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Reproductive biology of wahoo (*Acanthocybium solandri*) in the Canary Islands (eastern-central Atlantic)

Raül Triay-Portella [a,b,*], José A. González [c], José M. Lorenzo [c], Sandra Correia [d], José G. Pajuelo [c]

[a] *Grupo en Biodiversidad y Conservación, IU-ECOAQUA, Universidad de Las Palmas de Gran Canaria, Las Palmas, Spain*
[b] *MARE - Marine and Environmental Sciences Centre, Agência Regional para o Desenvolvimento da Investigação, Tecnologia e Inovação (ARDITI), Funchal, Portugal*
[c] *Grupo de Ecología Marina Aplicada y Pesquerías, Instituto Universitario de Estudios Ambientales y Recursos Naturales i-UNAT, Universidad de Las Palmas de Gran Canaria, Las Palmas de Gran Canaria, Spain*
[d] *Instituto do Mar (IMar) – Cabo Verde, Mindelo, São Vicente, Cabo Verde*

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ABSTRACT

The reproductive status of wahoo (*Acanthocybium solandri*) in the eastern-central Atlantic was investigated to better understand their migration and breeding patterns. The waters around the Canary Islands are considered a breeding area for wahoo; and this study documents the first described breeding activity found in the eastern Atlantic. The presence of many mature and spawning capable wahoo reported in this study confirms its spawning activity in this region. Off the Canary Islands, only mature individuals spawn in the region where no immature individuals were observed to date. Most of the specimens captured in Canary Islands waters exceed 100 cm TL (about 2 years old). Values of the gonadosomatic index (GSI) of males were much lower than those estimated for females. Testes showed little changes in size throughout gametogenesis, while ovaries increased significantly (p<0.05). The low values make it inadvisable to use GSI in males to determine spawning activity. In the Canary Islands, wahoo females spawn (fishes with tertiary vitellogenic oocytes, postovulatory follicles or germinal vesicle migration, yolk coalescence, germinal vesicle breakdown and hydrated oocyte) mainly during a 4-month period in summer. Both females of spawning capable outside the main summer breeding period and females in regressing phase during the spawning period have been observed in the Canary Islands. Males were found in the spawning capable phase throughout the year, with greater prevalence between May and October.

1. Introduction

Wahoo, *Acanthocybium solandri* (Cuvier, 1832), is a large pelagic scombrid distributed throughout the subtropical and tropical oceanic waters of the Indian, Atlantic, and Pacific oceans, including the Mediterranean and Caribbean seas (Collette and Nauen, 1983; Theisen and Baldwin, 2012; Viana et al., 2013; Gao et al., 2020). Wahoo is classified as a single panmictic species and is the only species of the genus *Acanthocybium* (Theisen et al., 2008). Recent genetic studies provide evidence of differentiation between the Indo-Pacific and Atlantic populations, and a global connectivity of wahoo populations from the Indo-Pacific into the Atlantic was observed via advection of warm water off the southern African coast, the Agulhas Rings, by the Benguela Current (Haro-Bilbao et al., 2020). Wahoo is a gonochoristic species

that has multiple spawning of buoyant eggs (Brown-Peterson et al., 2000; Theisen et al., 2008; Zischke, 2012; Zischke et al., 2013a), and spawns in areas near open-ocean currents, to likely promote larval dispersion (Wollam, 1969; Hogarth, 1976; Brown-Peterson et al., 2000; Theisen et al., 2008). It occurs seasonally in temperate waters of the North Atlantic and is present throughout the year in the Gulf of Mexico and in the Caribbean, but with seasonal patterns of abundance in different locations (Oxenford et al., 2003). It is an apex piscivore species found in sea surface temperatures ranging between 18º and 30ºC at depths shallower than 250 m (Oxenford et al., 2003; Theisen and Baldwin, 2012; Gao et al., 2020; Madigan et al., 2021). According to ICCAT, wahoo is one of the thirteen most important species of small tunas caught in tropical oceans around the world and its catches are increasingly frequent worldwide, which makes it necessary to know its biological and migratory cycles throughout its range (Brown-Peterson et al., 2000; Oxenford et al., 2003; Viana et al., 2008, 2013).

