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THE REPRODUCTIVE BIOLOGY OF THE POUTING *TRISOPTERUS LUSCUS* FROM THE ATLANTIC COAST OF MOROCCO

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ABSTRACT

*The reproductive biology of the pouting, *Trisopterus luscus*, is not well known in the Moroccan coastal area and this work reports on a two-year study of this species from January 2018 to December 2019. A total of 2210 sampled specimens were examined, of which 1162 were males (52.57%) and 1048 females (47.42%), the males significantly outnumbering the females according to the chi-square test. Monthly monitoring of the gonado-somatic index (GSI) and macroscopic and microscopic gonad observations showed that *T. luscus* was reproductively active throughout the year with maximum peaks during January–February 2018 and March–April 2019. The condition index (K) also peaked in these two months. Changes in the reproductive characteristics of this sampled population of *T. luscus* are discussed in relation to fish size and season and to fecundity.*

Key words: *Trisopterus luscus*, condition index, gonado-somatic index, length at first maturity, Atlantic Moroccan coasts

LA BIOLOGIA RIPRODUTTIVA DELLA BUSBANA BRUNA *TRISOPTERUS LUSCUS* LUNGO LA COSTA ATLANTICA DEL MAROCCO

SINTESI

*La biologia riproduttiva della busbana bruna, *Trisopterus luscus*, non è ben conosciuta nell'area costiera marocchina e questo lavoro riporta uno studio biennale sulla specie da gennaio 2018 a dicembre 2019. Sono stati esaminati 2210 esemplari campionati, di cui 1162 maschi (52,57%) e 1048 femmine (47,42%), con una significativa prevalenza dei maschi sulle femmine secondo il test del chi-quadrato. Il monitoraggio mensile dell'in-*

dice gonado-somatico (*GSI*) e le osservazioni macroscopiche e microscopiche delle gonadi hanno mostrato che *T. luscus* è stato attivo dal punto di vista riproduttivo durante tutto l'anno, con picchi massimi nei mesi di gennaio-febbraio 2018 e marzo-aprile 2019. Anche l'indice di condizione (*K*) ha raggiunto un picco in questi due mesi. I cambiamenti nelle caratteristiche riproduttive della popolazione campionata di *T. luscus* sono discussi in relazione alle dimensioni e alla stagione dei pesci e alla fecondità.

Parole chiave: *Trisopterus luscus*, indice di condizione, indice gonado-somatico, lunghezza alla prima maturità, coste atlantiche del Marocco

INTRODUCTION

Knowledge of the reproductive biology of important fish species is essential for successful fishery management (e.g., Birkland & Dayton, 2005; Zhang, 2021). There is increasing awareness that the traditional indicators of stock viability are inadequate because it is the capacity of a fish population to produce viable eggs and larvae each year that is crucial for stock viability and recovery (Kraus *et al.*, 2002; Murua *et al.*, 2003). Accurate estimates of the population reproductive potential are also required to assess stock-recruitment relationships (Marshall *et al.* 1994).

The pouting *Trisopterus luscus*, a teleost of the Gadoid family, is of commercial importance for artisanal fleets of a number of European countries, primarily France, Portugal, and Spain, and of major commercial importance on the Atlantic coast of the Iberian Peninsula (e.g., Wheeler, 1978; Whitehead *et al.* 1986). The species' range extends from the North Sea, along the Atlantic coasts of western Europe to the southern Atlantic coast of Morocco and into the Mediterranean Sea. Information concerning this species is relatively scarce but there have been studies on its growth (Puente 1988; Merayo & Villegas 1994), distribution, fish assemblage (shoaling or species composition including age structure) and selectivity (Fonseca *et al.*, 2005), feeding ecology, and parasitology (Tirard *et al.*, 1996; Fowler *et al.*, 1999).

T. luscus is considered a batch spawner (Merayo, 1996a) with a protracted spawning season during winter and spring time (Desmarchelier, 1985; Gherbi-Barre, 1983; Merayo, 1996a). This pouting undergoes asynchronous ovarian development and females reach maturation at about 15 cm, based on histology (Alonso-Fernández, 2011). Despite the asynchronous ovarian organization, several authors consider *T. luscus* as a species with determinate fecundity, claiming it is possible to estimate its potential fecundity (Alonso-Fernández *et al.*, 2008; Merayo, 1996a).

However, other data about this species – on growth, for instance – remain sparse (Puente, 1988; Merayo & Villegas 1994).

The pouting is most frequent in coastal areas of the Bay of Biscay, but in the North Atlantic/North Sea it does not extend far northwards beyond the Shetland Islands (El Omrani *et al.*, 2021; Wheeler, 1978). According to Wheeler (1978), the great Norwegian coast acts as the northern barrier for the species. The



Fig. 1: Essaouira-Sidi Ifni sampling area for *Trisopterus luscus* and key fishing ports in the central and southern Moroccan Atlantic coastal area.

Sl. 1: Zemljevid obravnavanega območja s predelom Essaouira-Sidi Ifni in glavnimi ribiškimi pristanišči, kjer so bila opravljena vzorčenja vrste *Trisopterus luscus* v osrednjem in južnem maroškim atlantskim obalnim območjem.

important spawning areas for the species appear to be the English Channel (Chevey, 1929), Bay of Biscay, and south to Morocco. Inner coastal areas are preferred spawning areas; according to anecdotal accounts the adult fish move out of these sites and form shoals of homogenous sizes (20–40 cm), while the larger fish prefer rocky areas (Desmarchelier, 1986).

Although the pouting is of major commercial importance on the Atlantic coast of the Iberian Peninsula, it has received little scientific attention as it is not highly valued. Since the fish does not keep well, it must be consumed within a short time after capture. Nevertheless, in France attempts are being made to exploit this fish as a substitute for molluscan and crustacean foods (Desmarchelier, 1986). Knowledge of the pouting's reproductive biology is generally limited and this reproductive study of *T. luscus* is the first to be carried out for Moroccan Atlantic waters.

The Moroccan Atlantic coast is among the richest in exploitable biological resources (El Omrani *et al.*, 2021). The shelf is characterized by the upwelling of deep Atlantic waters that contribute nutrients promoting primary productivity in superficial waters and increasing the productivity of the whole trophic food chain. Indeed, the Moroccan coast has the privilege to be among the five known zones in the world that are influenced by this beneficial upwelling phenomenon. A sequence of physical, chemical, and biological processes encourages primary production and increases the biomass of fish resources, thus, in order to maintain this productivity, continued upwelling of rich deep waters to the surface is essential.

These circumstances prompted the present study on the reproductive biology of *T. luscus*, probably the most complex aspect of this fish's biology. The purpose of this work was to study the reproductive parameters, the sex ratio, the laying period, and the size at first sexual maturity of the Moroccan population of *T. luscus* using both macroscopic and microscopic observations of the gonads. The combination of these reproductive parameters with those of growth and exploitation will help formulate management measures for a rational exploitation of the stock.

MATERIAL AND METHODS

Samples were collected once a month between January 2018 and December 2019 from trawler landings at a port on the Moroccan Atlantic coast (Fig. 1). A total of 2210 individuals were sampled, ranging from 11 to 31 cm in total length. The following information was collected from each individual: total length (L), total weight (Wg), maturation stage, gonad weight (GW), and liver weight (LW). For each mature individual, the gonadosomatic-index (GSI), hepatosomatic-index (HSI) and condition factor (K) were estimated as follows:

$$GSI = GW/W * 100 \quad HSI = LW/W * 100 \quad K = W/L^3 * 100$$

The sex ratio was calculated monthly according to the following equation: sex ratio = (F/M), M: number of males, F: number of females. The sex ratio was analyzed using a 1-centimeter length class basis.

