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ARTICLE

Are the Temporal Changes Observed in the Reproductive Biology of the Estuarine Conguito Sea Catfish Related to Increased Small-Scale Fishing Effort on the Northwestern Pacific Coast of Mexico?

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Abstract

Biological parameters relating to the reproductive biology of Conguito Sea Catfish *Cathorops liropus* were investigated in 1979–1984 and 2015–2018 from an estuarine system on the northwestern Pacific coast of Mexico. In the first period, the spawning season occurred during the dry-warm season (April-June), according with the percentage of mature females and the highest gonadosomatic index (GSI) values. Mean TL was 12.3 cm, two cohorts were found, length at maturity was 18.6 cm, and fecundity was 24.47 oocytes/organism. In the second period, the spawning season extended to the rainy-warm season (July-November), as reflected by the percentage of mature females and the GSI values. Mean TL was 11.6 cm, length at maturity decreased to 17.1 cm, and fecundity decreased to 20.67 oocytes/organism, indicating a reduction in the size-based indicators and a change in the spawning period and reproductive effort as time passed. The number of fishing skiffs increased from 1,103 in 1980 to 2,434 in 2019, representing a 220% increase, and the landings increased from 400 to 3,432 metric tons in the same period. Temporal trends in surface water temperature, salinity, and the Oceanic Niño Index did not explain the observed changes between the study periods. These results suggest that the observed changes in the reproductive potential of Conguito Sea Catfish have been at least partially due to fishing.

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Fish species commonly exhibit variability in population structure, such as seasonal variations in body length at maturity, spawning strategy, the duration of the spawning period, and gonad weight, which may result from biotic and abiotic factors (Fowler et al. 2000) but also from high rates of mortality that can alter life cycle and life history traits and, therefore, the reproductive characteristics of populations (Worden et al. 2010; Botsford et al. 2011; Rouyer et al. 2011). If increased mortality occurs over a long time, the demographic changes can be substantial and can carry important ecological implications, such as diminished reproductive potential (Birkeland and Dayton 2005; Berkeley et al. 2012), changes in stock productivity (Conover and Munch 2002; Hsieh et al. 2006; Anderson et al. 2008; Stenseth and Rouyer 2008), and long-term changes in life history traits (Jørgensen et al. 2007), thus potentially affecting the growth and abundance of a population in the long term (Marshall et al. 1998).

Inevitably, intensive commercial fishing is one factor with the potential to critically affect fish stock biomass and productivity (Christensen et al. 2003); thus, an understanding of these effects is important for fisheries ecology in terms of both management and conservation. For example, larger fishes with higher gonad volume are expected to make a larger contribution to overall egg production than their smaller counterparts. However, if large fish are most likely to suffer fishing mortality, individuals that delay maturation might never have the opportunity to spawn (Rochet 2000). In populations where fishing mortality increases with size, early maturation may help to ensure future egg production and population stability, as well as potentially extending reproductive life (Roff 1992). However, this may compromise growth, resulting in smaller individuals being more vulnerable to predation (Rochet 1998).

To identify which parts of a population are involved in egg production, it is necessary to estimate size at maturity together with the body length structure of the population (Anastasopoulou et al. 2006). This information is also useful in setting and refining size restrictions by fisheries managers and, along with mean body size, is an important predictor of exploitation risk (Reynolds et al. 2005).

In the southeastern Gulf of California, four species of the Ariidae family are commonly captured by the small-scale fisheries under the generic name of "bagre" (catfish): Widehead Sea Catfish *Ariopsis guatemalensis*, Tete Sea Catfish *A. seemanni*, Conguito Sea Catfish *Cathorops liropus*, and Cominate Sea Catfish *Occidentarius platypogon*. These species are grouped together during the landing process, with no distinction being made among them, as all are categorized as "catfish" for the fisheries statistics (SAGARPA 2013). In addition, catfish species are captured with most fishing gears (i.e., gill nets, trawls, cast nets, longlines, etc.) utilized by commercial fishers in the

area, and they are commonly caught as bycatch in the artisanal and industrial shrimp fisheries (Amezcua et al. 2006; Madrid-Vera et al. 2007; Muro-Torres and Amezcua 2011). These practices impede a proper assessment of the exploited populations, and the fishery statistics elaborated in this way preclude a species-level assessment.

For the case of Conguito Sea Catfish, in general little is known about the biology or life history strategies of species belonging to the genus *Cathorops* (Marceniuk et al. 2016). This genus is distributed only in the Americas and can be easily misidentified due to the overall similarity of external morphology and coloration, combined with a lack of knowledge of ontogenetic and intersexual differences among *Cathorops* species, and sometimes they can even be identified as other unrelated species of the Ariidae family (Marceniuk et al. 2009). As a result of this, there is no adequate information on the commercial catch of this specific species, and very few studies have been carried out (Marceniuk 2007).

The Conguito Sea Catfish is common in the Mexican Pacific (Tapia-García et al. 1998; Velázquez-Veláquez et al. 2016; Del Moral-Flores et al. 2017; Palacios-Salgado et al. 2018) and has been exploited by the small-scale fisheries operating in the region of the mangrove-estuarine complex of Marismas Nacionales, the most extensive mangrove region in the American Pacific (Flores-Verdugo et al. 2014), at least since the early 1980s (Álvarez-Rubio et al. 1984; Amezcua-Linares et al. 1987). However, despite its abundance and economic importance, studies and information on its population ecology, demographic parameters, and reproductive ecology are lacking; as such, fishery regulation specific to this species is nonexistent in the Mexican Pacific. Such information forms the basis for species management. One of the main problems that the small-scale fishers report for this region is the high and uncontrolled increase in fishing effort over the years and the excessive catch of fish (Botello et al. 2010). However, possible changes in the reproductive ecology of this or other species as a consequence of these issues have never been assessed.

