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Comparative reproductive biology of Sciaenidae family species in the Río de la Plata and Buenos Aires Coastal Zone, Argentina

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A comparative analysis on various aspects of the reproductive biology of 7 Sciaenidae family species was done. In addition the reproductive parameters needed for stock assessment models were provided. The research covered the analysis of the duration of the breeding season and the estimation of reproductive variables such as size at maturity, fecundity and spawning frequency. When all species were considered together, some aspects of reproduction were similar, regarding the reproductive strategy; all species are batch spawners with indeterminate fecundity and an extensive reproductive season (approximately six months) except for Pogonias cromis, *which showed a more limited spawning season (three months). With regard to reproductive potential, wide differences in fecundity values mainly due to the different sizes attained by each species were observed (range in batch fecundity values between 5000 and 2,800,000 hydrated oocytes). However, when relative fecundity was compared, average values were generally similar, ranging approximately between 150 and 200 hydrated oocytes per female gram.* Pogonias cromis *is the exception within this group, because the mean relative fecundity ranged between 75 and 98 hydrated oocytes per ovary-free female gram. This difference may be a consequence of the greater oocyte size reached by* P. cromis *eggs (1100–1400 μm) compared to the rest of sciaenid analysed (750–900).*

Keywords: Sciaenidae, reproductive strategy, reproductive potential, length at first maturity, fecundity, spawning frequency

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INTRODUCTION

In the Argentine Sea, in particular in the Buenos Aires Coastal Zone (34°S–41°S), cohabit 94 fish species belonging to 49 families including marine and freshwater species (Jaureguizar *et al*., 2006). These species form an ecological ichthyc group known as *asociación íctica demersal costera bonaerense* (Díaz de Astarloa *et al*., 1999) or 'Bonaerense Coastal Ecosystem' (Jaureguizar *et al*., 2006). The Bonaerense Coastal Ecosystem supports a multispecific demersal fishery with different commercial fleet types (craft, bay or creek, coastal and off-shore). Sciaenidae and Rajidae families are the most important in terms of abundance and catch levels (Cousseau, 1985).

Within the Buenos Aires Coastal Zone, the Sciaenidae family is represented for seven species: whitemouth croaker (*Micropogonias furnieri*); striped weakfish (*Cynoscion guatucupa*); king weakfish (*Macrodon ancylodon*); black drum (*Pogonias cromis*); Argentine croaker (*Umbrina canosai*); banded croaker (*Paralonchurus brasiliensis*); and southern kingcroaker (*Menticirrhus americanus*). Some of these species are estuarine residents; others live in marine waters, while others develop part of their life cycle in estuaries and into adulthood living in marine environments. Rico (2000) analysed the abundance distribution (t/mn2) of sciaenids in the Buenos Aires Coastal Zone associated with bottom salinity, defining two groups. A first group with preferences for marine environments (striped weakfish, Argentine croaker, southern kingcroaker and banded croaker) whose abundances decrease as they enter the estuary and a second group composed of species that tolerate a wide range of salinity (whitemouth croaker, king weakfish and black drum) who increase their abundance in diluted water.

Carozza *et al*. (2001) and Fernández Aráoz *et al*. (2005) analysed the composition of commercial landings during 1986–2003. These authors found that catches of demersal species were composed of 30 species dominated by whitemouth croaker, striped weakfish, 3 flatfishes species (*Paralichthys patagonicus*, *Paralichthys orbignyanus* and *Xystreuris rasile*), 9 rays coastal species (Rajidae family) and shark species among others. From a commercial or operative standpoint, this group is known as *variado costero* (Carozza *et al*., 2001).

Research on reproduction of exploited fish stocks is essential in the development of fisheries science for several reasons. For example, age or size at sexual maturity is a parameter used in most stock assessment models, directly affecting the estimation of spawning biomass and productivity. Also, the reproductive effort measured by the size or age of a species is central in Stock–Recruitment models to understand the

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variability in the strength of recruitment. Other reproductive traits such as fecundity, spawning frequency and length of the spawning season are essential to properly estimate egg and larvae production, especially, in indeterminate fecundity species, such as many pelagic ones (Hunter & Macewicz, 1985). Annual changes in these variables could affect the stock productivity and produce variability in fish recruitment (Macchi *et al.*, 2004). On the other hand, some reproductive variables may be associated with changes in the population structure, as size or age at first maturity, which may decline over the years as a consequence of over-exploitation (Hubold, 1978; Beacham, 1983; Trippel, 1995).

Marine fishes exhibit wide heterogeneity in reproductive strategies and a key issue in the estimation of the egg production of any species is to correctly identify its reproductive strategy. Most marine fish species of commercial importance are iteroparous, gonochoristic and exhibit external fertilization without parental care (Murua & Saborido-Rey, 2003). Based upon the rhythm that oocytes are spawned (ovulated), Tyler & Sumper (1996) described two types of spawning patterns: synchronous or total spawners (the whole clutch of developed oocytes is shed in a unique event or ever a short period time); and asynchronous or batch spawners (eggs are released in batches usually over a protracted spawning period). Only a portion of the yolked oocytes is selected to be spawned and hydrated in each batch. Within the Sciaenidae family, batch spawning with indeterminate fecundity (potential annual fecundity is not fixed before the onset of spawning: Hunter *et al.,* 1992) is the spawning pattern adopted by all species, in particular those inhabiting the Bonaerense Coastal Ecosystem (Vizziano & Berois, 1990; Macchi & Christiansen, 1992; Macchi, 1998; Macchi *et al.*, 2002). This reproductive feature is difficult for estimating the annual fecundity because it is necessary to know the number of oocytes released per spawning (batch fecundity), the percentage of females spawning per day (spawning frequency) and the duration of the spawning season (Hunter *et al.*, 1992; Barbieri *et al.*, 1994).

In the Buenos Aires Coastal Zone, whitemouth croaker, striped weakfish and king weakfish have been most studied from the standpoint of reproduction (Cassia, 1986; Macchi & Christiansen, 1992; Macchi, 1998; Macchi & Acha, 1998; Acha *et al.*, 1999; Macchi, *et al.*, 2003; Militelli & Macchi, 2004, 2006), although no comparative studies have been conducted among the members of this family.

Given the economic importance of some members of this fish family in Argentina and Uruguay and the biological characteristics presented, the aim of this paper is to develop a comparative analysis on various aspects of the reproduction in sciaenids, that include the duration of the reproductive season, the assessment of length at first maturity and the estimation of batch fecundity, spawning frequency and size–mass of the oocytes.

