Reproductive ecology studies for sustainable fisheries management in Iberoamerica.
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Reproductive ecology as a tool for identifying stock components: the case of the blue whiting (*Micromesistius poutassou*) in the Northeast Atlantic

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Summary: Accurate fish stock evaluation requires proper identification of population structure, for which reproductive ecology studies are essential. This study examines blue whiting (*Micromesistius poutassou*), a widely distributed mesopelagic gadoid managed as a single stock in the Northeast Atlantic, despite ongoing debate about the existence of distinct spawning components. To investigate potential differentiation, we compared reproductive parameters between two regions: the Porcupine area in southwest Ireland (ICES division 27.7.c,k,h,j) and the Peninsula area off the northern Iberian Peninsula (ICES division 27.8.c-9.a.N). Using biological data from 2018 surveys of the Spanish Institute of Oceanography and commercial vessels, we analysed somatic attributes (length, weight and condition) and assessed the species' reproductive strategy. We also examined interannual variation in Peninsular females' somatic features, total and batch fecundity, and geographic variation in fecundity and spawning frequency in February–March. Blue whiting was confirmed as a capital breeder, spawning from February to April. Iberian individuals exhibited smaller sizes and lower condition but higher fecundity (mean potential and batch fecundity: 46.817 vs. 12.223 oocytes, 16.808 vs. 6.112 hydrated oocytes), releasing three batches per season at 11-day intervals, compared with one every ~15 days at Porcupine. These findings suggest a distinct southern component, reinforcing the relevance of reproductive studies for stock assessment and management.

Keywords: fecundity; bioenergetic strategy; population structure; fisheries assessment; reproductive ecology; blue whiting; spawning components; parental condition.

La ecología reproductiva como herramienta para identificar c omponentes d e s tock: e l c aso d e l a bacaladilla (*Micromesistius poutassou*) en el Atlantico Noreste

Resumen: La correcta evaluación de los stocks pesqueros requiere identificar de manera precisa su estructura poblacional, siendo los estudios de ecología reproductiva esenciales para ello. Este estudio analiza la bacaladilla (*Micromesistius poutassou*), un gádido mesopelágico ampliamente distribuido y considerado como un único stock en el Atlántico Noreste (NEA), pese al debate existente sobre posibles componentes de puesta diferenciados. Para investigar su potencial diferenciación, comparamos los parámetros reproductivos entre dos regiones: el área de Porcupine, en el suroeste de Irlanda (ICES division 27.7.c,k,h,j), y el norte de la Península Ibérica (ICES division 27.8.c-9.a.N). A partir de datos biológicos de 2018, procedentes de campañas del IEO y flotas comerciales, se analizaron los atributos somáticos (talla, peso y condición) y se determinó la estrategia reproductiva de la especie. Además, se examinó la variación interanual de la fecundidad y la frecuencia de desove durante los meses de febrero y marzo. Los resultados confirman que la bacaladilla es un *capital breeder*, con un periodo de desove que se extiende de febrero a abril. Los individuos de la Península mostraron menor talla y condición, pero mayor fecundidad (media de fecundidad potencial y parcial: 46.817 vs. 12.223 ovocitos, 16.808 vs. 6.112 ovocitos hidratados), liberando tres lotes en cada estación reproductiva con intervalos de 11 días, frente a un lote cada ~15 días de la zona de Porcupine. Estos resultados sugieren la existencia de un componente de puesta distintivo en el sur, resaltando la relevancia de los estudios de reproducción para la evaluación y gestión de los stocks pesqueros.

Palabras clave: fecundidad; estrategia bioenergética; estructura poblacional; asesoramiento pesquero; ecología reproductiva; bacaladilla; componentes de puesta; condición parental.

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INTRODUCTION

Numerous definitions of the stock concept exist in fisheries literature (McBride 2014), all centred on the interaction between a fish species and its management. Here, we define a fish stock as a population unit, or set of subunits, with similar biological and ecological characteristics that is subjected to exploitation.

The essential requirement for the effective management of fish stocks and for preventing overexploitation is to correctly identify the population unit and its potential subcomponents (Gonçalves et al. 2017). A diverse range of approaches is used for this purpose, including catch data, tagging, reproductive and ecological traits, otolith microchemistry and morphology, meristics and morphometric analysis, parasite studies, genetics, protein variation and mitochondrial DNA analysis (ICES 2024). The most effective strategy should involve a holistic integration of various techniques, with the utility of each evaluated individually.

In fisheries stock assessment, the primary reference unit is the reproductive stock, typically quantified as the spawning stock biomass (Murua et al. 2003). Until the 1990s, stock assessment models assumed that recruitment (R) was directly proportional to spawning stock biomass, with adult abundance as the main driver of population renewal. In this context, Trippel (1999) defines the reproductive potential of a fish stock as its ability to produce viable offspring that successfully recruit into the population or fisheries. However, subsequent research has shown that recruitment is influenced by a complex interplay of factors and processes, including environmental conditions, parental traits and the reproductive ecology of the species, all of which shape offspring characteristics and survival (Lowerre-Barbieri et al. 2017). These interactions emphasize the need to move beyond simple biomass-based models in order to fully understand stock-recruitment dynamics. In this regard, Lowerre-Barbieri et al. (2017) updated the theoretical framework and introduced the concept of reproductive resilience, defined as the capacity of a population to maintain the reproductive success necessary for long-term population stability despite disturbances. Reproductive resilience extends beyond reproductive processes alone, encompassing all factors that contribute to offspring survival until reproductive age. Consequently, recruitment is determined not only by spawning stock biomass but also by the overall quality and condition of the stock. Since recruitment is a stock-specific process influenced by individual attributes, population characteristics and dynamics, as well as external factors, differences between stocks or their components are expected to result in variations in parental traits and reproductive capacity (Caddy and Cochrane 2001). Recognizing and understanding these differences (e.g. differences in spawning time, location, reproductive strategy, fecundity and maternal condition) is particularly important in spatially structured populations (Murua et al. 2003).

In the North Atlantic, most studied marine fish species of commercial importance are iteroparous (spawn more than once during their lives), are capital breeders (energy for reproduction comes from the energy stored in the tissues before the spawning season), exhibit determinate fecundity (fixed before the onset of spawning), are batch spawners (releasing eggs in several events over the spawning season) and show group-synchronous oocyte development (two populations of oocytes can be recognized at any given time in the ovary) (Domínguez-Petit et al. 2017). While broadly consistent, these reproductive patterns can exhibit regional variation within a single stock. Reproductive ecology provides a focused and effective framework for identifying spawning subunits and examining intra-stock variability (Lowerre-Barbieri et al. 2017). To demonstrate this approach, the present work uses blue whiting (*Micromesistius poutassou* Risso, 1827) in the Northeast Atlantic (NEA) as a case study to investigate the potential existence of one or two distinct stock units in the region. By analysing reproductive potential and maternal attributes (Hatún et al. 2009, Payne et al. 2012), this analysis provides updated insights into the population structure of blue whiting and illustrates the utility of reproductive ecology in identifying stock components.

The case of the blue whiting

Blue whiting is a small pelagic gadoid widely distributed in the North Atlantic as well as in the Mediterranean, although the populations are considered to be isolated from one another. In the NEA, the species ranges from the Barents Sea in the north to the Strait of Gibraltar in the south, extending westward to the Irminger Sea (Payne et al. 2012), inhabiting depths of 300 to 600 m. Adults reach maturity between 2 and 7 years of age, with an estimated L_{50} ranging from 15 to 20 cm (ICES 2024). During winter, adult fish migrate to the shelf edge and banks west of the British Isles, where spawning takes place between March and April. By late spring and summer, they move to feeding areas in the Norwegian Sea and nearby waters, returning annually to the same spawning grounds (Hatún et al. 2009, Heino et al. 2008) (Fig. 1). The largest spawning concentrations occur on the Rockall Bank Plateau, extending to the Porcupine Bank during years of particularly high biomass (Pointin and Payne 2014).