The potential for changes in Conguito Sea Catfish reproductive biology that might cause temporal and geographic variations in reproductive output has not been previously investigated. Furthermore, the effects of various fisheries on the population dynamics of this species have not been quantified. We sought to examine temporal variability in the reproduction of the Conguito Sea Catfish and relate it with fishing effort in the area, with the specific objectives of (1) identifying differences in spawning period duration and size at maturity between two time periods based on fish caught by the gill-net fishery during 1979–1984 and 2015–2018; and (2) identifying which sections of the population were being extracted by local fisheries during both periods and how operations may affect

the egg production overall. Finally, the results were related to the increase in fishing effort from 1980 to 2019.

METHODS

Sampling sites.—Conguito Sea Catfish specimens were collected from the Teacapán-Agua Brava mangrove-estuarine system (22°04′–22°35'N, 105°25′–105°45'W; Figure 1), the hydrology of which was severely modified by the construction of the Cuautla Channel at the Agua Brava Lagoon through the Federal Ministry of Hydrological Resources in 1974. According to Blanco y Correa et al. (2012) and Serrano et al. (2020), the hydrological conditions of the estuarine system were under a certain degree of stability before the opening of the Cuautla Channel, with a predominant oligonaline condition (0.5–3.0 psu) due to the presence of 12 unobstructed rivers and the lack of seawater intrusion through the Teacapán Inlet according to the sea-level elevation model designed by Serrano et al. (2020). However, based on a hydrological model, the same authors suggested that the entire mangrove-estuarine system reached salinity saturation 3 years after the channel's opening (~1977), which is the actual condition found through the estuarine system. The damming of all but one river and the hypersaline conditions commonly found through the extensive saltpan areas during the dry season, which present high water residence time, are believed to have caused a constant increase in salinity (with concentrations between 46 and 52 psu) and surface water temperatures of 28–30°C in the main lagoons, leading to major mangrove degradation throughout the area. Although the estuarine system presents a high evaporation rate, most of the hypersalinity found in the main water bodies is expulsed to the adjacent Pacific Ocean through the Cuautla Channel by the strong tidal currents (0.6 m/s) from the semidiurnal tide (1.5-m amplitude).

In total, 17 stations were sampled from fishing skiffs using the same fishing gear employed by the small-scale fishery operating in the area targeting finfish: a gill net with a mesh size of 8.9 cm and a total length of 80 m. Sampling was conducted during two periods. The first period extended from January 1979 to November 1984, with sampling conducted approximately bimonthly. Subsequently, at the same stations and using a net with the same characteristics, sampling was undertaken from July 2015 to August 2018 at 3-month intervals. In both cases, all of the climatic seasons in the area were covered (drycold, dry-warm, and rainy-warm seasons; Amezcua et al. 2019). In both periods, sampled specimens were stored on ice and transported to the laboratory for later analyses.

Data analysis.— In the laboratory, all organisms were measured to the nearest millimeter TL and weighed to the nearest gram. The fish were dissected and classified as male, female, or macroscopically undetermined sex. Both

gonad lobules were removed from female specimens and weighed (± 0.05 g). Adult sex ratios were calculated for comparison between seasons and periods by using a chi-square goodness-of-fit test with continuity correction (Zar 1999) to detect any deviation from the expected 1:1.

To determine temporal differences in length of Conguito Sea Catfish from both periods, the mean TL and length-frequency polygons were plotted and compared for both periods. Two-way ANOVA was used to determine whether the mean TL differed in both periods between males and females. Sex and period were used as categorical factors, and TL was used as the dependent variable. Homoscedasticity of variances was tested with Cochran's C-test, and normality was tested with a Kolmogorov–Smirnov test. If differences were found, no test for multiple comparisons was attempted, as there were only two categories in each factor.

Length-frequency polygons were elaborated for each period, and the cohorts were identified through kernel density estimation (KDE; Silverman 1986). The univariate kernel density estimator used is given by the equation

$$\hat{f}(x) = \frac{1}{nh} \sum_{i=1}^{n} K\left(\frac{x - X_i}{h}\right),$$

where h is the bandwidth and K(x) is the Gaussian kernel function. The Sheather–Jones bandwidth selection method for KDE was used. The KDE procedure was performed in R.

In the first period, there was no possibility of conducting a histological analysis of the gonads; therefore, in both periods the female gonadic stage was estimated macroscopically to maintain consistency. The gonadic stages were based on the scale proposed by Vazzoler (1982) but with adaptations for tropical marine catfishes in agreement with histological and macroscopic aspects of the ovaries (Fávaro et al. 2005; Table 1). On the assumption that the maturation of male and female specimens is synchronous (King 1995), ovaries alone were used for these analyses. Female gonads provide similar information to that provided by the examination of testes regarding reproductive condition and offer additional insights into fecundity and spawning time.

The reproductive cycle of adult female Conguito Sea Catfish was described for each period by differentiating the relative frequency of reproductive stages determined macroscopically using the information from Table 1 and, thus, the relative frequency of gonad development in each season for which samples were available. Combined with seasonal variations in the gonadosomatic index (GSI = [gonad weight/gutted body weight] \times 100), these data were used to infer spawning season dates in both periods. The use of GSI provided a measure of reproductive condition relative