To follow the developmental processes, the ovaries (n = 400) were removed from specimens for histology and fixed immediately in buffered Davidson preservative. Central portions of the fixed ovaries were extracted, dehydrated, embedded in paraffin, sectioned at 5 µm, and stained with haematoxylin-eosin for microscopic analysis performed through observation and photography of different stages using a camera (ToupCam™) attached to a light microscope (Olympus CX41). For each female, the follicles (oocytes and surrounding follicular layer) were classified into developmental stages based on histological criteria (Saborido-Rey & Junquera, 1998; Murua & Saborido-Rey, 2003). The stages assigned were primary growth, cortical alveoli, vitellogenesis, and hydrated. Other ovarian structures such as atretic oocytes and postovulatory follicles (POFs) were identified and their presences scored for every slide. Female maturity status was determined based on the most advanced oocyte development stage contained within the ovary, the presence of POFs, and percentage of vitellogenesis atresia (Dominguez-Petit, 2007).

All females with ovaries in above-defined maturity stages were considered mature. Females were considered immature when only primary-growth stage oocytes were present and there was no evidence of prior spawning activity, e.g., thick ovary wall.

Macroscopic observations classified female oocytes into five stages (I, II, III, IV, and V) (Holden & Raitt, 1974). Stage I and II oocytes were considered immature; the other stages mature. To define female maturity in terms of body length, a logistic equation was applied to the maturity-at-length data, based on the histological and macroscopic maturity classification methods:

$$P = 1 / (1 + e^{-(a + b * L)}) \quad (1)$$

where: P = percentage of mature individuals by size class; L = total length (mm); "a" and "b" = constants. Parameters "a" and "b" were obtained by a logarithmic transformation of the expression (1) which enabled the linear equation (2):

$$\ln (P / (1 - P)) = a + b * L \quad (2)$$

Length at first sexual maturity was defined as the length at which 50% of the individuals were mature (L50), i.e., $L50 = -a / b$ (3).

Tab. 1: Relation between macroscopic evolution of ovaries and microscopic evolution of oocytes.**Tab. 1: Povezava med razvojem ovarijev na makroskopskem nivoju in razvojem oocit na mikroskopskem nivoju.**

Maturation stage of the ovaries	Macroscopic state of the ovaries	Microscopic evolution of oocytes
1. Immature	Ovary small and pink, homogeneous appearance	Numerous oogonia and oocytes grouped in islands, which are separated by a thin conjunctive blade weft
2. Start of development	Pink ovary, size between 4 and 5cm	Scarce oogonia, appearance of increasing oocytes
3. Vitellogenesis	Orange-coloured ovary, grainy appearance. A few hyaline oocytes are visible through the ovarian membrane	All stages of maturation are present: oocytes in the process of vitellogenesis are the most abundant
4a. Pre-spawning 4b. Spawning	a. The presence of many hyaline oocytes gives the ovary a speckled appearance. b. Significant vascularization of the ovarian membranes. Eggs begin to be released	a. The presence of many hyaline oocytes gives the ovary a speckled appearance. b. Significant vascularization of the ovarian membrane. Eggs begin to be released
5. Post-spawning and recovery	Flaccid and yellowish ovary, wrinkled envelope, numerous non-emitted oocytes still occupy the ovary. The ovary takes on its immature appearance	Disorganized ovary; numerous empty follicular envelopes which are reabsorbed. Abundant blood cells and atresia of all vitellogenic oocytes that were not been emitted

Oocyte diameter distributions

Ovarian histology was supplemented by analysis of the frequency distributions of diameters of the oocytes contained in the ovary. This study allowed us to ascertain whether spawning takes place at one time or several times during a single sexual cycle: strategy of laying (Le Duff, 1997). According Kartas & Quignard (1984), seasonal egg spawning, when examined in terms of size distribution of eggs in the ovary, may respond to one of the following models:

- Bimodal (or multimodal) distribution of eggs in which the laying of the most advanced group is followed by the development and laying of one or more groups developed from the secondary groups;
- Bimodal distribution of eggs in which the most advanced group is laid and the next secondary group resorbed. *T.* resembles unimodal distribution except for the oocytes maturing again within the annual sexual cycle allowing a second spawning;
- Unimodal distribution of eggs, corresponding to a single laying per season (concentrated or spread over time);
- Unimodal distribution of eggs laid immediately before or after a secondary group derived from the development of cells without vitellus.

Batch fecundity and relative fecundity: according to Bagenal (1966), batch fecundity is the number of eggs ripening in a female just before laying, whereas

Aboussouan & Lahaye (1979) define it as the number of oocytes destined for laying. The method of studying individual absolute fecundity that we adopted was that of “volume sampling” as used by many authors (Simpson, 1951; Bagenal, 1966). The mature stage IV ovaries were collected from 30 females of *T. luscus*.

After a histological confirmation that the diameter of the oocytes was homogeneous between the 3 median, posterior, and anterior parts of the ovary and between the 2 ovary lobes, a sample was collected from the ovary central area and weighed in grams to two decimal places. Samples were stored in a neutralized 10% formaldehyde solution. This method gives better results than the one using Gilson's liquid, as it and makes it possible to dissociate connective tissue of the ovary and thus isolate the oocytes, essential for subsequent counts. In the case of environment procedure, Gilson's fluid is renewed about every 10 days to promote the dissociation of the oocytes. The latter can be accelerated by frequent agitation of samples stored in pill boxes.

After separating the stroma, the oocytes were washed with fresh water to remove excess formalin and concentrated detritus from the supernatant. They were then diluted with 1 liter of salt water. Mechanical homogenization of the liquid column was required before removing 1 ml of subsamples using a graduated pipette. This subsample was then counted using a Dollfus tank. This operation was repeated 3 times for each ovary sample and the absolute in-

Tab. 2: Annual sex ratio of *T. luscus* in the Moroccan Central Atlantic coastal area from January 2018 to December 2019.

Tab. 2: Letno razmerje med spoloma pri vrsti *T. luscus* na maroškem obalnem območju srednjega Atlantika od januarja 2018 do decembra 2019.

Year	N	Females	Males	Females (%)	Males (%)
2018	1391	539	852	39%	61%
2019	819	509	310	62%	38%
2018-2019	2210	1048	1162	47%	53%

dividual fecundity was determined according to the formula of Le Bec (1985): $F = n (V_d / V_{se}) \times (P_g / P_e)$, where F = batch fecundity; n = mean of the 3 subsamples; V_d = dilution volume (ml); V_{se} = volume of a subsample (ml); P_g = mass of ovaries (g); P_e = ovarian sample weight (g).

Statistical treatment

Statistical analyses were performed using the null hypothesis test of observed differences between estimated variables (proportion of males and females), and the chi-square test.

The ANOVA statistical analysis was performed under R 4.0.4 using the R Commander package. It was used to analyze the results of GSI, HSI and the condition factor (K) data.

RESULTS

Sex ratio

Of a total of 2210 specimens, 1162 were males (53%) and 1048 females (47%). The overall sex ratio (SR) determined in the two cycles equaled 0.90 ($X^2=5.9$, $P \leq 0.001$). The males outnumbered the females and the sex ratio was consistently in favor of males during the first year (2018) of sampling, while the females outnumbered the males during the January–December 2019 period (Tab. 2).

Sex distribution by size class

The distribution of the sexes (male and female) according to length was determined by grouping the specimens into 1 cm interval size classes, ranging from 11 to 31 cm. The sex ratio with regard to fish size showed that females dominated in the 19–31 cm size range, with males being well represented in small size classes (11–13 cm) and dominating the 14–17 cm size classes, while in size classes 18–20 cm the distribution of specimens was balanced between females and males (Fig. 2).