Blue whiting fisheries are among the largest in the North Atlantic and have been extensively exploited by European nations, particularly since the late 1990s, with the catch primarily used for feed production (Trenkel et al. 2015). In the NEA and adjacent waters (ICES subareas 1-9, 12 and 14), 16 national fleets are involved in the fishery under a long-term management strategy coordinated by the main catch contributors, Norway, the EU, the Faroe Islands, Iceland and the UK, who operate within the framework of the Northeast Atlantic Fisheries Commission (NEAFC) (ICES 2024). The bulk of the catch is taken by large pelagic trawlers, with most fishing activity occurring in the first quarter of the year and peaking in March-April, when fleets target spawning aggregations. These catches

are concentrated west of the British Isles, on the Rockall and Hatton Banks and around the Faroe Islands. In the following quarters, fishing shifts further north to the Norwegian Sea, Icelandic waters and the North Sea, coinciding with the species' feeding grounds (NEAFC 2024).

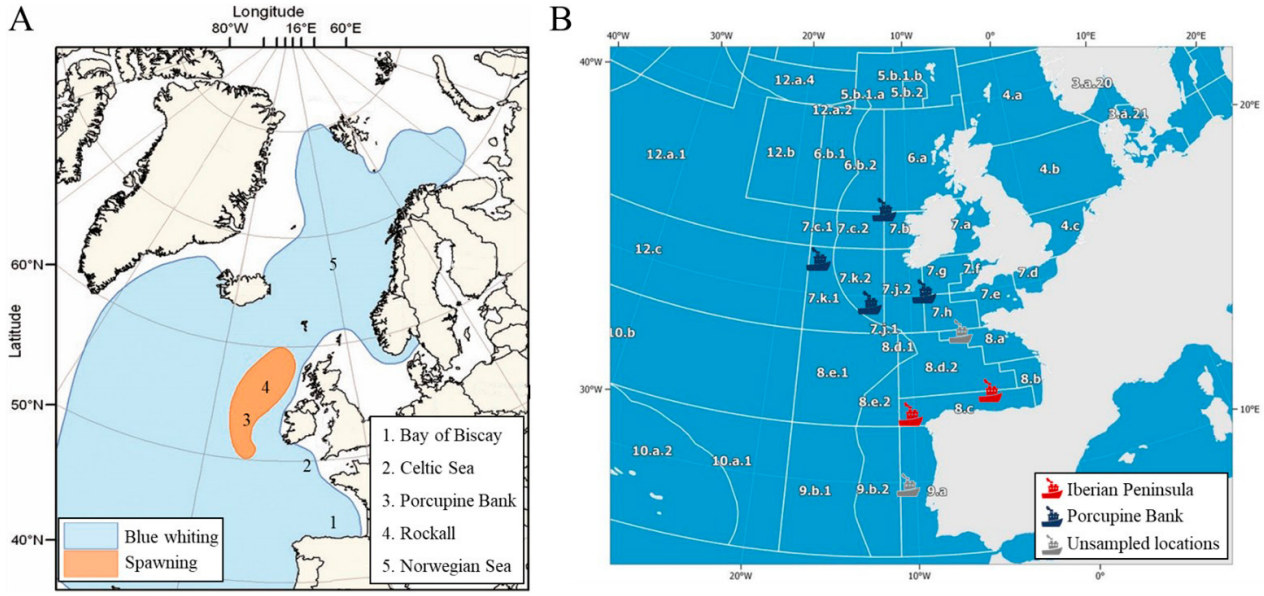

Fig. 1. – A, distribution of the blue whiting in the Northeast Atlantic. Source: modified from NEAFC 2024. B, boundaries of the Northeast Atlantic (Major Fishing Area 27), showing ICES subareas 27.4, 27.5, 27.6, 27.7, 27.8 and 27.9. Symbols indicate sampling sites. Source: modified from ICES 2022.

Although the blue whiting is currently not listed as at risk (ICES 2024), the latest ICES advice forecasts a decline in spawning stock biomass due to elevated fishing mortality and potentially underestimated recruitment, probably because of incomplete survey coverage and fisheries-dependent bias in fleet behaviour (influenced by factors such as TAC/quota allocations, profitability, market demand, and access restrictions), which together prevent the full representation of the biomass distribution (NEAFC 2024). Additionally, despite its significant economic value, updated reproductive information for this species is limited (Heino et al. 2008). Since 1993, it has been managed as a single stock ranging from the Gulf of Cadiz to the Norwegian Sea, but a 2009 review by the Stock Identification Methods Working Group recommended a precautionary delineation into two main stocks (ICES 2024). Furthermore, there is great controversy over whether the NEA population comprises a single stock with two spawning subpopulations (Mahe et al. 2016) or two completely independent stocks, with their boundary established north of the Porcupine Bank (Was et al. 2008). The division line seems to vary between years, influenced by environmental factors such as salinity, currents, food availability and population abundance (Pointin and Payne 2014). In this structure, the subpolar gyre plays a key role in determining the northward or southward drift of larvae (Heino et al. 2008, Hatún et al. 2009, Payne et al. 2012). While the largest specimens are found in the northern part of its distribution (reaching as much as 50 cm), studies carried out in the north of Spain and Portugal (Gonçalves et al. 2017) reveal active spawning on the Atlantic Iberian coast, although spawning individuals are usually below 35 cm in length, and no further studies on offspring viability or contribution to the recruitment have been delivered. Moreover, a notable gap in information exists regarding the distribution of the species between the Porcupine Bank and the Cantabrian Sea (ICES 2024). Therefore, to address the issue of blue whiting population structure in the NEA, this study compares the reproductive parameters of individuals from southeast Ireland (ICES division 27.7.c, k, h, j) and the north of the Iberian Peninsula (ICES division 27.8.c-9.a.N), to determine whether one or two spawning components exist.

MATERIALS AND METHODS

Sampling

Biological data were collected from oceanographic surveys (PELACUS, IBWSS-ES, DEMERSALES, and PORCUPINE) and commercial landings sampled by the Spanish Institute of Oceanography (IEO, CSIC) within the European Fisheries Monitoring Programme. All individuals were caught in 2018 in the NEA, specifically in the areas of southeast Ireland (ICES division 27.7.c, k, h, j) and north of the Iberian Peninsula (ICES division 27.8.c-9.a.N) (Fig. 1) For clarity, we will refer to the former as the "Porcupine area" and the latter as the "Peninsula area" throughout this article. The PELACUS and IBWSS-ES surveys were conducted in spring (March and April), target-

ing the spawning stock using acoustic methods coupled with pelagic mid-water trawls (63.5/51) with net lengths of 50 or 100 m, while the DEMERSALES and PORCUPINE surveys were carried out in autumn (September and October), obtaining juvenile (sexually immature) individuals and employing bottom trawling with the sweep method. The PELACUS and DEMERSALES surveys covered the northern and northwestern waters of the Iberian Peninsula, while the IBWSS-ES and PORCUPINE surveys covered the southeastern waters of Ireland. Commercial samples were collected all year round along the northern and northwestern shelf of the Iberian Peninsula, primarily using bottom trawlers.

A total of 2781 individuals were sampled, for which length (to 1 mm), total weight (to 1 g), gutted weight (to 1 g), sex (male, female or indefinite) were recorded, as well as the macroscopic ovary maturity stage. From the total of specimens sampled, 582 ovaries were collected and fixed in a 4% buffered formaldehyde solution for microscopic maturity and fecundity studies. Histological processing of the gonads was carried out at the IEO's laboratories. Transversal slices from the central area of each ovary were embedded in paraffin, cut into 3 µm slices and stained with haematoxylin and eosin.

Microscopic maturity staging

Microscopic maturity staging was based on the scale of Brown-Peterson et al. (2011), relying on the fish reproductive cycle and considering the characteristics of oocytes and ovarian structures. The oocyte development stages considered in this study were primary growth, cortical alveoli, vitellogenic and hydrated oocytes. Additionally, other ovarian structures considered for maturity classification included post-ovulatory follicles (POFs), atresia and coalescent oocytes (Murua et al. 2003, Brown-Peterson et al. 2011) (Fig. 2). All ovarian sections were examined with a Leica DM4000B light microscope with a Leica DFC420 camera incorporated and the LAS V3.1 software (Leica 2008). Microscopic gonadal grading is considered to provide higher precision and confidence (i.e. higher reliability) in the assessment of reproductive status (Murua et al. 2003).

