Mediterranean Marine Science

Vol 17, No 2 (2016)

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doi: 10.12681/mms.1156

To cite this article:

GRAU, A., SABORIDO-REY, F., PASTOR, E., PALMER, M., MASSUTÍ-PASCUAL, E., QUETGLAS, A., RIERA, I., & MORALES-NIN, B. (2016). Reproductive strategy of common dentex Dentex dentex: management implications. *Mediterranean Marine Science*, *17*(2), 552–566. https://doi.org/10.12681/mms.1156

Research Article

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net
DOI: http://dx.doi.org/10.12681/mms.1156

Reproductive strategies of common dentex *Dentex dentex*: management implications

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Handling Editor: Kostas Stergiou

Received: 2 December 2014; Accepted: 15 March 2016; Published on line: 29 July 2016

Abstract

The common dentex *Dentex dentex* is an iconic endangered species in the Mediterranean, where it is a target species that is sought after for small-scale, recreational and spearfishing fisheries. The reproductive biology of *D. dentex* in the natural environment is poorly known; therefore, the reproductive strategy of the species was assessed through a combination of reproductive traits and growth characteristics (estimated from length-at-age data), the size/age of sexual maturity and the energetic dynamics. A total of 358 wild fish, ranging in total length (L_T) from 19 to 84.7 cm, was sampled at Mallorca Island (Western Mediterranean) from March 1996 to June 1999. The sex ratio was skewed towards females (1.361); however, the length composition was not different between sexes ($p = 0.551$). Three young immature individuals (< 28 cm L_T, 0.8% individuals) were rudimentary hermaphrodites, offering support for classification as a late gonochoristic species. The age composition, determined based on the sagittal otolith, ranged from 0 to 26 years (yr). The von Bertalanffy growth function did not differ between sexes ($F = 2.58$, $p = 0.762$): L_∞=76.581 cm, $K = 0.127$ yr^{-1}, $t_0 = -2.335$ in a combined function. The maturity ogives for size and age showed that females achieved 50% maturity at 34.922 cm L_T and 3.3 yr, and males, at 33.812 cm L_T and 2.5 yrs. The onset of annual ripening took place in December, whereas vitellogenesis occurred from February to April. The spawning peak was in April and May for both males and females. A generalised linear model (GLM) showed that female size did not significantly affect the spawning season, whilst the seasonal component affected both the onset and end of spawning (GLM, $p < 0.005$). The gonadosomatic index (I_G), hepatosomatic index (I_H) and relative condition index (K_R) varied significantly with the reproductive season for females, and I_G varied for males. The microscopic observation of the gonads showed that fecundity is likely determinate, with an asynchronous oocyte development before spawning and a clear ovarian bimodal organization after the onset of spawning. The oocyte density variance of 85% was explained by the oocyte diameter, which also offered support for the trait of determinate fecundity. Female weight explained 84% of the observed variance for fecundity. Liver storage seemed to be the primary source of energy for maturity, which suggests a combination of capital and income breeding. The results suggested a reproductive strategy of type A, with balanced trade-offs between survival, growth and reproduction. At present, no management measures are being directed to *D. dentex;* herein, we suggest a minimum landing size of 35 cm L_T to ensure a higher proportion of larger fish to preserve the stock.

Keywords: Fecundity, age, growth, Western Mediterranean.

Introduction

Life history strategies are complex patterns of life history traits and refer to the coordinated evolution of these traits (Roff, 1983; Saborido-Rey & Kjesbu, 2005). Among the most important life history traits in all living organisms are the growth pattern, timing of maturity, reproductive investment, offspring size, mortality and lifespan. The trade-offs linking those life history traits ultimately determine the population dynamics. Therefore, exploited resources should be managed by taking into account the life history traits and their trade-offs. However, management of exploited fish is usually based on a limited knowledge of some of these traits and mostly ignores the current or future reproductive capability of the population, which may lead to stock collapses (Saborido-Rey & Trippel, 2013). The life history strategy reflects how an organism's income (energy) is optimally allocated to either growth or reproduction.

However, optimal allocation implies that traits are not combined at random. Instead, successful life histories at the evolutionary scale are those combinations that maximize the reproductive output accumulated across the entire lifespan. For example, in the case of sexual maturity, the longer a fish delays initiating reproduction, the greater its cumulative chance of dying without reproducing at all (costs). However, the longer a fish delays reproduction, the larger its size and the greater its reproductive ability because larger fish are able to obtain more resources and invest them in reproduction (benefits). The optimal balance between costs (risk of death) and benefits (reproduction rate) determines the optimal size at which a fish should start to reproduce (Charnov *et al*., 2013). Moreover, such an optimal size is attained at an age that depends on the growth curve. Most fish have a type of indeterminate growth that is well represented by the von Bertalanffy growth model, and a number of empirical or mechanistic relations have been derived between the von Bertalanffy parameters (i.e., how fish grow) and the reproductive effort or mortality/lifespan (Charnov, 2008; Charnov *et al.*, 2013). Life history strategies can be better understood in terms of energy balances after these relations have been identified. At the temporal scale of the entire lifespan, fish that invest more energy in growing (i.e., growing faster) before maturation would mature at a relatively larger size (at a high proportion of maximum size), but then, it should also invest a higher amount of energy in reproduction. As a consequence, these fish would show higher reproductive effort and mortality rate, i.e., a shorter life span (Ware, 1984; Winemiller, 2004; Charnov, 2008).

In these species, the cost of reproduction in a given year is usually financed using the current energetic income, i.e., income breeders and oocyte recruitment are indeterminate, or asynchronous within a protracted spawning season (Lowerre-Barbieri *et al*., 2011a; McBride *et al.,* 2013). On the other extreme is the strategy of growing more slowly, delaying maturation, which would occur at a relatively smaller size compared with the maximum size that can be attained, i.e., investing energy on growth after maturation. The lower reproductive effort and mortality rate implies a longer life span, and often, the reproductive costs depend on energetic reserves acquired before the reproductive season (capital breeders). For these breeders, oocyte recruitment would be determinate and group-synchronous within a restricted spawning season (*op. cit.*).

Overall, all these trade-offs suggest that increasing mortality (e.g., fishing) cannot be expected to be compensated with, for example, maturing at an earlier age; the remaining life history traits may change in undesired (from fisher's perspective) directions because most combinations of life history traits are evolutionarily constrained. For example, fishing-induced evolution (Heino & Godø, 2002) tends to favour not only early sexual maturation but also fish of smaller adult sizes when fishing is size-selective (Law, 2000; Alós *et al.,* 2014).

Life history traits related to the reproductive capability are especially difficult to assess. These traits are well known only for a limited number of exploited fish but are ignored for most other species, even for commercially relevant fish. This is, for example, the case with the common dentex *D. dentex* L. 1758 (Sparidae), a relevant species both for small-scale commercial and recreational fisheries (Marengo *et al*., 2014). Due to its potential for aquaculture (Rueda & Martínez, 2001), this species has been extensively studied in captivity (Glamuzina *et al*., 1989; Bibiloni *et al*., 1993; Pastor *et al*., 1995; Koumoundouros *et al*., 1998; 1999; 2001; Mourente *et al*., 1999a,b,c; Crespo *et al*., 2001; Machias *et al*., 2002; Loir *et al*., 2001; *inter al*.), but most of the life history traits remain poorly known for wild populations. The knowledge of the species in the natural environment is limited to its distribution (Mediterranean and Atlantic, from the Bay of Biscay to White Cape and Madeira, with the exception of the British Isles; Bauchot & Hureau, 1986), the growth of young fish and some fishery-related aspects (Morales-Nin & Moranta, 1997), and the length-weight relation (Morey *et al*., 2003) (but see review in Marengo *et al*., 2014). In this study, the trade-offs between reproductive and growth traits, including energetic storage as a growth factor, were explored in *D. dentex* to define the life history strategy for this relevant and iconic species in the Mediterranean.

Therefore, we explored four reproductive traits of *D. dentex*: sex, oocyte recruitment, fecundity type and seasonal spawning pattern. The reproductive strategy of the species was assessed by combining these reproductive traits with the growth characteristics (estimated from length-at-age data), the size/age of sexual maturity and the energetic dynamics. Those reproductive issues have been addressed for the first time with wild *D. dentex*, using data gathered with histological methods rather than through macroscopic observation of the gonads, the latter being prone to provide biased and uncertain inferences (Lowerre-Barbieri *et al*., 2011b). The results obtained do not support the use of stock management based only on minimum legal size and effort limitation and illustrate the relevance of an in-depth knowledge of reproductive traits in order to advise which management alternatives should be a priori explored for ensuring stock sustainability.

Material and Methods

Sampling

D. dentex is fished in Mallorca by a small-scale fleet using bottom longlines at depths of 30-60 m, whereas juvenile fish are caught by trammel net and surface trolling (Morales-Nin & Moranta, 1997), as well as by recreational fishing (Coll *et al*., 2004). A total of 358 wild fish were obtained on the Central Sales Wharf of the Island of Mallorca (Western Mediterranean) during monthly visits made from March 1996 to June 1999. The samples were pooled across years for inferring reproductive parameters and growth. The number of fish and the range in length by sampling period and sex are summarized by quarters in Table 1. Additionally, a sample of aquaculture-reared fish was used for validating the periodicity of the growth increments on the otolith.

Once in the laboratory, the fish were measured for L_T to the nearest mm, and the weight (W) and eviscerated weight (W_E) were determined to the nearest gram. The abdominal cavity was opened, the fish were sexed,

Table 1. Summary of the number of *D. dentex* fish studied and their length range (L_T cm) during the three sampling years, the quarters (Q) and by sex (F: Female, M:Male, I: Indeterminate, and HF.