MATERIALS AND METHODS

Sample collections

Specimens of the Sciaenidae family and oceanographic data were obtained from the Bonaerense coastal area (34°–41°S) during 13 Instituto Nacional de Investigación y Desarrollo Pesquero research cruises carried out between 1999 and 2005; most of them corresponded to fisheries evaluation cruises (Figure 1). Furthermore, in some years samples from commercial landings coming from San Clemente port became available. Table 1 shows a summary of the basic data obtained from each sampling trawl. Total length (TL) in centimetres and total weight (TW) in grams were recorded for each fish sampled. Individuals were sexed and the stage of reproductive development was determined macroscopically. For this, a five-stage maturity key was employed: (1) immature; (2) developing; (3) spawning capable; (4) regressing; and (5) regenerating (Brown-Peterson *et al.*, 2011).

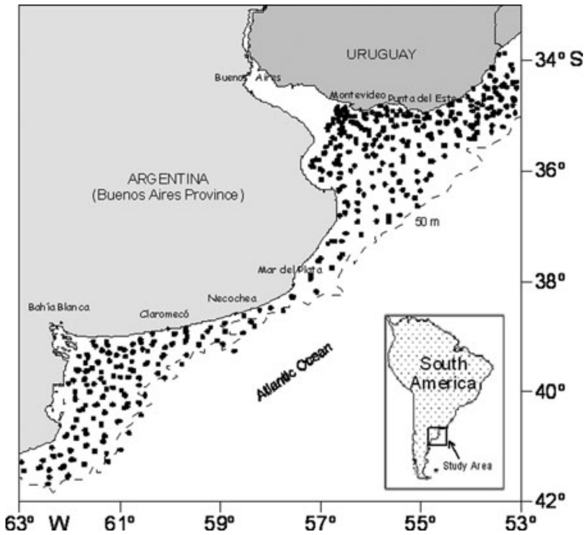

Fig. 1. Spatial distribution of demersal trawl stations during Instituto Nacional de Investigación y Desarrollo Pesquero research cruises carried out between 1999 and 2005.

For histological examinations, ovaries in different maturity stages were removed after capture and preserved in 10% neutral buffered formalin (Table 1). Fixed gonads were weighed (GW) to the nearest 0.1 g and a portion of tissue was removed from the centre of each ovary, dehydrated in ethanol, cleared in xylol and embedded in paraffin. Tissues were sectioned at approximately 4 µm thick and stained with Harris's haematoxylin followed by eosin counterstain (García del Moral, 1993). Histological classification of the ovaries was adapted from Brown-Peterson *et al.* (2011). A maturity scale for sciaenids was established that basically coincides with the macroscopic classification (Table 2). The main difference lies in the recognition of different microscopic substages in the developing phase.

Reproductive parameters

Analysis of the duration of the breeding season was based both on observation of the maturation stages (macroscopic and microscopic) as well as in the case of some species in the literature. The seasonal appearance of the developing stages was used to describe the reproductive cycle. Females were considered as reproductively active when they were capable of spawning at the time of capture or in the near future (Hunter *et al.*, 1992). Description of the stages of postovulatory follicle (POF) degeneration was adapted from that reported for *M. furnieri* and *M. ancylodon* of the Río de la Plata estuary (Macchi *et al.*, 2003; Militelli & Macchi, 2004).

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Table 1. Basic data from research surveys, commercial landings, number of individuals sampled per species (N ind.) and number of ovaries collected for histological examinations (N ov.).

Year	Month	Number of trawl stations	Species	N ind.	N ov.
1999	November	141	*M. furnieri**	917	117
			C. guatucupa	754	246
			M. ancylodon	1075	140
			U. canosai	140	64
			P. brasiliensis	295	2
			M. americanus	2	
2000	March	44	*M. furnieri*	814	104
			C. guatucupa	518	30
			M. ancylodon	610	150
			U. canosai	57	
			P. brasiliensis	184	
			M. americanus	8	
2000	June	50	*M. ancylodon*	30	30
2000	July	51	*M. ancylodon*	47	47
2000	October	29	*C. guatucupa*	229	83
2000	November	45	*M. furnieri*	194	78
			C. guatucupa	240	68
2001	March	43	*M. furnieri*	1246	80
			C. guatucupa	392	106
			M. ancylodon	2395	575
			P. brasiliensis	401	155
			M. americanus	25	5
2001	November	16	*M. furnieri*	188	27
			M. ancylodon	234	86
2003	December	154	*M. furnieri*	1215	302
			C. guatucupa	978	148
			M. ancylodon	580	5
			U. canosai	394	
2005	November	184	*M. furnieri*	864	
			C. guatucupa	2200	
			M. ancylodon	393	
			U. canosai	251	
			P. brasiliensis	93	
			M. americanus	121	35
Year	**Month**	**Port**	**Species**	**N ind.**	**N. ov.**
2000	January	San Clemente	*M. ancylodon*	206	60
	February	San Clemente	*M. ancylodon*	46	44
	May	San Clemente	*M. ancylodon*	85	37
	October	San Clemente	*M. ancylodon*	60	44
Totals				18,840	2868

*, for species names in full see text.

In these species the degenerative process of the POFs was faster than that observed for other species (Hunter & Goldberg, 1980). The highest speed of degeneration was associated with the higher water temperatures in the Río de la Plata estuary during summer (Macchi *et al.*, 2003).

The size at first maturity (L50) was obtained by logistic regression by length-class using the maximum likelihood method (Kendall & Stuart, 1967); all individuals with gonad stages other than immature (1) were considered reproductive, thus the frequency of mature individuals was used as a response variable and the total length as the explanatory variable. This analysis was performed only for fish species with sufficient sample numbers of immature and mature gonads.

The material used for fecundity and spawning frequency estimations came from three research cruises carried out in the spawning peak (November 1999, December 2001 and December 2003) and from two surveys performed at the end of the spawning period (March 2000 to March 2001) (Table 1).

Batch fecundity (BF, number of oocytes released per spawning) was estimated gravimetrically with the hydrated oocyte method (Hunter *et al.*, 1985). Samples were examined histologically to determine the presence of POFs and hydrated oocytes. To avoid biases when estimating batch fecundity, only ovaries with hydrated oocytes and without POFs were used. Three pieces of ovary of approximately 0.1 g each were sampled from the anterior, middle and posterior section of each gonad, weighed (0.1 mg) and the number of hydrated oocytes counted. Batch fecundity was the product of the mean number of hydrated oocytes per unit ovarian weight and total ovarian weight (GW). Relative fecundity (RF, number of hydrated oocytes per gram of ovary-free body weight) was estimated as the batch fecundity divided by female weight (without ovaries).

Table 2. Sciaenids ovary maturity scale.

