

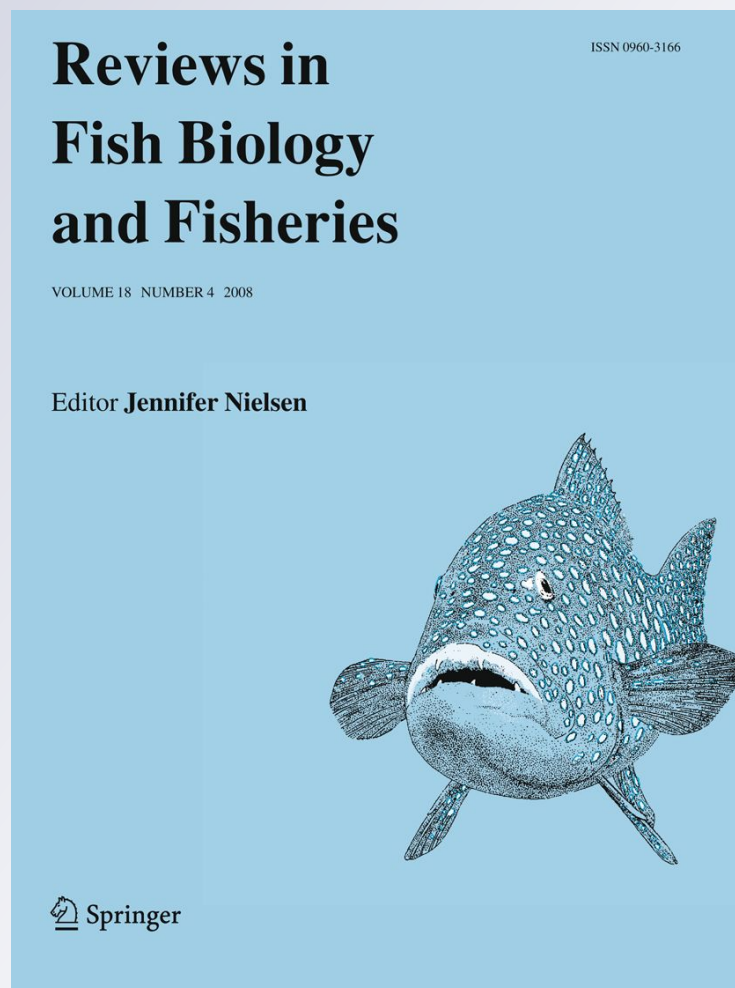
*Reproduction of the wedge sole
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captivity: spawning parameters and
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**Reviews in Fish Biology and
Fisheries**

ISSN 0960-3166
Volume 21
Number 3

Rev Fish Biol Fisheries (2011)
21:517-526
DOI 10.1007/
s11160-010-9172-8



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Reproduction of the wedge sole (*Dicologlossa cuneata* Moreau) in captivity: spawning parameters and influence of the natural temperature

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Received: 20 April 2010 / Accepted: 14 August 2010 / Published online: 27 August 2010
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Abstract In this work, the wedge sole (*Dicologlossa cuneata*) spawning under a natural thermocycle has been studied. The spawning parameters were similar to those of other flatfish in captivity, the relative fecundity being very high ($1.7 \pm 0.1 \times 10^6$ eggs kg female⁻¹ per spawning season). The percentage of floating eggs decreased with time and was directly related to egg diameter, daily relative fecundity and fertilization rate. Nevertheless, the hatching rate variations were not correlated to any other spawning parameter. The temperature range during the spawning season was very wide (11–21°C) though the largest spawns occurred between 12 and 16°C. The natural temperature cycle influenced wedge sole egg production, the winter temperature minimum indicating the onset of spawning, but the variations in the reproductive season did not appear to affect the daily egg production. Future research should focus on the photoperiod and its interaction with temperature as key factor for spawning.