Year	Quarter	M	F	I	HF	L_T range
	Q1	5	12	1	0	39.3 - 84.3
	Q2	37	43	1	1	21.5 - 84.7
1996	Q3	1	3	0	0	52.6 - 80.5
	Q4	0	0	0	0	-
	Total	43	58	1	1	21.5 - 84.7
	Q1	13	16	0	0	37.9 - 72.5
	Q2	18	33	0	0	30.2 - 77.4
1997	Q3	6	6	0	0	32.0 - 79.0
	Q4	19	30	5	1	19.0 - 79.8
	Total	56	85	5	1	19.0 - 79.8
	Q1	16	13	2	1	24.3 - 72.0
	Q2	1	4	0	0	63.5 - 77.3
1998	Q3	2	1	3	0	56.3 - 69.0
	Q4	13	21	0	0	21.0 - 73.7
	Total	32	39	5	1	21.0 - 77.3
	Q1	6	7	0	0	22.0 - 69.4
1999	Q2	8	9	0	0	24.0 - 68.5
	Total	14	16	0	0	22.0 - 69.4
Total		145	198	12	3	19.0 - 84.7

gonads and the visceral cavity (VC) sizes were measured, and the liver (W_L) and gonads (W_G) were weighed to the nearest 0.01 g.

Age determination and growth calculation

Sagittal otoliths were dissected, cleaned, stored dry and read whole while immersed in glycerol against a dark background using the protocol developed for the species (Morales-Nin & Moranta, 1997). The periodicity of the annual increments in the otoliths was directly validated from cultured fish of known age (24 fish, 2 and 3 years old) and indirectly validated following the evolution of the marginal increments throughout the year (Campana, 2001) of 351 wild fish ranging in L_T from 19 to 84.7 cm.

The *D. dentex* used for direct validation were reared at the LIMIA aquaculture facilities following the procedures described elsewhere (Pastor *et al*., 2000). Briefly, juveniles born in captivity were reared in tanks and transferred to 5.5 m diameter floating cages at 70 days old. Then, the fish were fed *ad libitum* once a day with fresh fish. Two groups of fishes were used for validation: 5 fishes born on May 1994 and sacrificed on May 1996 (mean length 35.3 cm L_T) and 19 fishes born on May 2002 and sacrificed on April 2005 (mean length 37.4 cm L_T).

The indirect methods of validation assume that the formation of opaque increments begins roughly simultaneously for all fish (usually in spring) and that the increments increase in width until a new increment is generated (in the next spring). Therefore, if, and only if, the putative increments are annual, the monthly percentage of individuals with an opaque border follows, at a population level, a unimodal curve from spring to spring (Morales-Nin & Panfili, 2005).

Length-at-age data of 331 wild fish were used to estimate the von Bertalanffy growth model. Between-sex differences in growth were tested using the Chow test (Chow, 1960; Saborido-Rey *et al*., 2004).

Seasonal trends in I_G, I_H and K_R

Monthly variation in the gonadosomatic and hepatosomatic indices (the ratio of gonad and liver weight with gutted weight, respectively) was estimated using the gutted weight of 134 and 108 mature females and males, respectively. The same sample was used to assess the monthly variation in body condition. The analysis of the log-transformed weight-length relation (330 sexed wild fish, both mature and immature) showed that the allometric index did not differ between males and females but was significantly different from three. Therefore, K_R, which was proposed by Le Cren (1951), was used. This index was the ratio between the observed (W_{obs}) and the expected weight (W_{exp}) estimated from the W_E - L_T relation, as described above.

Seasonal trends in ovarian development

The reproductive phase was determined in 343 fish (198 females and 145 males, Table 1) based on microscopic observations of the gonad; estimates of the stage of ovarian development based on macroscopic inspection of the gonads has proven to be imprecise and may lead to biased inferences (Murua *et al*., 2003). Six phases were established (Table 2) following the terminology of Brown-Peterson *et al*. (2011). A sample of the gonads was taken, weighed and preserved in 10% phosphate-buffered formalin. A preliminary test was conducted on 12 female fish to determine if oocyte development was homogeneous throughout the gonad. No significant differences were observed among samples for the number of oocytes and reproductive stage from the anterior, central and posterior regions; therefore, only a sample from the central part of the right lobe was taken for the remaining fish.

Gonad samples were dehydrated in alcohol and embedded in paraffin wax or in 2-hydroxyethyl methacrylate (Kulzer). The embedded gonads were sectioned transversely at 3-4 μm or 1-2 μm thickness, depending on the objective (see below), and stained with Mayer's haematoxylin and eosin or with toluidine blue. Ovary reproductive phases were determined based on the most advanced oocytes, the occurrence of postovulatory follicles (POF), atretic vitellogenic oocytes (AO) and the amount of lamellar stroma. Male gonad stages were based on male germ cell development and the presence of spermatozoa in the lumen of lobules and in the vas deferens.

GLMs were used to determine the duration and the influence of maternal effects on the spawning season. The probability of a female being in either of the two spawning stages tested was the response variable. To assess the onset of the spawning, these two stages were classified as females in the development phases (0) or spawning capable (1). To assess the end of the spawning, the females were classified as spawning capable (1) or regressing and regenerating (0). The female size and the week of the year were included as explanatory variables.

Sexual maturity

Maturity curves were estimated using a generalised linear model with a logit link function and binomial error distribution (Collet, 1991; Heino *et al.,* 2002) using fish L_T and sex as the response variables, so between-sex differences were tested. A second GLM was performed for maturity relative to fish age and sex. The data were not grouped by size classes, and each individual was included as an independent observation in the model.

Table 2. Histological description of microscopic ovarian phases of the gonads of *D. dentex*. The mean diameters of the gametogenic stages (μm) are indicated.

Phase	Histological description
Ovary	
I Immature	Small ovarian cavity. Lamellae containing numerous oogonia (O) (12.11±2.64), chromatin-nucleolus stage (CN) (17.60±4.16) and perinucleolar oocytes (PN) (52.42±.22.62). Some oocytes (but scarce) at lipid globule stage (LG) (121.92±14.27) during the entire year.
II Early developing	Numerous primary oocytes, together with secondary oocytes at the LG and cortical alveolus stage (CA) (228.08±30.55). Very few O. No oocyte atresia (OA) is observed.
III Late developing	Oocytes at all stages of developing, including batches of secondary vitellogenic oocytes at Yolk granule stage I (248.33±28.79), II (307.05±52.22) and III (531.65±72.11). Very few O. Occasional OA, mainly of advanced Vitellogenic oocytes (VO). Post-ovulatory follicles (POF) were not observed.
IV Spawning capable	Presence of POF and/or oocytes at final maturation and hydrated oocytes (H) (833.60± 93.42). Oocytes in all stages of development. Few (or none) O. A large population of oocytes remains in the PG phase. Rare vitellogenic OA. Ovarian cavity increases in size as spawning proceeds.
V Regressing	Wide ovarian cavity. Vascularized, empty and irregular ovigerous lamellae with numerous POF and some AO, together with residual healthy, yolked oocytes. A large population of primary oocytes present at the periphery of the ovigerous folds.
VI Regenerating (resting)	Wide ovarian cavity and thick ovarian wall. O and primary oocytes numerous. Some LG. Corpus albicans (belonging to POF or atretic oocytes) and melanomacrophage centres (MMC) present. No vitellogenic oocytes. Abundant stroma in the inner of bloodshot ovigerous folds. No vitellogenic oocytes.
Testes	
I Immature	Very small gonads with well-developed tubules. Abundant spermatogonia (14.23±1.95). Spermatogenic activity during all the year, more intense in the reproductive season. Spermatozoa (1.62±0.09) are present in the lumen of tubules and vas deferens during the reproductive season.
II Early developing	Spermatogenic activity is generalised in testes, with abundant spermatocytes (I, 4.23±0.18; II, 3.24±0.35). Spermatozoa can be observed in tubules but not in all of them
III Late developing	Intense spermatogenic activity. Abundant spermatids (2.77±0.41). Spermatozoa are present in the tubules but do not fill all the lumen.
IV Spawning capable	Intense spermatogenic activity. Dilated tubules and vas deferens fully filled with spermatozoa.
V Regressing	No spermatogenic activity or very limited. Tubules and vas deferens continue full of residual spermatozoa.
VI Regenerating	Wall of spermatogenic tubules is full of spermatogonia. Residual spermatogenic activity and scattered residual spermatozoa are still present in the tubules and vas deferens. Abundant stroma in the testes.

Type of fecundity

The type of fecundity of a species not only determines the methodology for estimating fecundity (Hunter *et al*., 1992; Murua & Saborido-Rey, 2003) but is a relevant reproductive trait in itself. Capital breeders tend to have determinate fecundity. Fecundity can be determinate (the number of eggs released during the spawning season is fixed prior to the onset of spawning) or indeterminate (not fixed prior to the onset of spawning). In determinate species, the number of developing oocytes (NDO) is equivalent to the potential annual fecundity (*Fp*), which can be estimated by counting the number of vitellogenic oocytes in females just before spawning. However, in indeterminate species, the annual fecundity should be calculated from the batch fecundity, the percentage of females spawning per day (spawning fraction) and the duration of the spawning season (Hunter *et al*., 1985).

Determining the type of fecundity may be challenging. Following West (1990) and Murua & Saborido-Rey (2003), three lines of evidence were used to compare several parameters immediately before and during the spawning season: i) the development of a hiatus separating the stock of vitellogenic oocytes from the pre-vitellogenic oocytes in the oocyte size-frequency distribution, ii) the variation in the mean diameter of advanced vitellogenic oocytes, and iii) the variation in the proportion of vitellogenic oocytes (NDO) in the oocyte size-frequency distribution throughout the breeding season.