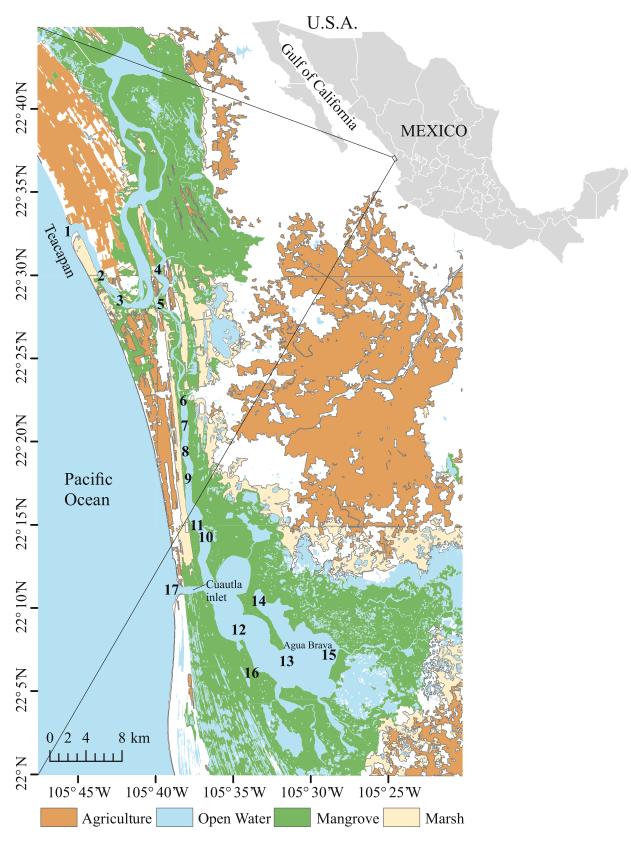


FIGURE 1. Location of the study area along the northwestern Pacific coast of Mexico, indicating the 17 sampling stations for Conguito Sea Catfish.

TABLE 1. Reproductive stages and macroscopic characteristics of female Conguito Sea Catfish.

Stage	Macroscopic characteristics		
I. Immature	Ovaries are small, filiform, slender, whitish, and translucent, without evidence of previous spawning. Oocytes are not visible to the naked eye.		
II. Vitellogenesis (ripening)	Ovaries have a pale yellowish color, blood vessels are visible on the dorsal side, and oocytes are clearly visible. Gonad is lobular and fills two-thirds of the abdominal cavity. Oocytes are mature.		
III. Ripe	Ovaries are orange-yellow in color, with many blood vessels. Gonad occupies up to two- thirds of the abdominal cavity. Oocytes are vitellogenic, are golden-yellow, have a higher diameter than those in the previous stage, and are visible to the naked eye.		
IV. Spent and atretic oocytes	Ovaries are reduced, wrinkled, flaccid, and either empty or with few yolked oocytes remaining. Color is dark reddish at the posterior portion. Hemorrhagic appearance. Oocytes are heterogeneous, with some being residual or in degeneration. Gonad occupies about half of the abdominal cavity.		
V. Resting–recovering	Ovaries are pale cream or light yellow in color, with few blood vessels. Subtle granulation is visible to the naked eye. The gonad increases in size, occupying up to half of the abdominal cavity. Oocytes are beginning to be visible to the naked eye.		

to body size since it calculates the relative proportion of gonad relative to body weight (gutted). To determine differences in GSI between periods and seasons, a two-way ANOVA was undertaken with period and season as factors. Variations in GSI were only analyzed for mature fish (as indicated by gonadic stage). Homoscedasticity and normality were also tested with Cochran's *C*-test and the Kolmogorov–Smirnov test. If differences were found, Tukey's honestly significant difference test was performed.

Mean body length at maturity (L_{50}), defined as the TL at which at least 50% of all females are sexually mature, was estimated. A female was considered mature if gonadal development was at stage III (ripe) or beyond, with the gonad yellowish and oocytes evident to the naked eye (Table 1). If these criteria were not met, a female was considered immature. Fish were grouped into 1-cm size-class intervals, and a logistic model was created that described the proportion of mature females as a function of TL using the equation

$$P = \left(\frac{1}{1 + e^{r + L_{50} \times L}}\right),\,$$

where P is the proportion of mature fish in length-class L; r is the width of the maturity curve; and L_{50} is body length at maturity. We estimated the model parameters using a square difference function through Newton's direct search algorithm in Microsoft Excel (Kutner et al. 2004). Percentage values for maturity were then fitted to body length-class for the females in each sampling zone (coast or open sea).

An analysis of residual sum of squares (RSS) was used to compare the maturity curves between zones and, thus, to determine whether the females from different zones varied in terms of length at maturity (Chen et al. 1992). This analysis tested the difference between two curves by calculating the RSS (RSS_i) and degrees of freedom (DF_i) for each data set i in both analyzed periods. The resultant RSS_i and DF_i values for each curve were added (Σ RSS_i and Σ DF_i), data from both curves were pooled, a new curve was fitted to the combined data, and pooled values for both RSS and DF (RSS_p and DF_p) were calculated. A final F-statistic was calculated using the equation

$$F = \frac{\frac{\text{RSS}_p - \sum \text{RSS}_i}{\text{DF}_p - \sum \text{DF}_i}}{\frac{\sum \text{RSS}_i}{\sum \text{DF}_i}} = \frac{\frac{\text{RSS}_p - \sum \text{RSS}_i}{3(K-1)}}{\frac{\sum \text{RSS}_i}{N-3K}},$$

where F is the F-statistic with 3(K-1) and N-3K degrees of freedom; K is the number of curves being compared (two in this case); and N is the pooled sample size. A detailed explanation of this analysis is given by Haddon (2010). The analysis was performed in Microsoft Excel.

Fecundity was estimated by counting all oocytes from female gonads in stages III and IV after they had been separated from the ovarian tissue by leaving the gonads in Gilson's fluid for 48 h; the number of oocytes was then related with the TL. To determine whether a mathematical function adequately described this relation and to test differences between the two periods, ANCOVA was undertaken using Statistica software (StatSoft).

Fishing effort was estimated as the number of small-scale boats (skiffs or Mexican pangas, as defined by Johnson et al. 2017) operating in the study area adjusted by the number of people in local coastal populations or, as in this case, the small-scale fishers inhabiting the zone.