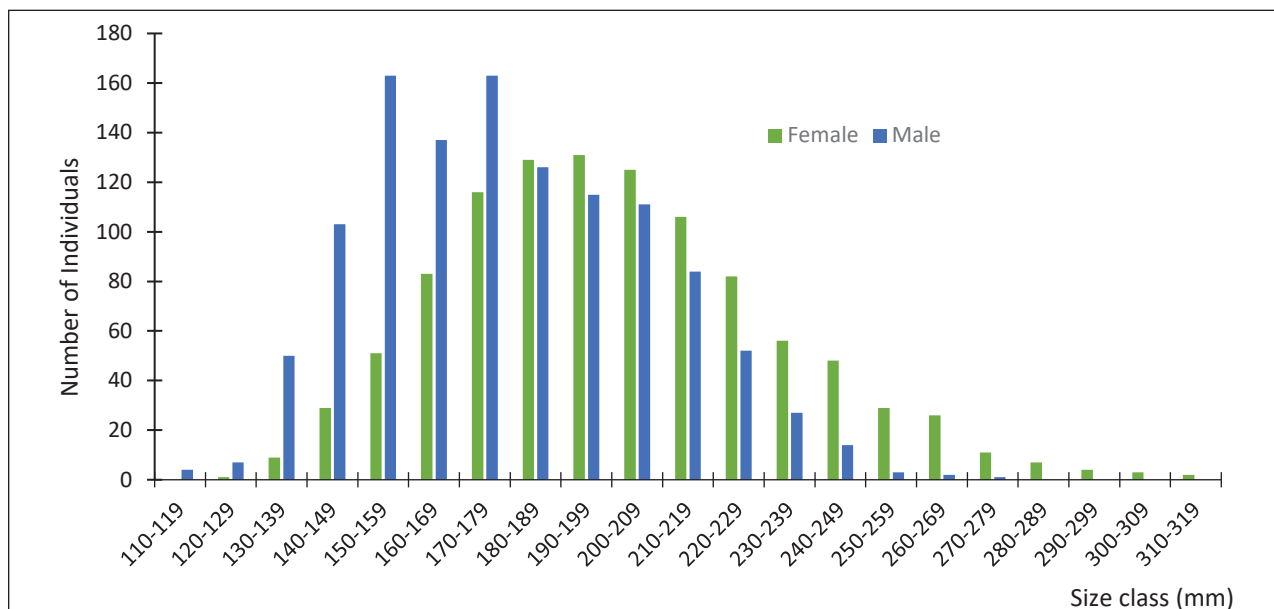


Fig. 2: Sex distribution by size class (male and female) of *T. luscus* in the Moroccan Central Atlantic coast over the period between January 2018 and December 2019 (size in mm).

Sl. 2: Porazdelitev spola po velikostnih razredih (samci in samice) vrste *T. luscus* na maroški obali srednjega Atlantika v obdobju med januarjem 2018 in decembrom 2019 (velikost v mm).

Seasonal sex ratio

The sex ratio is inconstant over the life of most fish species. The femininity and masculinity frequency changes of *T. luscus* were determined monthly from January 2018 to December 2019 (Fig. 3). The sex ratio showed irregular frequencies of females in the catches and their predominance during breeding periods. The values fluctuated between 20.22% in September 2018 and 48.44% in February 2019, with peaks of 70.58% in December 2018 and 90.90% in November 2019. The chi-square test showed that the difference between the frequencies of males and females was very significant, however, males showed high proportions only in 2018 (Fig. 3). The male sex ratio fluctuated between 29.41% in December 2018, 79.77% in September 2018, 9.09% in November 2019, and 51.55% in February 2019 (Fig. 3).

Average sizes of males and females of *T. luscus*

During the sampling period (2018–2019), the average length in females was 199.8 mm (standard error=32.04587, N=1048) and 175.5 mm in males (standard error=27.63253, N=1162). A statistical comparison (using R software) yielded an average length value of $t = 2.2e-16$ for both sexes, less than the theoretical value of 1.96 given in the Student's *t*-test tables. The results confirm that females were consistently more numerous than males.

Breeding season

a. Sexual maturity by sex

A macroscopic examination of the testes and ovaries showed the monthly development of sexual maturity in stages as presented below, with seasonal variation in the percentages indicating that males and females at all different stages of sexual maturity occur throughout the year but in varying ratios (Fig. 4). Pouting in post-lay or emission (stage V) were poorly represented in our samples. Early maturation (stage III) and mature (stage IV) females were encountered throughout each year but it was in the November to April period that the percentages of these two stages were the highest. The lowest percentages of mature individuals were observed in the May to July period. During this season, most individuals finished breeding and entered a period of sexual rest.

b. Monthly evolution of the gonado-somatic index

The bimonthly variations of the gonado-somatic index (GSI) were similar in both sexes during 2018–2019 and showed an ascending phase from September–October (2018) to April–May (2019) when the maximum values were reached, 3.50 for females and 3.30 for males; the descending phases occurred during January–June 2018 and March–May 2019 (Fig. 5). In both years the index dropped to minimum values for both sexes (0.57

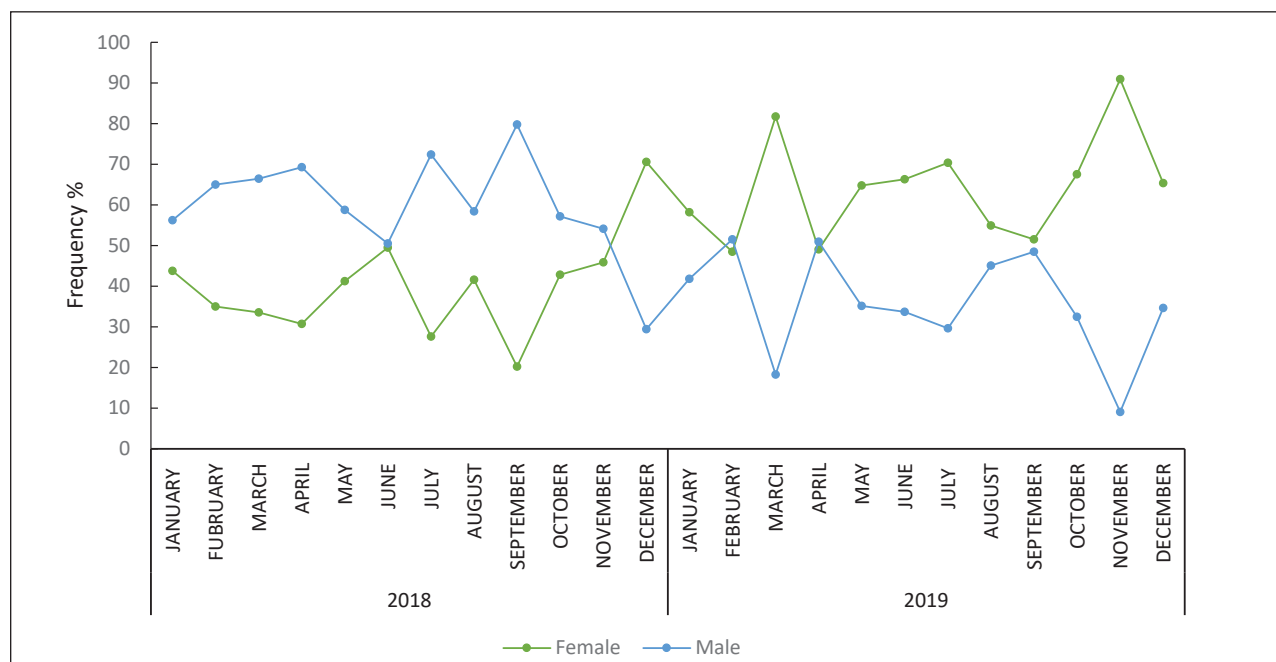


Fig. 3: Monthly and annual distributions of females and males of *T. luscus* in Moroccan Central Atlantic waters.
Sl. 3: Mesečne in letne porazdelitve samic in samcev vrste *T. luscus* v maroških vodah srednjega Atlantika.