Oocyte size-frequency distributions were determined from histological sections, as this technique allows developmental characteristics to be associated with any given oocyte size class (West, 1990). The number of NDOs was estimated by a volumetric method in 61 randomly chosen mature females (45 to 79 cm L_T) in pre-spawning and spawning condition, i.e., at stages II to IV (Table 2). A subsample from each ovary was removed and stored in Gilson fluid. Only the cortical alveolus and vitellogenic oocytes were counted. Twenty random subsamples of 5 ml (approximately 0.5% of the total volume) were taken, and the oocytes were counted under a dissecting microscope. The average of the 20 counts was used to estimate the NDO. Relative NDO was estimated as the number of vitellogenic oocytes per gram of somatic eviscerated weight (W_E).

Oocyte measurements were performed on maturing and spawning ovaries from the same 61 females as indicated above. In order to minimize bias towards any particular oocyte size, measurements were made of all oocytes present in five microscopic fields using a 4x objective. Oocyte size, obtained as the average of the shorter and longer diameters, was only recorded for those oocytes that had been sectioned through the nucleus (Foucher & Beamish, 1980). Measurements ranged from 16 to 75 oocytes per gonad (mean 38.7 ± 9.1 S.D.). The nucleus increased relatively little in size with oocyte growth, and thus, the bias towards larger cells is minimal (Foucher & Beamish, 1980); therefore, a correction factor was not applied to the observed oocyte size frequency measured in the histological sections because the purpose of our analysis was only to compare oocyte size-frequency distributions between individuals and not to quantify oocyte abundances.

Potential fecundity

As fecundity in the *D. dentex* is determinate (see results and discussion), the potential fecundity, Fp, was defined as the number of mature oocytes per female in a reproductive season, which was not corrected for atretic losses (Hunter *et al.*, 1992). Fp was estimated in 46 females (size ranging from 33 to 84 cm) in pre-spawning condition, i.e., with the presence of oocytes in secondary growth (cortical alveoli or vitellogenesis) but without any spawning marker. Finally, the relations between the fecundity of the 46 females above and their maternal features (size, weight, age and body indexes) were assessed by fitting GLM with a normal error distribution and a power link function.

Results

Age and growth

The annual periodicity of the growth marks was validated by both the direct and the indirect method. Concerning the 24 reared fish, the agreement between the known age and the count of the putative annual growth marks was very high. All fish confirmed this method, except in one case when three growth marks were counted for a 2-year-old fish. These otoliths had frequent small abnormal crystallizations (31% of the fishes), which is a common feature of reared fish (Tomás & Geffen, 2003). Similarly, the first translucent increment was not as well defined as it appears in wild fish. However, the second and third increments were distinct. In April 2005, all the fish showed a new opaque increment in the process of forming on the otolith edge.

Concerning the periodicity of the otolith growth marks of the wild fish, the percentage of otoliths with an opaque marginal increment was always low, probably due to difficulties in observing the marginal increment, which was larger in fall and attained its maximum increment in winter (2.5%, 6.7%, 15% and 20% in the four quarters, respectively); this result was in contrast to the reared immature fish, which showed the maximum increment in spring. Although these contrasting results deserve further future analysis by age class, we consider that annual periodicity of the putative annual increments as being indirectly validated.

The ages of 331 fish were estimated. Ages ranged from 0 to 26 years for females and from 0 to 22 years for males. Data fitted significantly to the von Bertalanffy growth function ($p < 0.001$ for both sexes; Table 3 and Fig. 1). Growth trajectories did not differ between

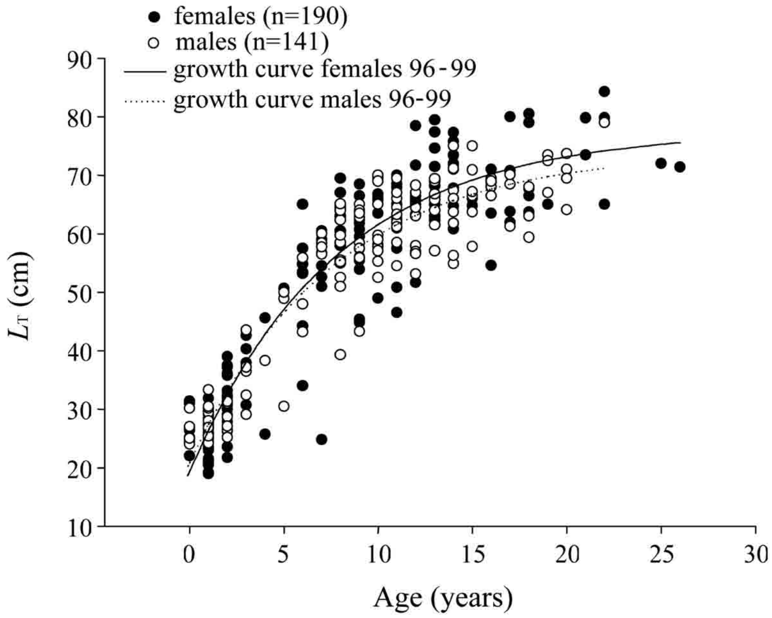

Fig. 1: *D. dentex* age composition and von Bertalanffy growth curves by sex and for all years combined.

the sexes (F = 2.58, p = 0.762). The asymptotic length for the combined function was 76.6 cm, and 75% of this size was reached by age 9, indicating a relatively slow growth.

Table 3. Von Bertalanffy growth parameters for *D. dentex*.

	L∞ cm	**K yr^{-1}**	**t_0**
Males	74.123	0.132	-2.504
Females	77.588	0.129	-2.22
Total	76.581	0.127	-2.335

Sex ratio and sexual maturity

Of the 358 fish analysed, the sex was determined in 343 (198 females and 145 males), whereas the sex was not determined for 12 small individuals. Interestingly, three fish were hermaphrodites. These hermaphrodites measured 20.7, 25.2 and 27.6 cm L_T and were 0 and 1-year-old. They had immature testes with an immature ovarian section located in a dorsomedial position, near the gonadal artery and the primordial central cavity. The size distribution was not different between the sexes (ANOVA, p = 0.551). The overall sex ratio was skewed to females (1.36, females/males).

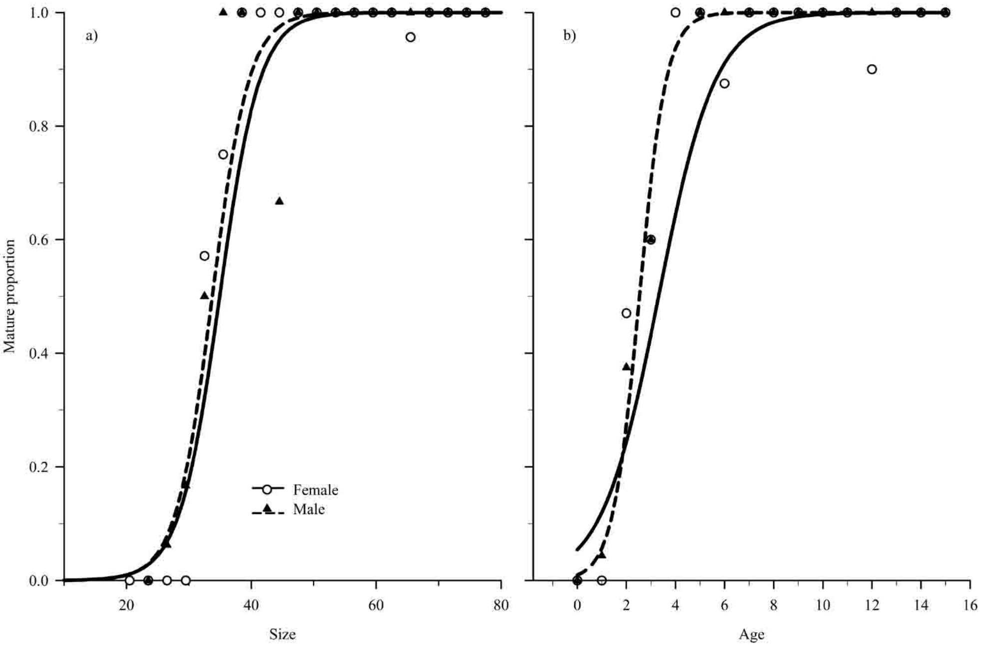

Fig. 2: *D. dentex* maturity ogive at a) size (L_T cm) and b) age for females (solid line) and males (dashed lines).

Table 4. The results of the generalised linear models (GLM) for maturity ogives in *D. dentex*.

Response variable	Explanatory variables	Estimate	Std. Error	Wald Stat	*p* value
Maturity DE = 80.4 n = 343	Intercept	11.262	1.768	40.559	< 0.001
	Size	-0.327	0.055	35.224	< 0.001
	Sex	-0.181	0.296	0.374	0.541
Maturity DE=98.6 n = 332	Intercept	3.144	0.438	51.503	< 0.001
	Age	-1.032	0.164	39.522	< 0.001
	Sex	-0.089	0.266	0.111	0.739

The smallest mature female observed was 32 cm L_T and 2 years old. Most of the females longer than 36 cm and more than 4 years old were mature. Similarly, the smallest mature male was 26 cm L_T and 2 years old, but most males longer than 33 cm and older than 4 years were mature. Full maturity was reached in an interval of 20 cm for both sexes (Fig. 2a) and at 6 and 4 years for females and males, respectively (Fig. 2b). Maturity ogives for the size and age were not significantly different between the sexes (Table 4). Females achieved 50% maturity at 34.9 cm L_T and 3.3 years, whereas males achieved maturity at 33.8cm L_T and 2.5 years.