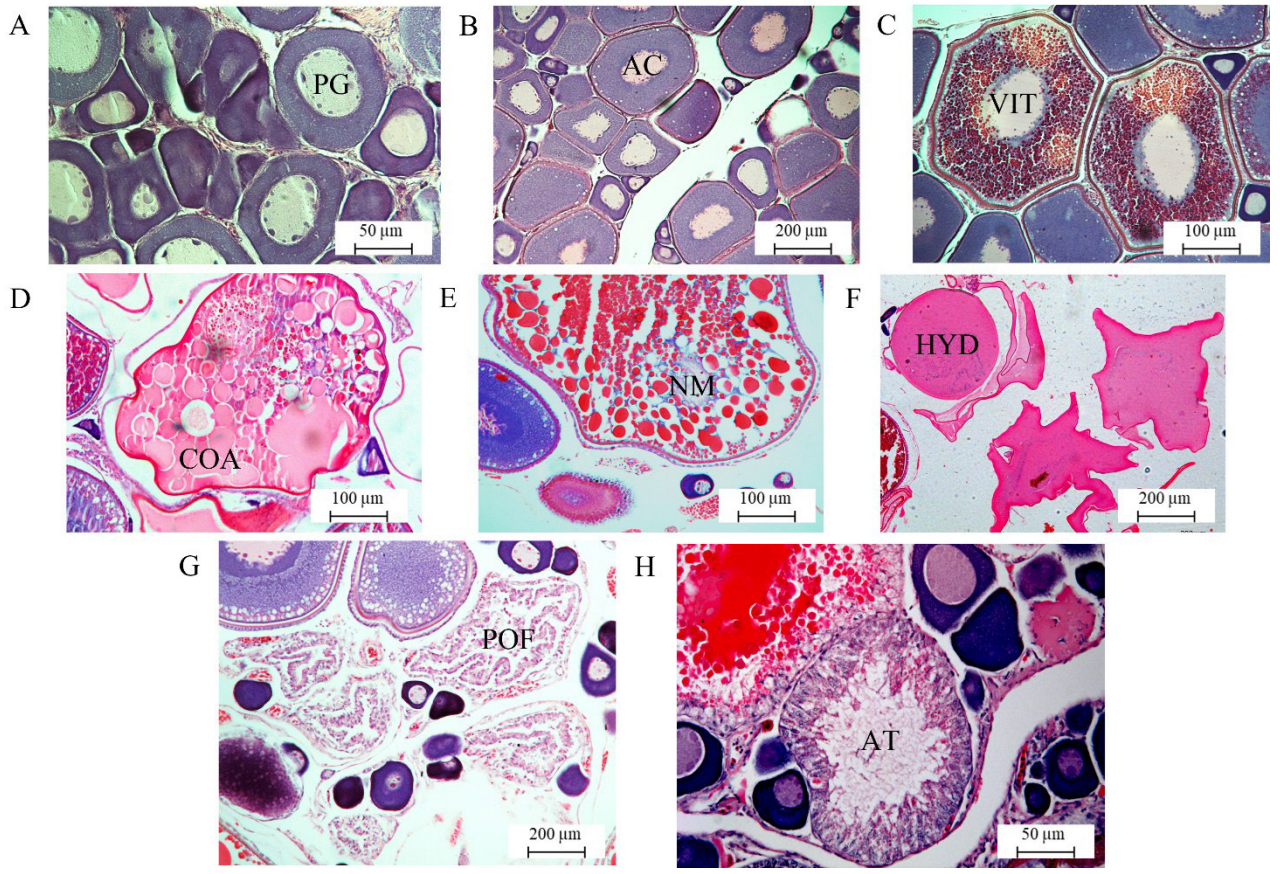

Fig. 2. – Oocyte development stages during the reproductive cycle of blue whiting. A, primary growth (PG); B, cortical alveoli (AC); C, vitellogenesis (VIT); D, coalescence (COA); E, migratory nucleus (NM); F, hydrated oocytes (HYD); G, post-ovulatory follicles (POF); H, atresia (AT). Observed under a Leica Microscope with a 40´ objective. Reference bar: 50 µm in A and H, 100 µm in C, D and E, and 200 µm in B, F and G.

Physiological condition indices

To define females' physiological condition and test the existence of maternal effects, the gonadosomatic index (GSI), hepatosomatic index (HSI), and Le Cren's relative condition factor (K´) were calculated using the following equations (Murua et al. 2003):

$$GSI = \frac{gonad\ weight\ (g)}{gutted\ weight\ (g)} \times 100$$

$$HSI = \frac{liver\ weight\ (g)}{gutted\ weight\ (g)} \times 100$$

$$K = \frac{gutted\ weight\ (g)}{calculated\ weight\ (g)} \times 100$$

These indices were also used to characterize the reproductive bioenergetics strategy of blue whiting, serving as proxies of energy allocation.

Fecundity

Fecundity analysis was based on the histological readings of 60 ovaries selected for the presence of mature (late vitellogenic or hydrated) oocytes with no signs of recent spawning, such as POFs. Of these, 24 ovaries were chosen for fecundity estimations following the criteria described by Murua et al. 2003. Potential fecundity (number of mature oocytes in the ovary) was estimated in individuals with mature oocytes and no signs of recent spawning (POFs), while batch fecundity (number of hydrated oocytes in the ovary) required the additional absence of residual hydrated oocytes (Murua et al. 2003). Fecundity was calculated using the gravimetric method, which links weight and ovary density (number of oocytes per gram of ovary) from a series of subsamples of known weight (Ganias et al. 2010) using the following equation:

$$F = \frac{gonad\ weight\ (mg)\ \times\ subsample\ oocyte\ count}{subsample\ weight\ (mg)}$$

Spawning frequency

Spawning frequency was estimated as the ratio between potential fecundity (total number of mature oocytes) and batch fecundity (number of oocytes released per spawning event). Given that the main spawning period typically lasts around one month, we assumed a reproductive season duration of 30 days. Thus, the interval between spawning events (days per batch) was calculated by dividing this ratio by 30, yielding an estimate of the average number of spawning events per female during the spawning season (Pájaro and Macchi 2001).

Oocyte analysis

To study the oocyte distribution in the ovary, three subsamples (0.05-0.1 g) were taken from the anterior (A), central (C), and posterior (P) parts of the lobules of each gonad. The oocytes were separated into size classes using different meshes (600, 300, and 150 μm width). Observation and photography were carried out using a Leica M165C stereomicroscope with a Leica DMC4500 camera and the LAS X program (Leica 2008). The number and diameter of the oocytes were estimated using the ImageJ analysis program. No significant differences were found between parts of the ovary, so a mean of the three subsample values (A, C, and P) was used for every female.

Statistical analysis

Statistical analysis was conducted in R and RStudio version 4.3.3 (R Core Team 2023). Preliminary data visualization and plotting were performed using the ggplot2 package. Descriptive statistics were conducted using the *describe* function from the psych package. A significance level of p-<0.05 was applied for all tests.

The population analysis (length-weight relationship and maturity ogive) was carried out on the complete dataset. The length-weight relationship was modelled using the *lm* function from the R *stats* package (R Core Team 2023). The Akaike information criterion (AIC) was used to select the model with the best combination of variables, based

on the lowest AIC value. Given the volume of data obtained for each site and the spawning season, the temporal analysis focused on mature females from the Iberian Peninsula, while the geographic analysis was conducted for spawning females from both sites during February and March. To analyse monthly and geographic variation of continuous variables (length, weight, condition indices, fecundity and oocyte diameter), we first tested for normality and homoscedasticity using the Shapiro-Wilk test (from the *stats* package) and the Levene test (from the *cars* package), respectively. When these assumptions were not met, the Kruskal-Wallis nonparametric test [the *kruskal.test* function was applied, followed by the Wilcoxon post hoc test (*pairwise.wilcox.test* function (R Core Team 2023)]. To analyse monthly and geographic variation in the categorical variable (microscopic maturity), Fisher's exact test was applied (*fisher.test* function (R Core Team 2023)). The last three functions can be found in the R *stats* package.

RESULTS

Population features

In the Peninsula area the length of the sampled specimens ranged between 13.7 and 39.5 cm (mean=23.55 cm) and total weight between 18.36 and 369 g (mean=110.01 g), while in the Porcupine area length ranged between 19.9 and 34 cm (mean=27.5 cm) and total weight between 44.4 and 173.3 g (mean=97.02 g) (Table 1). The length-weight relationship differed between sites (p=0.003, R^2=0.851), with both fitting a potential curve. Positive allometry was observed only in the Peninsula area (Peninsula a=0.0024, b=3.2908; Porcupine a=0.0111, b=2.7315) (Fig. 3A). Despite the broader size range in the Peninsula area (13.7–39.5 cm), individuals from this site exhibited higher weights for the same length as those from the Porcupine area in the overlapping size range (19.9–34 cm). Size frequency in February and March showed that only larger individuals were represented in the Porcupine area (Fig. 3B).