Fig. 4: Bimonthly percentages of stages of sexual maturity on a macroscopic scale in (a) males and (b) females of *T. luscus* in the Moroccan Central Atlantic coastal area over the period January 2018 – December 2019.

Sl. 4: Dvomesečni deleži faz spolne zrelosti na makroskopskem nivoju pri (a) samcih in (b) samicah vrste *T. luscus* na maroškem obalnem območju srednjega Atlantika v obdobju januar 2018 – december 2019.

in females and 0.56 in males) during July–October and June–September, respectively. The most stable periods were those of vitellogenesis and laying during March–April. Despite overall similarities of the male and female GSI curves, the ANOVA test indicated a small significant difference between the two sexes ($p = 0.05$).

c. Monthly maturity stages in females on a microscopic scale

Seasonal variation in percentages of sexual maturity stages showed that females at different stages of sexual maturity can be found throughout the year (Fig. 6). As on a macroscopic scale, stage V individuals were poorly represented in our samples. Mature or laying individuals (stage IVa and IVb) were encountered throughout the year, but it was in the November 2018 to April 2019 period (late autumn, winter and spring) that their percentages were the highest. The lowest percentages of mature or laying individuals were observed from May to July, which corresponds to observations on a macroscopic scale. Towards the end of that season most individuals finished breeding and entered a period of sexual rest.

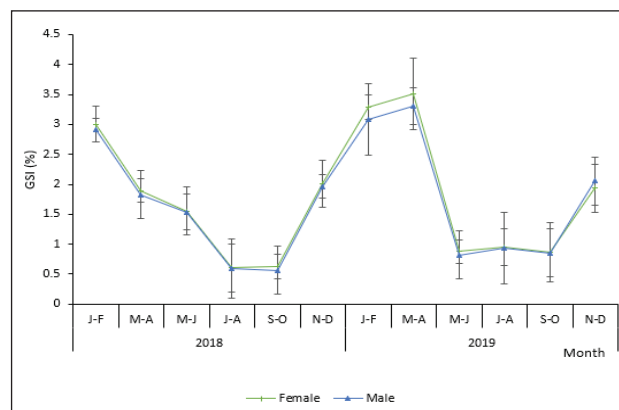


Fig. 5: Annual cycle of the gonadosomatic index GSI (mean $\pm$ SD) in males and females of *T. luscus*, in the Moroccan Central Atlantic coastal area over the January 2018 – December 2019 period.

Sl. 5: Letna dinamika gonadosomatskega indeksa GSI (povprečje $\pm$ SD) pri samcih in samicah vrste *T. luscus* na maroškem obalnem območju srednjega Atlantika v obdobju januar 2018 – december 2019.

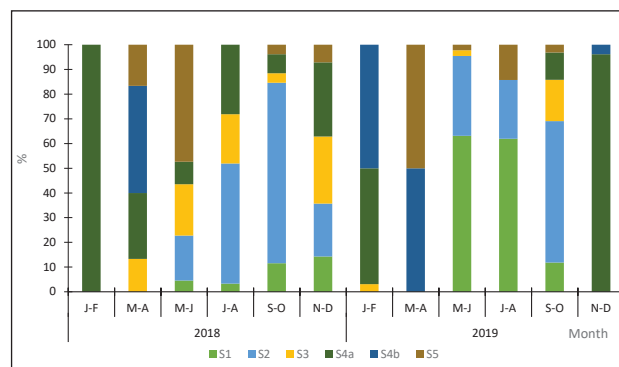


Fig. 6: Bimonthly percentages of stages of sexual maturity on a microscopic scale in females of *T. luscus*, in the Central Atlantic coast of Morocco over the January 2018 – December 2019 period.

Sl. 6: Dvomesečni deleži faz spolne zrelosti na mikroskopskem nivoju pri samicah vrste *T. luscus* na osrednji atlantski obali Maroka v obdobju januar 2018 – december 2019.

Hepatosomatic index (HSI)

Values of HSI increased sharply during September–October and November–December 2018, reaching a maximum value of 4.16 in females and 3.60 in males; a similar but somewhat smaller increase occurred in 2019 (Fig. 7). Curves of the monthly development of HSI followed the same trend in both sexes but the values showed a significant difference ($p = 0.05$).

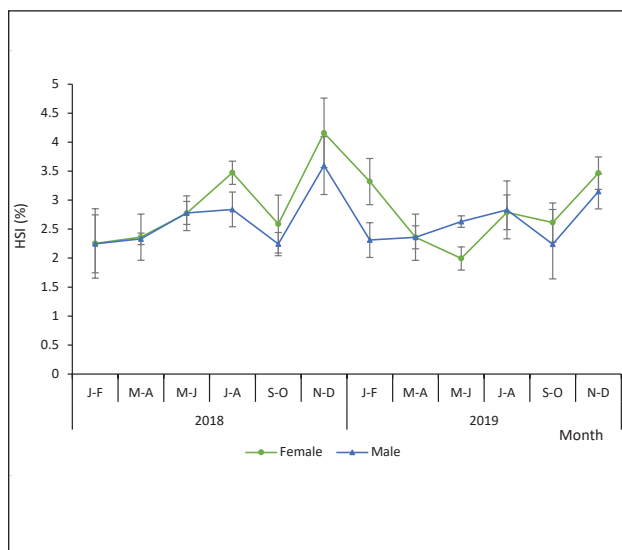


Fig. 7: Annual cycle of the hepatosomatic index HSI (mean $\pm$ SD) in males and females of *T. luscus* in the Moroccan Central Atlantic coastal area over the January 2018 – December 2019 period.

Sl. 7: Letna dinamika hepatosomatskega indeksa HIS (povprečje $\pm$ SD) pri samcih in samicah vrste *T. luscus* na maroškem obalnem območju srednjega Atlantika v obdobju januar 2018 – december 2019.

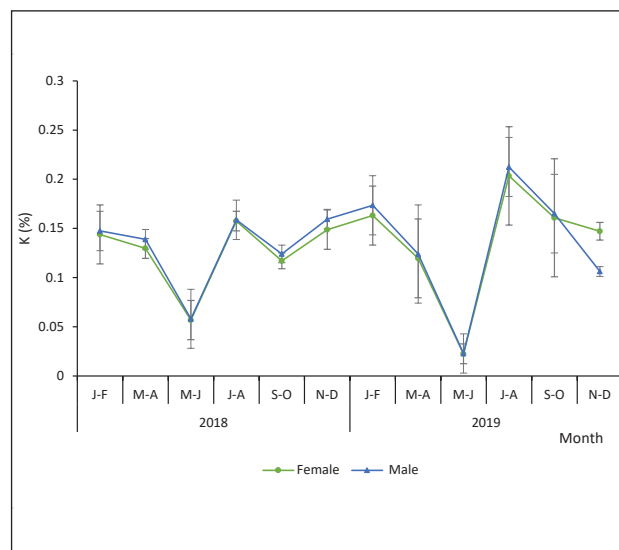


Fig. 8: Annual cycle of the condition index K (mean $\pm$ SD) in males and females of *T. luscus* in the central Atlantic Moroccan Coastal area, over the period January 2018 – December 2019.

Sl. 8: Letna dinamika indeksa kondicije K (povprečje $\pm$ SD) pri samcih in samicah vrste *T. luscus* na maroškem obalnem območju srednjega Atlantika v obdobju januar 2018 – december 2019.