According to Johnson et al. (2017), this method can accurately predict fisheries landings in the study area. The fisher population in the fisheries statistics books is accurate, as it is based on the number of permits given by the fishing authority; however, the small-scale fishing effort (i.e., number of skiffs) usually has no reliable record due to information gaps (Botello et al. 2010). Therefore, because the relationship between fisher populations and fishing boats was not correlated, it was necessary to estimate the fishing effort using the method employed by Johnson et al. (2017). With this information, the CPUE was estimated by dividing the yearly landed catfish from the study area (metric tons) between the number of boats.

Information on the small-scale fisher population and the number of small-scale boats and yearly data on catfish landings from the study area were obtained from the Yearbooks of Fisheries and Aquaculture of the Mexican government dating back to the 1980s (https://www.gob.mx/conapesca/documentos/anuario-estadistico-de-acuacultura-y-pesca) as well as from the Official Newsletter of the government of the State of Nayarit, where this system is located, and from reports of the National Commission on Fisheries and Aquaculture of Mexico (Comisión Nacional de Acuacultura y Pesca; https://www.gob.mx/conapesca).

Surface water temperature, the Oceanic Niño Index (ONI), and water salinity were plotted to determine whether changes in CPUE and our results could be related to variations in these factors. Temperature data were obtained from this study in both periods at every sampled station as well as from previous studies undertaken in the same area since the 1970s (Amezcua-Linares 1977; Alvarez-Rubio et al. 1984; Amezcua-Linares et al. 1987, 1992; Díaz-González and Soto 1988; Castillo-Rodriguez and Amezcua-Linares 1992; Muro-Torres and Amezcua 2011; Coiraton and Amezcua 2020). Surface temperature data were obtained from the Operational Sea Surface Temperature and Sea Ice Analysis project (Good et al. 2020) with a monthly resolution. Data were processed in R to generate time series from 1981 to 2020. The ONI was downloaded from the National Oceanic and Atmospheric Administration's National Weather (https://origin.cpc.ncep.noaa.gov/products/analysis_ obtaining data from 1975 to 2020. A plot including the surface

monitoring/ensostuff/ONI_v5.php), obtaining monthly data from 1975 to 2020. A plot including the surface water temperature and the ONI from 1974 to 2020 was constructed. Salinity was measured in both periods at every station and every season with a seawater refractometer, and results were plotted for both periods.

RESULTS

In total, 1,389 specimens of Conguito Sea Catfish were analyzed in this study, with TLs ranging from 7.0 to 24.3 cm (mean $\pm \text{SD} = 12.1 \pm 3.3 \text{ cm}$). In the first period,

the sample comprised 559 individuals, with TLs ranging from 6.1 to 24.3 cm (12.1 \pm 2.9 cm). Of these, 43 were organisms of undetermined sex, 248 were females, and 268 were males. Females had a length range of 7.0-24.3 cm TL $(13.1 \pm 2.9 \text{ cm})$, whilst the males had a length range of 7.0–19.3 cm TL (11.7 \pm 2.4 cm). The total sex ratio (male: female) for this period was 1.1:1.0, which was not significantly different from the expected ratio of 1:1 ($\chi_i^2 = 0.775$, P > 0.10). However, the ratio varied seasonally (Table 2). During the dry-cold season, the sex ratio was 2.88:1.00, which was significantly different from the expected ratio of 1:1. During the dry-warm season, the sex ratio was also statistically different, although in this case the number of females was higher (0.58:1.00). During the rainy-warm season, the observed sex ratio (1.13:1.00) was not significantly different from the expected ratio of 1:1.

In the second period, the sample comprised 830 specimens, with TLs ranging from 5.4 to 21.7 cm (mean \pm SD = 11.2 ± 3.9 cm). In this period, 58 were organisms of undetermined sex, 304 were males, and 468 were females. Females had a length range of 7.3–21.3 cm TL (12.4 \pm 3.7 cm), whilst males had a length range of 7.7-21.7 cm TL $(11.3 \pm 3.4 \,\mathrm{cm})$. The sex ratio (male : female) was 0.65:1.00. This relationship was significantly different from the expected 1:1 ratio ($\chi_i^2 = 34.839$, P < 0.01); therefore, in the second period the number of females was significantly higher. In this period, the ratio also varied seasonally (Table 2). In the dry-cold and dry-warm seasons, the number of males was significantly smaller, with sex ratios of 0.77:1.00 and 0.22:1.00, respectively. In the rainy-warm season, the sex ratio of 0.94:1.00 was not statistically different from the expected 1:1 ratio, an observation similar to that in the first period.

The ANOVA test indicated that the mean TL of organisms in the first period was higher than the mean TL in the second period ($F_{1, 1,284} = 8.287$, P < 0.01). In both

TABLE 2. Sex ratios (male: female) of Conguito Sea Catfish and results of chi-square analyses from the different seasons in both study periods (DC = dry-cold season [December-March]; DW = dry-warm season [April-June]; RW = rainy-warm season [July-November]). Asterisks (*) indicate statistically different results.

Season	Males	Females	Sex ratio	χ_i^2	P		
1979–1984							
DC	95	33	2.88	40.46*	< 0.05		
DW	67	119	0.58	34.39*	< 0.05		
RW	106	96	1.13	1.36	>0.05		
2015–2018							
DC	142	183	0.77	12.07*	< 0.05		
DW	32	147	0.22	402.02*	< 0.05		
RW	130	138	0.94	0.55	>0.05		

periods, the mean TL of females was higher than that of the males ($F_{1, 1,284} = 45.301$, P < 0.01). The mean TL for both sexes decreased by almost 1 cm between the two analyzed periods (Figure 2).