Keywords Wedge sole · Spawning · Fecundity · Temperature

Introduction

Most flatfish present non-synchronic ovarian development and are batch spawners, releasing several egg batches during the spawning period (McEvoy 1984; Houghton et al. 1985; Zamarro 1991; Manning and Crim 1998; Nagler et al. 1999; Smith et al. 1999; Anguis and Cañavate 2005). Only a few flounders (*Pseudopleuronectes americanus* Walbaum; *Kareius bicoloratus* Basilewsky; and *Pseudorhombus triocellatus* Bloch & Schneider) release gametes once during the spawning season (Burton and Idler 1984; Ramanathan et al. 1990; Park 1995). Similarly, pleuronectiformes normally present a single spawning period in a year. Nevertheless, some species (*Reinhardtius hippoglossoides* Walbaum; *Tarphops oligolepis* Bleeker; and *Engyproson grandisquama* Temminck & Schlegel) are able to produce and release gametes twice in a year (Minami and Tanaka 1992; Kamisaka et al. 1999; Albert et al. 2001).

Some cultured flatfish in Europe, mainly halibut (*Hippoglossus hippoglossus* Linnaeus) and turbot (*Psetta maxima* Linnaeus), require the stripping technique since they cannot release gametes spontaneously. This may be because large fish undergo a spatial limitation in culture tanks of inadequate size,

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inhibiting the typical nuptial behaviour (Gibson 2005), and hence Bromley et al. (1986) achieved spontaneous spawns of turbot in large tanks at low stocking density. However, farmed soleids such as Senegal sole (*Solea senegalensis* Kaup), common sole (*Solea solea* Linnaeus), and Egyptian sole (*Solea aegyptiaca* Chabanaud) can release gametes spontaneously into culture tanks, though the stripping technique has been recently performed with the former (Baynes et al. 1993; Anguis and Cañavate 2005; Bonaldo et al. 2006; Chereguini et al. 2007; Rasines et al. 2009).

Although many variables trigger the commencement of spawning, the most important factors are photoperiod and temperature, since they significantly affect gonadal maturation and gamete release (Bye 1984; Lam and Munro 1987; Bromage et al. 2001). In this sense, decreases in the temperature range and timing of the photophase are the two main inductive cues for the European perch (*Perca fluviatilis* Linnaeus) reproduction (Wang et al. 2006). Clark et al. (2005) stated that water temperature plays a prominent role in the initiation, maintenance, and termination of the reproductive cycle in striped bass (*Morone saxatilis* Walbaum). Also, gonadal maturation in Senegal sole can be stimulated by lowering the water temperature during early winter (García-López et al. 2009). As a result, in many intensive fish farms, it is possible to obtain eggs year round by controlling the photoperiod and temperature.

Wedge sole (*Dicologlossa cuneata* Moreau) is a valuable market species in the gulf of Cádiz, SW Spain (Sobrino et al. 1994; Jiménez et al. 1998). The IFAPA Agua del Pino research centre (Cartaya, Huelva, Spain) has studied the rearing of this species in captivity since 2002, and currently several research projects on the biology of this flatfish are under way (Herrera et al. 2005; Herrera 2006). The reproduction of this species has been studied in nature (Jiménez et al. 1998; Vila et al. 2002; García-Isarch et al. 2006), although information on its spawning parameters in captivity are scarce. Only Herrera et al. (2008) presented general biological data of wedge sole in tanks, and therefore a thorough study of specific issues as spawning features would provide a better knowledge of the biology of this flatfish.

Thus, the present work examines wedge sole spawning in captivity, analysing spawning parameters, finding interrelations among them and studying

the influence of natural temperature cycle on egg production.

Materials and methods

Experimental design

For the establishment of the broodstock, professional fishing boats that regularly captured the species through gillnet were contracted. The specimens were caught off the coast of Huelva (SW Spain) during July 2002, November 2002 and May 2003 and were adapted to captivity according to Herrera et al. (2008).

Spawners were held in three 5,000 L rectangular tanks (4.2 m²), at 0.3–0.4 kg m⁻², in the IFAPA Agua del Pino (Huelva, Spain). The water (flow-through system) was sterilised with an UV filter (>32 MV cm⁻²) and followed natural temperatures except between July and September, when it was cooled to 21°C by means of a titanium-plate heat exchange. The daily water renewal was 200–250% and the light intensity varied from 50 to 100 lux, with a natural photoperiod (latitude 37°12'N). In all tanks, aeration was applied through two air-stones, and temperature and dissolved oxygen were measured daily.

At the end of each spawning season, all fish were sampled ($n = 103$; 75 and 57 for 2004, 2005 and 2006 respectively), determining sex by gonadal palpation (female gonads are very large and sited from the visceral cavity to near the tail) and maintaining a sex ratio of 1.5 females male⁻¹. Each specimen was identified with a passive integrated transponder (PIT) tag.