Seasonal pattern of ovarian development

Most fishes had gonads of the same size, but relative asymmetry existed mainly in the immature fish (equal size gonads: females, 81.93%; males, 77.34%; immature, 66.67%; hermaphrodites, 50%). When the gonads were asymmetric, a predominance of a larger left gonad (left 13.38%, right 7.02%) was observed. The size of the gonad relative to the visceral cavity showed a marked increase, with the available space being almost completely filled in the mature and post-spawning fishes.

The ovarian development (Fig. 3) showed that the onset of annual ripening took place in December, whereas vitellogenesis occurred from February to April. The spawning period extended from March to June, with a peak in April and May showing 78 and 93%, respectively, of the females at spawning phase. Females with regressing ovaries were first observed in May, whereas regenerating individuals appeared in June. In July, all mature females were at the resting stage. Running males were found from March to June, showing the same extension of the spawning period as for the females (Fig. 3b). At the peak of spawning activity (April and May), more than 65 and 80%, respectively, of the testes were running.

The model used to assess the onset, end and duration of the spawning (binomial GLM) included a seasonal variable, expressed by week as the variable and by size as the maternal effect. Size did not significantly affect either the onset or the end of the spawning, and consequently, the duration of the spawning season was not determined by female size. In contrast, the seasonal component significantly affected the onset and end of spawning (GLM, $p < 0.005$). A total of 50% of the females were at the onset of spawning at week 12.7 (mid-March), and 50% of the females were at the end of spawning at week 23.7 (early June); that is, the average duration of spawning was estimated to be 11 weeks (Fig. 4).

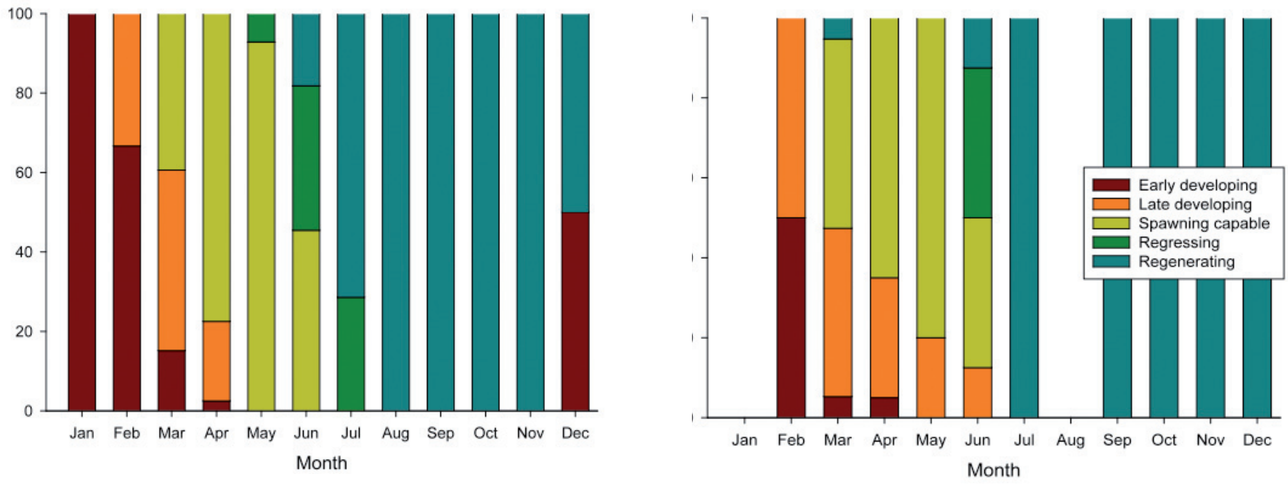

Fig. 3: *D. dentex* reproductive phases proportion by month for mature females (left) and males (right).

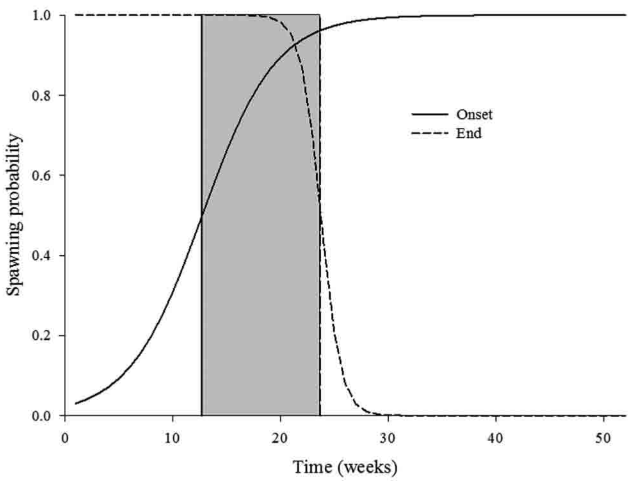

Fig. 4: Female *D. dentex* prediction of onset and end of the spawning season as a result of the generalised linear model (binomial). The shadow area represents the average spawning duration framed by the time at which 50% of females are at the onset of spawning (solid vertical line) and when 50% of the females are at the end of spawning (dashed vertical line).

Seasonal pattern of I_G, I_H and K_R

The average values of I_G, I_H and K_R varied significantly during reproduction for the females, but only I_G varied for the males (Table 5). I_G showed a clear spring reproductive peak in both sexes (Fig. 5). Vitellogenesis, as indicated by the I_G peak, matched well with the seasonal pattern of ovarian development observed using the above-described histological methods. The I_G value was at the minimum level between August and January and peaked in April and May during the spawning. After the spawning, the I_G sharply decreased in both sexes (Fig. 5). The liver storage, I_H, showed a parallel pattern to I_G in the females ($r = 0.951$, $p < 0.005$; Fig. 5). No clear trend was observed in the male I_H. In contrast, the female K_R steadily decreased from February to June and increased sharply in summer, remaining high until the beginning of vitellogenesis. The K_R level did not correlate with the I_G (r =-0.476, $p = 0.118$).

Variation in the I_G, I_H and K_R among the different female reproductive phases was also significant for females, but was significant only for I_G in the males (Table 5). I_G and I_H showed the same trend; maximum values were observed in spawning females, and minimum values, in the recovering phase (Fig. 6). In the case of K_R, the maximum value was found in the recovering phase, whereas the minimum was located in the spent phase, right after the end of the spawning (Fig. 6).

Type of fecundity

The oocyte size-frequency distributions of *D. dentex* showed an asynchronous pattern before spawning, but a hiatus occurred by the end of the spawning season (Fig. 7). Accordingly, the mean vitellogenic oocyte diameter significantly increased through the year, both by sampling date and week ($r^2 = 0.590$, $p < 0.001$ and $r^2 = 0.925$, $p < 0.001$, Fig. 8a). Similarly, the mean oocyte diameter increased significantly among months and between pre-spawning and spawning females ($p < 0.001$ in both cases).

However, the NDO did not change between the pre-spawning and spawning females ($p = 0.311$ and 0.385, respectively). In spite of the lack of differences, a clear increase in the relative NDO was observed during vitellogenesis, followed by a decrease during spawning (Fig. 8b). However, the relative NDO significantly decreased ($F = 4.20$, $p < 0.05$) between March and April. A generalised prevalence of atresia at the end of the spawning season was never observed, likely because the majority of oocytes were spawned, as indicated by the hiatus in the formation. In contrast, some empty, flaccid, bloodshot, spent ovaries, which were reddish-brown in colour, could be observed at the end of the spawning period (from the middle of June to the beginning of July).

Table 5. The results of an analysis of variance of somatic indices of *D. dentex* by sex, month and reproductive phase.

			***F* value**	***p* value**
Month	Females	I_G	11.84	<0.001
		I_H	7.43	<0.001
		K_R	2.93	<0.005
	Males	I_G	9.70	<0.001
		I_H	1.08	0.3852
		K_R	1.07	0.3934
Phase	Females	I_G	79.19	<0.001
		I_H	34.94	<0.001
		$K\mathrm{r}$	3.39	<0.05
	Males	I_G	22.22	<0.001
		I_H	1.18	0.3200
		K_R	0.052	0.9842

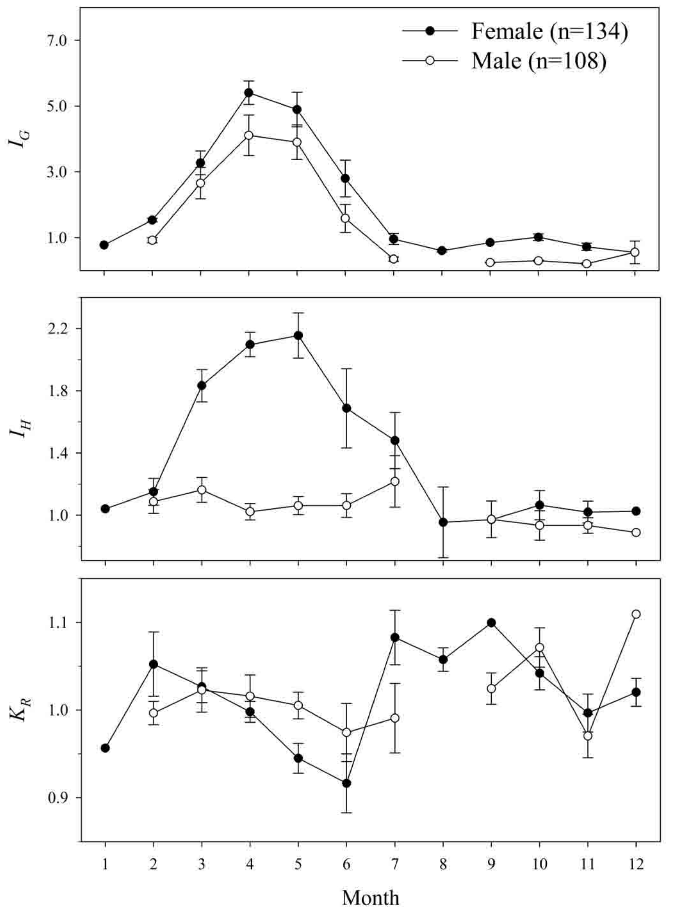

Fig. 5: Monthly average of gonadosomatic (I_G), hepatic (I_H) indexes, and condition (K_R) indexes by sex of mature *D. dentex*. Bars indicate the standard error.