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* Corresponding author at: Grupo en Biodiversidad y Conservación, IU-ECOAQUA, Universidad de Las Palmas de Gran Canaria, Las Palmas, Spain.
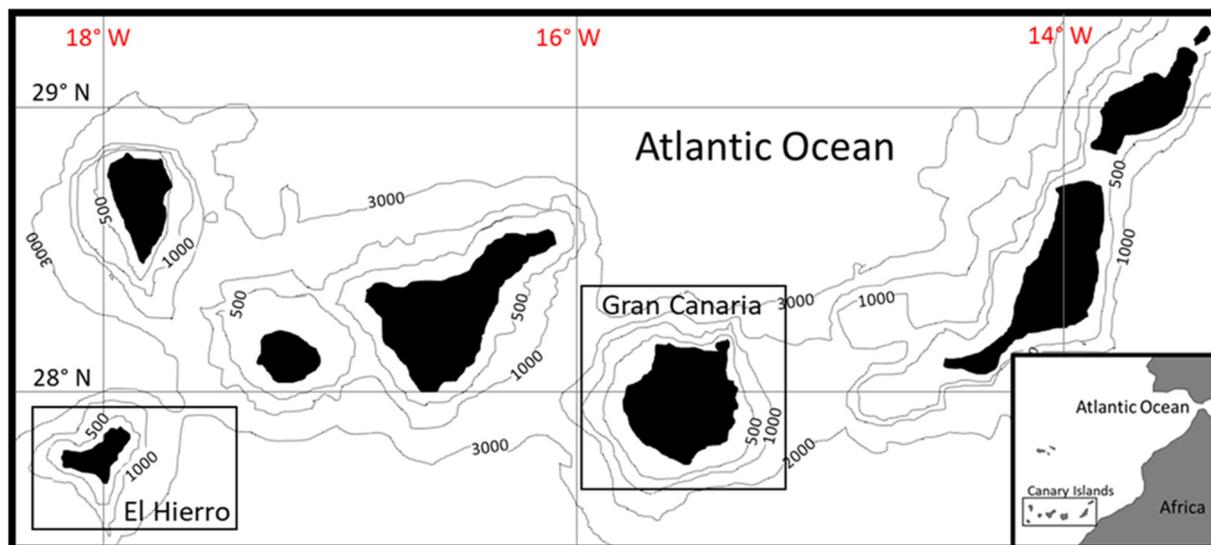*E-mail address:* raul.triay@ulpgc.es (R. Triay-Portella).

Fig. 1. Location of the sampling areas off the Canary Islands.

In the Canary Islands, wahoo is fished all year round but with marked seasonality, with maximum catches in spring and summer (González et al., 2020). In the last 16 years, wahoo catches in the Canary Islands ranged from 79.5 tons in 2009 to 36.2 tons in 2012, with an average catch of 56.6 tons. According to the website of the Canary Islands Government, between 30 and 77% of the total regional catch is caught around the island of El Hierro, with an average catch of over 30 tons per year*.

Given the scarcity of published data on the breeding areas of wahoo in the Atlantic Ocean, the reproductive biology of wahoo caught around the Canary archipelago was investigated to better understand their migration pattern and breeding locations.

2. Materials and methods

Individuals of *A. solandri* were collected monthly from January to December of 2019, from the artisanal fleet of the islands of El Hierro and Gran Canaria (Fig. 1), as well as by sport fishers (Mena et al., 1993; González et al., 2020). Around El Hierro, artisanal catches are made with a special hook-based fishing gear, which uses a large wooden or fiberglass lure in the shape of wahoo, which floats on the surface and is tied to a 6m-long rod that carries a large pointed hook or harpoon at its end (Mena et al., 1993; González et al., 2020). When the wahoo approaches this lure, the fisherman spears the animal with the harpoon of the "rod".

For each fish, total length (TL, cm), fork length (FL, cm), total weight (TW, g) and eviscerate weight (EW, g) were recorded, and gonads were removed and weighed (GW, 0.01 g). Sex of individuals was macroscopically assigned as either female (F) or male (M) and verified histologically afterwards. The Student t-test was used to evaluate the null hypothesis of equality in mean TL and equality in mean TW between sexes (H_0: $\mu_1 = \mu_2$) with a significance level of 5% ($\alpha = 0.05$). Differences in TL distribution between males and females were analysed using the Kolmogorov–Smirnov non- parametric Z-test. This test evaluated the null hypothesis of equality in TL distribution between sexes (H_0: $F_1(x) = F_2(x)$) with a significance level of 5% ($\alpha = 0.05$) (Sachs, 1982; Sokal and Rohlf, 2012).