Table 1. – Descriptive statistics of the somatic variables analysed in each study area. N, number of sampled specimens; sd, standard deviation; se, standard error; K´, Le Cren's relative condition factor; GSI, gonadosomatic index; HSI, hepatosomatic index.

Peninsula							
Variable	n	mean	sd	median	minimum	maximum	se
Length (cm)	2815	23.5	4.5	24.6	13.7	39.5	0.1
Weight (g)	1654	110	37.2	104.1	18.4	369	0.9
K´	1654	1.02	0.13	1.03	0.69	1.46	0
GSI	894	1.31	1.71	0.47	0.002	11.8	0.06
HSI	828	4.11	2.6	3.62	0.02	15.24	0.09
Porcupine							
Variable	n	mean	sd	median	minimum	maximum	se
Length (cm)	52	27.5	2.6	27.5	19.9	34	0.4
Weight (g)	51	97	27.6	92.8	44.4	173.3	3.9
K´	51	1	0.03	1	0.89	1.14	0.01
GSI	48	1.86	1.6	1.05	0.37	6.45	0.23
HSI	42	3.28	2.19	2.66	0.54	10.07	0.34

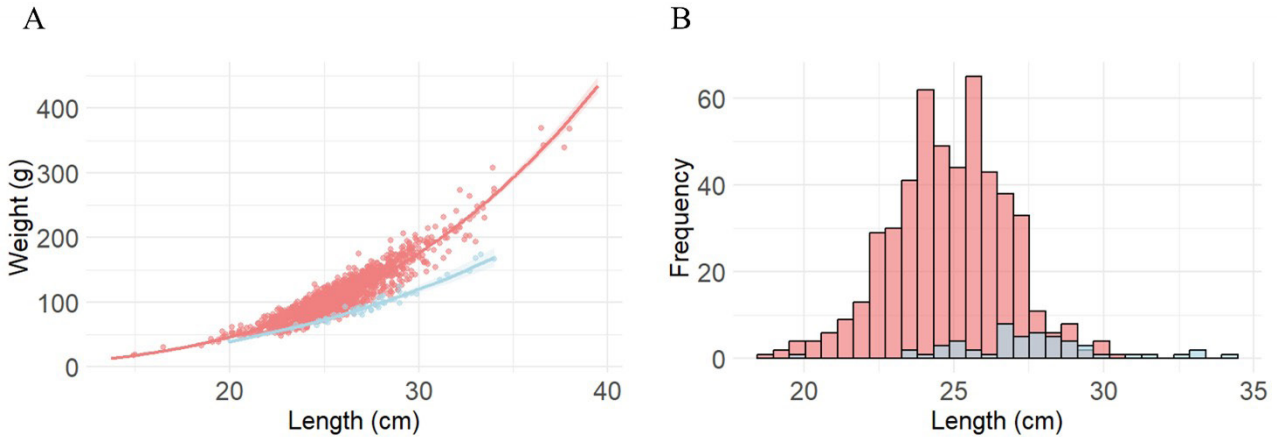

Fig. 3. –Length-weight relationship for the entire sampling period (A) and length-frequency for spawning peak (February and March) exclusively (B). Lines, modelled relationship; shaded area, 95% confidence interval; dots, observed data. Red, Iberian Peninsula; blue, Porcupine area.

Intra-annual variability

Monthly trends in length and weight followed similar patterns throughout the study period, gradually increasing from February (means of 25.45 cm and 97.1 g, respectively) to December (means of 27.17 cm and 135.69 g, respectively). Significant differences were observed between certain months (Fig. 4A, B) (p<0.001), particularly February, March and April, and the remaining months of the year. A noticeable peak was observed in July (means of 29.09 cm and 172.29 g for length and weight).

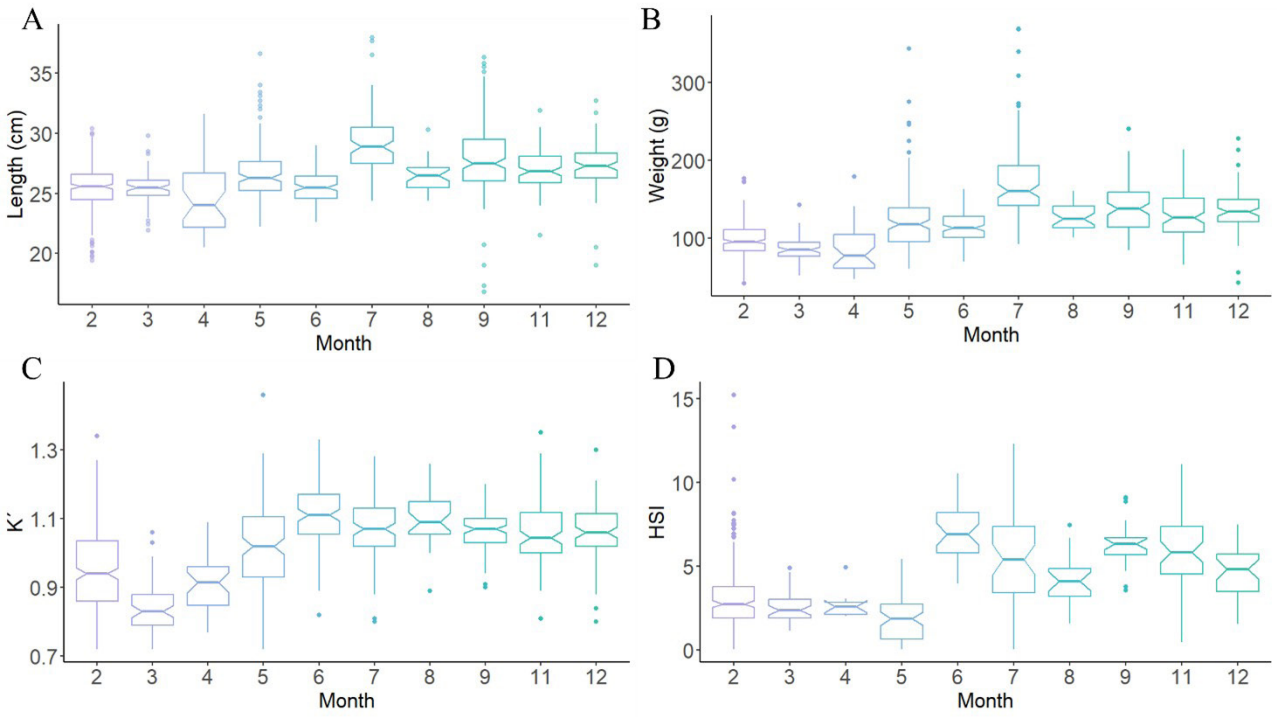

Fig. 4. – Boxplot of the monthly variation of length (cm) (A), weight (g) (B), condition index (K´) (C), and hepatosomatic index (HSI) (D) for mature females from the Iberian Peninsula. Numbers on the x-axis correspond to the months of the year. Horizontal line inside the box, median; box, interquartile range (IQR=Q1–Q3); fork, confidence interval of the median; vertical lines ±1.5*IQR; dots, outliers. October data were excluded due to missing values in most variables.

Condition indices exhibited a clear seasonal pattern (p<0.001). K´ ranged from 0.72 to 1.46 (mean=1.01) (Table 2), showing low values from February (mean=0.95) to March (mean=0.84), after which it recovered and remained

stable for the rest of the year (Fig. 4C). HSI varied between 0.02 and 15.24 (mean=3.9) (Table 2) and its values were low during the first part of the year (from February to May, with means between 2.71 and 3.17), increasing in June (mean =7) and fluctuating around a mean of 5.66 during the remaining months (Fig. 4D). GSI ranged from almost 0 to 11.67 (mean=1.54) (Table 2). Maximum values were recorded in February (mean=3.07), with a 93.1% decrease in May (mean=0.21). Afterward, they remained constant until the end of the year, when a slight increase was observed in December (mean=0.65) (Fig. 5).

Table 2. – Descriptive statistics of the somatic and reproductive variables analysed for mature females from the Peninsula and Porcupine areas. n, number of sampled specimens; sd, standard deviation; se, standard error; K´, Le Cren's relative condition factor; GSI, gonadosomatic index; HSI, hepatosomatic index; HYD diameter, diameter (µm) of hydrated oocytes.