For the egg collection, 250 L egg collectors with a 450 µm net were installed in the tank drain. From 2004 to 2006, spawn parameters were registered daily: floating and non-floating eggs, fertilization and hatching rates, and egg diameters (only in 2005). Daily relative fecundity (DRF) and relative fecundity (RF) were calculated as follows: DRF = eggs/female biomass in a tank per day; RF = eggs/female biomass in a tank per spawning season. During 2006, prophylactic baths in incubation tanks were applied to each spawn for pathology prevention; for this, Ox-Aquaculture[®] (OX-CTA, Cuarte, Huesca) was used at 200 ppm for 15 min.

A sample of 70–80 floating eggs was taken from each spawn and incubated (at 19°C) in a 24-well microtiter plate (approx. 3 eggs/well) to determine fertilized eggs (24 h) and newly hatched larvae (48 h). Fertilization and hatching rates referred to floating and fertilized eggs, respectively. Egg diameter ($n = 10\text{--}15$ eggs day⁻¹) was measured with a microscope (10×) connected to a camera with a liquid crystal display and measurement-specific software (Digital Sight® DS-L1, Amstelveen, The Netherlands).

Statistical analysis

Numerical data are presented as mean ± SE (standard error of the mean). Differences between groups ($P < 0.05$) were tested with a one-way ANOVA or Student-*t* tests when normality and homoscedasticity occurred. In cases of non-normality and heteroscedasticity, Kruskal-Wallis or Mann-Whitney were used to analyse the data. The normality and homoscedasticity were tested by means of the Kolmogorov-Smirnoff and Levene tests, respectively.

For correlations, Pearson and Spearman correlation coefficients were used for parametric and non-parametric data, respectively. The Maximum Likelihood Estimation (MLE) method was applied to curve adjustments. All statistical analyses were performed through the software SPSS 13.0 for Windows.

Results

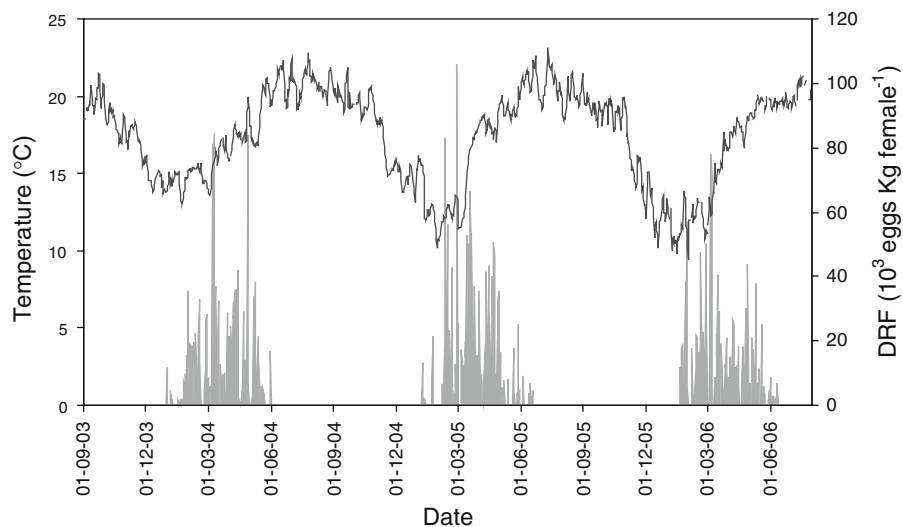
The breeders began to spawn 6 months after their arrival at the research centre. The spawning seasons started on 30 December 2003, 7 January 2005 and 20 January 2006; and finished on 31 May 2004, 17 June 2005 and 11 June 2006, respectively. The maximum values of daily relative fecundity (DRF) occurred within the first 80 days (Fig. 1) but in 2004, when it was close to the end of the reproductive season (120 days). In 2004 and 2005, the FE (percentage of floating eggs) and *F* (fertilization rate) showed a decreasing trend for the season, the DRF remaining stable. However, FE and DRF diminished and *F* augmented during 2006 (Fig. 2). Overall, all parameters were found to remain stable throughout the spawning period except for the DRF, which declined at late spawning (Fig. 2).