Macroscopic stage	Microscopic stage	Histological description
I. Immature	I. Immature	Small ovaries with a thin tunica, compact and ovarian ridges with mainly basophils cells, oogonias and primary oocytes. Smaller components have a nucleus with a central nucleolus; while the most developed have several nucleoli in the periphery (perinucleolar stage)
II. Developing	II. Early developing	During this phase, ovarian ridges remain compact. This stage begins secondary growth stage, characterized by the development of colourless inclusions in oocytes cytoplasm, called cortical alveoli, the rest of components are maintained in primary phase
	III. Developing	The mature oocytes are in vitellogenesis, characterized by the presence of eosinophilic droplets in the cytoplasm, composed of yolk protein. In addition to cortical alveoli other colourless larger droplets are observed around the nucleus composed of lipids. At this stage it becomes clear as the zona radiata, which is distinguished as eosinophilic layer between the plasma membrane and granulosa layer
III. Spawning capable	IV. Advanced developing	Large proportion of ovaries with vitellogenic oocytes with cytoplasm filled with yolk droplets. The nucleus has irregular contours due to the accumulation of reserves in the cytoplasm. In later stages of maturation lipid droplets begin to fuse to originate the oil droplet. The follicular cells grow in height and pellucid membrane is thickened, observed at higher magnification channels that connect the ovoplasma with granulosa cells
	V. Partial spent	At this stage ovarian ridges are lax, showing signs of spawning. Inflammatory reactions can be observed, bleeding and postovulatory follicles at different stages of resorption. Along with these evacuation indicators, oocyte yolks in maturity are expelled at the next spawn
	VI. Total developing and ripe	At this stage ovary reaches its maximum development and fills most of the body cavity. Prior to spawning, mature oocytes enter in tertiary stage of growth characterized by cytoplasmic hydration. This process begins with the migration of nucleus toward the animal pole and the formation of oil droplet. Then the nuclear membrane dissolved and a rapid incorporation of water by the cytoplasm occurs, which increases the size of oocytes
IV. Regressing	VII. Regressing	At this stage there has been total removal of mature oocytes, indicating the end of the reproductive process. Vitellogenic residual elements are observed at different stages of resorption (atresia). The tunica albuginea appears thickened due to the retraction which occurred after spawning
V. Regenerating	VIII. Regenerating	Upon completion of spawns, ovaries go through a process of reversal to the next spawning period. Only primary oocytes are found. Adults at rest are different from juvenile stage for holding thickened tunica albuginea and ovarian ridges with some degree of laxity

Spawning frequency was only estimated for whitemouth croaker. This variable was obtained from the incidence of females with POFs, following the method described by Hunter & Goldberg (1980). The description of the stages of POF degeneration in March was based on that given by Macchi *et al.* (2003) who observed that POF degradation in *M. furnieri* was faster than that reported by Hunter & Goldberg (1980) for northern anchovy (*Engraulis mordax*). 24-hours-old POF showed advanced signs of degeneration similar to those observed in *E. mordax* 48 hours after spawning. This more rapid degeneration was attributed to water temperature in the spawning area, which was higher (20–25°C) than that recorded for the northern anchovy (Hunter & Goldberg, 1980). Because of this, spawning frequency at the end of the reproductive period (March) was estimated by taking the total of females with POF, which correspond to a period of less than 24 hours from spawning (Hunter *et al.*, 1986). For samples taken in December 2003, as temperature in the spawning area was similar to that reported for *E. mordax* (about 16°C: Hunter & Goldberg, 1980), spawning frequency was estimated using the criteria given by Hunter & Goldberg (1980), who considered only the day 1 POF (24–48 hours from spawning) to calculate the daily spawning proportion.

The size and appearance of unfertilized eggs can tentatively be used to evaluate or estimate the overall developmental potential of the eggs after fertilization. For instance, the size of the egg was sometimes considered to be beneficial for the future development of the embryo. In order to obtain an estimate of the quality of spawning in different species, diameter (OD) and dry weight (DW) of hydrated oocytes were measured. For these, ovarian samples of whitemouth

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croaker (N = 40), Argentine croaker (N = 9), banded croaker (N = 16) and southern kingcroaker (N = 8) were collected and samples of 100 hydrated oocytes were removed from each individual. The oocyte diameter was measured and each sample was rinsed in distilled water, dried for 20 hours at 60°C and weighed (0.1 mg).

In the case of black drum, striped weakfish and king weakfish batch fecundity, spawning frequency, OD and DW values estimated by Macchi *et al.* (2002) and Militelli & Macchi (2004, 2006) were used for comparison between different species.

Statistical analysis

Coefficients of the logistic regressions obtained to estimate L50 for males and females and from the different sampled years were compared using a Chi-square test (Aubone & Wöhler, 2000). The relationships between BF and the variables TL and TW (ovary-free) were described using simple standard regression (Draper & Smith, 1981). A power model and a linear model were fitted to the relationships of BF versus TL and BF versus TW (ovary-free), respectively. Comparisons between the relationships BF versus TL obtained from different spawning seasons were based on the overlapping length-ranges of females applying an analysis of covariance (Draper & Smith, 1981). Differences in spawning frequency between years were tested using a Chi-square test. Diameter and dry weight of the hydrated oocytes were related to female size by linear regression. Values obtained during the spawning peak (November–December) and at the end of the breeding season were compared by analysis of variance. Results were considered significant if $P < 0.05$.

RESULTS

Spawning period

Figure 2 shows the extent of breeding season for different sciaenid species in the Buenos Aires Coastal Zone. The determination thereof was based on the presence of female reproductive activity; in cases that were not available samples were considered as described in the literature. The reproductive season in general was extensive (approximately six months) covering the spring–summer period. An exception to this pattern was observed in black drum, which showed its main spawning activity between October and December, for samples collected in Samborombon Bay.

Length at first maturity

The estimates of length at first maturity (L50) in whitemouth croaker, obtained from samples collected during different seasons, showed highly significant differences between the sexes ($\chi^2 = 27.85$, df = 1, $P < 0.01$). Despite some differences observed between years, these were not significant. Figure 3A shows the logistic regression obtained grouping the values of all years. Males reached first sexual maturity at smaller size than females. By bringing together individuals of both sexes, the length at first maturity had an average of 32.2 cm TL.

The size at maturity for *C. guatucupa* was evaluated fitting a logistic regression combining the values obtained in 1999 and 2005 (Figure 3B). Females matured at larger sizes than males, with estimated sizes at first maturity of 30.7 cm TL for females and 27.93 cm TL for males ($\chi^2 = 33.3$, df = 1, $P < 0.001$).

For king weakfish, as in the above mentioned species, the L50 estimated showed highly significant differences between sexes ($\chi^2 = 20.02$, df = 1, $P < 0.001$). Non-significant differences were observed between years and grouping the values of different years, the size at maturity for *M. ancylodon* obtained was 19.27 cm TL and 23.07 cm TL for males and females, respectively (Figure 3C).

