Variability in reproductive traits in the sex-changing fish, *Coris julis*, in the Mediterranean

A. ALONSO-FERNÁNDEZ1, J. ALÓS2 and M. PALMER2

1 Instituto de Investigaciones Marinas, Consejo Superior de Investigaciones Científicas, IIM-CSIC. 
C/ Eduardo Cabello 6, 36208, Vigo, Pontevedra, Spain

2 Instituto Mediterráneo de Estudios Avanzados, Consejo Superior de Investigaciones Científicas, IMEDEA (CSIC-UIB). 
C/ Miquel Marqués 21, 07190, Esporles, Illes Balears, Spain

Corresponding author: alex@iim.csic.es

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Abstract

The quantity and quality of propagules, i.e. reproductive output, play a key role in the dynamics of exploited populations, with particular implications for sex-changing fish. Here, we studied for the first time the effects of maternal traits on the reproductive output of the Mediterranean rainbow wrasse *Coris julis*, a sequential hermaphroditic fish widely distributed in temperate marine coastal regions. The quantity of the reproductive output (batch fecundity) was significantly related to maternal size, which is of special interest in a species submitted to size-selective harvesting (recreational angling). However, egg quality (egg size) was not significantly related to any maternal factor and the spawning fraction was related to a seasonal pattern only. These results should contribute to improving estimations of the annual reproductive output and the stock assessment of this species. Certain implications for management are discussed.

Keywords: Batch fecundity, egg quality, maternal effects, Sex-change, Mediterranean, *Coris julis*.

Introduction

The quantity and quality of reproductive output play a key role in understanding the population dynamics and life-history characteristics of exploited fish stocks (Hilborn & Walters, 1992; Marshall et al., 2003). Reproductive output is usually estimated by measuring fecundity (Lambert, 2008). However, estimating the number of eggs released by a female during a year is challenging or even impossible, especially in indeterminate-fecundity fish species (Hunter et al., 1989, 1992; Murua & Saborido-Rey, 2003). In such cases, estimating the spawning frequency and the number of spawning events within a spawning period (Lowerre-Barbieri et al., 2011) is crucial for a proper estimation of annual egg production (Murua et al., 2003). Besides, the quality of the reproductive output of a population refers to the egg and larval potential viability (Trippel, 1999). Therefore, both the ability of a female to produce viable eggs (Nissling et al., 1998) and the egg’s potential to produce viable fry (Kjorsvik et al., 1990) play a key role in determining the fate of harvested populations.

The quantity and quality of the reproductive output are generally affected by the characteristics of the mother (Solemdal, 1997). Therefore, discriminating the role of the quantitative and qualitative maternal effects should be considered as a correct way to estimate reproductive potential. Fish size is the most commonly reported maternal feature affecting reproduction, and both the quantity and quality of the reproductive output seem to improve in larger individuals (Birkeland & Dayton, 2005). However, the individual variability in reproductive timing is typically not considered when estimating reproductive output (Murua et al., 2003; Murua & Saborido-Rey, 2003). Spawning frequency, however, has been shown to increase with both size and age (Gianias et al., 2003; Claramunt et al., 2007; Fitzhugh et al., 2012) and is affected by other factors, such as the amount of energy available to the spawning females (Hunter & Leong, 1981; McBride et al., 2013). Therefore, maternal factors exert a key influence in determining the reproductive output at individual level and, thus, at population level (Trippel & Neil, 2004), although they can be modulated by other environmental factors, such as seasonal trends (Trippel & Neil, 2004; Murua et al., 2006; Treasurer & Ford, 2010).

Unfortunately, detailed information on reproductive output and the factors affecting output is limited in species with low interest for commercial fisheries, such as those that are only targeted by recreational fisheries (Alós et al., 2013). This is the case for the Mediterranean rainbow wrasse, *Coris julis* (Linnaeus, 1758), a labrid species widely distributed in temperate coastal areas...
C. julis, a low-value commercial fishery species, is one of the most frequently captured species in recreational fishing (Morales-Nin et al., 2005; Cardona et al., 2007; Lloret et al., 2008). C. julis is a diandric protogynous hermaphrodite with two types of coloration (Bacci & Razzauti, 1958; Bruslé, 1987): i) an initial phase displayed by all females and a variable proportion of males (Bentivegna & Rasotto, 1983); and ii) a terminal phase displayed only by males. Little is known about the reproductive biology of C. julis, and available information is limited to a number of studies focusing on the process of sex change or sexual patterning (Bacci & Razzauti, 1958; Bentivegna et al., 1985; Bruslé, 1987; Lejeune, 1987; Alonso-Fernández et al., 2011).