The spawning parameters registered for 3 years (2004–2005–2006) are shown in Table 1. The relationship between egg diameter and spawning day is presented in Fig. 3, giving a cubic equation adjustment: $\text{Diam} = 777.5 + 3.92t - 0.05t^2 + 0.0001t^3$ ($R^2 = 0.804$).

The correlations between the different spawning parameters are presented in Table 2, reflecting some significant and positive correlations with coefficients less than 0.5.

With regard to the influence of temperature on spawning parameters, it was found that egg release

Fig. 1 Water temperature (line) and daily relative fecundity (bars) between 2004 and 2006



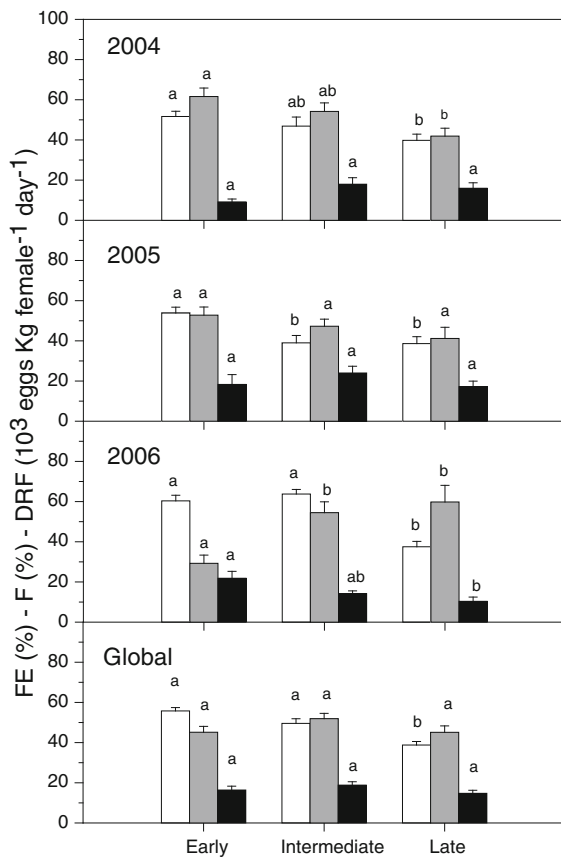


Fig. 2 Mean FE (white bars), F (grey bars) and DRF (black bars) during the spawning season each year. Spawning was divided in three stages: early (days 1–50), intermediate (51–100) and late (101–end). Bar errors are SE and same letters indicate statistically homogenous groups

began when temperatures rose just after the annual minimum values: 13, 10.2 and 10.3°C for 2004, 2005 and 2006, respectively (Fig. 1). Table 3 presents data on temperature values related to egg production. All spawns took place between 10 and 21°C, although the most abundant ones occurred in a range of (12–18°C; Fig. 4). Moreover, a weak but significant inverse correlation ($R = -0.148$) was detected between temperature and DRF. Similarly, the FE and temperature correlation was inverse and significant ($R = -0.419$) and, hence, egg diameter was also inversely related to the latter ($R = -0.636$).

DRF increased only after temperature increases (TV) for 2 days before spawn (Fig. 5). FE and F did not vary significantly in any case: increasing, decreasing or stable temperature (data not shown).

Discussion

Wedge sole spawned in less than a year of captivity, demonstrating fast adaptation, contrary to common sole, halibut, and turbot, which needed 2–3 years to reproduce effectively in tanks (Devauchelle et al. 1987, 1988; Brown et al. 2006). Spontaneous spawning is advantageous because the broodstock do not have to be handled, thereby minimizing stress to the breeders and reducing labour costs (Leu et al. 2009). The wedge sole spawning period in captivity (January–May) appears to begin later and to be shorter than that of wild conspecifics (Jiménez et al. 1998; Vila et al. 2002). Like the Pacific halibut (*Hippoglossus stenolepis* Schmidt) but unlike the Senegal sole, the wedge sole is a winter spawner, showing an unique spawning period (Dinis et al. 1999; Stickney and Liu 1999).