Sex ratio was calculated as females:males (F:M) and the relationship between sex ratio and TL was determined. The Pearson chi-square goodness-of-fit test was used to evaluate the null hypothesis of equality of frequencies between sexes (H_0: 1:1 ratio) with a significance level of 5% ($\alpha = 0.05$) (Sachs, 1982; Sokal

and Rohlf, 2012). Maturity phases were established following Brown-Peterson et al. (2011): immature; regenerating, developing, spawning capable, and regressing. In the case of wahoo, the spawning capable phase includes two subphases: a first with tertiary vitellogenic oocytes (Vtg3) and/or postovulatory follicules (POF's), followed by an actively spawning subphase with germinal vesicle migration (GVM), yolk coalescence (YC), germinal vesicle breakdown (GVBD), and hydration (H). Testes were classified according to the most-advanced stage of spermatogenesis observed and the morphological feature in the germinal epithelium (Brown-Peterson et al., 2011). Stage of spermatogenesis can be differentiated by a decrease in size of cells and an increase in basophilic staining as development progresses from spermatogonia (Sg) to spermatozoa (Sz) (Brown-Peterson et al., 2011). Terminology for oocyte development including atresia follows Brown-Peterson et al. (2011) and Lowerre-Barbieri et al. (2011): oogonia, primary growth oocytes, alveolar cortical oocytes, primary, secondary and tertiary vitellogenic oocytes, mature oocytes (including germinal vesicle migration, yolk coalescence, germinal vesicle breakdown, and hydration) and postovulatory follicles. All vitellogenic oocytes were considered as secondary growth oocytes. Cortical alveolar (CA) oocytes were also considered to be secondary growth oocytes since their formation is gonadotropin-dependent (Wallace and Selman, 1981; Lubzens et al., 2010; Brown-Peterson et al., 2011; Lowerre-Barbieri et al., 2011) and fish with CA oocytes were considered sexually mature. The relationship between maturity and histological phase of ovaries and testis of wahoo was established following Brown-Peterson et al. (2011), Farley et al. (2014) and Okochi et al. (2016). To assess maturity phases, all testes and ovaries were fixed and preserved in 4% buffered formalin and processed histologically. Tissues were embedded in paraffin, sectioned at 5 μm and stained with Harris haematoxylin and eosin. Spawning activity in the area was estimated by monitoring monthly changes in the frequency of maturity phases, in combination with the gonadosomatic index (GSI) calculated from the weight of the gonads as a percentage of total weight minus gonad weight (Griffiths et al., 2019). The mean GSI values among months were compared between sexes with ANOVA. This analysis was used to evaluate the null hypothesis of equality in mean GSI values among months (H_0: $\mu_1 = \mu_{2=\ldots} = \mu_n$) with a significance level of 5% ($\alpha = 0.05$). Once the null hypothesis was rejected, Dunnett's T3 post-hoc test was applied to determine which month differed. The post hoc test identifies
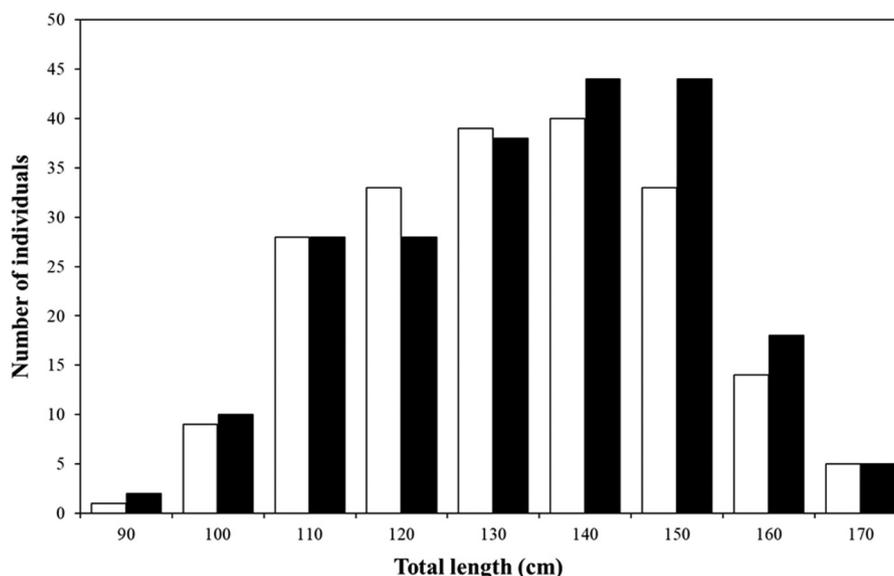
Fig. 2. Number of specimens of males and females of wahoo sampled. Black are females, white are males.

homogeneous subsets where means that do not differ within each subset, testing the null hypothesis of equality in GSI values with a significance level of 5% ($\alpha = 0.05$). All statistical analyses were performed with the SPSS package.