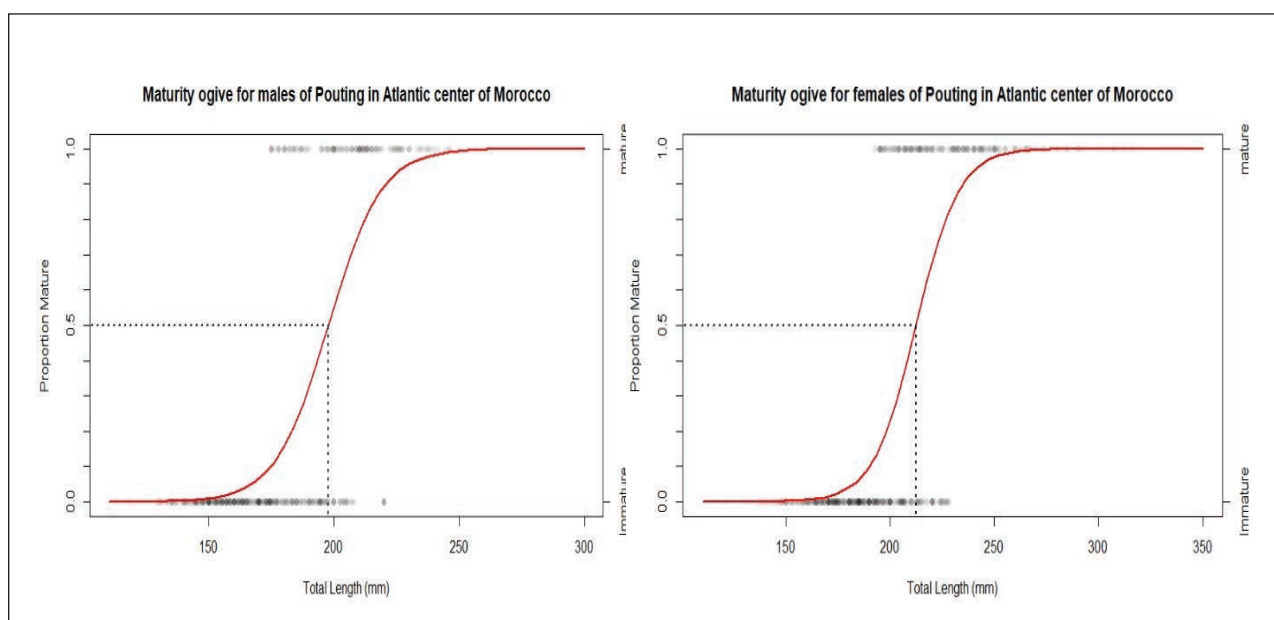


Fig. 9: Maturity ogive and length at first maturity (L50) in (a) males and (b) females of *T. luscus* from the Moroccan Central Atlantic coastal area over the period January 2018 – December 2019.

Sl. 9: Zrelostna ogiva in dolžina pri spolni zrelosti (L50) pri (a) samcih in (b) samicah vrste *T. luscus* na maroškem obalnem območju srednjega Atlantika v obdobju januar 2018 – december 2019.

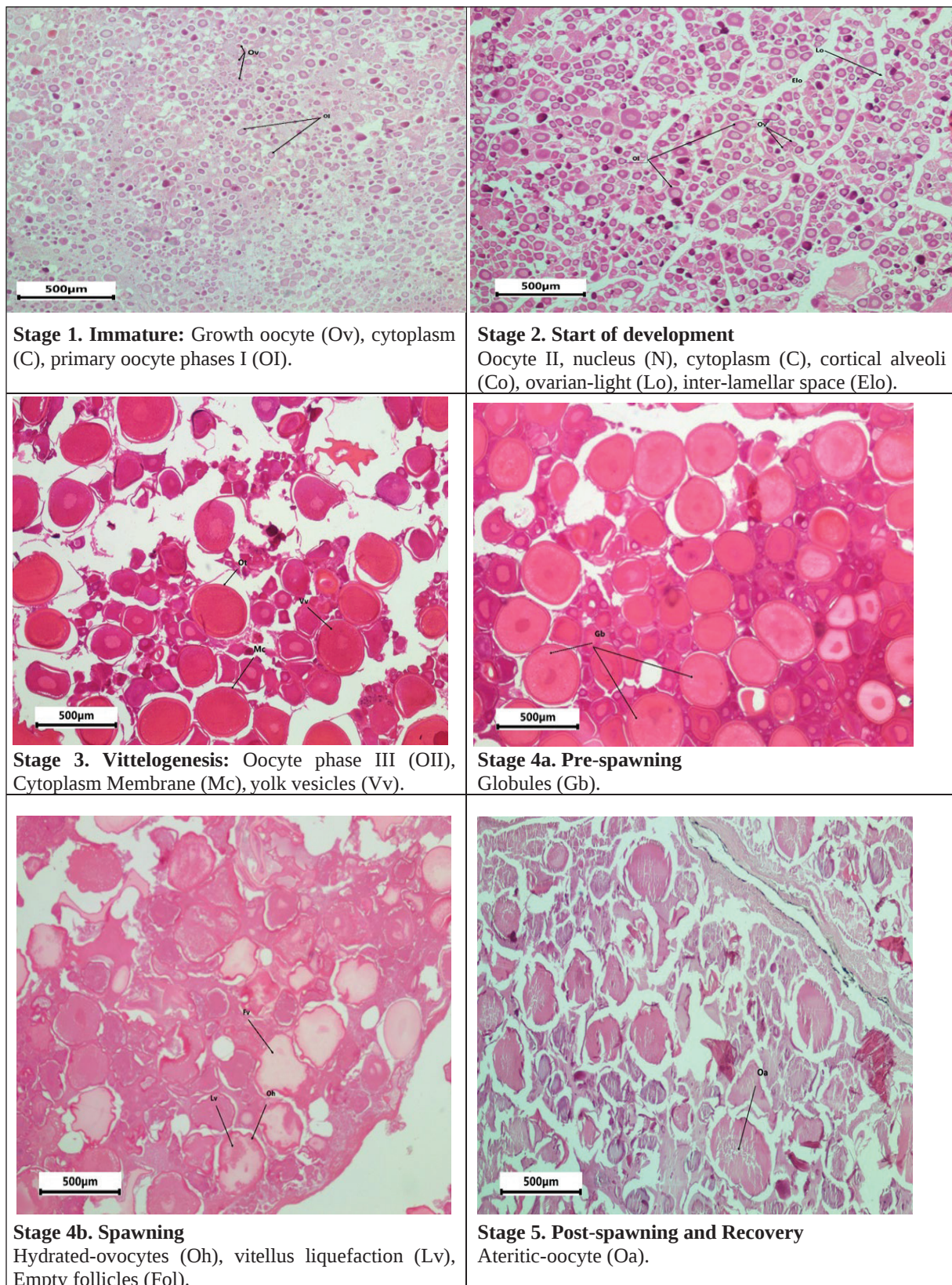


Fig. 10: Microscopic sexual maturity stages in oocytes of the *T. luscus* from the Moroccan Central Atlantic coast.
Sl. 10: Faze razvoja jajčnih celic na mikroskopskem nivoju pri vrsti *T. luscus* iz maroške srednje atlantske obale.

Condition index (K)

Condition index K values ranged from 0.02 to 0.21 in females and from 0.01 to 0.22 in males (Fig. 8). A good condition phase occurred in winter, peaking during January–February 2019 at 0.17 in females and 0.18 in males, and in summer 2019, with a marked peak in July–August at 0.20 in females and 0.21 in males. (Fig. 8). The statistical analysis showed a significant difference between the two sexes in condition index values ($p = 0.05$).

Maturity ogive and length at first maturity (L50)

The average sizes (lengths) corresponding to L50 for the study period (January 2018 to December 2019) were 19.8 cm and 21.5 cm for males and females, respectively (Fig. 9). They varied marginally according to sex. The curves indicate that males reached sexual maturity at a smaller size than females.