The KDE function identified two modes for the first period (mean₁ \pm SD = 10.47 \pm 3.4 cm; mean₂ \pm SD = 17.4 \pm 2.54), and one mode was identified for the data from the second period (mean \pm SD = 13.8 \pm 2.24 cm; Figure 3). This is in agreement with the results from ANOVA, as in the first period the mean TL of the organisms caught was larger.

Five gonadic stages were described based on the macroscopic characteristics of the oogenesis stage in female Conguito Sea Catfish (Table 1). Oocyte development was generally synchronous in both gonads, and the species was an isochronal spawner. When spent gonads were found during the spawning season, both gonads were empty, likely indicating that any developing oocytes reached maturity and were used during spawning or were reabsorbed.

In both periods, the Conguito Sea Catfish showed one reproductive event per year, with a spawning peak during late spring and early summer, which corresponds to the dry-warm season (April-June). During the first period (1979–1984; Figure 4A), approximately 30% of the females were ripe and 25% showed spent gonads in the dry-warm season. The reproductive period seemed to extend until the rainy-warm season (July-November), although the number of ripe and spent female gonads decreased considerably to approximately 5% in both cases, and the number of females in stages I and II increased. During the late

autumn and winter (dry-cold season), the majority (~70%) of the gonads analyzed were in stage I.

In the second period (2011–2014; Figure 4B), a similar pattern was observed in the dry-warm season; a reproductive peak was apparent during this period, in which approximately 28% of the gonads were ripe and 8% were spent. However, in these years, the reproductive period continued to the next season (rainy-warm), in which a considerable number of ripe and spent individuals were observed (20% and 4%, respectively). During the rainywarm season in the second period, the number of mature ripening ovaries (stage III) was considerably higher than that observed during the rainy-warm season in the first period (19% in 2011–2014 versus 6% in 1979–1984). In the second period, even in the cold months, higher numbers of ripening and ripe ovaries were found (~15% for both cases), exceeding the number of ovaries in these stages found in cold months during the first period (6% and 4%, respectively).

The GSI values were in agreement with the observed pattern of gonad stages. During the first period, a clear peak in GSI was observed in late spring and early summer (dry-warm season), which decreased considerably in the other two seasons. In the second period, the GSI also reached its maximum mean value during the dry-warm season; however, the mean value remained similar in the rainy-warm season but decreased in the dry-cold season. Analysis of variance showed differences in the mean GSI between periods ($F_{1, 168} = 9.55$, P < 0.05), with the mean GSI being higher in the second period, and differences were also found between seasons ($F_{2, 168} = 5.01$, P <

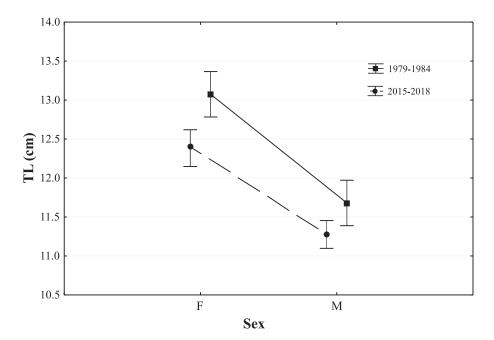


FIGURE 2. Differences in the mean TL (cm) for both sexes of Conguito Sea Catfish between the two analyzed periods. Vertical lines are SDs.

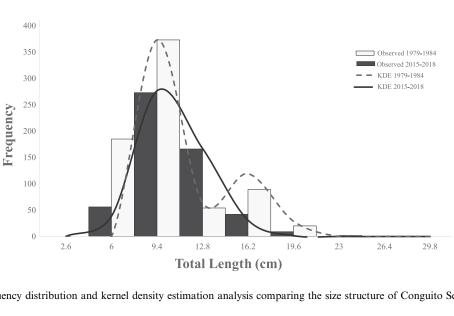
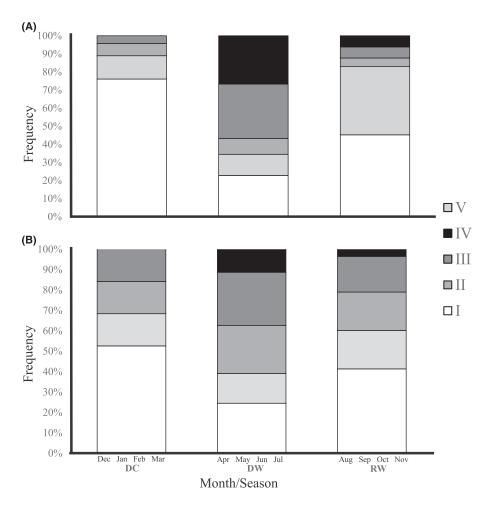


FIGURE 3. Length-frequency distribution and kernel density estimation analysis comparing the size structure of Conguito Sea Catfish in the two analyzed periods.



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FIGURE 4. Seasonal variation in reproductive stages of female Conguito Sea Catfish in both study periods: (A) 1979–1984 and (B) 2015–2018 (DC = dry-cold season; DW = dry-warm season; RW = rainy-warm season). Roman numerals indicate the macroscopic gonadal stages identified (see Table 1 for stage descriptions).

0.05), as the mean GSI was significantly higher during the dry-warm season in both periods. Differences were also found in the period \times season interaction ($F_{2, 168} = 6.85$, P < 0.05), as the mean GSI was significantly higher during the rainy-warm season in the second period (Figure 5).

In the first period, the smallest female with mature gonads had a TL of 10.9 cm; the L_{50} for sampled females was 18.6 cm. The logistic model was as follows:

$$P = 1/\left[1 + e^{(0.42 + 18.6 \times L)}\right].$$

In the second period, the smallest female with mature gonads was 9.1 cm long and the female L_{50} was 17.1 cm. The logistic model was

$$P = 1/\left[1 + e^{(0.49 + 17.1 \times L)}\right].$$

These differences were statistically significant according to the analysis of RSS ($F_{31, 34} = 43.44$, P < 0.01), indicating that the females in the second period matured at a shorter body length than those in the first period. At 21.5 cm, 90% of females in the second period had attained sexual maturity, while in the first period the smallest body length-class exhibiting 90% maturity was 24 cm (Figure 6).