3. Results

A total of 419 wahoo were sampled, of which 202 were males and 217 females (Fig. 2). The estimated sex ratio was 1:1.07 (F:M), which did not differ from unity ($\chi^2 = 0.53$; p = 0.46). There were no differences between the frequencies observed for size classes. The minimum size observed was 94 cm FL for males and 91 cm FL for females. The maximum size was 170 cm FL for males and 171 cm FL for females. The maximum weight recorded was 45050 g TW for males and 44520 g TW for females. Wahoo did not show significant differences in mean FL or TW between sexes (t<1.062, p>0.289). The Kolmogorov–Smirnov Z-test did not show significant differences in the FL distribution between sexes (Z = 0.713, p = 0.689).

The ovaries increased from 27 g in regenerating to 957 g in spawning capable. No pattern was observed between GSI and total body weight, both in males and females. For females, mean GSI value peaked in July–September. Individual GSI values for females showed a few cases with high values from November to February. For males, GSI values were low, with 50% of individuals lower than 0.31 and 95% below 1.25 (Fig. 3). ANOVA analysis indicated significant differences in mean GSI values among months for males and females (ANOVA: males F = 3.63, p<0.0001; females F = 11.83, p<0.0001). Dunnett's T3 post-hoc test showed significant differences in GSI values among June–August for males and from May to September for females (p<0.05). ANOVA analysis also indicated significant differences in mean GSI values among months between sexes (ANOVA: F = 19.85, p<0.0001). Dunnett's T3 post-hoc test showed a subset of months (October–April) where means do not differ within of the subset, testing the null hypothesis of equality in mean GSI value.

Wahoo gonads are suspended by a dorsal mesentery in the posterior region of their visceral cavity. Testes are elongate in mature individuals, while ovaries are elongate and ovoid in females, with both lobules equally developed. Histological analysis verified that the specimens had only either ovarian or testicular tissue. All maturity phases (except immature) were recorded in the Canary Islands (Table 2). Regenerating individuals were present all year around, with higher values from October to April, indicating the main inactive period of reproduction (Table 2). Regenerating females were characterized by primary growth oocytes (PG), late-stage of atresia, and a thicker ovarian wall. This phase was more frequently observed from October to April (Fig. 4a). Fish in the regenerating phase are sexually mature but reproductively inactive. Developing males were observed all year round (Table 2). Developing females were mainly observed between May and July, with a few until August, and again a few in November and January (Table 2). Females were in the early developing (CA) mainly in May showing with time the expected progression of females in the late developing phase (June–July). Developing females were characterized by primary growth oocytes (PGO) and cortical alveolar oocytes (CA) (Fig. 4b). Late developing phase were characterized by primary (Vtg1), and secondary (Vtg2) vitellogenic oocytes (Fig. 4c). Spawning capable males were dominant from June to September and in December (Table 2). Spawning capable females appeared in May in a low percentage and were dominant from June to September (Table 2). Spawning capable females were also observed in low percentages from November to February. Spawning capable ovaries were histologically characterized by the presence of tertiary (Vgt3) oocytes (first subphase, Fig. 4d) or oocytes in mature phase (actively spawning subphase): oocytes in yolk coalescence (YC), germinal vesicle migration (GVM), germinal vesicle breakdown (GVBD) or hydration (H), and the presence of postovulatory follicles (POFs) (Fig. 4e–g). Spawning capable females in the actively spawning subphase were mainly observed from June to September. Also, females in the actively spawning subphase were observed in some individuals from December to January. Regressing females were mainly recorded from June to October (Table 2); characteristically, their ovaries showed massive atresia and POF's (Fig. 4h). Mature males in developing and spawning capable phase were found all year round.