Gonadal kinetics and dynamics study

Microscopic anatomy of the ovary

The cytological follow-up of ovarian dynamics in the female pouting through its sexual cycle showed that the ovary contained oogonia scattered between follicular cells, oocytes in pre-vitellogenesis, and oocytes in various stages of vitellogenesis. (Fig. 10). The ovary initially consists of a set of ovarian follicles and connective tissue (Fig. 10, stage I). Oocyte growth is divided into two phases: the pre-vitellogenic phase, which marks the establishment of the metabolic machinery essential for the development of the germ cells, and the phase of vitellogenesis, which serves the accumulation of gametes (at different stages of maturation), surrounded by a theca and separated by connective tissue. Observations of ovary cross-sections correspond to the five stages selected by macroscopy (cf. Table 1) according to the descriptions in Figure 10.

Oocyte population size structure and laying strategy

The histological study was supplemented by the determination of size and number of oocytes in the ovaries of females selected as representing the different phases of the cycle (Fig. 11).

Each ovarian histological type corresponded to one or more distributions of oocyte diameters observed in the females selected as representative of the population. The succession of distributions over time traced the development of vitellogenic oocyte batches to maturity, thus

defining the spawning strategy of the species. The spawning or egg laying strategy constitutes the basis for assessing fish fecundity (Dominguez *et al.*, 2008).

In immature females, the distribution of oocyte diameters was unimodal: a single batch of oocytes with a mode of 100 μm was distinguished. It was mainly formed by stage I oocytes and some stage II oocytes with diameters between 150 and 200 μm (Fig. 11).

At the beginning of development, the distributions of oocyte diameters were formed mainly of stage II oocytes and a few stage I oocytes of 100 μm . In the vitellogenic stage (stage III), oocyte diameters ranged from 250 to 400 μm .

Distributions of female fish in vitellogenesis were heterogeneous – bimodal, tri-modal or multimodal. The oocytes were divided into a number of modes corresponding to successive oocyte emissions. Maturation of the oocytes therefore occurred in successive waves. As the first group of oocytes matured, a second group took its place, and so on. A widening of the histogram base could be observed as vitellogenesis progressed and the distribution of oocytes developed (Fig. 11), with the largest oocytes attaining a diameter of 700 μm .

All distributions had a first batch of pre-spawned oocytes, with the highest number exhibiting a modal diameter of 300 μm . They differed by the emergence of one or more modes in the vitellogenic oocyte population present. The plurimodal distributions consisted of three batches of vitellogenic oocytes. The first two modes were at 300 and 400 μm , the third at 500 μm . Batches observed in polymodal distributions likely presented bimodal or tri-modal distribution patterns, but overlap prevented their detection.

Pre-vitellogenesis oocytes were present throughout the vitellogenesis stage in the ovary.

The distribution of oocytes according to size indicated continuity between pre-vitellogenic and vitellogenic oocytes. The transition of oocytes to vitellogenesis was continuous during the maturation phase.

In spawning females, the size distributions of oocytes are from November to February (Fig. 6). The last batch of oocytes in tertiary vitellogenesis was converted, by successive hydration, into batches of oocytes to be emitted in different waves of laying.

In the population of opaque vitellogenic oocytes, lighter and larger oocytes corresponded to oocytes in the process of hydration, exhibiting diameters of 400 to 500 μm (450 μm mode), or hyaline oocytes with diameters of 600–700 μm .

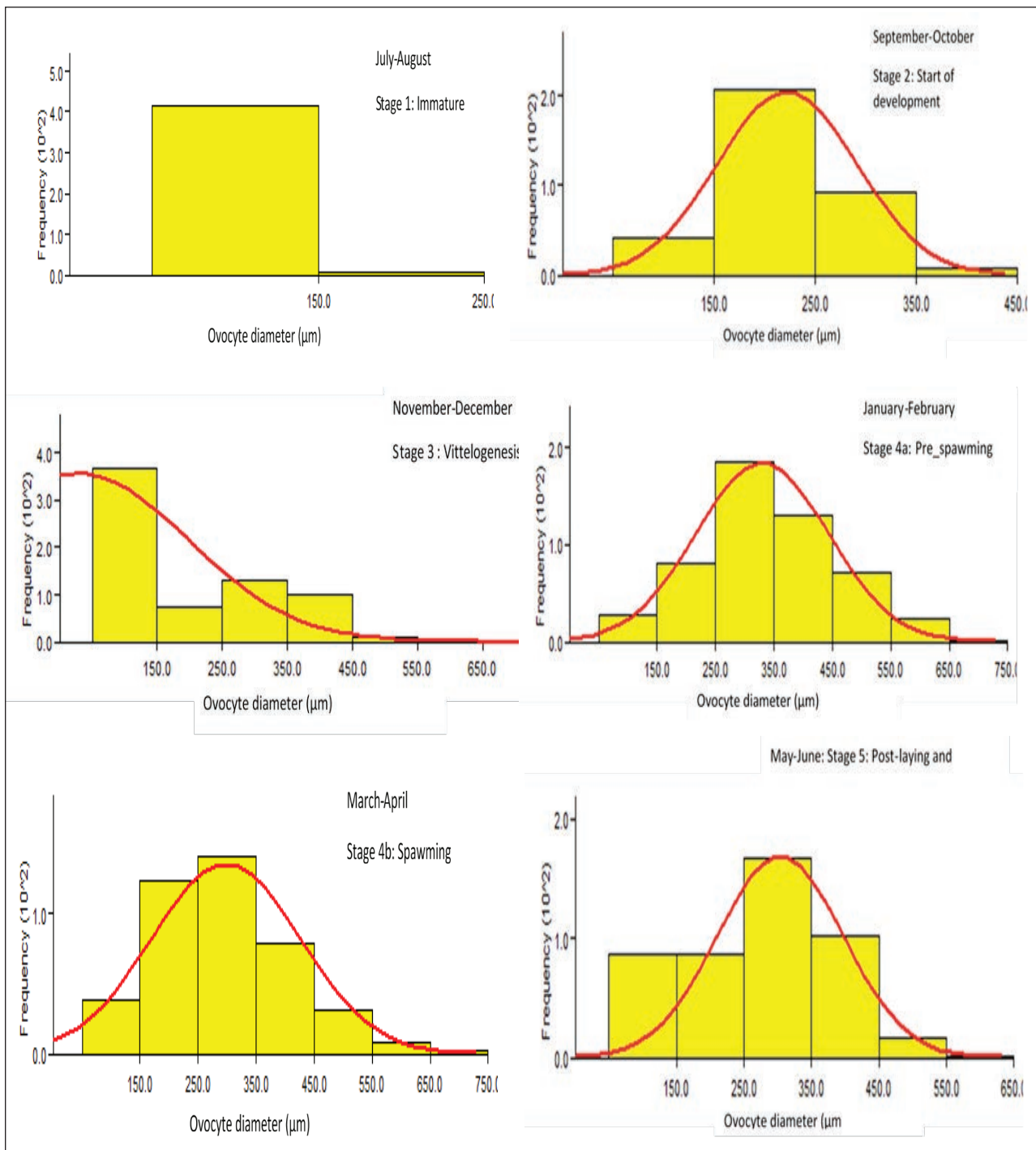


Fig. 11: Size structure of the oocytes in *T. luscus*.

Sl. 11: Velikostna struktura jajčnih celic pri vrsti *T. luscus*.

Recruitment of egg cells into vitellogenesis continued throughout the spawning phase.

Oocytes filled with vitellin reserves occupied most of the ovary and stood alongside smaller oocytes at the beginning and during maturation (Fig. 10).