Regarding the variation in fecundity, the egg output of female Conguito Sea Catfish increased with size in both periods (Figure 7). In the first period, 73 females were analyzed for fecundity, with a TL range of 10.9–24.3 cm. The mean fecundity was 24.47 oocytes/organism, and the linear equation describing this relationship was

$$F = 0.695 \times TL + 8.84$$
.

In the second period, 131 females were analyzed for fecundity, with a TL range of 9.1–21.3 cm. The mean fecundity was 20.67 oocytes/organism, and the linear equation describing this relationship was

$$F = 0.25 \times TL + 15.01$$
.

In both cases, F is the fecundity and TL is total length (cm). The ANCOVA indicated that the two slopes were statistically different ($F_{3, 298} = 354.3$, P < 0.01). The univariate results indicated that the relationship between length and fecundity was statistically significant (TL: $F_{1, 298} = 507$, P < 0.01). The main effect testing for the difference between the periods indicated that the constants were different between the two analyzed periods (period: $F_{1, 298} = 410$, P < 0.01). The interaction term, indicating that the period affected the relationship between TL and fecundity, was also statistically significant (period × TL interaction: $F_{1, 298} = 112$, P < 0.01).

A significant positive relationship was found between the logarithm of the number of fishing boats and the logarithm of the coastal human population ($\log_{10}[boats] = 0.8673 \cdot \log_{10}[fisher population]; r^2 = 0.9996$; Supplementary Material Figure 1). The population-driven number of small-scale boats in the area can be predicted by the fisher population elevated to the exponent of 0.8673 in this case. Using this result, the yearly effort (as given by the number of boats) was obtained from 1980 to 2019. Catfish landings in the study area increased from 400 metric tons in 1980 to 3,432 metric tons in 2019, representing an increase of more than 800%. With the landings data, the yearly

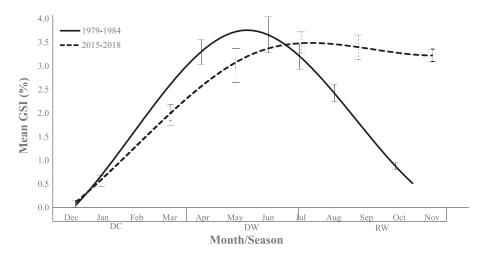


FIGURE 5. Seasonal variation in the gonadosomatic index (GSI) of female Conguito Sea Catfish in both analyzed periods (DC = dry-cold season; DW = dry-warm season; RW = rainy-warm season). Vertical lines represent SDs from the months for which data were available. The numbers of females analyzed for every period and season are shown in Table 2.

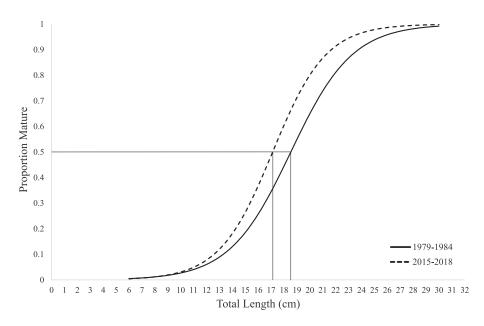


FIGURE 6. Length at maturity of female Conguito Sea Catfish in both analyzed periods. Lines indicate the TL (cm) at which 50% of individuals were mature for each period.

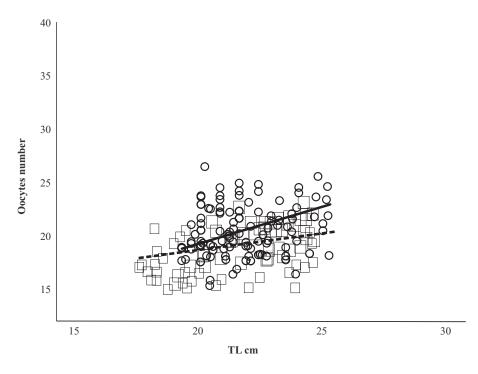
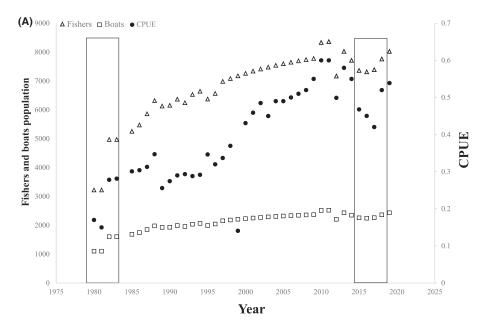


FIGURE 7. Relationship between TL (cm) and fecundity (number of oocytes) of female Conguito Sea Catfish in both analyzed periods. Circles represent the observed fecundity during the first period, and the solid line represents the predicted relationship. Squares represent the observed fecundity during the second period, with the dotted line representing the predicted relationship.