The outcome of the maternal effects on reproductive output are unknown in C. julis, even though they could play a major role in the case of protogynous species (Hawkins & Roberts, 2004; Fenberg & Roy, 2012). In sex-changing fish, size-dependent fishing activity preferentially targets large individuals. This bias alters the sex ratio and age structure of the population, which in turn appears to change the sex-change moment to earlier ages and render smaller females more vulnerable (Collins & McBride, 2011; Fenberg & Roy, 2012). Therefore, if the reproductive output of the females is related to the maternal size (Birkeland & Dayton, 2005), such biased harvesting pressure could decrease the population’s reproductive output (Armsworth, 2001; Alonzo & Mangel, 2004; McBride et al., 2008), which suggests special care in stock management (Brooks et al., 2008). Therefore, the main objective of this study was to determine the annual reproductive output of C. julis females and identify its major causes of variability. In addition to the likely existence of maternal effects, we also tested the possible existence of temporal variation in three specific reproductive parameters: i) batch fecundity; ii) egg quality and iii) spawning activity. This new information on reproductive characteristics may be useful for improving the estimation of biologically sound reference points.

Material and Methods

Biological sampling

C. julis individuals were collected during experimental fishing sessions along the south-western coast of Mallorca Island (north-western Mediterranean Sea; Fig. 1). The selected sites had optimal habitat characteristics for the studied species (10-20 m depth with a bottom habitat dominated by Posidonia oceanica seagrass). Individuals were captured using conventional recreational gear from February to October 2007, which fully covered the spawning season (Alonso-Fernández et al., 2011). In total, 1,038 C. julis individuals were sampled (Table 1) and measured (Total length, TL; nearest mm). The gonads were removed and weighted (nearest 0.01 g) from all specimens and fixed immediately in a 10% solution of formalin buffered with Na₂HPO₄·2H₂O (molar concentration = 0.046 M) and Na₂HPO₄·H₂O (0.029 M). Central portions of the fixed gonads were extracted, dehydrated, embedded in paraffin, sectioned at 3 μm, and stained with hematoxylin and eosin for microscopic analysis with a Leica Series RE digital microscope (Leica Microsystems, Wetzlar, Germany). Firstly, histological slides were examined to check sex. Then, for each ovary, the oocytes

Fig. 1: Map showing A) the spatial location of Mallorca Island and B) the sampling stations within the study area in the waters of Mallorca Island (NW Mediterranean).
of each slide were classified into stages of development using conventional histological criteria (West, 1990; Tyler & Sumpter, 1996).

**Batch fecundity**

Batch fecundity (the number of eggs spawned per batch) was estimated for all females with hydrated oocytes and no newly collapsed post ovulatory follicles (which indicate recent spawning) according to previous recommendations (Hunter et al., 1985). We used the gravimetric method, in which fecundity is determined as the product of gonad weight and oocyte density (number of hydrated oocytes per gram of ovarian tissue) (Murua et al., 2003). An ovarian subsample of approximately 150 mg (which comprises approximately 15% of the gonad weight) was extracted, and the hydrated oocytes were separated manually and counted applying a semiautomatic image analysis protocol (Alonso-Fernández et al., 2008).

**Egg quality**

The dry weight (mg/oocyte) of the hydrated oocytes was used as a proxy of egg quality (Kjorsvik et al., 1990; Kamler, 1992; Brooks et al., 1997). The same hydrated oocytes obtained after batch fecundity estimation were used to determine their dry weight. Dry weight was determined after drying the sample for 24 h at 110°C. The mean dry weight of a single hydrated oocyte was estimated by dividing the dry weight of the sample by the number of hydrated oocytes per sample.