In the case of Argentine croaker (*Umbrina canosai*) and southern kingcroaker (*Menticirrhus americanus*) L50 was only estimated with data collected in 2003 and 2005, respectively, due to the small number of samples and low representation of juveniles in other years. In December 2003 the L50 obtained for Argentine croaker showed significant differences between sexes ($\chi^2 = 4.33$, df = 1, $P < 0.05$) and was 23 cm TL for males (N = 196) and 25.9 cm TL for females (N = 198). L50 estimated by taking both sexes together was 24.3 cm LT. For southern kingcroaker length at first maturity estimated in November 2005 was 20 cm TL for males (N = 67) and 22.27 cm TL for females (N = 54). The L50 obtained for both sexes combined was 21.58 cm TL. It should be noted that *M. americanus* is often found in very low density in the Río de la Plata Estuary compared to other sciaenids as whitemouth croaker or king weakfish.

For black drum and banded croaker it was not possible to estimate L50 in any of samples taken. In the case of banded croaker, mature individuals lower than 14 cm TL were not found and all specimens larger than 22 cm LT corresponded to adults.

Fecundity

Batch fecundity (BF), estimated for whitemouth croaker in March 2000 (N = 10), March 2001 (N = 18) and December 2003 (N = 12) showed a potential relationship with total length and lineal with total weight (ovary-free) of individuals (Figure 4). BF estimated for females caught in March 2000 ranged between 53,600 (43 cm TL) and 315,000 (61 cm TL) hydrated oocytes, with a mean value of 134,673 (±50,290) hydrated oocytes. In March 2001, the BF values were significantly higher ($t = 2.39$; df = 22; $P < 0.05$) and ranged between 70,300 (42 cm TL) and 498,000 (61 cm TL) hydrated oocytes with a mean value of 204,202 (±55,483) hydrated oocytes. In December 2003 BF values ranged between 101,445

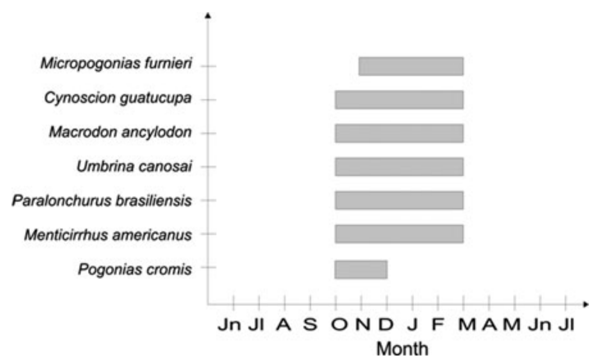

Fig. 2. Range of the spawning season for sciaenids species inhabiting the Río de la Plata Estuary and Buenos Aires Coastal Zone.

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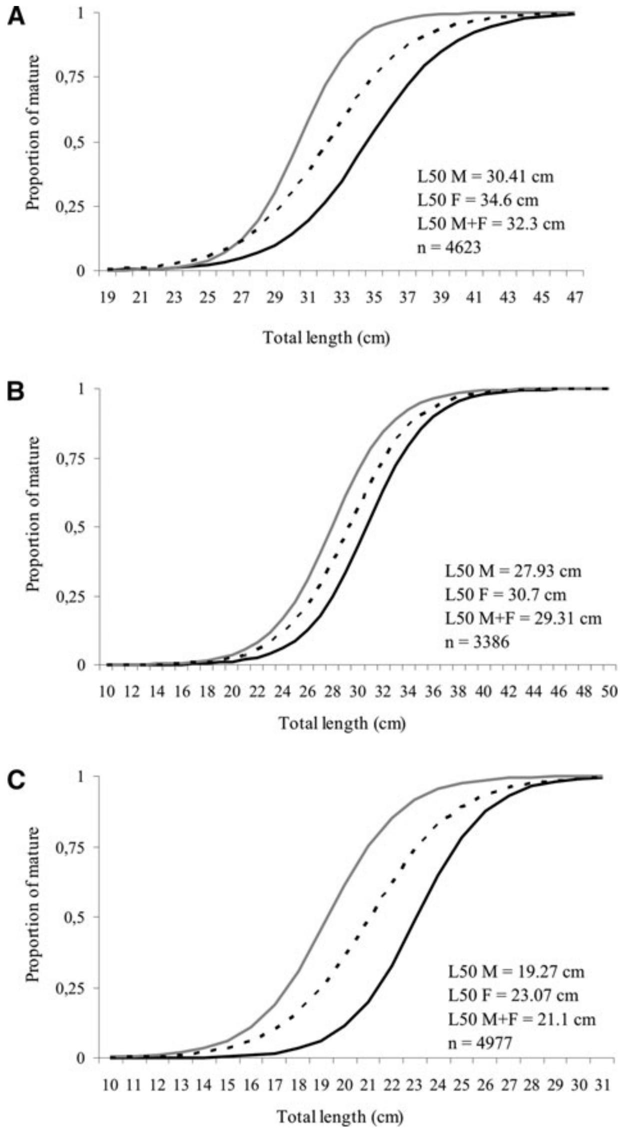

Fig. 3. Length at first maturity of females (black fill line), males (grey fill line) and both sexes combined (dashed line) for (A) *Micropogonias furnieri*, (B) *Cynoscion guatucupa* and (C) *Macrodon ancylodon*.

(49 cm TL) and 460,230 (58 cm TL) hydrated oocytes, with a mean value of 206,866 (±59,913) hydrated oocytes. Comparisons of mean values and covariance analysis made for the data set corresponding to the same size-range showed no significant differences with March 2001 ($t = 0.95$, df = 24, $P > 0.05$). However, these estimates were significantly higher than those obtained in March 2000 ($t = 3.19$, df = 16, $P < 0.01$). Relative fecundity (RF), estimated with data of the three cruises, ranged from 50 to 276 hydrated oocytes/g of female (ovary-free). This variable showed a great dispersion based on the length of the females and it did not demonstrate any tendency in relation to the female size. As with BF, the RF values estimated for March 2000 were significantly lower than those obtained for March 2001 and December 2003 ($t = -3{,}86$; df = 26; $P < 0.01$). The mean RF obtained for every year was 97 ± 19, 161 ± 26 and 148 ± 28 oocytes/g, respectively.

Batch fecundity obtained for *Umbrina canosai* in November 1999 and December 2003 ranged between 53,200 and 197,000 hydrated oocytes for a size-range between 29 cm and 39 cm TL. This variable showed a positive relationship with size and weight of females (ovary free) (Figure 5). Relative fecundity ranged between 105 and 207 oocytes/g of female (ovary-free) with a mean value of 161 ± 25 oocytes/g of female (ovary-free), and no relationship with total size or weight was observed.