CPUE was estimated for the same period, and the yearly variation in the number of fishers and the number of boats was plotted versus time (years; Figure 8A). The CPUE was less than 0.2 metric tons/boat during 1980 and 1981 but increased to almost 0.3 metric tons/boat in the

following 2 years, when the effort increased as well. During the second period, the number of boats ranged from 2,259 (2015) to 2,364 (2018), representing more than twice the number of boats initially recorded in 1980. The CPUE also increased in a trend similar to the increased effort. As



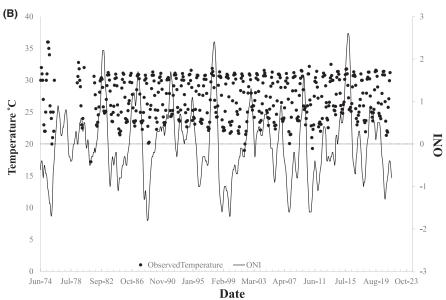


FIGURE 8. (A) Fisher population, the estimated number of fishing boats (skiffs), and the estimated CPUE (metric tons/boat) of Conguito Sea Catfish in the study area from 1980 to 2019 (columns indicate the periods in which this study was undertaken) and (B) temporal variation in surface water temperature (°C) and the Oceanic Niño Index (ONI) in the study area. The horizontal line represents an ONI value of zero.

a result of this, the CPUE was 0.47 metric tons/boat in 2015 and 0.51 metric tons/boat in 2018. Information on previous years (1979 and before) was not available.

Temperature values (°C) from 1974 to 2020 varied seasonally, with the highest temperatures recorded during the rainy–warm season (July–November) and the coldest temperatures observed during the dry–cold season (February–March; Figure 8B). However, a trend that could be related to an increase in sea surface temperature was not observed; in fact, the warmest readings were from 1975.

The ONI values showed a cycled variation that remained similar during the period of our study.

Salinity also followed a pattern similar to that of the temperature in both periods; salinity values were less than 10 psu during the peak of the rainy-warm season, as a consequence of the increased precipitation and the input from the rivers at that time, whereas values were close to 40 psu during the dry-warm season (Supplementary Material Figure 2). Therefore, a relationship between variations in temperature, salinity, or the ONI and the observed

changes in the CPUE or reproductive output of Conguito Sea Catfish could not be established.

DISCUSSION

Our results indicate that the size structure and reproductive biology of Conguito Sea Catfish have changed over 30 years; the mean TL and the length at maturity have decreased, and the reproductive cycle has changed. During the first period, the sex ratio (male : female) was not significantly different from 1:1 except during the reproductive season, a result that has been observed also for other catfish species in the area (Muro-Torres and Amezcua 2011; Amezcua and Muro Torres 2012). However, in the second period, the number of females was significantly higher than the number of males. A similar tendency previously observed for the Guri Sea Catfish Genidens genidens (Mishima and Tanji 1981) was attributed to a spawning aggregation of females. However, a similar observation from other teleost species caught as bycatch in the shrimp trawl fishery of the tropical eastern Pacific concluded that the difference was attributable to differential survival rates between females and males (Domínguez-López 1989; Lucano Ramirez et al. 2001), implying higher mortality of males, likely due to fishing, which is consistent with the findings from this study, as the effort increased by more than two times between the analyzed periods.

In the first period, the mean TL was larger and the length structure consisted of two modes. In the second period, the frequency distribution for TL consisted of only one mode, mean TL was shorter, the organisms caught were generally smaller, and the larger specimens were absent. Most of the individuals caught during both periods were small stage-1 fish or were of undetermined sex (likely juvenile organisms), implying that the study site likely functions as a nursery area for this species and that the small-scale fishery is probably removing a large number of fish representing this part of the population.

Evidence of temporal variability in the duration of spawning activity, reproductive investment, and body length at maturity was found between the two periods. In the first period, a clear and well-defined spawning season was observed during late spring and early summer, corresponding to the dry-warm season. This observation agreed with the seasonal variation in the GSI, as seasonal changes in GSI were very marked in this period. Previous studies on catfish species from the area have also found that spawning takes place in the dry-warm season (April-June), as the number of ripe females and GSI are higher (Muro-Torres and Amezcua 2011; Amezcua and Muro Torres 2012).

On the other hand, in the second period, Conguito Sea Catfish appeared to mount a higher reproductive effort,

exhibiting a greater reproductive potential, as the spawning season apparently extended through the following season (rainy-warm). This is supported by the fact that in the second period, ripening, ripe, and spent stages represented almost 40% of females, in comparison to the previous period, in which these stages represented less than 20% of females, in addition to the GSI still being high during this season. Previous studies suggest that seasonal changes in GSI are an indicator of reproductive investment (Devlaming et al. 1982; Tamate and Maekawa 2000). Therefore, the presence of high GSI values suggests a high reproductive investment that extended over two seasons during the second period.

The results of the GSI and gonadal development stage data can be used to reliably estimate the duration of the reproductive season (Fowler et al. 2000; Brown-Peterson et al. 2001). The obtained values of both parameters indicated a reproductive period that lasted from April to June during 1979–1984, whereas the reproductive period extended to November during the years 2015-2018. Decreases in the L_{50} and fecundity from the first period to the second period were also observed. These results are consistent with previous works indicating that increased fishing pressure in dioecious stocks induces maturation at smaller lengths (Hunter et al. 2015) as well as a reduction in overall population fecundity—even in the absence of decreased fertilization rates (Alonzo and Mangel 2004). The observed reduction in fecundity could be related to the fact that the mean TL decreased in the second period. However, the egg production rate was lower as well. Previous studies have indicated that high fecundity is correlated with rapid growth and vice versa (Schultz and Warner 1991). If changes in the growth rate also occurred from one period to another, this could explain the observed results, but estimation of growth was beyond the scope of this study.

Results obtained from the present work, when comparing the length and reproductive strategy of Conguito Sea Catfish for two periods that were more than 30 years apart, could be related to plasticity in reproduction and maturation schedules that are triggered with an increase in temperatures and also could be due to food availability (Hunter et al. 2015). Furthermore, size selection patterns can vary over time due to stochasticity of environmental conditions, and such patterns can also be affected by variation in age and body size at maturity over time (Kendall and Quinn 2009). Size at maturity is influenced by many factors, including but not limited to the density of conspecifics, the density of other fish species, and ocean conditions (Ruggerone et al. 2003).