**Spawning activity**

Histological indicators of spawning differ in their duration. These differences determine how they should be interpreted. Ovulation oocyte stages are extremely short-lived histological indicators and were used as the most conservative method to assess spawning time (Lowerre-Barbieri et al., 2011). For example, in spotted sea trout, ovulation can last from 6 to 14 h (Brown-Peterson, 2003). Therefore, oocyte maturation stages (germinal vesicle migration to hydration) are interpreted as markers of imminent spawning to assess the spawning fraction, i.e. the proportion of mature females spawning daily (Hunter & Macewicz, 1985; Brown-Peterson, 2003). Spawning fraction was then assessed using the proportion of actively spawning females within the total number of spawning capable females (Brown-Peterson et al., 2011). After estimating the fraction of the population spawning on a single day, the time between spawning events is simply calculated as the reciprocal of the spawning fraction (Murua & Motos, 2006). Finally, spawning frequency at population scale results from dividing the number of days in the spawning season by the spawning interval (Murua et al., 2003; Murua et al., 2006).

**Data analysis**

We used a generalised linear model (GLM) (McCullagh & Nelder, 1989; Zuur et al., 2007) to evaluate the significance of the effects of maternal factors (i.e. fish total length) and seasonal trend (i.e. sampling month) on individual reproductive output (batch fecundity, oocyte dry weight and spawning fraction). Different distributions were assumed regarding the response variables: i) Negative binomial for batch fecundity (to address over-dispersed count data); ii) Gaussian for oocyte dry weight and iii) Binomial for spawning probability. Model assumptions were evaluated based on the study of residuals patterns (Zuur et al., 2010). Stepwise backward selection was used to select the optimal model according to the Akaike information criterion (AIC) and likelihood ratio tests (Zuur et al., 2007). All statistical analyses were conducted using R software, version 3.0 (R Development Core Team, 2013).

**Results**

**Batch fecundity**

Although the spawning season of *C. julis* lasts from April to July, we restricted the statistical analysis of batch fecundity variation to May and June due to the low number of samples available for the rest of the spawn-

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**Table 1. Coris julis.** Estimates of the total length (TL) range of the Mediterranean rainbow wrasse based on samples collected from the waters of Mallorca Island (NW Mediterranean) during the course of the reproduction assessment study (2007).

<table>
<thead>
<tr>
<th>Month</th>
<th>Total individuals (n)</th>
<th>Length range (mm)</th>
<th>Females (n)</th>
<th>Length range (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>February</td>
<td>1</td>
<td>131-131</td>
<td>1</td>
<td>131-131</td>
</tr>
<tr>
<td>March</td>
<td>121</td>
<td>84-160</td>
<td>70</td>
<td>84-154</td>
</tr>
<tr>
<td>April</td>
<td>160</td>
<td>78-208</td>
<td>71</td>
<td>78-178</td>
</tr>
<tr>
<td>May</td>
<td>164</td>
<td>91-194</td>
<td>89</td>
<td>94-166</td>
</tr>
<tr>
<td>June</td>
<td>160</td>
<td>90-198</td>
<td>96</td>
<td>90-157</td>
</tr>
<tr>
<td>July</td>
<td>189</td>
<td>79-166</td>
<td>93</td>
<td>82-154</td>
</tr>
<tr>
<td>August</td>
<td>176</td>
<td>89-177</td>
<td>78</td>
<td>89-177</td>
</tr>
<tr>
<td>September</td>
<td>25</td>
<td>105-154</td>
<td>16</td>
<td>105-153</td>
</tr>
<tr>
<td>October</td>
<td>42</td>
<td>88-192</td>
<td>25</td>
<td>88-154</td>
</tr>
<tr>
<td>Total</td>
<td>1,038</td>
<td>78-208</td>
<td>539</td>
<td>78-178</td>
</tr>
</tbody>
</table>
ing period (Table 2). Mean batch fecundity (all values expressed as the mean±sd) for the entire study period, May-July, was 2,362±2,153 hydrated oocytes and the mean total length of the analyzed individuals was 119±12 mm. Mean relative batch fecundity was 78±53 hydrated oocytes/g of the total weight of the female, but batch fecundity significantly and exponentially increased with length (Table 3). In contrast, there was no significant difference between May and June (Table 3); thus, a single batch fecundity-size relationship was considered by pooling all fish regardless of the sampling date (Fig. 2, Table 3). Batch fecundity largely decline in July to 706±193 hydrated oocytes.