Peninsula							
Variable	n	mean	sd	median	minimum	maximum	se
Length (cm)	1149	26.7	2.7	26.5	16.8	38	0.1
Weight (g)	1028	119.4	39.4	113.6	42.3	369	1.2
K´	1028	1.01	0.12	1.03	0.72	1.46	0
GSI	623	1.54	1.82	0.61	0.002	11.67	0.07
HSI	551	3.9	2.42	3.27	0.02	15.24	0.1
Potential fecundity	41	47099	18311	48592	13298	72615	2860
Batch fecundity	18	16779	11134	13694	2792	36041	2624
HYD diameter	18	567.9	60.4	550.7	488.8	714	14.2
Porcupine							
Variable	n	mean	sd	median	minimum	maximum	se
Length (cm)	52	27.50	2.64	27.50	19.90	34.00	0.4
Weight (g)	51	97.02	27.56	92.80	44.40	173.30	3.9
K´	51	1.00	0.06	1.00	0.89	1.14	0.01
GSI	48	1.86	1.60	1.05	0.37	6.45	0.23
HSI	42	3.28	2.19	2.66	0.54	10.07	0.34
Potential fecundity	15	12223	9221	9159	2567	33501	2381
Batch fecundity	6	6112	5728	3998	1152	16169	2339
HYD diameter	6	740.78	216.15	678.04	513.73	1068.68	88.24

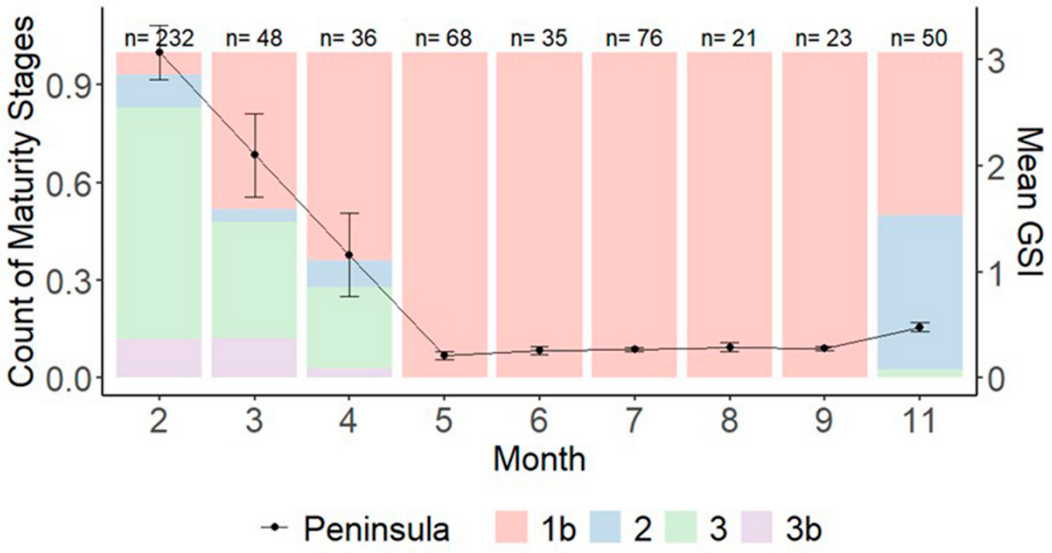

Fig. 5. –Monthly prevalence of microscopic maturity stages (bars) and mean ± se of the gonadosomatic index (GSI) (whisker and line plot) values for mature females from the Iberian Peninsula. n=number of observations for the GSI. Microscopic scale modified from Brown-Peterson et al. 2011 (1b, inactive; 2, developing; 3, spawning-capable; 3b, active spawning). October and December data were excluded due to missing values.

The prevalence of the different maturity stages in females varied throughout the year (p<0.001). Most females were in spawning-capable or actively spawning stages in February (71% and 12%, respectively). Spawning activity continued in March and April (48% and 27.7% of the ovaries were in stages 3 and 3b, respectively), although the prevalence of inactive specimens increased notably (48% in March and 64% in April). Between May and September, all sampled females were in the inactive stage (1b). Afterward, the females begin to develop their ovaries for the next spawning season, with 41% of females in the developing stage by November (Fig. 5).

Potential fecundity varied between 13298 and 72615 oocytes per female (mean=47099) (Table 2). It decreased significantly from February (mean=50704 oocytes, n=36) to March (mean=20821 oocytes, n=4), and in April it rose to a mean of 41284 oocytes (n=3) (Fig. 6A) (p= 0.012). Batch fecundity ranged between 2792 and 36041 hydrated oocytes per female (mean=16779) (Table 2). Although it decreased from February (mean=18928 hydrated oocytes, n=14) to March (mean=6914 hydrated oocytes, n =3), and only one hydrated female was found in April (mean=16287, n=1); the difference was not statistically significant (p=0.227) (Fig. 6B).

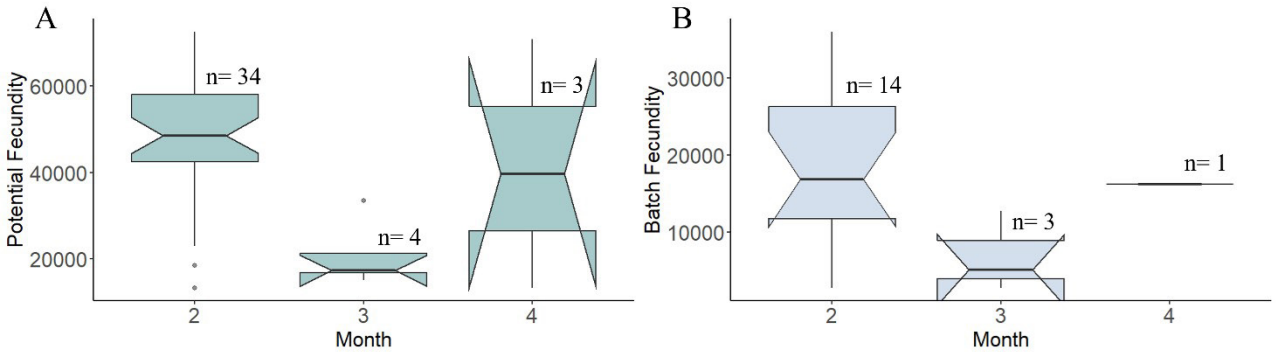

Fig. 6. – Boxplot of the monthly variation of potential (A) and batch (B) fecundity of females from the Iberian Peninsula. Numbers on the x-axis correspond to the months of the year. Horizontal line inside the box, median; box, interquartile range (IQR=Q1–Q3); fork, confidence interval of the median; vertical lines ±1.5*IQR; dots, outliers.

Geographical variability

Comparisons were limited to February and March due to data availability for the Porcupine area and their correspondence with peak spawning activity. Length range showed significant differences between the Porcupine (19.9–34 cm) and the Peninsula (19.6–30.4 cm) areas (p< 0.001), with individuals from the Peninsula area showing smaller sizes (mean=25.26 cm) than those from the Porcupine area (mean=27.5 cm) (Table 3) (Fig. 7A); however, no significant differences in weight were observed between areas (Fig. 7B) (p=0.223).

K´ ranged between 0.89 and 1.14 in the Porcupine area and between 0.69 and 1.34 in the Peninsula area, with significantly higher values in the north (mean=1.00 vs 0.91) (p<0.001) (Table 3) (Fig. 7C). No significant differences in HSI values were observed between the study areas (p=2.243) (Fig. 7D), although the range was broader in the Peninsula (0.02-15.24) than in the Porcupine area (0.54-10.07) (Table 3).

Differences in GSI between the Porcupine and the Peninsula areas were also detected during the spawning peak (February and March) (p<0.001), with higher values in the southern area (mean=3.29) than in the northern one (mean=1.60) (Table 3), as shown by the black whiskers in Figure 8. Similarly, for females exhibiting imminent spawning activity (stages 3 and 3b), GSI was higher in the Peninsula (mean=4.22) than in the Porcupine area (mean=2.27) (77% and 42.3% of ovaries in stages 3 and 3b, respectively), as illustrated by the dashed blue whiskers in Figure 8.