When comparing the observed results with the longterm trends in temperature, the ONI, and salinity from the study area, it seems that the observed changes were not driven by these climatic factors. It is possible that the evaporation and precipitation rates also did not have any effect on the observed changes if we consider that the variation in salinity is a response to these two factors. The salinity values remained constant in both periods, indicating that the rates of evaporation and precipitation have remained similar. With respect to food availability, previous trophic studies undertaken in the area indicate that food availability in the study region is plentiful (Muro-Torres et al. 2020). This suggests that lengths at maturation and reproductive output have declined in response to temporal trends in some other biotic and environmental conditions and fishing.

As previously stated, the fishing effort in the study area doubled from one period to another and the landings increased by more than eight times. During the first period, the number of boats ranged from 1,103 (1980) to 1,607 (1984), an increase resulting from the support given by the federal government to the small-scale fisheries in Mexico (Cruz-Romero et al. 1996). Currently, the effort in terms of boats, as well as the fisher population in the area, seems to have reached an asymptote, given that the number of fishing permits has not increased recently (https://www.conapesca.gob.mx/wb/cona/permisos_de_pesca_ comercial), and a reduction was observed, likely due to the economic crisis and a reduction in catches (from the year 2015 onwards), among other factors. According to fisheries-induced evolution theory, this will have generated a selective pressure to increase the reproductive effort and favor early maturation at small sizes. Although we cannot assert a causal link based on these observations, it does appear likely that fishing is at least partially responsible for the observed results (Hunter et al. 2015). As time passes, older (and larger) fish in a population become fewer because cohorts accumulate the effects of fishing mortality through time, so larger fish form a smaller proportion of the population (Shin et al. 2005). Additionally, high exploitation due to fishing leads to substantial modifications in the size structure of exploited communities, such as a reduction in size at maturity and decreases in the mean and mean maximum TLs (Shin et al. 2005; Kendall et al. 2009).

The complementary information provided by different size-based indicators also supports the hypothesis that the changes found are related to fishing (Shin et al. 2005). Our findings are consistent with the expectation that fisheries-induced changes cause harvested fish populations to become shorter, as was expressed for iteroparous species (Law and Grey 1989), and also these changes are related to an increase in fishing effort.

The reproductive capacity of fishes is known to be strongly influenced by body length (Marteinsdottir and Begg 2002); thus, a population consisting of larger individuals—with consequently larger gonads—may be deemed to have greater reproductive potential than a population

of smaller individuals. From the current results, it is apparent that in the first period, the population of Conguito Sea Catfish had a higher reproductive capacity and a well-defined reproductive season. In the second period, and probably as a way to compensate for the loss of reproductive potential, this species started to expand the reproductive season. Even though the study periods were more than 30 years apart, the first sample period was performed after the construction of the Cuautla Channel, and as mentioned before, the hydrological conditions of the entire estuarine system have not changed since 1977. Regarding the reduction of larger specimens in the second period, this could be a result of overexploitation practices rather than climatic variability. For instance, it has been pointed out that the original estuarine forests of white mangrove Laguncularia racemosa changed into more tidaldominated red mangrove Rhizophora mangle forests due to the opening of the Cuautla Channel (Serrano et al. 2020). In fact, it is common to find major dead trunks (>1 m diameter) of white mangrove throughout the estuarine system, while a dense cluster configuration of fringe red mangrove is usually found along the main lagoons and tidal channels. It is well known that the dense aerial roots of the red mangrove act as a nursery ground for fish and thus should increase their overall number and production. However, the results of this investigation suggest otherwise based on the recent decrease in the number of fish along with an increase in fishing effort and CPUE.

The Conguito Sea Catfish is a small species in comparison with other catfish species from the area. The largest specimen caught was 21.7 cm, while the Cominate Sea Catfish and the Chihuil *Bagre panamensis*, for example, reach lengths of more than 50 cm; furthermore, the Conguito Sea Catfish seems to exclusively inhabit estuarine systems with low dispersal capacity, as is the case for all other species from the genus *Cathorops* (Barletta et al. 2005; Fávaro et al. 2005; Betancur-R et al. 2007; Marceniuk 2007; Marceniuk et al. 2016). The results of our study might be a consequence of these characteristics, as the size and habitat preferences of the Conguito Sea Catfish indicate that it has a low capacity for movement between zones as well as a small response to the effect of the fishery.

Assuming that reproduction is the main contributor to stock restoration, the observed variability could significantly impact the conservation status for future generations of this population. Thus, in estuarine zones where small-scale fisheries operate, it may be necessary to manage and preserve the reproductive stock of this species. At present, there are no specific fishing regulations aimed at managing the Conguito Sea Catfish in the Mexican Pacific and no proper management plan is in place (SAGARPA 2013). The only regulation currently enforced in this area is for finfishes in general and relates to the number of fishing skiffs that are in operation.

Our results point out that the removal of all cohorts of individuals by the small-scale fishery appears to be at least partially responsible for the changes in reproductive potential and the reductions in length at maturation, which could potentially affect the long-term stability of the population (Bani and Moltschaniwskyj 2008). Establishing the spawning time of Conguito Sea Catfish may help to manage fishing activity, especially in heavily exploited populations. However, while the risk of fishing in spawning grounds is higher during spawning periods, overfishing of immature individuals is potentially no less damaging given that the sustainability and productivity of a fishery are dependent on the continued availability of juveniles. Management through the establishment of a biomass closed season and/or minimum size limits may be sufficient for this species, considering that it seems to be secluded in estuarine systems and is targeted only by the gill-net finfish fishery. However, it is necessary to consider that small-scale fishers in tropical and subtropical zones of countries with low institutional capacity are usually very poor and such measures may have significant economic and social implications. Consideration should be given to the economic and social aspects of the fishers as well as the ecology of the target species before developing adequate and effective methods for fisheries management in the area.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.