Table 4 presents flatfish spawning parameters described in the literature. The relative fecundity of the wedge sole was high ($1,600\text{--}1,800 \times 10^3$ eggs kg female⁻¹ per spawning season), surpassing that reported for other flatfish species in Europe (common sole, halibut and turbot) but similar to Senegal sole (Devauchelle et al. 1987, 1988; Tilseth 1990; Baynes et al. 1993; Anguis and Cañavate 2005; Brown et al. 2006). Some flatfish species (Senegal sole; Southern flounder *Paralichthys lethostigma* Jordan & Gilbert; New Zealand turbot *Colistium nudipinnis* Waite; and New Zealand brill *Colistium guntheri* Hutton) showed lower fertilization rates than in wedge sole (Smith et al. 1999; Tait and Hickman 2001; Anguis and Cañavate 2005). Nevertheless, the fertilization rates were lower than for commercially cultured flatfishes: halibut and turbot (Forés et al. 1990; Norberg et al. 1991). DRF, FE, and F increased or remained stable (no significant differences) between 2004 and 2005, this probably being due to better adaptation to captivity. This positive adaptation could be linked to a higher ingestion rate and hence a better nutritional status, which would improve the spawn quality (Brandsen et al. 2007; Bentley et al. 2009). The same was found from 2005 to 2006: DRF decreased but not significantly so, and FE, a typical indicator of egg quality, increased (Kjorsvik et al. 1990; Sargent et al. 1995). In this sense, Bromley et al. (1986) described a significant improvement in turbot egg production after 4 years in captivity, while Tveiten and Johnsen (1999) stated that larger fish

Table 1 Spawning parameters between 2004 and 2006

Year	2004	2005	2006	Global
TE (10 ³ eggs)	17,045	20,142	17,317	18,157 ± 979
RF (10 ³ eggs kg female ⁻¹ spawn season ⁻¹)	1,591	1,817	1,597	1,668 ± 74
DRF (10 ³ eggs kg female ⁻¹ day ⁻¹)	14.4 ± 1.5 ^a	19.9 ± 2 ^b	16 ± 1.5 ^{ab}	16.6 ± 1
FE (%)	45.7 ± 2.1 ^a	40.9 ± 2.2 ^a	55.4 ± 1.9 ^b	47.3 ± 1.2
F (%)	68.2 ± 2 ^a	48.4 ± 2 ^a	43.9 ± 3.4 ^a	47.4 ± 1.7
H (%)	74.4 ± 1.6 ^a	81.1 ± 2.1 ^a	53 ± 4.7 ^b	68.3 ± 2.2
Time	Dec 30–May 31 (153 days)	Jan 7–Jun 17 (162 days)	Jan 19–Jun 11 (144 days)	153 ± 5 days
Spawns	109	91	100	100 ± 5
Diameter (µm)	–	828 ± 7	–	828 ± 7

Diameter unit is µm. Data are expressed as mean ± SE except those presented as absolute value. Different letters in DRF, FE, F and H indicate significant differences (*P* < 0.05)

TE, F and H for 2004 and 2005 have been published in Herrera et al. (2008)

TE total eggs, RF relative fecundity, DRF daily relative fecundity, FE percentage of floating eggs, F fertilization rate, H hatching rate

Fig. 3 Wedge sole egg diameter for the spawning season

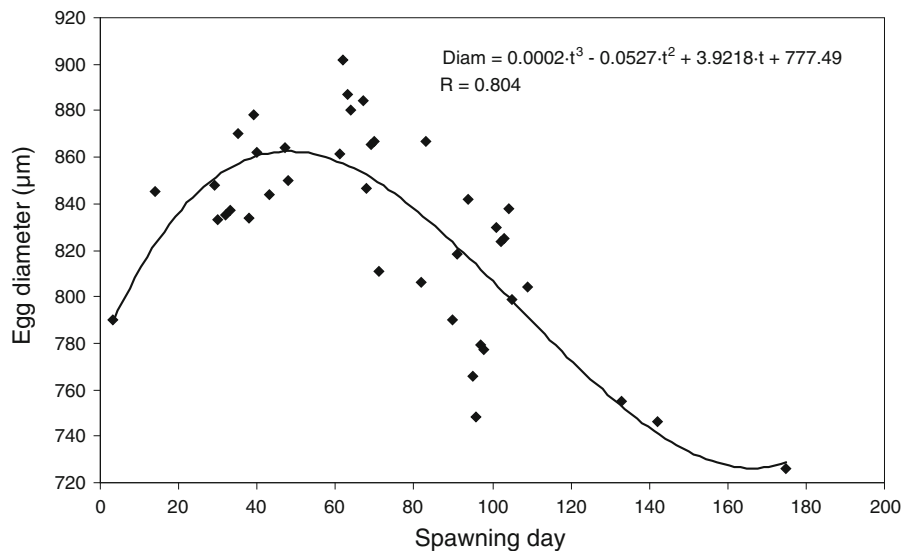


Table 2 Correlation coefficients between different spawning parameters (see Table 1 legend)