Regarding the spatial variability in maturity stages during the spawning peak, the percentage of spawning females in the Peninsula area was 77% (65% in stage 3 and 12% in stage 3b), compared with 42% in the Porcupine area (31% in stage 3 and 11% in stage 3b) (p<0.01). The proportion of regenerating females in the same period (1b) was 14% and 58% for the Peninsula and Porcupine areas, respectively (Fig. 8). Fecundity differed significantly between the Porcupine and the Peninsula areas, with both potential and batch fecundity higher in the southern area (mean =46817 oocytes, n =39, and 16808 hydrated oocytes, n =17, respectively; p=0.01) than in the northern area (mean=12223 oocytes, n=15, and 6112 hydrated oocytes, n=6, respectively; p=0.025) (Table 3) (Fig. 9A, B).

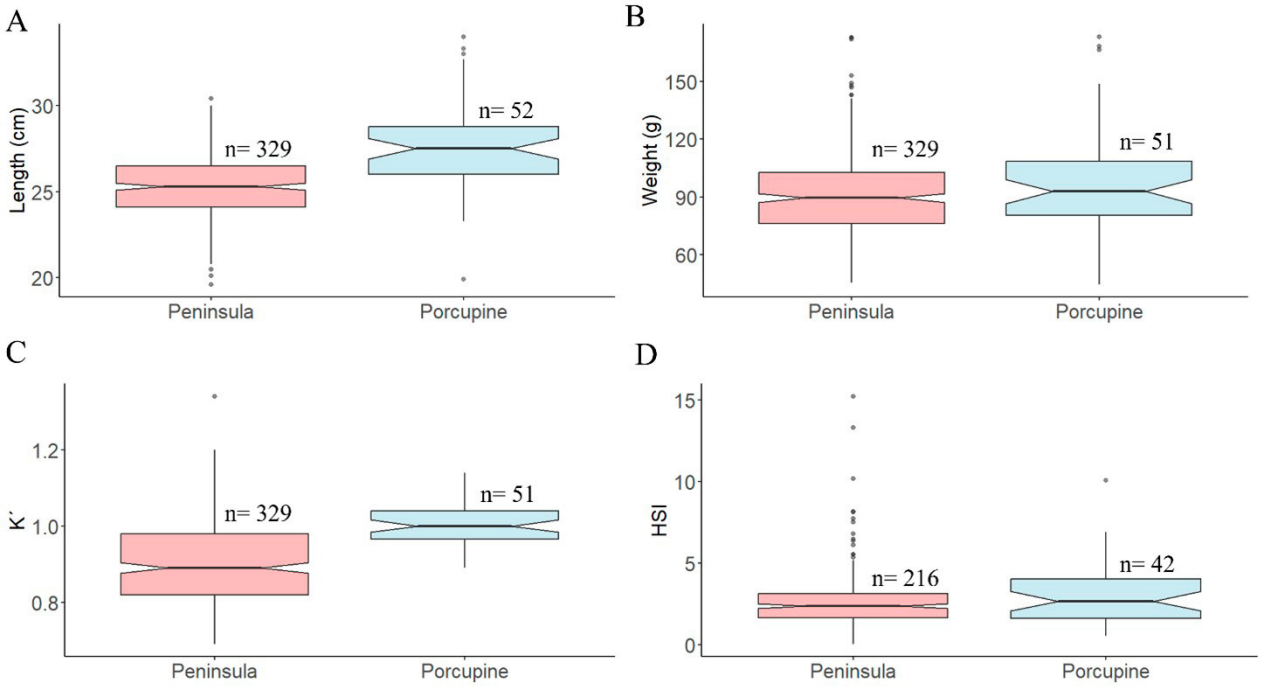

Fig. 7. –Boxplot of the site variation of length (A), weight (B), condition index (K´) (C) and hepatosomatic index (HSI) (D) of spawning females for February and March. Numbers on the x-axis correspond to the months of the year. Horizontal line inside the box, median; box, interquartile range (IQR=Q1–Q3); fork, confidence interval of the median; vertical lines ±1.5*IQR; dots, outliers.

Table 3. – Descriptive statistics of the somatic and reproductive variables analysed per study area for February and March. n, number of sampled specimens; sd, standard deviation; se, standard error; K´, Le Cren's relative condition factor; GSI, gonadosomatic index; HSI, hepatosomatic index; HYD diameter, diameter (μm) of hydrated oocytes.

Peninsula							
Variable	n	mean	sd	median	minimum	maximum	se
Length (cm)	329	25.3	1.7	25.3	19.6	30.4	0.1
Weight (g)	329	91	22.2	89.5	45.2	173	1.2
K´	329	0.91	0.11	0.89	0.69	1.34	0.01
GSI	248	2.73	1.85	2.28	0.01	11.67	0.12
HSI	216	2.73	1.84	2.36	0.02	15.24	0.13
Potential fecundity	40	46817	17723	48592	13298	72615	2802
Batch fecundity	17	16808	11476	12803	2792	36041	2783
HYD diameter	17	564.6	60.5	534.6	489	714	14.7
Porcupine							
Variable	n	mean	sd	median	minimum	maximum	se
Length (cm)	52	27.5	2.6	27.5	19.9	34	0.4
Weight (g)	51	97	27.6	92.8	44.4	173.3	3.9
K´	51	1	0.06	1	0.89	1.14	0.01
GSI	48	1.86	1.6	1.05	0.37	6.45	0.23
HSI	42	3.28	2.19	2.66	0.54	10.07	0.34
Potential fecundity	15	12223	9221	9159	2567	33501	2381
Batch fecundity	6	6112	5728	3998	1152	16169	2339
HYD diameter	6	740.8	216.1	678	513.7	1068.7	88.2

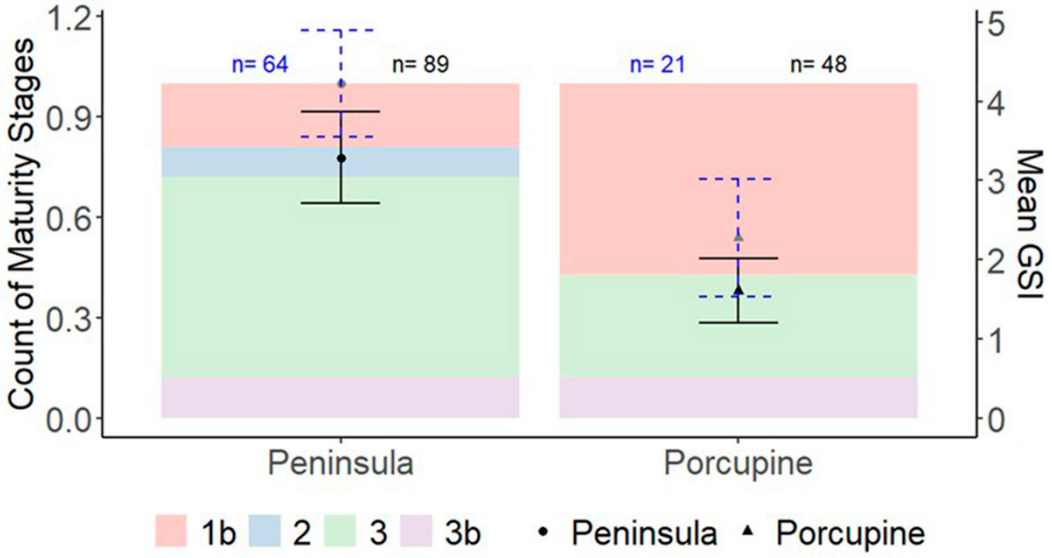

Fig. 8. – Prevalence of microscopic maturity stages (bars) and mean ± se of the gonadosomatic index (GSI) (whisker plot: black, mean GSI for all microscopic maturity stages; dashed blue, mean GSI for stages 3 and 3b) of females sampled during the spawning peak in the Peninsula area (February and March) and Porcupine area (March). n=number of observations for the GSI. Microscopic scale modified from Brown-Peterson et al. 2011 (1b, regenerating; 2, developing; 3, capable of spawning; 3b, active spawning).

The ratio between potential and batch fecundity for February and March suggests that each female from the Peninsula area could release approximately three batches in every spawning season, whereas those from the Porcupine area could release two batches in the same period. Assuming a spawning season of one month (approximately 30 days), we conclude that the spawning interval for blue whiting in the Peninsula area is 11 days, while in the Porcupine area it is 15 days.