In the case of *Paralonchurus brasiliensis*, samples of gravid female were only obtained in March 2001. BF estimations ranged between 5560 (19 cm TL) and 32,400 (21 cm TL) hydrated oocytes, with an average value of 18,683 (±4,552) hydrated oocytes. This variable did not show a relationship with total length or weight of females; this may be due to the narrow size-range of the samples. RF ranged from 58 to 320 hydrated oocytes per gram of female (ovary-free) with a mean value of 199 ± 49 oocytes/g of female (ovary-free).

As mentioned previously, *Menticirrhus americanus* is a species whose abundance in the area of the Rio de la Plata is very low, which makes it very difficult to obtain samples of gravid females. Only in November 2005 eight hydrated females of southern kingcroaker were captured to estimate the reproductive potential. BF ranged between 45,115 and 273,188 hydrated oocytes and RF ranged between 143 and 374 hydrated oocytes per gram of female (ovary-free) with a mean value of 217 ± 70. BF showed a positive relationship with length (TL) and weight of females (ovary-free) described by the equations:

$$BF = 312.13\ TW^{*} - 40677\ (r^2 = 0.58)$$
$$BF = 0.0054\ TL^{4.72}\ (r^2 = 0.71)$$

Spawning frequency

Spawning frequency of whitemouth croaker was estimated for March 2000, March 2001 and December 2003. In March 2000, 33.2% (N = 77; CV = 0.49) of females had POF <24 hours, indicated an interval between spawning close to 3 days during this month. In March 2001 the percentage of females with POF <24 hours was 26.25% (N = 240; CV = 0.09) which corresponds to a spawning frequency of 4 days. The daily percentage of mature females with day 1 POF in December 2003 was 18.58% (N = 226; CV = 0.8), equivalent to a frequency close to 5 days for this month. These differences between sampled years were highly significant ($\chi^2 = 12.07$, df = 2, $P < 0.005$).

Size and weight of the oocytes

Whitemouth croaker oocyte diameter and oocyte dry weight were estimated for March 2000, 2001 and December 2003. The diameter of hydrated oocytes showed no significant differences between the three years sampled ($t = 1.90$, df = 25, $P > 0.05$) and showed an average of 868 μm. This variable did not show a significant relationship to the size or weight of females. With regard to oocyte dry weight, the average value obtained for a sample of 100 hydrated oocytes during March 2000 (2.1 ± 0.1 mg) and March 2001 (2.3 ± 0.2 mg) showed no significant differences ($t = 1.33$, df = 28, $P > 0.05$), however in December 2003 (3.1 ± 0.1 mg) ($t = -12.48$, df = 25, $P < 0.01$) was significantly higher. These results suggest that yolk reserves of hydrated oocytes were lower in samples collected at the end of the spawning season (March).

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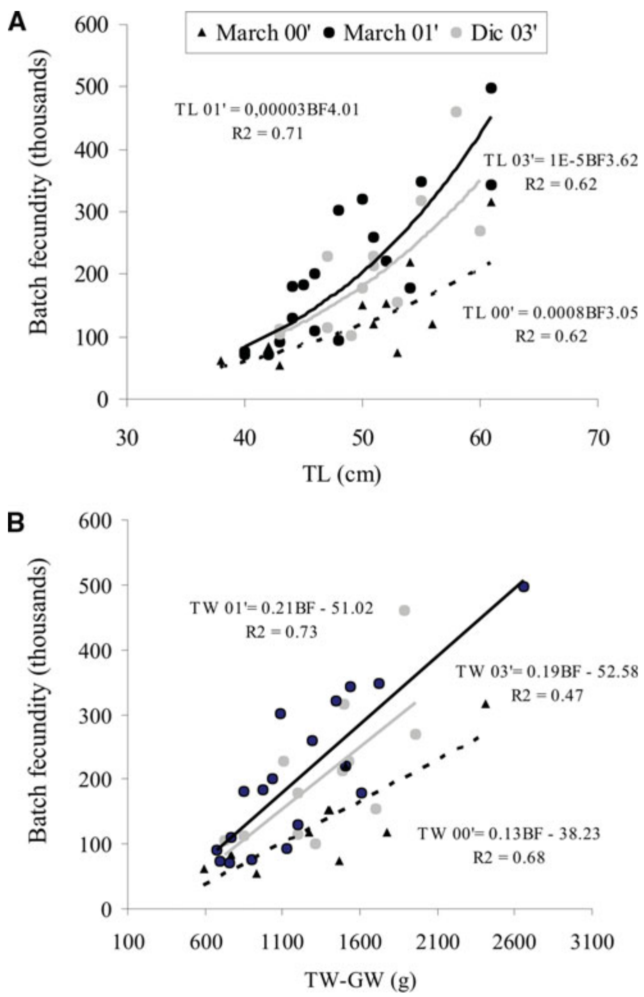

Fig. 4. Batch fecundity of *Micropogonias furnieri* as a function of total length (A) and total weight (without ovary) (B) obtained from March 2000 (triangles and dashed line), March 2001 (black dots and black fill line) and December 2003 (grey dots and grey fill line).

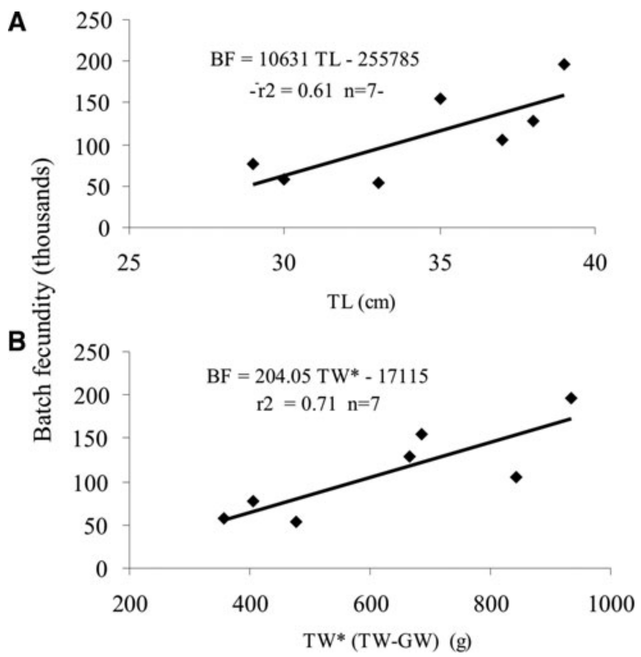

Fig. 5. Batch fecundity of *Umbrina canosai* as a function of total length (A) and total weight (without ovary) (B).