	Diameter	H	F	FE
DRF	ns	ns	ns	0.293
FE	0.450	ns	0.133	–
F	ns	ns	–	–
H	ns	–	–	–

ns no significant correlation (*P* > 0.05)

produced higher-quality eggs. However, Rideout and Morgan (2010) did not find any relationship between body size and fecundity in wild flatfishes

(American plaice *Hippoglossoides platessoides* Fabricius, yellowtail flounder *Limanda limanda* Linnaeus, and witch flounder *Glyptocephalus cynoglossus* Linnaeus).

The hatching rates found were similar to those reported for Senegal sole and other pleuronectiformes such as turbot and halibut (see Table 4). The significantly lower *H* in 2006 could be a result of the use of an inadequate egg disinfection protocol with Oxi-Aquaculture® (a product which contains hydrogen peroxide). The antibiotic application is an alternative to this method, since it is less toxic and

Table 3 Temperature data registered for this study

	2004	2005	2006	Global
Range (°C)	13–20.7	11.5–21.6	10.7–20.1	10.7–21.6
Min. <i>T</i> (°C)	13	10.2	9.4	9.4–13
Day DRFmax (date)	70 (Mar 9)	51 (Feb 26)	46 (Mar 5)	55.7 ± 7.3
<i>T</i> DRFmax (°C)	15.8	13.5	12.7	14 ± 0.9
TV DRFmax	0.2	0.3	0.1	0.20 ± 0.06

Global data are indicated as mean ± SE (except range and min. *T*)

Range minimum and maximum temperatures for spawning season, *Min. T* year lowest temperature, *Day DRFmax* spawning day (from the first spawn) and date when the highest DRF occurred, *T DRFmax* temperature of that day, *TV DRFmax* temperature variation from 2 days before

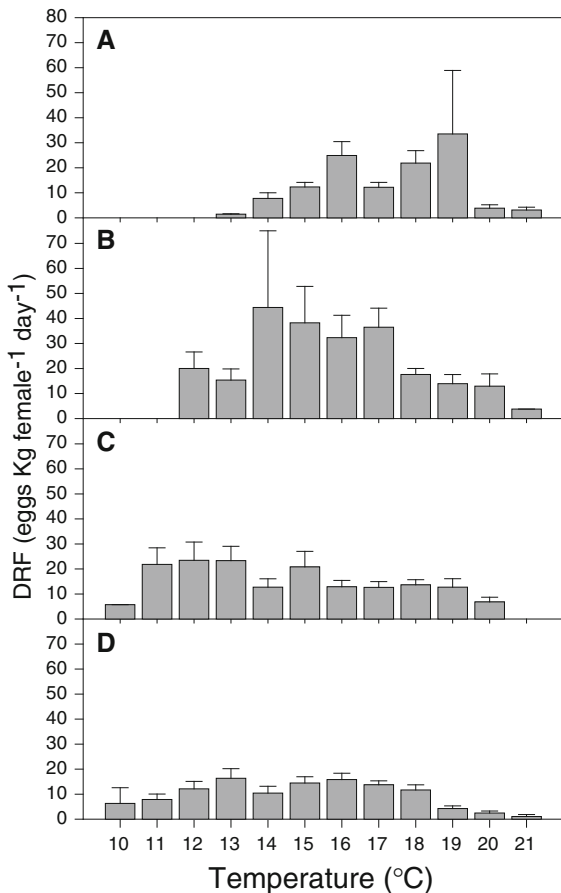


Fig. 4 Daily relative fecundity (mean + SE) depending on water temperature for the wedge sole spawning season (a 2004; b 2005; c 2006; d global)

causes lower mortality (Jones 1989; Nissling et al. 2006).