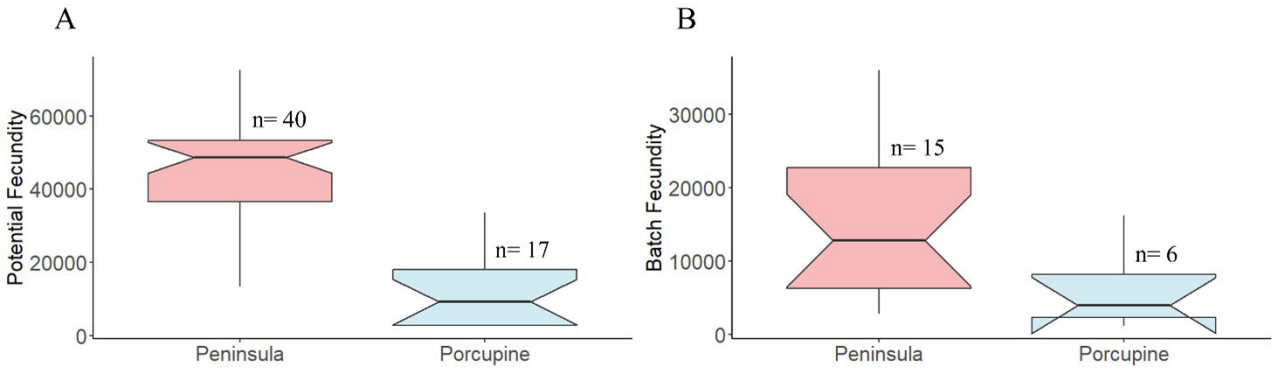

Fig. 9. – Boxplot of potential (A) and batch (B) fecundity calculated during the spawning peak of the species in the study areas. Names of the x-axis correspond to the sites. Horizontal line inside the box, median; box, interquartile range (IQR=Q1–Q3); fork, confidence interval of the median; vertical lines ±1.5*IQR; dots, outliers.

Hydrated oocyte diameter ranged from 489 to 714 µm (mean=564.6 µm) in the Peninsula area and from 513.7 to 1068.7 µm (mean=740.8 µm) in the Porcupine area. However, no significant differences were found between areas (p>0.05) (Fig. 10).

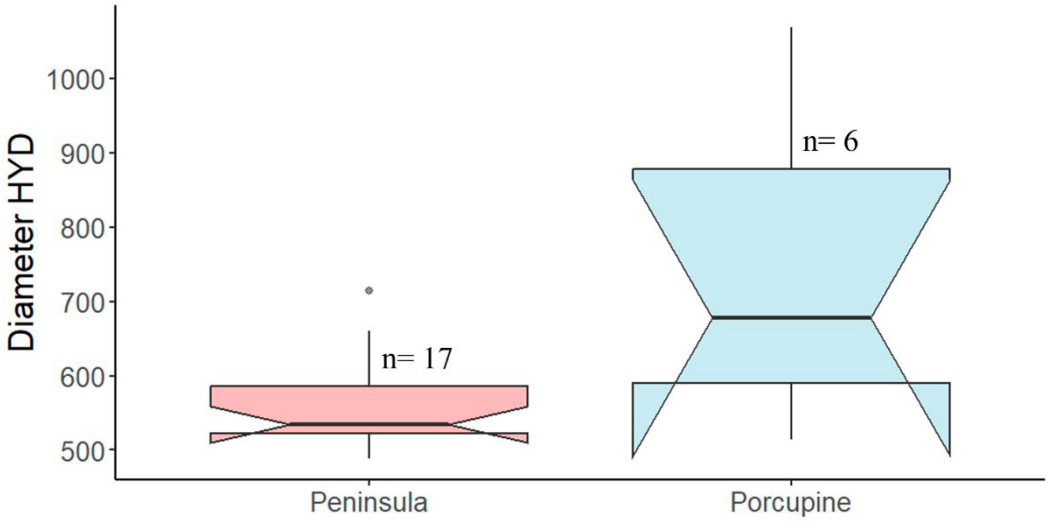

Fig. 10. – Boxplot of hydrated oocyte diameter (µm) calculated during the spawning peak of the species in the study areas. HYD, hydrated oocyte. Names of the x-axis correspond to the sites. Horizontal line inside the box, median; box, interquartile range (IQR=Q1–Q3); fork, confidence interval of the median; vertical lines ±1.5*IQR; dots, outliers.

DISCUSSION

In the present study, though they were few in number, the largest individuals (35–39 cm) were observed in the Peninsula area. However, the greater lengths exhibited by Porcupine specimens during the spawning period (February and March) than by those from the Peninsula area likely reflects reproductive migration, with a modal length of 28 cm in the former and a bimodal distribution of 23 and 27 cm in the latter. Gonçalves et al. (2017) also reported specimens over 40 cm on the Portuguese coast, and our length-frequency data align with the ICES (2024) assessment reports from the Faroe Islands to the Porcupine Seabight. Similarly, the typical length of the species in the Mediterranean is approximately 20–25 cm, with a maximum length of 39 cm (Serrat et al. 2019, Mir-Arguimbau et al. 2020), while in the Western Atlantic its congeneric species, *Micromesistius australis*, found around Argentinian Patagonia, the Falkland Islands and New Zealand, exhibits a typical length of 60 cm and a maximum length of 90 cm (ICES 2024). Building upon these findings and those reported in other areas, it currently does not seem feasible to maintain the hypothesis that the large spawners are in the waters north of the British Isles (the Porcupine area), while only juveniles are found in the Bay of Biscay and further south (the Peninsula area). Regarding the length-weight relationship, specimens from the Iberian Peninsula appear to be in better condition than those from the Porcupine region. However, given the relatively small sample size from the Porcupine area (n=52 vs n=1149 in the Peninsula area), these results should be interpreted with caution.

In our monthly analyses, the peak in length and weight observed in mature females from the Iberian Peninsula in July can be attributed to sampling bias, as the majority of data were collected from commercial fleets that preferentially target larger individuals. This pattern aligns with the expected annual growth for the species. Seasonal trends in the condition indices are clearly linked to reproduction: K´ begins to recover immediately after the spawning peak, while HSI remains low until May, three months after the maximum reproductive activity, suggesting that early gonad development, i.e. vitellogenesis, which begins in October–November, depends initially on energy stored in the liver, where vitellogenin, the precursor of egg yolk, is synthesized. Additionally, the sharp decline observed in K´ from February to March, followed by a relatively rapid recovery, indicate that actively spawning females temporarily cease feeding during reproduction (Varne and Mork 2004, Gonçalves et al. 2017). Low levels of K´ and HSI during the spawning season have also been reported in other studies of the same species (Gonçalves et al. 2017, Serrat et al. 2019), as well as other species of gadoids, e.g. cod (*Gadus morhua*) (Mello and Rose 2005) and pout (*Trisopterus luscus*) (Alonso-Fernández et al. 2008). This is also consistent with the species' physiology, as it possesses white muscle with minimal fat content, making it less efficient as the primary source of energy. The delayed recovery of hepatic reserves could be linked to environmental factors such as food availability, but more studies would be necessary for corroboration. These observations indicate that blue whiting is a capital breeder (Murua et al. 2003, Serrat et al. 2019) that uses the energetic reserves stored in its tissues for reproduction.

The present study demonstrates that effective spawning occurs in the Iberian Peninsula between February and April (likely starting in January, although data for this month were unavailable), with peak spawning in February, coinciding with the spawning season previously reported along the Portuguese coast (Gonçalves et al. 2017). Un-

fortunately, maturity information for the Porcupine area was only available for March, preventing us from estimating the spawning peak there for the study period. However, previous research indicates that spawning in the main grounds west of the British Isles occurs from March to May, with a peak in April, while in Icelandic and Norwegian waters, it typically takes place between May and June (Varne and Mork 2004), following a latitudinal gradient that extends from southern regions (starting in January) to northern regions (as late as June). In the Mediterranean, the spawning season occurs from December to March, with a peak in January (Mir-Arguimbau et al. 2020). These temporal shifts in spawning across locations appear to be linked to the environment, particularly salinity (optimal range 35.3–35.5), temperature (optimal ~11 ºC), and food availability, all of which are influenced by the oceanographic conditions at each site (Varne and Mork 2004, ICES 2024). The existence of effective spawning in the Iberian Peninsula contradicts the study by Carrera et al. (2001), which suggests that the southern part of the distribution is a nursery area for first- or second-year individuals, which then migrate northward for reproduction once they reach a sufficient size. According to these authors, individuals migrate from the spawning grounds of western Ireland (the Porcupine area) to the feeding grounds in the Norwegian Sea (NEAFC 2024), never returning to the southernmost waters. This behaviour is observed in other small pelagic species from the North Atlantic that undertake spawning migrations, such as herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), in which first-year females remain in feeding areas, while only second- or third-year individuals migrate to spawning areas (Laurien et al. 2024). Furthermore, the length of mature females observed in the Iberian Peninsula is similar to that reported in other areas (20–30 cm west of the British Isles) (ICES 2024), and the spawning season seems to takes place in the same period (February–March) both in the Porcupine and the Peninsula areas, as explained above, suggesting that the migration of old and large specimens northward would not be plausible. Although Varne and Mork (2004) defend the spawning migration of blue whiting based on its combination of pelagic and demersal traits, the results of the present study do not support this hypothesis. Moreover, the morphology of blue whiting is not as hydrodynamic as that of pelagic swimmers, raising questions about its ability to migrate long distances, particularly when smaller in size.