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In the case of Argentine croaker, banded croaker and southern kingcroaker hydrated females were obtained only from one year. The average values of diameter and dry weight of 100 hydrated oocytes was: 860 ± 55 μm and 1.7 ± 0.07 mg for *U. canosai* (November); 758 ± 17 μm and 1.3 ± 0.09 mg for *P. brasiliensis* (March) and 999 ± 14 μm and 2.5 ± 0.03 mg for *M. americanus* (November).

Table 3 summarizes the results obtained in the present study including the values of length at first maturity (L50), batch fecundity, oocyte size and spawning frequency obtained for the different species of the sciaenid family, including data reported by Macchi *et al.* (2002) for *Pogonias cromis* and by Militelli & Macchi (2004, 2006) for *Macrodon ancylodon* and *Cynoscion guatucupa*, respectively.

DISCUSSION

The size at maturity is subject to variation between species and within species. Thus all fishes of the same cohort or size need not attain maturity at some fixed age or length. In the case of *M. furnieri* and *C. guatucupa*, length at first maturity (L50) values estimated in this work were similar to those previously reported for these species in coastal waters of the Buenos Aires Coastal Zone (Cousseau *et al.*, 1986; Macchi & Acha, 1998; Militelli & Macchi, 2006). The difference between the sexes indicates that females tend to mature at larger size than males. L50 obtained for *M. ancylodon* was lower than other estimates reported for the Rio de la Plata area (Norbis & Pagano, 1985; Cordo, 1986) and for the southern Brazil population (Juras & Yamaguti, 1989). L50 estimated for *U. canosai* was higher than those estimated for this species in southern Brazil. Haimovici (1982), working with samples from Rio Grande do Sul, considered a L50 for males between 17.1 and 18.8 cm TL and between 19.8 and 22.9 cm TL for females. L50 obtained for *M. americanus* was higher than other estimates obtained for this species with individuals collected in waters of Santos Bay, San Pablo (Brazil) (Giannini & Paiva, 1992), in the North Atlantic region (Smith & Wenner, 1985) and in the Gulf of Mexico (Harding & Chittenden, 1987); however, these estimates should be used as preliminary due to small sample size. A recent study carried out by Lewis & Fontoura (2005) in southern Brazil reported a length at first maturity for *P. brasiliensis* of 15.4 cm TL. At present, no information about length at first maturity of *P. cromis* inhabiting Argentine waters has been reported. In north-eastern Florida (USA) it was found that L50 of this species differ between sexes, as in the rest of the sciaenids. This parameter was about 59 cm TL (4–5 years) for males and ranged between 65 and 69.9 cm TL (5–6 years) for females (Murphy & Taylor, 1989). On the other hand, in Laguna Madre (Texas coast) these differences were not found and the age at first maturity for both sexes was estimated around 4 years (Bumguardner *et al.*, 1995).

Some biomass assessment models such as the egg production method require an estimate of spawning frequency. This requirement exists because the method was developed for fishes, such as sciaenids, which have indeterminate annual fecundity. Thus, the rate of egg production can be calculated only from estimates of spawning frequency and batch fecundity made during a survey period (Hunter & Macewicz, 1985). In this paper, estimates of fecundity and spawning frequency of sciaenids were compiled, which can serve to obtain

Table 3. Values of reproductive variables of Sciaenidae family species in Buenos Aires Coastal Zone. TL, total length; L50, length at first maturity; BF, batch fecundity; RF, relative fecundity; SF, spawning frequency; HD, hydrated diameter; DW, oocyte dry weight (100 eggs).

Species	*Micropogonias furnieri* (whitemouth croaker)	*Cynoscion guatucupa* (striped weakfish)	*Macrodon ancylodon* (king weakfish)	*Umbrina canosai* (Argentine croaker)	*Paralonchurus brasiliensis* (banded croaker)	*Menticirrhus americanus* (southern kingcroaker)	*Pogonias cromis* (black drum)
Maximum TL (cm)	67	53	40	39	21	40	150
Spawning season	October–March	October–March	October–March**	Spring–summer	Spring–summer	Spring–summer	October–December+
L50 (cm)	32.2	29.3	21.1	24.3	15.4	21.6	62•
BF (ooc.)	53,600–498,000	14,500–208,000*	12,400–225,700**	53,200–197,000	5560–32,400	45,115–273,180	90,000–2,800,000+
RF mean (ooc./g)	97–161	107–135*	285–349**	161	199	217	75–98+
SF (days)	3–5	6–8	6**	—	—	—	3–4+
HD mean (μm)	868	786–870*	974–1162**	860	758	999	1036–1271+
DW (mg)	2.1–3.1	1.91–2.21*	3.3–5.1**	1.7	1.3	2.5	3.43–4.24+

*Militelli & Macchi (2006); **Militelli & Macchi (2004); +Macchi *et al.* (2002); •Murphy & Taylor (1989).

spawning-stock biomass estimates for the assessment of these stocks in the Buenos Aires Coastal Zone. Daily percentage of spawning females estimated for whitemouth croaker was consistent with the values reported by Macchi *et al.* (2003), who reported a spawning frequency between 3 and 4 days during 1995–1996 spawning season. These estimates of daily percentage of spawning females were also similar to those reported for black drum (*P. cromis*) (Macchi *et al.*, 2002), but higher than those estimated for other sciaenids, such as *M. ancylodon* (Militelli & Macchi, 2004) and *C. guatucupa* (Macchi, 1998).

Descriptions of reproductive strategies and the assessment of fecundity are the fundamental topics in the study of the biology and population dynamics of fish species (Hunter *et al.*, 1992 in Murua & Saborido-Rey, 2003). Batch fecundity estimates for *M. furnieri* showed interannual variations, based on samples collected in the Río de la Plata estuary (Macchi *et al.*, 2003). Data from the reproductive seasons 1995–1996 and 1997–1998, showed that fecundity of whitemouth croaker decreases at the end of the reproductive period, coinciding with an increase in atresia percentages. In fact, during December 2003 fecundity values were much higher than those estimated in March 2000 and 2001. Nevertheless, this variable varies among years, depending on environmental or nutritional factors (Nieland & Wilson, 1993). This result agrees with analysis of the oocyte dry weight in hydrated females, which showed lower values in March. Seasonal decrease in egg size was reported for this and other species (Kjesbu *et al.*, 1996; Macchi *et al.*, 2003), which may be associated with temperature or nutritional condition of the spawning females (Hinckley, 1990; Wooton, 1994). Similar results were reported for *Cynoscion guatucupa* (Militelli & Macchi, 2006) and *Macrodon ancylodon* (Militelli & Macchi, 2004).