**Egg quality**

As for batch fecundity, we restricted egg quality variation analysis to May and June (Table 2). Mean oocyte dry weight was 0.0051±0.0010 mg/oocyte in individuals with a mean total length of 119±12 mm. The oocyte dry weight did not present any significant temporal trend (i.e. between-month differences). Similarly, regarding maternal factors, oocyte quality was not significantly related to fish size (Table 3).

**Spawning activity**

We modelled the probability that a *C. julis* female would be at the spawning stage (assuming a ~24 h dura-

### Table 2. *Coris julis*. Estimates of total length (mm), batch fecundity (nº hydrated oocytes) and egg dry weight (mg/egg) for the Mediterranean rainbow wrasse, based on sub-sampling selection for batch fecundity and egg quality estimations for the reproduction assessment study (2007).

<table>
<thead>
<tr>
<th>Month</th>
<th>number (n)</th>
<th>Length range (mean±sd)</th>
<th>Batch fecundity (mean±sd)</th>
<th>Egg dry weight (mean±sd)</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
<td>32</td>
<td>118±11</td>
<td>2,142±1,964</td>
<td>0.0053±0.0011</td>
</tr>
<tr>
<td>June</td>
<td>49</td>
<td>119±12</td>
<td>2,782±2,288</td>
<td>0.0050±0.0009</td>
</tr>
<tr>
<td>July</td>
<td>5</td>
<td>122±18</td>
<td>706±193</td>
<td>0.0050±0.0015</td>
</tr>
<tr>
<td>Total</td>
<td>86</td>
<td>119±12</td>
<td>2,362±2,153</td>
<td>0.0051±0.0010</td>
</tr>
</tbody>
</table>

**Fig. 2: Coris julis**. Fish total length-batch fecundity relationship in the waters of Palma Bay and Cabrera Archipelago National Park (NW Mediterranean) during the study.

### Table 3. *Coris julis*. Summary of parameters of the generalised linear models performed to test the relationship of maternal (total length in mm) and seasonal factors with batch-fecundity and spawning fraction. April was selected as the reference month.

<table>
<thead>
<tr>
<th>Response</th>
<th>Explanatory</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>t/Z value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Batch fecundity</td>
<td>Intercept</td>
<td>2.4667</td>
<td>0.7615</td>
<td>3.24</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Deviance explained=39.46%</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Length</td>
<td>0.0441</td>
<td>0.0064</td>
<td>6.89</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Spawning fraction</td>
<td>Intercept</td>
<td>2.1401</td>
<td>0.7475</td>
<td>2.86</td>
<td>0.0042</td>
</tr>
<tr>
<td></td>
<td>Deviance explained=8.71%</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>-0.1942</td>
<td>0.8141</td>
<td>-0.24</td>
<td>0.8115</td>
</tr>
<tr>
<td></td>
<td>June</td>
<td>0.2464</td>
<td>0.8339</td>
<td>0.30</td>
<td>0.7676</td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>-1.5737</td>
<td>0.7959</td>
<td>-1.98</td>
<td>0.0480</td>
</tr>
</tbody>
</table>
tion of the histological markers used) as a function of total fish length and seasonality (i.e. between-month differences). Female length was not significantly related to spawning probability, whereas between-month differences were significant (Table 3). The temporal pattern indicated a more or less stable spawning fraction along the spawning season but showed a significant decrease in July, the last month of the spawning season (Fig. 3). The spawning interval for each month was estimated to be 1.1 days from April to June and 1.6 days in July. For April and July it was not possible to construct a reliable batch fecundity-size relationship due to the low number of samples available. Therefore, we used a single batch fecundity-total length relationship for the complete spawning period based on statistical results (Table 3). Combining the point estimations for batch fecundity and spawning fraction, we estimated egg production per individual and month. A similar egg production rate per individual was estimated for all months, except for July, when females experienced a significant reduction of nearly 30% (Fig. 4). All this variation is due to monthly variation of the spawning fraction since batch fecundity was assumed to be constant throughout the period.