4. Discussion

The Canary Islands can be considered a breeding area for wahoo. The presence of many mature and actively spawning subphase fish (with postovulatory follicles or germinal vesicle migration, yolk coalescence, germinal vesicle breakdown and hydrated oocyte) during this study confirms the spawning activity of wahoo in this region. Wahoo may migrate from the open ocean
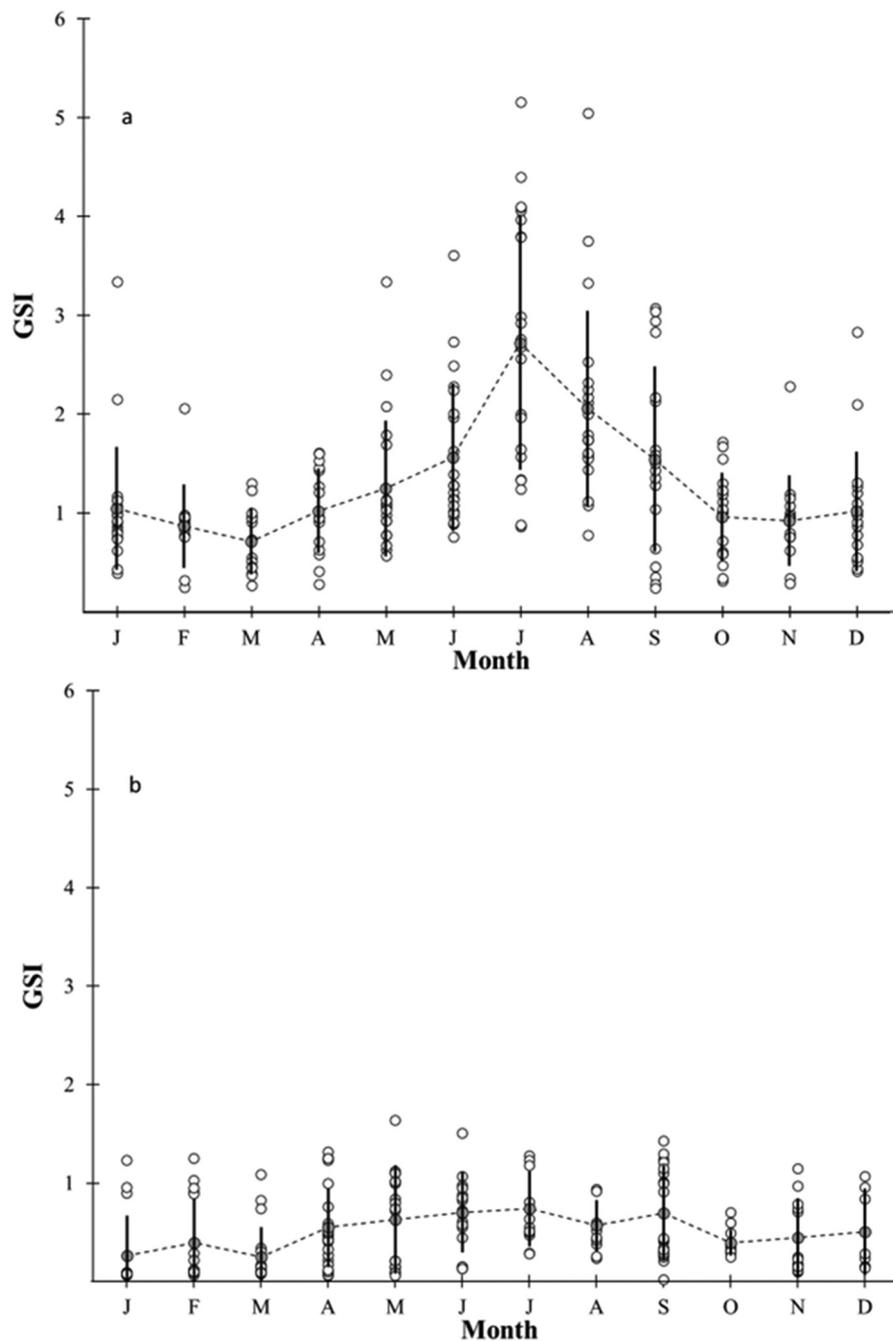
Fig. 3. Mean GSI values and standard deviation for (a) females (n = 217) and (b) males (n = 202). Circles indicate individual GSI values.