When considered together some aspects of reproduction were similar for all sciaenid species inhabiting the Río de la Plata estuary and Buenos Aires Coastal Zone (Table 3). For example, all species are multiple spawners with indeterminate fecundity, the reproductive season in general is extensive (approximately six months) covering the period spring–summer (Militelli, 2007), except for black drum whose spawning season is more delimited (Macchi *et al.*, 2002). However, there are differences between the spawning areas and some reproductive tactics. Militelli (2007) taking into account temperature and salinity ranges of the spawning areas, grouped the sciaenids into three spawning tactics: (a) estuarine spawner associated with the bottom salinity front: the species that spawn in the inner area of the estuary in accordance with the main horizontal salinity gradients in the bottom (*M. furnieri*, *P. cromis* and *M. ancylodon*); (b) estuarine spawner non-associated with the bottom salinity front: the spawning of these species was mainly located in the middle of the estuary in brackish water with salinities ranging between 24 and 30 psu (*P. brasiliensis* and *M. americanus*); and (c) marine spawner: reproduction occurred always in salt water (values higher than 30 ups) in the outer area of the Rio de la Plata estuary or El Rincón, at the south of Buenos Aires Province (*C. guatucupa*, *U. canosai* and *M. furnieri*).

With regard to reproductive potential, there are wide differences in fecundity values mainly due to the different sizes attained by each species (batch fecundity ranged between 5000 and 2,800,000 hydrated oocytes). But, when relative fecundity values (size independent variable) were compared, average values of this variable in general were similar, ranging approximately between 150 and 200 hydrated oocytes per female gram. Black drum is the exception within this group, because the mean relative fecundity mean ranged between 75 and 98 hydrated oocytes per ovary-free female gram. This difference may be as consequence of the greater oocyte size reached by *P. cromis* eggs (1100–1400 μm) compared to the rest of sciaenids. In the particular case of black drum, the largest diameter reached by hydrated oocytes was also associated with an increase of dry weight (Macchi *et al.*, 2002), so that low relative fecundity recorded in this species may be compensated in part for increased egg quality, which would encourage the survival of early life stages. At the time of using these data for biomass estimates it should be noted that in 4 (*M. furnieri*, *C. guatucupa*, *M. ancylodon* and *P. cromis*) of the 7 species, significant differences in reproductive parameters values obtained for the spawning peak and end of the spawning season were observed.

From species studied, whitemouth croaker, striped weakfish and Argentine croaker are those with higher biomass in the Buenos Aires Coastal Zone. These species have in common the fact of sharing areas of distribution and reproduction larger than black drum, king weakfish or banded croaker. Moreover, these most abundant species are also characterized by reproductive periods generally more extensive, as is the case at least of whitemouth croaker and striped weakfish (Militelli, 2007). These aspects of reproductive strategy may be associated with differences in abundance recorded for these species, since greater extension of the area and spawning period involves higher reproductive potential and a greater chance of survival of spawning products. These characteristics may influence the possibility of colonizing new areas and eventually the development of more abundant populations.

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REFERENCES

Acha E.M., Mianzan H., Lasta C.A. and Guerrero R.A. (1999) Estuarine spawning of whitemouth croaker *Micropogonias furnieri* (Pisces: Sciaenidae), in the Río de la Plata, Argentina. *Marine and Freshwater Research* 50, 57–65.

Aubone A. and Wöhler O.C. (2000) Aplicación del método de máxima verosimilitud a la estimación de parámetros y comparación de curvas de crecimiento de Von Bertalanffy. *Serie INIDEP Informes Técnicos* 37, 21.

Barbieri L.R., Chittenden M.E. Jr and Lowerre-Barbieri S.K. (1994) Maturity, spawning, and ovarian cycle of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters. *Fishery Bulletin* 92, 671–685.

Beacham T.D. (1983) *Growth and maturity of Atlantic cod (*Gadus morhua*) in the southern Gulf of St Lawrence.* Canadian Technical Report of Fisheries and Aquatic Science 1142.

Brown-Peterson N.J., Wyanski D.M., Saborido-Rey F. Macewicz B.J. and Lowerre-Barbieri S. (2011) A standardized terminology for describing reproductive development in fishes. *Marine and Coastal Fisheries* 3, 52–70.

Bumguardner B.W., Colua R.L., Young E., Westbrook D. and Buckley R. (1995) *Black drum life history in Texas Bays with emphasis on the Upper Laguna Madre*. Texas Parks and Wildlife Department, Coastal Fisheries Division. Final Report for project F-36-R.

Carozza C., Navarro L., Jaureguizar A., Lasta C. and Bertolotti M.I. (2001) *Asociación íctica costera bonaerense 'Variado Costero'. Informe I*. INIDEP Technical Report 48, 28 pp.

Cassia M.C. (1986) Reproducción y fecundidad de la pescadilla de red (*Cynoscion striatus*). *Publicación de la Comisión Técnica Mixta del Frente Marítimo* 1, 191–203.

Cordo H.D. (1986) Estudios biológicos sobre peces costeros con datos de dos campañas de investigación realizadas en 1981. IV. La pescadilla real (*Macrodon ancylodon*). *Publicación de la Comisión Técnica Mixta del Frente Marítimo* 1, 47–52.

Cousseau M.B. (1985) Los peces del Río de la Plata y de su Frente Marítimo. In Yañez Arancibia A. (ed.) *Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration*. DR (R) UNAM Press México, pp. 515–534.

Cousseau M.B., Cotrina C.P., Cordo H.D. and Burgos G.E. (1986) Análisis de datos biológicos de corvina rubia (*Micropogonias furnieri*) y pescadilla de red (*Cynoscion striatus*) obtenidos en dos campañas del año 1983. *Publicación de la Comisión Técnica Mixta del Frente Marítimo* 1, 319–332.

Díaz de Astarloa J.M., Aubone A. and Cousseau M.B. (1999) Asociaciones ícticas de la plataforma costera de Uruguay y norte de Argentina, y su relación con los parámetros ambientales. *Physis* 57, 29–45.

Draper N. and Smith H. (1981) *Applied regression analysis*. 2nd edition. New York: John Wiley and Sons.

Fernández Aráoz N.C., Lagos N. and Carozza C. (2005) *Asociación ictica costera bonaerense 'variado costero' evolución de las capturas desembarcadas por la flota comercial argentina (1990–2003)*. INIDEP Technical Report 4, 21 pp.

García del Moral R. (1993) *Laboratorio de anatomía patológica*. Madrid: McGraw-Hill and Ed. Interamericana.

Giannini R. and Paiva-Filho A.M. (1992) Aspectos da Bioecologia de *Menticirrhus americanus* (Teleostei, Sciaenidae) na Bahía de Santos, SP, Brasil. *Boletim do Instituto de Pesca* 19, 1–15.

Haimovici M. (1982) *Estructura y dinámica poblacional del pargo blanco* Umbrina canosai *(Sciaenidae, Pisces) del litoral de Rio Grande do Sul, Brasil*. PhD thesis. Universidad Nacional de Buenos Aires, Facultad de Ciencias Exactas y Naturales, Buenos Aires, Argentina, 273 pp.