Distributions of post-spawning females can be tri-modal. The only visible batch in this study consisted of pre-vitellogenic oocytes and vitellogenic, i.e., stage III and IV oocytes. The frequency of vitellogenic oocytes was lower than that found

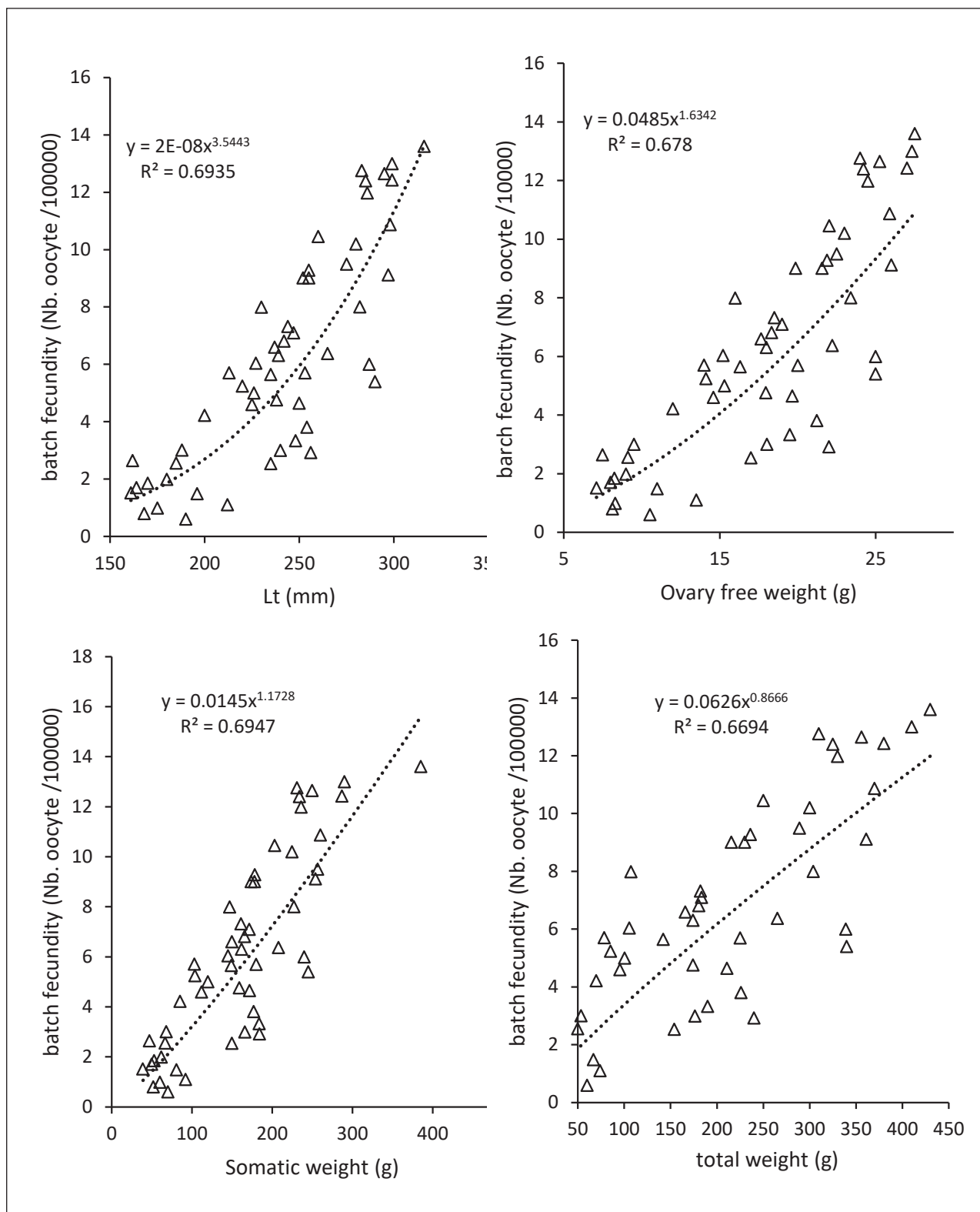


Fig. 12: Relationships between batch fecundity and total length (upper), ovary free weight (lower), somatic weight, and total weight of the *T. luscus* from the Moroccan Central Atlantic coast.

Sl. 12: Razmerja med drstitveno plodnostjo in skupno dolžino (zgornja), prosto težo jajčnikov (spodnja), somatsko težo in celotno težo primerkov vrste *T. luscus* z maroške obale srednjega Atlantika.

in laying females, but their presence indicates that oocytes progressed to vitellogenesis continually throughout the spawning period (Fig. 11).

Batch and relative fecundity

Batch fecundity (number of viable eggs usually released by a serial spawner during a pulse of spawning) is between 15,146 and 136,031 eggs with an average value of 61,848 eggs per pulse. The relative fecundity oscillated between 15,146 (Lt = 161 mm, Pe = 38.9 g) and 136,031 (Lt = 316 mm, Pe = 385.1 g) with an average of 325.37 and 142.48 eggs/g, respectively. The relationships observed between fecundity and the different biological parameters are shown graphically (Fig. 12), the highest correlation being between somatic weight and batch fecundity:

- Total length; $Fa = 2 \cdot 10^{-8} Lt^{3.443}$, $r = 0.693$ (Fig. 12);
- Ovary free weight; $Fa = 0.048 Pg^{1.634}$, $r = 0.678$ (Fig. 12);
- Somatic weight; $Fa = 0.0145 Pe^{1.728}$, $r = 0.964$ (Fig. 12);
- Total weight; $Fa = 0.0625 Pt^{0.866}$, $r = 0.699$ (Fig. 12).

DISCUSSION

Several indices are used to determine and visualize the breeding periods of many demersal fish species. Their selection is based on the quasi-simultaneity of the maximum index values associated with the spawning periods. At least two indices are needed to assess the reproduction and fecundity in *Trisopterus luscus*.

Determination of the maximum egg-laying period of the pouting in European waters of the North-East Atlantic is based on the abundance of eggs and larvae, ovarian histology, and development of the gonado-somatic index (GSI) (Lahaye, 1972; Dominguez *et al.*, 2008).

To investigate sexual maturity changes and identify the spawning periods in the Moroccan population, this study used a variety of variables and indices, including the GSI (gonad development phases) and HSO (hepatosomatic condition) indices, the condition factor (K), gonad histology, size at first sexual maturity (L50), and the sex ratio. Monthly sampling (from January 2018 to December 2019) clearly showed two cycles in the overall sex ratio and a slight predominance of males in the catches. This dominance can be explained by either relative mortality of females during reproduction, differences in growth in favor of males or regrouping to reproduce during the intense laying season (Amenzoui *et al.*, 2004–2005).

The sex ratio in terms of size indicated a dominance of females in larger size classes and males in the small ones. This dominance of older females could, according to several authors, have several explanations, including greater availability or capturability of males, a higher natural mortality of males, sexual inversion, or more simply differential growth with different longevity of the two sexes favoring females (Amenzoui *et al.*, 2004–2005). The gonad maturation index (GSI) increase for this species coincided with gametogenesis and its decrease indicated active egg laying (cf. Lahaye, 1972). The GSI values of females were higher than those of males due to the large size of the ovaries. Seasonal development of the GSI showed the periods of sexual activity for the Moroccan pouting which, combined with data on sexual maturity stages, indicated that this population can reproduce throughout the year, with a maximum peak registered between January and February 2018 and between March and April 2019. We also observed the presence of some spawning females throughout the year. The results did show some variation between 2018 and 2019 in spawning time and coincidence with findings of other authors covering different areas of the Atlantic Ocean where breeding seasons seem to vary depending on the region. Indeed, for the pouting this extends from February to June in the English Channel, from March to July in the French part of the North Sea (Desmarchelier, 1985), and from January to April in the south of the Bay of Douarnenez, France (Gherbi-Barre, 1983). A shift in the laying period further into spring thus appears to gradually occur from the south to the north of France, with a delay of about one month in the beginning of spawning between one zone and another (Desmarchelier, 1985). In north-west Spanish waters female pouting reaches higher maturity and exhibits asynchronous oocyte development (Alonso-Fernández, 2008), which corresponds well to the results of our study, but further monitoring of Moroccan stock is needed to draw firm comparative conclusions about the timing of spawning sequences.