Discussion

In this study, we investigated a fundamental but frequently neglected aspect of the population dynamics of *C. julis* in the NW Mediterranean Basin. As in many other species with no or limited interest for commercial fisheries (Alonso-Fernández et al., 2011), information on the quantity and quality of the reproductive output is limited. However, *C. julis* is frequent in the creel of recreational anglers, and due to the growing interest for such fisheries in the Mediterranean, data on reproductive characteristics will play a key role in designing proper management and ensuring sustainable yield (Morgan, 2008). Here we describe, for the first time, the variability of the reproductive output of *C. julis* and the factors affecting output. We provide evidence of the existence of maternal effects (a positive exponential relationship between fish size and batch fecundity). This exponential relationship between fish size and number of eggs produced per batch should have a relevant influence on harvested populations of *C. julis* due to the strong size-selective mortality associated with this type of recreational (i.e. hook-and-line) fishing (Cerdà et al., 2010) and the expected reduction in size and age of sex-change (Collins & McBride, 2011; Fenberg & Roy, 2012). Therefore, the results obtained here can be useful for ecologists and fisheries scientists and help them to gain a better understanding of the population dynamics of this widely distributed species in the Mediterranean (Marshall et al., 2003).

Morgan (2008) demonstrated that fecundity data can be incorporated into indices of reproductive potential, which can have a great impact on estimates of reference points and recognition of stock status. Furthermore, Lambert (2008) has emphasized the importance of adding measures of fecundity to other parameters for exploited marine fish stocks, in order to improve assessment of reproductive potential. In this respect, this is the first study carried out to demonstrate the existence of a relationship between batch fecundity and fish size for *C. julis* total egg production. Our results on the number of eggs released per batch are close to those reported for other members of the Labridae family, such as *Notolabrus fucicola*, for which 75±35 hydrated eggs per gram of female have been described (Harwood & Lokman, 2006), while considerably different from others, such as *Semicossyphus pulcher*, with 38±28.5 hydrated eggs per gram of female (Loke-Smith et al., 2012). Generally, fecundity and female length are well related (Birkeland &
Dayton, 2005). However, in species with indeterminate fecundity (i.e. batch spawners), this relationship is usually estimated from batch fecundity rather than potential fecundity, which introduces an additional level of variation (between-batch variability) and tends to reduce the explanatory power of fish length in predicting fecundity (Wootton, 1990; Fitzhugh et al., 2012). This seems to be the case for C. julis, for which there is clear evidence of a positive exponential relationship between fecundity and fish size, but the predictive power of this relationship is relatively poor. Seasonal patterns in egg production have been previously reported in fish species with determinate (Trippel and Neil, 2004) an indeterminate (Macchi et al., 2004; Murua et al., 2006) fecundity strategies. These changes are generally associated with fish condition and nutritional status of females (Trippel & Neil, 2004; Murua et al., 2006). During peak spawning activity in Coris julis, May and June (Alonso-Fernández et al., 2011), no temporal changes were detected. However, batch fecundity at the end of the spawning season suffered a large decline, in agreement with other indeterminate fecundity species (Macchi et al., 2004). Despite this decreasing trend at the end of the spawning season, it is not possible to draw robust conclusions due to the low number of samples available. Increased sampling effort is required throughout the entire spawning season in order to obtain a sample size that is adequate for statistical modelling of egg production.

We refer to “egg quality” as “egg size” (expressed as oocyte dry weight) under the assumption that “bigger is better” (Birkeland & Dayton, 2005). Maternal effects on egg quality have been widely recognized in temperate fish species (Martineidottir & Steinarssson, 1998; Vallin & Nissling, 2000); however, several counter-examples have been documented (see references in Kamler, 1992). In C. julis, the maternal effects (female size) were not significant within the sampled size range. In this respect, it has been suggested that there are likely confounding factors associated with different environmental cues (temperature and/or salinity) that they could obscure the relationship between egg and fish size (Chambers, 1997). Moreover, considering the short life-span and size range of C. julis females (i.e. sex change occurs at approximately 4 years old and around 13 cm in the area studied; Alonso-Fernández et al., 2011; Linde et al., 2011), the maternal effects on egg quality are difficult to detect in comparison to species with long life-spans, such as Sebastes spp (Berkeley et al., 2004).