Harding S.M. and Chittenden M.E. Jr (1987) Reproduction, movements and population dynamics of the southern kingfish *Menticirrhus americanus* in the northwestern Gulf of Mexico. *NOAA Technical Report NMFS* 49, 1–21.

Hinckley S. (1990) Variation of egg size of walleye pollock *Theragra chalcogramma* with a preliminary examination of the effect of egg size on larval size. *Fishery Bulletin US* 88, 471–483.

Hubold G. (1978) Variations in growth rate and maturity of herring in the North Sea in the years 1955–1973. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* 172, 154–163.

Hunter J.R. and Goldberg S.R. (1980) Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. *Fishery Bulletin US* 77, 641–652.

Hunter J.R. and Macewicz B.J. (1985) Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. *Fishery Bulletin US* 83, 119–136.

Hunter J.R., Lo N.C.H. and Leong R.J.H. (1985) Batch fecundity in multiple spawning fishes. In Lasker R.M. (ed.) *An egg production method for estimating spawning biomass of pelagics fish: application to the northern anchovy*, Engraulis mordax. NOAA Technical Report NMFS 36, pp. 67–77.

Hunter J.R., Macewicz B.J. and Sibert J.R. (1986) The spawning frequency of Skipjack Tuna, *Katsuwonus pelamis*, from the South Pacific. *Fishery Bulletin US* 84, 895–903.

Hunter J.R., Macewicz B.J., Lo N.C.H. and Kimbrell C.A. (1992) Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fishery Bulletin US* 90, 101–128.

Jaureguizar A.J., Menni R.C., Lasta C.A. and Guerrero R.A. (2006) Fish assemblages of the northern Argentine coastal system: spatial patterns and their temporal variations. *Fisheries Oceanography* 15, 326–344.

Juras A.A. and Yamaguti N. (1989) Sexual maturity, spawning and fecundity of king weakfish *Macrodon ancylodon*, caught off Rio Grande do Sul State (southern coast of Brazil). *Boletim do Instituto Oceanográfico da USP* 37, 51–58.

Kendall M.G. and Stuart A. (1967) *The advanced theory of statistics*. London: Charles Griffin and Company Limited, 690 pp.

Kjesbu O.S., Solemdal P., Bratland P. and Fonn M. (1996) Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 53, 610–620.

Lewis D. dos S. and Fontoura N.F. (2005) Maturity and growth of *Paralonchurus brasiliensis* females in southern Brazil (Teleostei, Perciformes, Sciaenidae). *Journal of Applied Ichthyology* 21, 94–100.

Macchi G.J. (1998) Preliminary estimate of spawning frequency and batch fecundity of striped weakfish, *Cynoscion striatus*, in coastal waters off Buenos Aires province. *Fishery Bulletin US* 96, 375–381.

Macchi G.J. and Acha M.E. (1998) Aspectos reproductivos de las principales especies de peces en la Zona Común de Pesca Argentino–Uruguaya y en El Rincón. Noviembre 1994. In Lasta C.A. (ed.) *Resultados de una campaña de evaluación de recursos demersales costeros de la provincia de Buenos Aires y del Litoral Uruguayo. Noviembre 1994. INIDEP Technical Report* 21, 67–89.

Macchi G.J. and Christiansen H.E. (1992) Estimación de la fecundidad de la corvina rubia (*Micropogonias furnieri*) mediante la aplicación del método estereométrico. *Publicación de la Comisión Técnica Mixta del Frente Marítimo* 12, 17–22.

Macchi G.J., Acha E.M and Lasta C.A. (2002) Reproduction of black drum (*Pogonias cromis*) in the Río de la Plata estuary, Argentina. *Fisheries Research* 59, 83–92.

Macchi G.J., Acha E.M. and Militelli M.I. (2003) Seasonal egg production pattern of whitemouth croaker (*Micropogonias furnieri*) of the Río de la Plata estuary, Argentina–Uruguay. *Fishery Bulletin US* 101, 332–342.

Macchi G.J., Pájaro M. and Ehrlich M. (2004) Seasonal egg production pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fisheries Research* 67, 25–38.

Militelli M.I. (2007) *Biología reproductiva comparada de especies de la familia Sciaenidae en aguas del Río de la Plata y Costa Bonaerense*. PhD thesis. Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales, Mar del Plata, Argentina, 145 pp.

Militelli M.I. and Macchi G.J. (2004) Spawning and fecundity of king weakfish, *Macrodon ancylodon*, in the Río de la Plata estuary, Argentina–Uruguay. *Journal of the Marine Biological Association of the United Kingdom* 84, 443–447.

Militelli M.I. and Macchi G.J. (2006) Spawning and fecundity of striped weakfish, *Cynoscion guatucupa*, in the Río de la Plata estuary and adjacent marine waters, Argentina–Uruguay. *Fisheries Research* 77, 110–114.

Murphy M.D. and Taylor R.G. (1989) Reproduction and growth of black drum, *Pogonias cromis*, in the Northeast Florida. *Northeast Gulf Science* 10, 127–137.

Murua H. and Saborido-Rey F. (2003) Female reproductive strategies of marine fish species of the North Atlantic. *Journal of Northwest Atlantic Fishery Science* 33, 23–31.

Nieland D.L. and Wilson C.A. (1993) Reproductive biology and annual variation of reproductive variables of black drum in the northern Gulf of Mexico. *Transactions of the American Fisheries Society* 122, 318–327.

Norbis W. and Pagano D. (1985) Aspectos biológicos de *Macrodon ancylodon. Comunicación Preliminar Actas Jornadas de Zoología de Uruguay*: 12–13.

Rico M.R. (2000) *La salinidad y la distribución espacial de la ictiofauna en el estuario del Río de la Plata.* Tesis de Licenciatura. Facultad de Ciencias Exactas y Naturales, UNMdP, 74 pp.

Smith J.W. and Wenner C.A. (1985) Biology of the southern kingfish in the South Atlantic Bight. *Transactions of the American Fishery Society* 114, 356–366.

Tyler C.R. and Sumper J.P. (1996) Oocyte growth and development in teleosts. *Reviews in Fish Biology and Fisheries* 6, 287–318.

Trippel E.A. (1995) Age at maturity as a stress indicator in fisheries. *Bioscience* 45, 759–771.

Vizziano D. and Berois N. (1990) Ciclo histológico del ovario de *Macrodon ancylodon* (Bloch & Shneider, 1801) (Teleostei: Sciaenidae). *Biología Pesquera* 19, 39–47.

and

Wootton R.J. (1994) Life histories as sampling devices: optimum egg size in pelagic fishes. *Journal of Fish Biology* 45, 1067–1077.

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