In the Moroccan sample no females at rest (stage V) were observed from June to August and in the fall, and few at this stage were encountered in winter and spring. This would lead us to conclude that egg spawning in *T. luscus* in the studied area takes place all year round with varying intensities depending on the season. However, the morphological development of the gonads is an imprecise indicator of the state of reproduction as it does not determine the degree of ovarian mortality. Therefore, microscopic analysis was essential to determine the timing of gamete maturation stages within the limits of the bimonthly sampling program.

On a microscopic scale, histological examination of female *T. luscus* gonads indicates somewhat asynchronous ovary maturation for this species (Wallace and Selman, 1981; Murua and Saborido-Rey, 2003). The ovary contains oocytes at all stages of development throughout the year and the simultaneous presence of walled oocytes and post-ovulatory follicles in female ovaries indicates that *T. luscus* is a partial breeder. This was also observed for the same species in Galician coastal waters (Alonso-Fernández, 2008). It should also be noted that the spawning season of pouting is long and some females are in a state of spawning throughout the year. However, most females from our sample began spawning in the first part of the year, peaking between February and April, which corresponds to results reported by Labarta & Ferreira (1982) and Merayo (1996a).

Monthly monitoring of the hepatosomatic index (HSI) showed a similar development pattern to that of the GSI with maximum values being reached at the same time, indicating that the liver does not intervene strongly in the transfer of lipid reserves necessary for vitellogenesis. The HSI in males showed similar variations as in females, and maturation of the male gonads therefore also required much energy with the liver losing its reserves in November, when the testes were mature. Weight was regained and was highest in December when testes were poorly developed. It was also noted that the final maturation of oocytes seemed to be associated with a rapid use of liver reserves. This caused lowering of the HSI during the final phase of vitellogenesis (February–March). During periods of sexual rest, the liver accumulates reserves that represent about 4.5% of the body weight (Desmarchelier, 1985).

In *T. luscus*, some lipid storage occurs in muscles within or between muscle fibers according to Desmarchelier (1985). The monthly change in the condition coefficient (K) in this study followed both the GSI and his indices indicating that muscle fat reserves were used in the female development at the end of vitellogenesis. The energy developed during the spawning and the lack of food clearly contributed to the weight loss of females at this time. In June, the pouting begins to recharge and takes on a more rounded shape. This period corresponds to more favorable growth in the summer and fish are in best condition in October–November before losing weight again in winter. In males, the K factor is correlated with the GSI showing an inverse trend with the GSI; however, reproductive performance in both males and females ultimately depends on the prevailing environmental conditions. The K weight index also serves as an indicator characterizing the

pouting as a “fatty” as opposed to “lean” fish, such as the horse mackerel. Our observations on the development of these indices generally confirm those of studies carried out in the English Channel (Desmarchelier, 1986).

This interannual variability is principally caused by prevailing environmental conditions, including date of initiation of laying (early or late laying depending on the year), the corresponding annual recruitment and food availability (Abad *et al.*, 1993). The L50 can also vary according to sex and size at first sexual maturity (L50); in the Moroccan pouting it was 21.5 cm in females and 19.8 cm in males, whereas in Galicia (Spain) the L50 in females was estimated at 18.2 cm (Labarta *et al.*, 1982) and 22 cm in males (Alonso-Fernández *et al.*, 2008). The variations in size at first maturity may also reflect the different strategies developed by fish in different environments to better adapt to the environmental conditions.

The development of mean oocyte diameter showed a small but important decrease over the spawning season, possibly suggesting recruitment of new oocytes to the stock of developing oocytes throughout the spawning season, a characteristic of species with indeterminate fecundity (Hunter *et al.*, 1989). The observed decrease may also have been a consequence of asynchronous development of the oocytes. However, when mean oocyte diameter was analyzed in the successive ovary developmental stages (instead of over the season), it showed a slight increase suggesting no *de novo* vitellogenesis after the onset of ripening, i.e., determinate fecundity (Alonso-Fernández *et al.*, 2008). Consequently, the issue of determinate or indeterminate fecundity in the Moroccan *T. luscus* stock remains inconclusive, although the latter is considered most probable.

The relative batch fecundity of pouting in this study ranged from 5 to 67 eggs g⁻¹ (fish weight range: 108–366 g). This contrasts with other indeterminate spawning species, which produce larger batches, such as *Merluccius merluccius*, *M. capensis* and *M. paradoxus*, with 123, 160, and 306 eggs g⁻¹ of relative batch fecundity, respectively, or with clupeids, e.g., *Sardina pilchardus* with close to 350 eggs g⁻¹ (Ganias *et al.*, 2004; Murua *et al.*, 2006). The ratio between the number of developing oocytes and batch fecundity displayed an average value of 20. Therefore, assuming a spawning season of 4–5 months, the pouting could produce a batch every 6–7 days. This means that if the pouting is a determinate spawner, a female will spawn an average of 20 batches during the spawning season: a figure very close to that for other determinate fecundity species (Kjesbu 1989; Kjesbu *et al.*, 1996). Fertility will always be af-

fects by the changing environmental conditions including predation and exploitation (Mura *et al.*, 2003; Ganas, 2009), thus challenging predictive modeling of stock sustainability.

CONCLUSIONS

This is the first investigation of the reproductive biology of the pouting *Trisopterus luscus* in the Moroccan Central Atlantic fishery area. Random bimonthly sampling of the Moroccan pouting population showed a dominance of the males during two

annual cycles (2018–2019) and indicated that reproduction probably took place during most of the year, but maximum spawning occurred during the January–February 2018 and January–March 2019 periods. The 50% level of population maturity (L50) at a total length of 19.8 cm in males and 21.5 cm in females compares fairly closely with that of more northern stocks. Nevertheless, further sampling and study are required in order to confirm the frequency and differentiation of sex ratios according to season and other aspects of the reproductive biology of *T. luscus* in Moroccan waters.

REPRODUKTIVNA BIOLOGIJA FRANCOSKEGA MOLIČA (*TRISOPTERUS LUSCUS*) IZ ATLANTSKE OBALE MAROKA

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POVZETEK

Avtorji poročajo o izsledkih dvoletne raziskave (januar 2018 – december 2019) o reproduktivni biologiji francoskega moliča (*Trisopterus luscus*) na maroškem obalnem območju, o kateri sicer ni veliko znanega. Pregledali so 2210 vzorčenih primerkov, od katerih je bilo 1162 samcev (52,57%) in 1048 samic (47,42%), pri čemer so bili samci statistično značilno (hi kvadrat test) bolj številčni. Mesečni monitoring gonadosomatskega indeksa (GSI) in makroskopski ter mikroskopski pregled gonad so pokazali, da so se francoski moliči aktivno razmnoževali skozi vse leto z viškoma v januarju–februarju 2018 in marcu–aprilu 2019. V obeh primerih je bil tudi višek indeksa kondicije (K). Nadalje avtorji razpravljajo o spremembah razmnoževalnih značilnosti francoskega moliča v povezavi z dolžino telesa, sezono in plodnostjo.

Ključne besede: *Trisopterus luscus*, indeks kondicije, gonado-somatski indeks, dolžina ob spolni zrelosti, atlantska maroška obala

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