Studies on the fecundity of blue whiting are limited, particularly those employing methodologies comparable to ours. The few available studies focus on populations in the Mediterranean (Serrat et al. 2019) and the southern blue whiting (*Micromesistius australis*) (Pájaro and Macchi 2001). There is some debate over whether the species exhibits determinate or indeterminate fecundity in the Mediterranean (Serrat et al. 2019), but the majority of studies support determinate fecundity in the species and its congenerics (Pájaro and Macchi 2001, Mir-Arguimbau et al. 2020, ICES 2024). In our study, the sharp decline in the number of oocytes observed from February to March further supports determinate fecundity. The peak in April is likely attributable to the low number of observations and is therefore not considered a genuine increase or representative of the overall population. In comparison with previous studies, our estimates of potential and batch fecundity (46431 and 16779 oocytes on average, respectively) are similar to those reported in the Mediterranean (mean batch fecundity of 13570 oocytes) (Serrat et al. 2019), but differ markedly from those of the southern blue whiting (mean potential and batch fecundity of 477700 and 706, respectively) (Pájaro and Macchi 2001), likely because it is a different species and the size differences mentioned above are considerable.

Based on our observations, blue whiting has a relatively low fecundity compared with other gadoids with determinate fecundity, such as the NE pout (*Trisopterus luscus*) (mean potential and batch fecundity of 210560 and 10805, respectively) (Alonso-Fernández et al. 2008) and cod (*Gadus morhua*) whose potential fecundity can be up to millions of eggs per female (Mello and Rose 2005). Our samples were collected when the spawning season had already started, which could imply an underestimation of potential fecundity; however, since only ovaries without signals of recent spawning activity (i.e. without POFs) were considered for potential fecundity estimations, we assume our calculations are representative of the species' reproductive potential. Nevertheless, for robust estimations, fecundity calculations should be based on samples collected before the spawning season, preferably in December and January. Moreover, batch fecundity is known to vary significantly throughout the reproductive period (Pájaro and Macchi 2001), which may help explain the monthly differences observed in our study.

Spawning females from the Peninsula area had lower length and K´ than those from the Porcupine area, but the high proportion of inactive females during the spawning peak in the Porcupine area may indicate a lower spawning fraction at this site or suggest that spawning peaked before March, contradicting Kloppmann et al. (2001), who reported a substantial number of eggs in March–April in this region. Reproductive parameters are highly plastic phenotypic traits, so observed differences may be due to a combination of environmental drivers and stock structure, as observed by Mir-Arguimbau et al. (2020) for blue whiting in the Mediterranean Sea. Unfortunately, the lack of data in January and February from the Porcupine area prevents us from concluding whether the spawning fraction in this area was low or just a phenological effect. Nevertheless, based on our data, March does not seem to correspond to the spawning peak.

Despite their smaller size and lower condition, Peninsular females exhibited higher potential and batch fecundity, although their oocytes were smaller than those from the Porcupine area. Trade-offs between the number and size of offspring are an adaptive response to environmental conditions (Domínguez-Petit et al. 2017), with smaller, more numerous eggs typically being found in highly dynamic environments. However, the limited number of fecundity observations (<20 samples of batch fecundity from the Peninsula area and <10 samples from the Porcupine area) prevents us from drawing robust conclusions regarding the reproductive potential in each area.

The spawning frequency of blue whiting estimated in the present study for the Peninsula (1 batch every 11 days) and Porcupine (1 batch every 15 days) areas is low compared with that of other gadoids with determinate fecundity, such as the Atlantic cod (1 batch every 3 days) (Kjesbu 1989) and pouting (1 batch every 6–7 days) (Alonso-Fernández et al. 2008). However, these species release millions of eggs per spawning season, an amount two orders of magnitude greater than that of blue whiting. Assuming our estimates of spawning frequency and a one-month individual spawning period, blue whiting release two or three batches in the NEA, which aligns with values reported for southern blue whiting in Argentina (Pájaro and Macchi 2001). The frequency and duration of spawning in fish are key components of their reproductive strategy, influencing reproductive potential and shaped by environmental factors and life-history trait trade-offs (McBride 2014). Changes in spawning phenology driven by ocean warming may affect recruitment and, hence, stock dynamics (Slesinger et al. 2021); therefore, studying in depth the reproductive phenology of the blue whiting population and the factors that regulate it will allow us to anticipate the impact of climate change on this species, which sustains the highest catches in the NEA.

Although our study did not encompass the entire distribution of blue whiting, most previous research has focused on higher latitudes up to the Porcupine Bank (Mahe et al. 2016). The Iberian Peninsula is considered the southernmost extent of the stock (ICES 2024), and little to no differentiation has been made between the two areas (Was et al. 2008). ICES advice reports, which constitute the most commonly cited corpus on the reproductive ecology of blue whiting, are based on data primarily obtained from the International Blue Whiting Spawning Stock survey, which covers the main spawning grounds, from Porcupine Bank northwards, as well as other surveys that cover the northern part, including the Nordic Sea and adjacent waters (International Ecosystem Survey in the Nordic Seas; International Survey in Nordic Seas and adjacent waters), the Barents Sea (Barents Sea Ecosystem Survey, BarSea), and Icelandic and Faroese waters (bottom-trawl surveys) (ICES 2024). Surveys conducted in less-known zones, such as the Spanish surveys in the Bay of Biscay, from which the data for this study were obtained, and the French surveys EVHOE (groundfish survey) and PELGAS (acoustic-trawl survey) (ICES 2024), have not focused on analysing the reproductive ecology of the species.

Despite the value of reproductive traits as indicators, they should be interpreted with caution and ideally integrated with other data sources (e.g. genetics, tagging and morphometrics) in a multi-disciplinary framework to robustly infer stock structure. Nevertheless, our findings offer significant insights for stock assessment and fisheries management, as this is one of the few studies that have addressed the southern component of the blue whiting population. Aligning assessment units with biologically meaningful boundaries—such as reproductive traits, otolith morphology and genetic markers—can reduce bias in stock estimates, mitigate management risk, and ultimately influence policy decisions (e.g. delineating separate quotas, implementing area closures, or adopting spatially explicit assessment models that better reflect the stock's true biological structure).

CONCLUSIONS

Thorough investigations into reproductive potential and parental attributes are recommended to identify stock components, as these factors are specific to each stock and shape their life history (Lowerre-Barbieri et al. 2017). Furthermore, integrating reproductive potential with other life history traits, such as growth and oceanographic variables, could provide a unique approach to resolving the population structure dilemma of blue whiting in the NEA, as there is currently no available information to serve as the basis for generating advice on the status of individual stocks (ICES 2024). Although our study indicates clear differences in reproductive traits between the Porcupine Bank and the Iberian Peninsula, the limitations in temporal and geographical sampling coverage prevent us from confirming with certainty the existence of two independent stocks or spawning components. Nevertheless, this study demonstrates that effective spawning takes place off the Iberian Peninsula and attributes of spawning females differ significantly between the two study areas, supporting the hypothesis of a complex stock structure for blue whiting, as suggested by Mahe et al. (2016).

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DECLARATION OF COMPETING INTERESTS

The authors of this article declare that they have no financial, professional or personal conflicts of interest that could have inappropriately influenced this work.

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AUTHORSHIP CONTRIBUTION STATEMENT

Mónica González Castrillón: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. **Rosario Domínguez-Petit**: Conceptualization, Funding acquisition, Investigation, Proyect administration, Writing – review & editing.

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