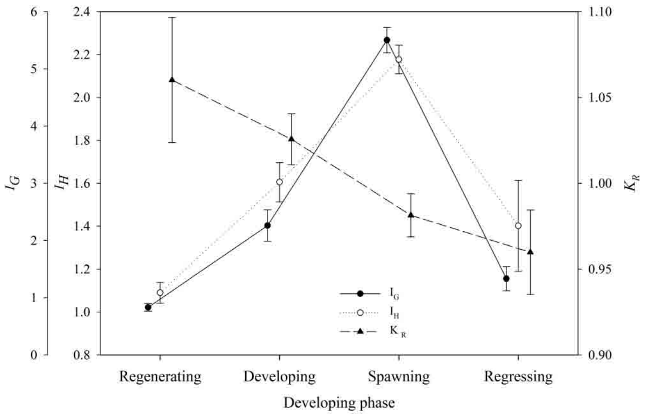

Fig. 6: Variation of somatic indexes by reproductive phases of female *D. dentex*. The *early* and *late developing* phases are merged into the *Developing* phase.

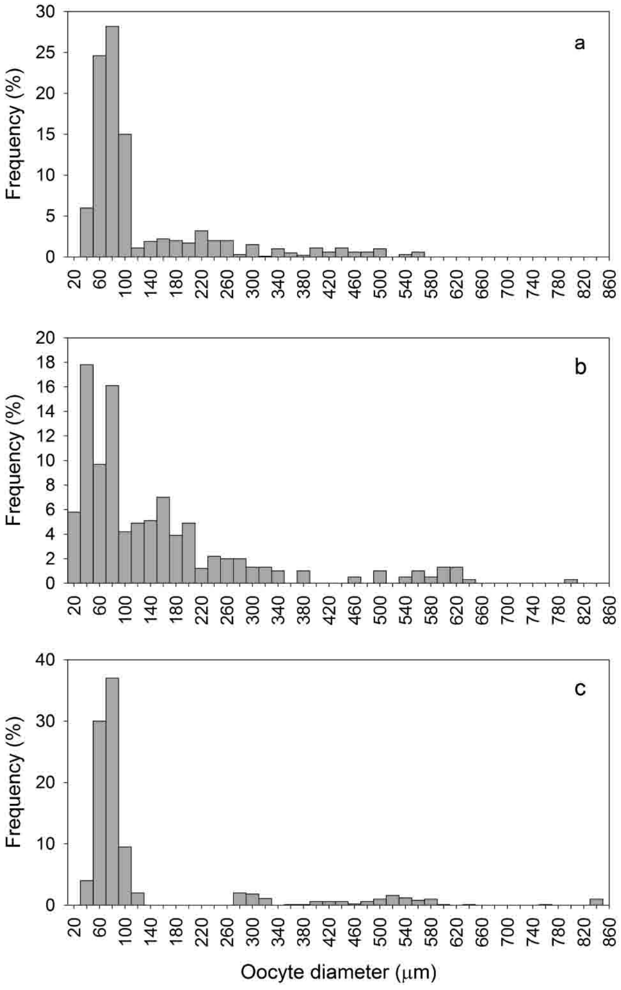

Fig. 7: Size frequency distribution of oocyte diameter grouped per 20 μm from histological sections of three *D. dentex* females. a) a 57.4 cm L_T female captured in March, maturity stage 3; b) a 75.8 cm L_T female captured in the middle of April, maturity stage 4; c) a 65.7 cm L_T female captured at the end of May, maturity stage 4.

The relationships between the NDO and female length and weight between pre-spawning and spawning females did not differ (GLM, p = 0.519 and 0.503, respectively, Fig. 8c and Fig. 8d). However, the regression with length and weight in pre-spawning females showed a high goodness of fit (r^2 = 0.88 and 0.913, respectively; Fig. 8c and Fig. 8d). The oocyte density, defined as the number of vitellogenic oocytes per gram of ovary, showed a significant relation with the oocyte diameter in a nonlinear power model (r^2 = 0.854, Fig. 9). This evidence indicates that oocyte development is asynchronous but that fecundity is likely determinate.

Potential fecundity

Given that fecundity is likely determinate, the NDO estimated above in the pre-spawning females should be considered as potential fecundity (Fp). Fp ranged between 154,000 (in a female of 34 cm L_T) and 29,382,500 (in a female of 84.3 cm L_T), as shown in Figure c and 8d. All maternal features significantly and positively influenced potential fecundity (Table 6), especially female length and weight. When the generalised linear models were run with the female features as the explanatory variables, the best model included total length, gutted

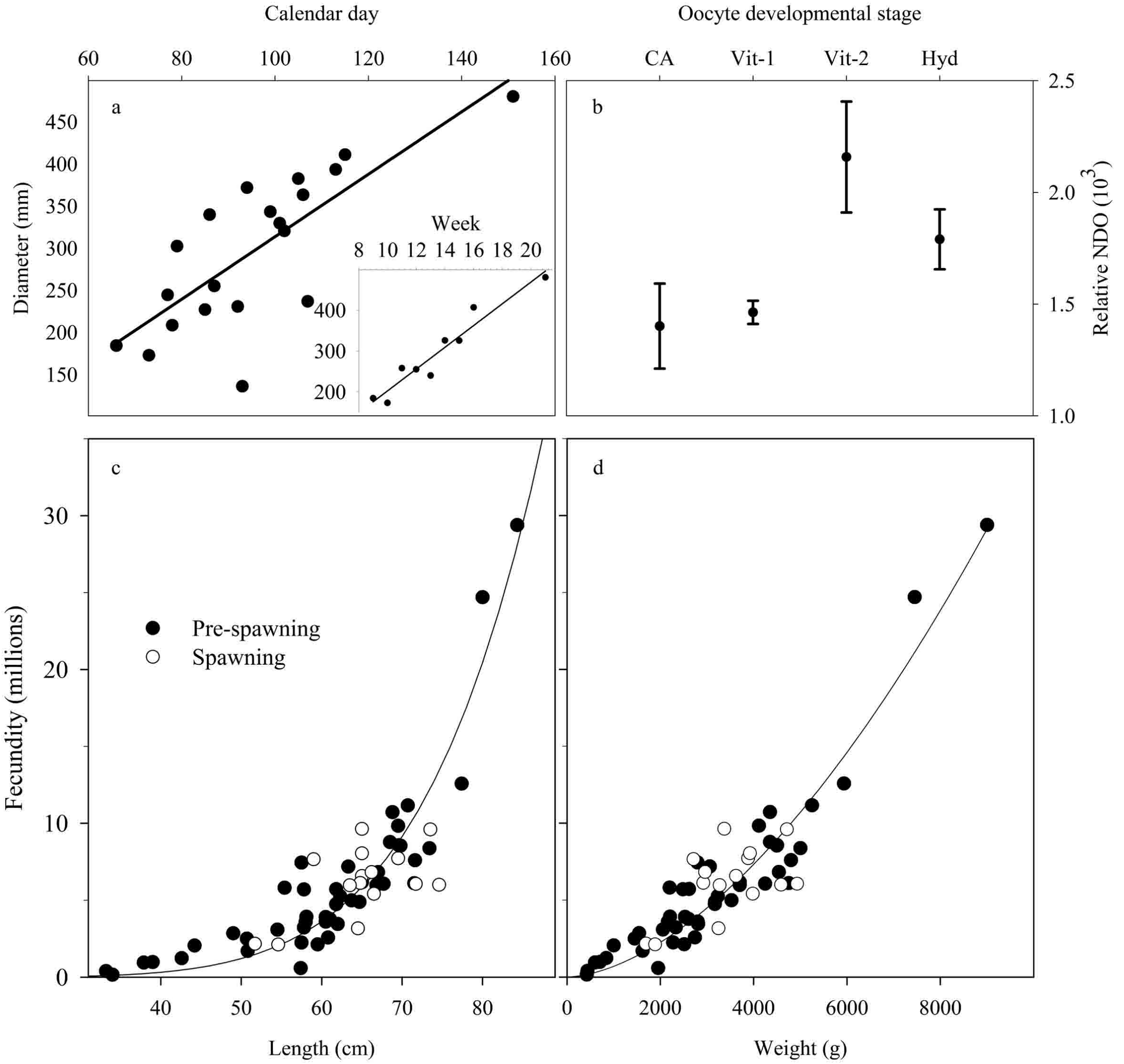

Fig. 8: Fecundity analysis of *D. dentex*. a) progression and linear regressions of mean oocyte diameter along the year by sampling day and week; b) mean and standard deviation of the relative number of developing oocytes (NDO) during the oocyte developmental stage; relations and fitted curves between fecundity and length (c) and weight (d) in pre-spawning and spawning females.