to the islands coasts and reproduce and then leave the islands to feed in the open ocean, and in surface currents and the eddies generated among the islands (Arístegui et al., 1994; Barton and Arístegui, 2004; Uchiyama and Boggs, 2006). The oceanographic characteristics of the Canaries, oligotrophic islands, coincide very well with the preferences of the species (Arístegui et al., 2003; Arístegui and Montero, 2005). In this regard, migrations and the selection of spawning grounds are linked to oligotrophic waters as spawning grounds, since there is a lower abundance of potential predators for their larvae (Nakagawa et al., 2007; Relano and Pauly, 2022). In addition, the presence of eddies in the south of the islands explains the abundance of this species in the area, since subtropical gyres are areas that increase the abundance of mesopelagic prey in cores that attract predators such as the wahoo, forming ecological hotspots (Arístegui et al., 1994; Barton and Arístegui, 2004; Arostegui et al., 2022).

In the Canary Islands, females spawn mainly during a 4-month period in summer. In the Atlantic Ocean, an extended spawning period in warm waters during the summer has been previously recorded (Wollam, 1969; Hogarth, 1976; Brown-Peterson et al., 2000; Oxenford et al., 2003; Maki and McBride, 2007; Figuerola-Fernández et al., 2008; Jenkins and McBride, 2009; Viana et al., 2013), and in both hemispheres in the Pacific Ocean (Zischke, 2012; Zischke et al., 2013a; Luan et al., 2017; Gao et al., 2020) (Table 1). The presence of females in actively spawning subphase (with oocytes in germinal vesicle migration, yolk coalescence, germinal vesicle breakdown and hydrated stage) outside the main summer breeding period, as well as the observation of females in regressing phase during the spawning period in the Canary Islands have also been observed in the western-central Atlantic by Brown-Peterson et al. (2000) and Maki and McBride (2007),

Table 1
Spawning period recorded for wahoo.

Area	Spawning period	Authors
Western Central Atlantic	May–October[b]	Wollam (1969)
Western Central Atlantic	June–August[a]	Hogarth (1976)
Western Central Atlantic	May–August[a]	Brown-Peterson et al. (2000)
Western Central Atlantic	May–August[a]	Oxenford et al. (2003)
Western Central Atlantic	May–August[a]	Maki and McBride (2007)
Western Central Atlantic	June–August[a]	Jenkins and McBride (2009)
Western Central Atlantic	May–September[a]	Figuerola-Fernández et al. (2008)
Western Equatorial Atlantic	February–September[a]	Viana et al. (2013)
Eastern Equatorial Atlantic	December–January[a]	Kindong et al. (2022)
Eastern Central Atlantic	June–September	Present work
Western Central Pacific	February–March[b]	Matsumoto (1968)
Eastern Central Pacific	May–October[b]	Matsumoto (1968)
Central Pacific	Spring and winter[a]	Iversen and Yoshida (1957)
Western Equatorial Pacific	January–December[b]	Matsumoto (1968)
Western Equatorial Pacific	January–December[a]	Zischke (2012)
Western South Pacific	October–February[a]	Zischke et al. (2013a)
Western South Pacific	Winter to spring[a]	Gao et al. (2020)
Eastern South Pacific	Winter to spring[a]	Luan et al. (2017)

[a] Recorded by gonadal analysis.
[b] Recorded by larval occurrence.

Table 2
Maturity phases for males (n = 202) and females (n = 217) wahoo. Numbers indicate the percentage of males and females analysed in each month.

Months	Males				Females				
	RE	DV	SC	RG	RE	DV	SCI	SCII	RG
January	35.29	41.18	23.53	0.00	73.68	5.26	5.26	5.26	10.53
February	50.00	33.33	11.11	5.56	80.00	0.00	6.67	0.00	13.33
March	55.00	45.00	0.00	0.00	100.00	0.00	0.00	0.00	0.00
April	21.74	69.57	8.70	0.00	100.00	0.00	0.00	0.00	0.00
May	15.79	57.89	26.32	0.00	45.00	40.00	10.00	5.00	0.00
June	14.29	42.86	35.71	7.14	9.52	52.38	23.81	14.29	0.00
July	6.67	40.00	46.67	6.67	4.55	18.18	18.18	45.45	13.64
August	8.33	33.33	41.67	16.67	9.52	9.52	14.29	42.86	23.81
September	0.00	38.89	50.00	11.11	21.05	0.00	5.26	36.84	36.84
October	46.67	40.00	6.67	6.67	94.12	0.00	0.00	0.00	5.88
November	41.67	41.67	16.67	0.00	80.00	13.33	6.67	0.00	0.00
December	25.00	37.50	31.25	6.25	83.33	0.00	5.56	5.56	5.56