Neither *F* nor DRF could be related to the egg batch quality, since these parameters remained unchanged throughout the spawning period; however,

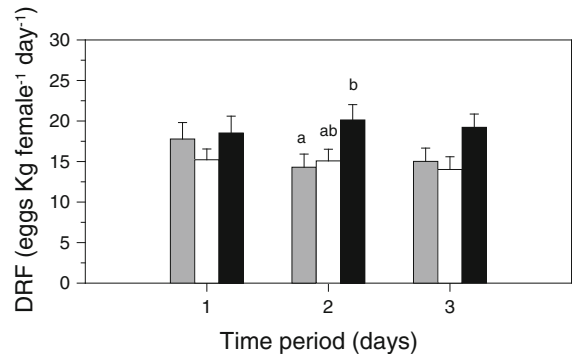


Fig. 5 DRF values (mean + SE) after temperature variations for 1, 2 or 3 days. Grey, white and black bars indicate decreasing, stable, and increasing temperatures, respectively. Same letters indicate statistically homogeneous groups

the FE decreased in parallel to the time (Fig. 2). Therefore, the fall in FE values indicates the end of the spawning season. In other adaptation trials of new pleuronectiforme species, no correlation was found between *F*, FE, and progress of the reproductive season (Hachero-Cruzado et al. 2007).

For the spawning seasons, approximately 100 spawns were collected in 153 days. As the broodstock was composed of 103, 75, and 57 females between 2004 and 2006, it appears that some or the most of females (at least for the last 2 years) released eggs more than once. This indicates that wedge sole is a batch spawner, like most flatfish species.

The wedge sole eggs measured 828 μm, being the smallest diameter of all marine fishes commercially cultured in Europe, though very close to that of the tropical flounder *Paralichthys tropicus* Ginsburg (Rosas et al. 1999; Herrera et al. 2008). The egg diameter varied during the spawning season, reaching its highest values at 60–80 spawning days (Fig. 3).

Table 4 Relative fecundity (RF), fertilization (*F*) and hatching rates (*H*) for different pleuronectiformes species reared in captivity

Species	RF (10 ⁵ /kg ♀)	<i>F</i> (%)	<i>H</i> (%)	References
<i>Psetta maxima</i>	0.8–4.3	–	10–97	Devauchelle et al. (1988)
	–	–	30–54	Jones (1989)
	–	75.4–78.9	39–40	Forés et al. (1990)
	10	–	–	Tilseth (1990)
<i>Hippoglossus hippoglossus</i>	0.08–0.2	30–100	–	Norberg et al. (1991)
	0.95–2	31–59	28–51	Mazorra et al. (2003)
	1.9–2.6	27–54.8	3.1–25.6	Brown et al. (2006)
<i>Solea solea</i>	1.4	–	60.4–100	Devauchelle et al. (1987)
	0.1–1.4	25–80	–	Baynes et al. (1993)
<i>Solea senegalensis</i>	5.1 ^a	–	12–89	Dinis (1986)
	11.6–16.5	39.8–67.6	55.4–70.9	Anguis and Cañavate (2005)
<i>Psetta maxima maeotica</i>	–	39.5	–	Hara et al. (2002)
	–	3.19	–	Basaran and Samsun (2004)
<i>Scophthalmus rhombus</i>	0.51–1.65	66.7–79	0–38.9	Hachero-Cruzado et al. (2007)
	–	1–37.5	0–46.2	Basaran et al. (2008)
<i>Paralichthys lethostigma</i>	–	32.8	–	Smith et al. (1999)
<i>Colistium nudippinis</i> and <i>C. guntheri</i>	–	<50	–	Tait and Hickman (2001)
<i>Dicologlossa cuneata</i>	15.9–18.1	46.9–52	71.7–79	Present work

^a Data from wild specimens

This pattern differs sharply from that of halibut and some soleids, where an egg size decreases over the spawning season (Baynes et al. 1993; Dinis et al. 1999; Brown et al. 2006). However, this measurement did not vary in other flatfish species (Nagler et al. 1999; Hachero-Cruzado et al. 2007).

The FE was directly related to other parameters such as egg diameter, DRF, and *F*, the former having the strongest correlation coefficient (Table 2), so higher viability spawns presented the largest eggs. These relationships could be affected by other factors since the correlation coefficients were low. In this work, no relationship between *F* and *H* was detected, though a high correlation was found in halibut ($R = 0.8$; Brown et al. 2006). According to our results, other studies are necessary to establish the main factors affecting egg viability (i.e. protein:lipid ratio in broodstock diet; egg morphology and lipid content) (Mazorra et al. 2003; Brandsen et al. 2007; Bentley et al. 2009; Hachero-Cruzado et al. 2009).