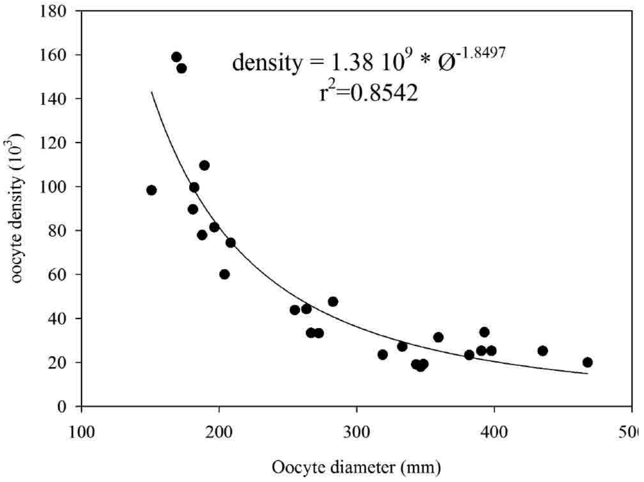

Fig. 9: Relation and fitted curves between oocyte density (number of oocytes per gram of ovary) and oocyte diameter for *D. dentex*.

weight and liver weight (AIC = 1,380.03, $p < 0.001$), although these three variables were highly correlated (0.93, 0.79 and 0.89, respectively). The coefficients of the fecundity-length and weight relations were significantly ($p < 0.001$) larger than the expected isometric values of three and one, respectively, indicating strong allometry and a higher reproductive potential for larger females.

The relative potential fecundity (Fr) varied greatly and ranged between 4,168 and 270 eggs g^{-1} (mean 1,589 ± 643 S.E.) from females of quite similar sizes (62 and 57 cm L_T). The Fr increased significantly with all maternal features (Table 6). Liver weight was the best predictor (r^2 = 0.41). The significant relations also indicate that larger females have higher reproductive potential. The oocyte diameter did not show significant relations with maternal features ($r^2 < 0.1$, $p > 0.05$).

Table 6. The results of the significant regression analysis for the effects of maternal features (LT, cm, Wg, and age) and body indexes (I_G, I_H, K_r and liver weight, M_L) on the potential (Fp) and relative fecundity (Fr) of *D. dentex.*

Fecundity	F	*p*	r^2
$Fp = 0.107\ LT^{4.275}$	182.31	<0.001	0.81
$Fp = 113.951\ Wg^{1.332}$	234.19	<0.001	0.84
$Fp = 234944.269\ Age^{1.278}$	39.02	<0.001	0.48
$Fp = 1.68E{+}06\ I_G^{0.822}$	29.51	<0.001	0.40
$Fp = 3.63E{+}06\ K_r^{7.029}$	26.18	<0.001	0.37
$Fp = 2.12E{+}06\ I_H^{1.067}$	5.18	<0.05	0.11
$Fp = 1.02\ 10^5\ LW - 5.70\ 10^5$	242.51	<0.001	0.85
$Fr = 29.5 + 27.47\ L_T$	14.56	<0.001	0.25
$Fr = 1043.96 + 0.21\ Wg$	22.39	<0.001	0.34
$Fr = 1174.93 + 50.76\ Age$	7.03	<0.05	0.14
$Fr = 1262.06 + 114.05\ I_G$	10.44	<0.05	0.19
$Fr = -1956.23 + 3577.64\ K_r$	15.26	<0.001	0.26
$Fr = 820.96 + 454.27\ I_H$	8.87	<0.05	0.17
$Fr = 1173.51 + 8.14\ LW$	31.08	<0.001	0.41

Discussion

Reproductive strategy

Despite previous studies on *D. dentex* (Morales-Nin & Moranta, 1997; but see Marengo *et al.*, 2014), the reproductive traits of this species in the wild were, until now, poorly known; moreover, data obtained from cultured fish are not readily applicable to wild fish (Loir *et al.*, 2001). In this study, we used a number of complementary approaches to better delineate the reproductive strategy of this coastal species. The most relevant life history traits of the reproductive strategy of *D. dentex* are as follows:

1) Gonochorism. The prevalence of hermaphroditism is residual and, in spite of its theoretical interest (see below), should not have any practical outcome on shaping the reproductive strategy.
2) *D. dentex* is a slow growing species with a long lifespan, as reported earlier (Morales-Nin & Moranta, 1997), with approximately 80% of the growth achieved in the first 10 years of life (the oldest fish detected were 22 years old).
3) Female sexual maturity is attained at nearly 50% of the maximum length but at a relatively young age (3 years). Given its slow growth, *D. dentex* experiences a relevant size increment after maturation, and an unavoidable trade-off between growth and reproduction should exist.
4) Fecundity is likely determinate, with an asynchronous oocyte development before spawning but a clear ovarian bimodal organization after the onset of spawning. Fecundity is (exponentially) related to the maternal traits. Female weight explained 84% of the observed variance in fecundity. This strong relation supports the hypothesis of determinate fecundity because, in indeterminate species, the oocytes are continuously recruited and spawned, and the annual fecundity of these species is not limited by body cavity size but instead by energetics and environment (Cooper *et al.*, 2013). However, only 85% of the variance in oocyte density (number of vitellogenic oocytes per gram of ovary) was explained by oocyte diameter, which is higher than that observed in indeterminate species, but is considerably lower than the values typical of determinate fecundity.
5) Storage seems to be the primary energy source for reproduction in *D. dentex*. In capital breeders, storage is produced during the favourable periods prior to the onset of ripening (McBride *et al.*, 2013). This is supported by the sharp increase in condition in summer and autumn, followed by a steady decrease during oocyte recruitment (winter to spring). In contrast, another typical storage tissue, the liver, shows a strong fluctuation concurrent with I_G and is highly correlated in females but not in males. This result may indicate that the liver is playing an important role in egg production too, which is not typical of capital breeders. Nevertheless, capital and income breeders represent the ends of a continuum, and some species are able to compensate for inadequate energy deposits with concurrent food intake (Henderson *et al.*, 1996). Moreover, the rapid vitellogenesis observed may indicate that while the energy allocated to oocyte recruitment and other reproductive traits is being taken from energy stored in the muscle, most of vitellogenesis is being financed with recently acquired energy that was temporarily stored in the liver (Ganias, 2013). This is in accordance with the observed in other species, such as pouting (Alonso-Fernández & Saborido-Rey, 2012), which exhibit determinate - or nearly

determinate - fecundity but also asynchronous oocyte development. This observation indicates that the species studied herein is a suitable candidate to possess an intermediate strategy, one that combines capital and income breeding. This storage dynamic seems to be in accordance with the relative short spawning period indicated both by histological observations and I_G, and the high degree of synchronization among individual spawning periods (81% of the females were spawning in April-May). Strong seasonality is typical of capital breeders, and although seasonality is common in cold-water habitats with restricted spawning seasons (Lowerre-Barbieri *et al*., 2011b), it has been reported also for temperate species with an intermediate strategy (Alonso-Fernández & Saborido-Rey, 2011; 2012; Alonso-Fernández *et al*., 2014). Nevertheless, additional effort is required to properly investigate the energy allocation strategy with biochemical data to better understand the relation between energy reserves and reproduction in *D. dentex*.

The growth coefficient has been largely linked to total mortality (Beverton & Holt, 1957; Pauly, 1980); slow-growing fish unavoidably should undergo lower mortality. The relations among these life history traits (maturation, growth and mortality) are also connected with the reproductive effort (Charnov, 2008) and with its major component, fecundity, as well with the way that the costs of reproduction are financed (Reznick, 1985; Stephens *et al*., 2009). The combination of these life history traits suggests that *D. dentex* has a reproductive strategy described by Ware (1984) as *type A*, where the reproductive rate is a function of the surplus energy; hence, balancing (trading-off) the energy invested in survival, growth and reproduction, i.e., where individual growth continues after the onset of maturation, is advantageous. The trade-off is possible because the fish is able to compensate negative energy balances through growth by metabolic or activity compensation. Likewise, fish with a limited food supply may partly or fully sacrifice egg production to preserve body condition, whereas others may maintain investment in reproduction at the expense of body reserves. This is equivalent to the *periodic* life history strategy (Winemiller & Rose, 1992) exhibited by fish that delay maturation in order to attain a size sufficient for the production of a large clutch and adult survival during periods of suboptimal environmental conditions. These include species with a high-fecundity strategy, where they frequently reproduce in synchronous episodes of spawning that coincides either with movement into favourable habitats or with favourable periods within the temporal cycle of the environment (e.g., spring). However, although *D. dentex* attain maturity at large size, maturity occurs at an early age, and part of the reproductive effort is financed using current energetic income, thereby leading to an intermediate strategy or strategy B in the conceptual model proposed by Saborido-Rey *et al*. (2010).

This trade-off implies that smaller fish are less productive, and to be productive, the species must survive beyond the age at maturation. In addition, larger females have better reproductive potential, and a well age- and size-structured population has greater reproductive potential, thereby favouring the survival of the early life stages and subsequent recruitment (Saborido-Rey *et al*., 2011).

Hermaphroditism

The unexpected finding of hermaphroditism deserves specific discussion. *D. dentex* belongs to the Sparidae family, where hermaphrodite species are common (Bauchot & Hureau, 1986); however, in this study, only three (0.8%) young, immature fish were hermaphrodites. No signs of sex change were found, indicating that *D. dentex* is likely a gonochoristic species, as has already been suggested (Grau *et al*., 2001; Loir *et al*., 2001). However, a few cases of juvenile rudimentary hermaphroditism have been observed (Grau *et al*., 2001). This pattern has also been reported for *Dentex gibbosus* (Grubisic *et al*., 2007) and other sparids (Matsuyama *et al*., 1988; Buxton & Garratt, 1990). As stated by Buxton & Garratt (1990), *D. dentex* would be considered a *late gonochoristic species*, distinguishing it from a *true* gonochorist, in which hermaphroditic tissue is never found. Moreover, those authors suggested that seabreams classified as true gonochorists may actually be rudimentary hermaphrodites because histological studies on their early developmental stages are often lacking. The reports of undifferentiated gonads (i.e., with a central cavity in immature stages; Yamamoto, 1969; Matsuyama *et al*., 1988; Buxton & Garratt, 1990) could corroborate this possibility.