RE, regenerating; DV, developing; SC, spawning capable; SCI, spawning capable first subphase; SCII, spawning capable actively spawning subphase; RG, Regressing.

who suggested an alternating or skipped spawning pattern and/or the existence of two temporally distinct groups of spawning females. In this regard, Brown-Peterson et al. (2000) pointed to the existence of a winter–spring spawning somewhere unknown. A possible explanation for this second group of spawning females observed in the Canary Islands is that winter migratory behaviour is a phenotype shown by only part of the total population. This group may move southward during the austral summer, to the south Atlantic islands where their abundance increases in December–January (Alasdair, 1990). Zischke et al. (2013b) suggested multiple discrete phenotypic stocks in the Pacific Ocean despite genetic homogeneity. Kindong et al. (2022) described a spawning of wahoo in the equatorial Atlantic (10oN to 5oS) in December-January (austral summer) along with the presence of specimens from 43 to 177 cm FL. Data by Kindong et al. (2022) also showed a reduction in catches between June and October, the presence of regressing females all year round and the minimal presence of spawning capable females between July and November. Intraspecific variations in migratory patterns have been described for many pelagic marine species (Theisen and Baldwin, 2012). Presence of regenerating females in the Canaries may be due to mature individuals spawning for a brief period in more northerly latitudes then migrating southward. This was noted by Zischke et al. (2013b). The presence of regressing and

regenerating females during the summer could also be an indication of asynchronic spawning, where females are not spawning at the same time. Brown-Peterson et al. (2000) indicated that wahoo is a multiple spawner with asynchronous oocyte development throughout the spawning season.

Male GSI values were much lower than for females. Testes showed little changes in size throughout gametogenesis, while the ovaries increase significantly as already described by Gao et al. (2020). Wahoo has a relatively low GSI, which is a typical feature of large and medium-sized pelagic oceanic fish species (Oxenford et al., 2003; Viana et al., 2013). In this regard, Brown-Peterson et al. (2000) noted that male GSI values are generally well below 1, and Zischke et al. (2013a) observed that GSI values for males ranged from 0.10 to 0.48. These low values make it inadvisable to use GSI to determine spawning activity in males. The present values for females are very similar to those found by Oxenford et al. (2003), Jenkins and McBride (2009) and Zischke et al. (2013a), with maximum values ranging from 4.30 to 5.85, except for one specimen in the Gulf of Mexico whose GSI was 9.50 (Brown-Peterson et al., 2000). Males around the Canary Islands were found in the spawning capable phase throughout the year, with higher prevalence between May and October. Oxenford et al. (2003) observed a wide range of spermatogenic stages in males through the year, and Brown-Peterson et al. (2000) and Kindong et al. (2022) commented that males are ready for spawning throughout the year. Together with a low GSI through the year, males are poor indicators of spawning activity in the region.