In nature, wedge sole reproduces within wide temperature ranges, varying depending on latitude: 13–20; 13.6–17.6; 14.5–18°C (Lagardère 1982; García-Isarch et al. 2003, 2006). Wider ranges have been recorded in captivity (13–20.7; 11.5–21.6;

10.7–20.1°C) and it appears that the reproductive period begins when temperature rises just after the minimum winter values (Fig. 1). In fact, in 2005 and 2006, the first spawn occurred when the temperatures increased 1°C after the winter minimum. In 2004 (a warm year), this happened at 13°C, the lowest value of the year. These results contrast to those found in the Bay of Biscay, where this species does not mature below 12°C (Lagardère 1982). Differences between latitudes of the Gulf of Cádiz and Bay of Biscay populations may explain this discrepancy.

The increase in spring temperature is a main cue for the reproduction of captive soleids. The temperature range depends on the species and latitude: common sole spawns at 8–12.5°C, while Senegal sole (southern distribution area) spawns in a broad range of higher temperatures, 13–23°C (Devauchelle et al. 1987; Baynes et al. 1993; Anguis and Cañavate 2005).

The optimum spawning temperature for Senegal sole is 16–22°C (Dinis et al. 1999; Anguis and Cañavate 2005), but the range is very short (1–2°C) for other pleuronectiformes submitted to natural conditions. However, the optimum temperature range can be changed by controlling temperature and

photoperiod; for example, relative fecundity in turbot is significantly improved when the temperature range is changed from 13–15 to 9.5–15.7°C (Devauchelle et al. 1988; Benetti 1997). According to our work, this would not be necessary for the wedge sole since the most of the spawns happened in a wide range (12–18°C), facilitating the culture procedures to obtain eggs. The maximum DRF in Senegal sole (29,600 eggs day⁻¹ kg female⁻¹) appears within 18–19°C (Anguis and Cañavate 2005). In wedge sole, the largest spawns (FRD = 78,000–1,05,000 eggs day⁻¹ kg female⁻¹) occurred between 12.1 and 15.8°C (mainly from February 26 to March 9). These data confirm the high relative fecundity of the wedge sole, being the highest within the soleids studied in Europe (Dinis 1986).

In the present work, negative correlations were found between temperature and parameters such as FE, DRF and egg diameter. These results indicate that temperatures above 20–21°C inhibit the spawning and its quality, as expected in a winter spawner. Moreover, inverse correlations between temperature and egg diameter have also been described for Senegal sole and turbot (Bromley et al. 1986; McEvoy 1984; Anguis and Cañavate 2005).

Temperature variations occurring 1 or 3 days before spawning did not seem to influence egg production, as opposed to 2-day intervals, where the DRF for increasing cases was higher than decreasing or stable temperatures (Fig. 5). In the Senegal sole, Anguis and Cañavate (2005) demonstrated that DRF during temperature increases (for 1, 2 or 3 days prior to spawning) was significantly higher than in other cases (falling or stable temperature). This finding indicates that the reproduction in Senegal sole is more temperature-dependent than in wedge sole, which had main spawns for minor temperature variations (Fig. 1). Moreover, wedge soles come from captive breeders and kept in constant water temperature (19°C) have been able to spawn (Herrera et al. 2008). According to our results, temperature influences wedge sole egg production but does not appear to be a key variable. In this way, the winter temperature minimum marks the onset of the spawning, and the variations for the reproductive season do not appear to affect the daily egg production. Therefore other variables such as photoperiod and lunar cycle could significantly affect spawning in wedge sole (Bromage et al. 2001; Oliveira et al. 2009).

In short, the present work describes, for the first time, the spawning of wedge sole in captivity. The main findings are: (1) wedge sole spawns in captivity without the use of hormones or other treatments; (2) captive wedge soles present very high fecundity; (3) the temperature range at which this species spawns is very broad; and (4) the winter minimum temperatures are the spawning cues but the variations during the reproductive season did not significantly influence egg release. Future research should focus on the photoperiod and its interaction with temperature as key factor for spawning.

Acknowledgment This work was partially funded by the project INTERREG 0251_ECOAQUA_5_E.

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