In addition to the estimates of batch fecundity per individual, an estimation of the annual realized fecundity in indeterminate species is needed to estimate the number of batches released within the spawning season, i.e. spawning frequency (Murua et al., 2003; Lowerre-Barbieri et al., 2011), which is estimated at population level from the fraction of females at the spawning stage at a given time (Armstrong & Withames, 2012). The spawning season of C. julis lasts approximately 4 months, when most females spawn daily or every 2 days. A proper estimate of the spawning fraction is highly dependent on correct definition of the spawning stage (Uriarte et al., 2012). Different histological spawning markers have different life-spans (i.e. are observable for more or less time after ovulation or oocyte hydration Lowerre-Barbieri et al., 2011; Armstrong & Withames, 2012). For example, in warm waters, an oocyte of Lutjanus campechanus was found to take approximately 10 h to fully hydrate (Jackson et al., 2006), and oocytes of Cynoscion nebulosus can last 6–14 h from ovulation to spawning (Brown-Peterson, 2003). In contrast, in deep sea species such as Hippoglossus hippoglossus, the complete hydration process can take 35–55 h (Finn et al., 2002). Egg size can also have an effect on timing of hydration, for instance McBride et al. (2003) reported a 30- 36-hour period for final oocyte maturation for Hemiramphus brasiliensis (2.0-3.5 mm egg diameter) in southern Florida.

Therefore, considering the temperature range of the Mediterranean Sea, C. julis oocyte size and the histological markers used, the assumption that a specific C. julis female has ovulated within 24 h seems reasonable. The high rate of females found at the spawning stage suggests that spawning events in C. julis take place often, almost every day, and that the high rate remains relatively constant throughout the spawning season. With such a high frequency of batches, our results, i.e. that the probability of being in the spawning stage does not depend on fish size, are not surprising. These results are in contrast with the general patterns observed in indeterminate fecundity species, which shows that the spawning fraction is positively size/age related (Claramunt et al., 2007; Ganias et al., 2007; Uriarte et al., 2012). However, in species that spawn every day there is a boundary effect that obscures our interpretation.

The clear effects of fish size on egg quantity (batch fecundity) should play an important role in the dynamics of an exploited population. C. julis is a sedentary species with high site fidelity and a small home range (Palmer et al., 2011), which makes this species particularly vulnerable to harvesting-related depletion at small spatial scales (Palmer et al., 2011). Therefore, spatially patchy harvest- ing pressure can directly reduce abundance and, thus, reproductive potential (i.e. the total egg production) of the stock. Secondly, due to the small mouth size of C. julis, recreational harvesting is highly size selective, with large fish being more vulnerable than smaller ones (Cerdà et al., 2010). In protogynous species, this size-selective mortality is indirectly sex selective, introducing a greater bias in operational sex ratios, i.e. males (older and larger) are more vulnerable to local depletion than females (younger and smaller) (Hamilton et al., 2007). According to the “size advantage model” (Ghiselin, 1969), the largest females and fastest growers (Linde et al., 2011) change sex in response to a modification of the social
structure of the population. Therefore, a higher probability of removing larger males could lead to a reduction of not only the total female population but, more importantly, large females. In fact, this expected response to anthropogenic harvesting has been confirmed in C. julis, and a larger and higher proportion of terminal males has been observed inside marine protected areas in the Mediterranean, where fishing activity is prohibited (Harmelin et al., 1995). Therefore, size-dependent harvesting activity can induce a “dwarfing” and “juvenescence” of females inhabiting harvested populations (Collins & McBride, 2011), which can induce a strong decrease in the reproductive output of exploited populations of protogynous hermaphrodites (Hawkins & Roberts, 2004; Hamilton et al., 2007). Populations with less fecund females will be more vulnerable to over-exploitation (Birkeland & Dayton, 2005), and effective management should incorporate some replenishment mechanism to alleviate the depletion of the number of individuals harvested and maintain sustainable density. In this sense, marine protected areas can play a role due to the limited movement of C. julis (Palmer et al., 2011).

Finally, this study deepens our understanding of the reproductive biology of C. julis and is key for developing future estimations of stock reproductive potential. Additionally, we have identified additional areas of research that will complement the findings reported here, such as i) confirming the assumption made for the duration of spawning markers and ii) completing more detailed demographic studies of other reproductive parameters in order to understand the spatio-temporal variation of reproductive output. This information should prove useful to managers, especially because the implementation of measures of spawning biomass used to estimate biological reference points. Fishery Bulletin, 106 (1), 12-23.


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