No functional hermaphrodites have been detected here, although they have been sporadically reported by other authors (Tortonese, 1975; Bauchot & Hureau, 1986). Nevertheless, in practice, this species should be considered as gonochoric but with few cases of bisexual juveniles.

Reproductive strategy and management

Presently, *D. dentex* is not being specifically managed, nor has it been scientifically assessed (STECF, 2013). Only general efforts to limit its exploitation have been applied to small scale fisheries and recreational fishing, and the species is sought after and has a high value (Marengo *et al*., 2014). *Dentex dentex* has sharply decreased in global catches (FAO, 2014) from more than 10,000 t in 1990 to 1,575 t in 2010, which may indicate an overfishing situation. In the Mediterranean, the progressive increase in catches until 1990 (6,825 t) was also followed by a sharp decrease (1,555 t in 2010). Now, *D. dentex* is classified as vulnerable on the Red List of Threatened Species in the Mediterranean.

Along with the regulation of effort, minimum catch sizes are by far the most common regulation tool in the management of a variety of fish stocks. Minimum catch sizes, established in an effort to allow the fish to reproduce at least once in their lives, usually protect the immature stock (Lowerre-Barbieri *et al*., 2011b). Considering the estimated mean size at maturity, 35 cm, a minimum landing size should be established at that size, which is a limit appropriate for both sexes. However, this type of management tool often leads to recruitment overfishing (Hilborn, 2012), which highlights the need of an in-depth knowledge of the reproductive strategy.

The need to understand the factors driving population productivity and the role of reproductive biology are being increasingly recognized (Kjesbu, 2009; Worm *et al.,* 2009; Saborido-Rey & Trippel, 2013) as needed to sustainably managing exploited fish stocks. In the case of *D. dentex*, given its reproductive strategy, when fishing mortality is at high levels, mature fish could reproduce only a few times before being caught. This has been documented as the cause of stock collapse in a number of species due to a diminished stock reproductive potential when large spawner fish are absent in the population (Saborido-Rey & Junquera, 1998; Trippel, 1999; Saborido-Rey & Trippel, 2013 and references therein).

Moreover, in *D. dentex,* the potential fecundity could be as high as nearly 30 million eggs produced by an 84-cm-long female. The relative fecundity resulted in up to 3 million eggs per kg of body weight, with an average of 1,7 million. This is more than twice the figure reported for captive *D. dentex* in Greece (Loir *et al*., 2001) but is similar to the reported fecundity *of D. gibbosus* (Grubisic *et al*., 2007). The exponent of the fecundity versus weight relation was significantly larger than 1 (1.7). This is particularly important because this value indicates that the egg production per spawning stock biomass will be positively related to the abundance of large females in the stock (Wright, 2013), highlighting the importance of the population having an age and size distribution with a higher proportion of older and larger fish to preserve the stock (Saborido-Rey & Trippel, 2013).

To address this scenario, a slot limit should be implemented, i.e., a minimum and a maximum landing size. However, the delineation of the upper size threshold is debatable, but it must consider the fecundity-length relation, i.e., the specific reproductive potential. This fishing regulation is feasible given the typical dome-shaped selectivity of the traditional fishing gears used in the Mediterranean for this species, but it may not be desirable from a fisher's point of view, as larger individuals are also the most economically profitable. However, the most effective way to protect larger fish is though the establishment of marine protected areas (MPAs), but that effort will require a better knowledge of *D. dentex* demography, spatial-temporal distribution and habitat use.

Acknowledgements

A. Grau and F. Saborido-Rey contributed equally to this manuscript. This work was funded by the Spanish Ministry of Education and Culture (Project CYTMAR ref nº MAR 95-1920-C02-01) and JACUMAR, Spanish Secretary General for Fisheries (Project: "Cultivo del denton: aspectos reproductivos, mejora del cultivo larvario y diseño de dietas artificiales para su engorde"). We are especially grateful to P. Tugores (COB – IEO), to the laboratory technicians at LIMIA, and S. Pérez-Máyol (IMEDEA) for their help and support on the development of this study. This is a result of the Joint Research Unit IMEDEA - LIMIA.

References

Alonso-Fernández, A., Saborido-Rey, F., 2011. Maternal influence on the variation of the reproductive cycle of *Trisopterus luscus* (Gadidae). *Ciencias Marinas*, 37, 619-632.

Alonso-Fernández, A., Saborido-Rey, F., 2012. Relationship between energy allocation and reproductive strategy in *Trisopterus luscus*. *Journal of Experimental Marine Biology and Ecology* , 416-417, 8-16.

Alonso-Fernández, A., Alós, J., Palmer, M., 2014. Variability in reproductive traits in the sex-changing fish, *Coris julis*, in the Mediterranean. *Mediterranean Marine Science*, 15, 106-114.

Alós, J., Palmer, M., Catalan, I., Alonso-Fernández, A., Basterretxea, G. *et al*., 2014. Selective exploitation of spatially structured coastal fish populations by recreational anglers may lead to evolutionary downsizing of adults. *Marine Ecology Progress Series* 503, 219-233.

Bauchot, M.L., Hureau, J.C., 1986. Sparidae. p. 883-907. In: *Fishes of the North-eastern Atlantic and the Mediterranean*. Vol. 2. Whitehead, P.J.P., Bauchot, M.L., Hureau, J.C., Nielsen, J., Tortonese, E. (Eds). UNESCO, Paris.

Beverton, R.J.H., Holt, S.J., 1957. *On the dynamics of exploited fish populations*. Ministry of Agriculture, Fisheries and Food, London, 533 pp.

Bibiloni, G., Cladera, A., Gomila M.A., Massuti, S., Zaratiegui, I., 1993. A small scale experiment on rearing of *D. dentex. European Aquaculture Society,* 19, 317.

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

Buxton, C.D., Garratt, P.A., 1990. Alternative reproductive styles in seabreams (Pisces: Sparidae). *Environmental Biology of Fishes*, 28, 113-124.

Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*, 59, 197-242.

Charnov, E.L., 2008. Fish growth: Bertalanffy k is proportional to reproductive effort. *Environmental Biology of Fishes*, 83, 185-187.

Charnov, E.L., Gislason, H., Pope, J.G., 2013. Evolutionary assembly rules for fish life histories. *Fish and Fisheries*, 14, 213-224.

Chow, G.C., 1960. Tests of equality between sets of coefficients in two linear regressions. *Econometrica, 28,* 591-605.

Coll, J., Linde, M., García-Rubies, A., Riera, F., Grau, A.M., 2004. Spear fishing in the Balearic Islands (west central Mediterranean): species affected and catch evolution during the period 1975-2001. *Fisheries Research*, 70, 97-111.

Collet, D., 1991. *Modelling binary data*. Chapman & Hall, London, 369 pp.

Cooper, W.T., Barbieri, L.R., Murphy, M.D., Lowerre-Barbieri, S.K., 2013. Assessing stock reproductive potential in species with indeterminate fecundity: Effects of age truncation and size-dependent reproductive timing. *Fisheries Research,* 138, 31-41.

Crespo, S., Martín de Mateo, M., Santamaría, C.A., Sala, R., Grau, A., 2001. Histopathological observations during larval rearing of common dentex, *D. dentex* L. (Sparidae). *Aquaculture,* 192, 121-132.

FAO, 2014. http://www.fao.org/fishery/species/3182/en. (Accessed 4 October 2014)

Foucher, R.P., Beamish, R.J., 1980. Production of Nonviable Oocytes by Pacific Hake (*Merluccius productus*). *Canadian Journal of Fisheries and Aquatic Sciences,* 37, 41-48.

Ganias, K., 2013. Determining the indeterminate: Evolving concepts and methods on the assessment of the fecundity patterns of fishes. *Fisheries Research,* 138, 23-30.

Glamuzina, B., Jug-Dujakovic, J., Katavic, I., 1989. Preliminary studies on reproduction and larval rearing of common dentex *Dentex dentex* (Linnaeus 1758). *Aquaculture*, 77, 75-84.

Grau, A., Morales-Nin, B., Quetglas, A., Riera, F., Massutí, E. *et al*., 2001. El modelo reproductivo del dentón *Dentex dentex* (L., 1758): bisexualidad juvenil y gonocorismo tardío. p. 555-560. In: Monografías ICCM 4, Spain.

Grubisic, L., Jelic-Mrcelic, G., Skakelja, N., Katavic, I., Ticina V. *et al*., 2007. Reproductive biology of pink dentex *Dentex gibbosus* (Rafinesque) from the Adriatic Sea, Croatia. *Aquaculture Research,* 38, 991-1001.

Heino, M., Godø, O.R., 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science,* 70, 639-656.

Heino, M., Dieckmann, U., Godø, R., 2002. Reaction norm analysis of fisheries-induced adaptive change and the case of Northeast Artic cod. *ICES Journal of Marine Science,* 59, 562-575.

Henderson, B.A., Wong, J.L., Nepszy, S.J., 1996. Reproduction of walleye in Lake Erie: allocation of energy. *Canadian Journal of Fisheries and Aquatic Sciences,* 53, 127-133.

Hilborn, R., 2012. *Overfishing: What Everyone Needs to Know*. Oxford University Press, USA, 160 pp.

Hunter, J.R., Lo, N.C.H., Leong, R.J.H., 1985. Batch fecundity in multiple spawning fishes. p. 67-77. In: *An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, Engraulis mordax.* Lasker, R. (Ed.), NOAA Technical Repport NMFS36.

Hunter, J.R., Macewicz, B.J., Lo, N.C.H., Kimbrel, C.A., 1992. Fecundity, spawning and madurity of female Dover sole, *Microstomus pacificus*, with an evaluation of assumption and precision. *Fishery Bulletin*, 90, 101-128.

Kjesbu, O.S., 2009. Applied fish reproductive biology: contribution of individual reproductive potential to recruitment and fisheries management. p. 321-368. In: *Fish Reproductive Biology: Implications for assessment and management*. Jokabsen, T., Fogarty, M.J., Megrey, B.A., Moksness, E., (Eds). Wiley-Blackwell, Oxford, UK.

Koumoundouros, G., Divanach, P., Kentouri, M., 1998. Embryonic and yolk-sac larval development of *Dentex dentex* (Linnaeus 1758) (Osteichthyes, Sparidae). *Marine Life,* 6, 41-50.

Koumoundouros, G., Divanach, P., Kentouri, M., 1999. Ontogeny and allometric plasticity of *Dentex dentex* (Ostheichtyes: sparidae) in rearing conditions. *Marine Biology,* 135, 561-572.

Koumoundouros, G., Divanach, P., Kentouri, M., 2001. The effect of rearing conditions on development of saddleback syndrome and caudal fin deformities in *Dentex dentex* L. *Aquaculture,* 200, 285–304.

Law, R., 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science,* 57, 659-668.

Le Cren, E.D., 1951. The Length-weight Relationship and Seasonal cycle in Gonadal Weight and condition of Perch (*Perca fluviatilis*). *Journal of Animal Ecology,* 20, 201-219.

Loir, M., Le Gac, F., Somarakis, S., Pavlidis, M., 2001. Sexuality and gonadal cycle of the common dentex (*Dentex dentex*) in intensive culture. *Aquaculture*, 194, 363-381.

Lowerre-Barbieri, S.K., Brown-Peterson, N.J., Murua, H., Tomkiewicz, J., Wyanski, D.M. *et al*., 2011a. Emerging issues and methodological advances in fisheries reproductive biology. *Marine and Coastal Fisheries,* 3, 32-51.

Lowerre-Barbieri, S.K., Ganias, K., Saborido-Rey, F., Murua, H., Hunter, J.R., 2011b. Reproductive Timing in Marine Fishes: Variability, Temporal Scales, and Methods. *Marine and Coastal Fisheries,* 3, 71-91.

Machias, A., Maraveyia, E., Pavlidis, M., Somarakis, S., Divanach, P., 2002. Ring formation on scales and otoliths of common dentex (*Dentex dentex*). *Fisheries Research,* 54, 287-294.

Marengo, M., Durieux, E.D.H., Marchand, B., Francour, P., 2014. A review of biology, fisheries and population structure of *Dentex dentex* (Sparidae). *Reviews in Fish Biology and Fisheries,* 24, 1065-1088.

Matsuyama, M., Torres Lara, R., Matsuura, S., 1988. Juvenile bisexuality in the red sea bream, *Pagrus major. Environmental Biology of Fishes,* 21, 27-36.

McBride, R.S., Somarakis, S., Fitzhugh, G.R., Albert, A., Yaragina, N.A. *et al*., 2013. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish and Fisheries*, 16 (1), 23-57.

Morales-Nin, B., Moranta, J., 1997. Life history and fishery of the common dentex (*Dentex dentex*) in Mallorca (Balearic Islands, western Mediterranean). *Fisheries Research,* 30, 67-76.

Morales-Nin, B., Panfili, J., 2005. Seasonality of the deep sea and tropics revisited: what can otoliths tell us? *Marine and Freshwater Research,* 56, 585-598.

Morey, G., Moranta, J., Massuti, E., Grau, A., Linde, M. *et al*., 2003. Weight–length relationships of littoral to lower slope fishes from the western Mediterranean. *Fisheries Research,* 62, 89-96.

Mourente, G., Rodríguez, A., Grau, A., Pastor, E., 1999a. Utilization of lipids by *Dentex dentex* L. (Osteichthyes, Sparidae) larvae during lecitotrophia and subsequent starvation. *Fish Physiology and Biochemistry,* 21, 45-58.

Mourente, G., Tocher, D.R., Diaz, E., Grau, A., Pastor, E., 1999b. Relationships between antioxidants, antioxidant enzyme activities and lipid peroxidation products during early development in *Dentex dentex* eggs and larvae. *Aquaculture*, 179, 309-324.

Mourente, G., Tocher, D.R., Diaz-Salvago, E., Grau, A., Pastor, E., 1999c. Study of the n-3 highly unsatured fatty acids requirement and antioxidant status of *Dentex dentex* larvae at the Artemia feeding stage. *Aquaculture,* 179, 291-307.

Murua, H., Saborido-Rey, F., 2003. Female Reproductive Strategies of Marine Fish Species of the North Atlantic. *Journal of Northwest Atlantic Fishery Science,* 33, 23-31.

Murua, H., Kraus, G., Saborido-Rey, F., Witthames, P.R., Thorsen, A. *et al*., 2003. Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *Journal of Northwest Atlantic Fishery Science,* 33, 33-54.

Pastor, E., Riera, F., Grau, A.M., Pou, S., Grau, A. *et al*., 1995. Growth of *Dentex dentex* in cages fed with three different diets. p. 226-227. In: *Quality in aquaculture*. *Aquaculture Europe, 1995*. Svennevig, N., Krogdahl, A. (Eds.). EAS Special Publication, nº 23, Gent, Belgium.

Pastor, E., Grau, A., Riera, F., Pou, S., Massutí, E. *et al*., 2000. Experiences in the culture of new species in the "Estación de Acuicultura" of the Balearic government (1980-1998). *Options Méditerranéennes Serie B. Etudes et recherché,* 47, 371-379.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science*, 39, 175-192.

Reznick, D., 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos,* 44, 257-267.

Roff, D.A., 1983. An allocation model of growth and reproduction in fish. *Canadian Journal of Fisheries and Aquatic Sciences,* 40, 1395-1404.

Rueda, F.M., Martínez, F.J., 2001. A review on the biology and potential aquaculture of *Dentex dentex*. *Reviews on Fish Biology and Fisheries,* 11, 57-70.

Saborido-Rey, F., Junquera, S., 1998. Histological assessment of variations in sexual maturity of cod (*Gadus morhua* L.) at the Flemish Cap (north-west Atlantic). *ICES Journal of Marine Science,* 55, 515-521.

Saborido-Rey, F., Kjesbu, O. S., 2012. *Growth and maturation dynamics*. Digital CSIC. pp. 26. http://hdl.handle.net/10261/47150. (Accessed 25 September 2014).

Saborido-Rey, F., Trippel, E., 2013. Fish reproduction and fisheries. *Fisheries Research,* 138, 1-4.

Saborido-Rey, F., Garabana, D., Cerviño, S., 2004. Age and growth of redfish (*Sebastes marinus*, *S. mentella*, and *S. fasciatus*) on the Flemish Cap (Northwest Atlantic). *ICES Journal of Marine Science,* 61, 231-242.

Saborido-Rey, F., Murua, H., Macchi, G. J., 2011. I Iberoamerican symposium on reproductive ecology, recruitment and fisheries. *Ciencias Marinas,* 37 (4B), 1-12.

Saborido-Rey, F., Murua, H. Tomkiewicz J., Lowerre-Barbieri S., 2010. Female reproductive strategies: An energetic balance between maturation, growth and egg production. p. 15-18. In: *Proceedings of the 4th Workshop on Gonadal Histology of Fishes*. Wyanski, D.M., Brown-Peterson, N.J. (Eds.). El Puerto de Santa Maria, Spain. Digital CSIC. http://hdl.handle.net/10261/24937. (Accessed 12 September 2014).

Scientific, Technical and Economic Committee for Fisheries (STECF), 2013. Review of scientific advice for 2014: Consolidated Advice on Fish Stocks of Interest to the European Union (STECF-13-27). *Publications Office of the European Union,* 575 pp.

Stephens, P.A., Boyd, I.L., Mcnamara, J.M., Houston, A.I., 2009. Capital breeding and income breeding: Their meaning, measurement, and worth. *Ecology,* 90, 2057-2067.

Tomás, J., Geffen, A. J., 2003. Morphometry and composition of aragonite and vaterite otoliths of deformed laboratory reared juvenile herring from two populations. *Journal of Fish Biology,* 63, 1-19.

Tortonese E., 1975. *Osteichthyes, (Pesci ossei). Fauna Italia, Parte seconda*. Edizioni Calderini, Bologna, 636 pp.

Trippel, E.A., 1999. Estimation of Stock Reproductive Potential: History and Challenges for Canadian Atlantic Gadoid Stock Assessments. *Journal of Northwest Atlantic Fishery Science*, 25, 61-81.

Ware, D.M., 1984. Fitness of different reproductive strategies in teleost fishes. p. 349-366. In: *Fish reproduction: strategies and tactics*. Potts, G.W., Wootton, R.J. (Eds). Academic Press, New York.

West, G., 1990. Methods of assessing ovarian development in fishes: A review. *Australian Journal of Marine and Freshwater Research,* 41, 199-222.

Winemiller, K.O., 2004. Box 4.2. Life-history strategies of fishes. p. 106-107. In: *Marine Conservation: Science, Policy, and Management*. Ray G.C., McCormick-Ray J. (Eds). Blackwell Science Ltd, USA.

Winemiller, K.O., Rose, K.A., 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences,* 49, 2196-2218.

Wright, P.J., 2013. Methodological challenges to examining the causes of variation in stock reproductive potential. *Fisheries Research,* 138, 14-22.

Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S. *et al*., 2009. Rebuilding global fisheries. *Science,* 325, 578-585.

Yamamoto, T., 1969. Sex Differentiation. p. 117-175. In: *Fish Physiology,* Vol. 3., Academic Press. New York and London.