Although the Canary Islands are likely a spawning area for wahoo, no immature individuals were observed. Most of the specimens caught in the Canarian waters exceed 100 cm TL (2 years old, unpublished data). The absence of immature wahoo in the area can be a result of these fish being small to be caught in fishery. The smallest individuals have been observed (Kindong et al., 2022) near equatorial Atlantic waters (from 43 cm fork length) and in the western Atlantic (Antilles) by Neilson et al. (1999) (from 32 cm standard length), by Viana et al. (2013) in St. Peter and St. Paul archipelago, Brazil (64 cm fork length), and by Alasdair (1990) in St. Helena Island (from 50 cm FL and 429 g). A hypothesis to explain this may be that the youngest specimens, with higher thermal requirements, are found in warmer waters than the recorded in the Canary Islands. Wahoo remains in warmer waters during its first year of life in search of food and spawning and, like other scombrids, constrained primarily by their physiological intolerance for colder water (Block and
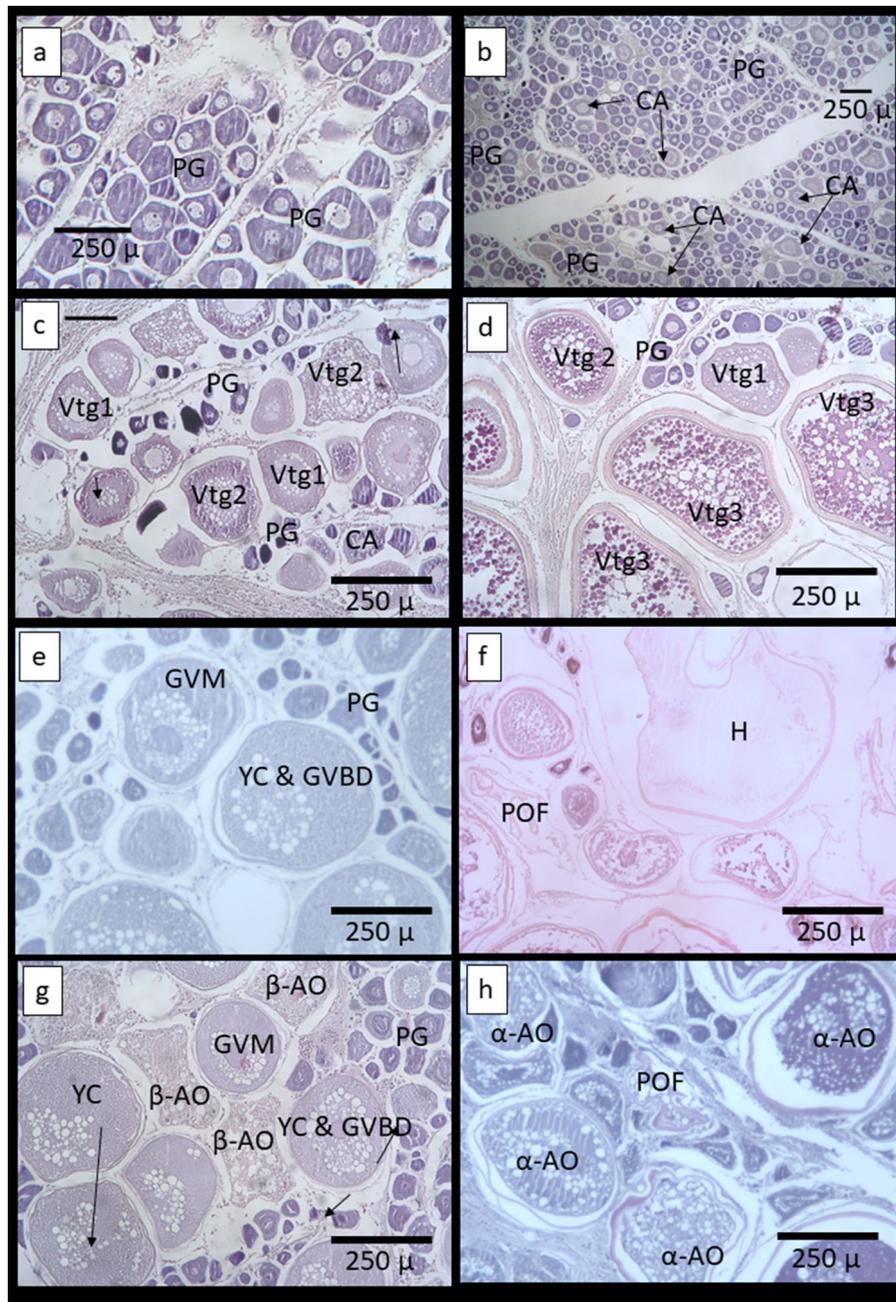
Fig. 4. Histological sections of wahoo ovaries. (a): regenerating, (b): early developing, (c): late developing, (d): early spawning capable subphase, (e–g): active spawning subphase (h) regressing. Oocyte stages: primary growth oocyte (PG), primary vitellogenic oocyte (Vtg1), secondary vitellogenic oocyte (Vtg2), tertiary vitellogenic oocyte (Vtg3), vesicle migration (GVM), yolk coalescence (YC), germinal vesicle breakdown (GVBD), hydration (H), postovulatory follicle (POF), alfa atretic oocyte (α-AO), and beta atretic oocyte (β-AO).

Stevens, 2001). In this regard, the presence of immature specimens has been observed in equatorial Atlantic waters, mainly in latitudes between 5ºN and 5ºS (Kindong et al., 2022) It to later expands its distribution area encompassing subtropical waters of the Macaronesian region sensu lato (Azores, Madeira, Canary, and Cape Verde archipelagos). The migratory pattern of wahoo in the Atlantic Ocean appears to be linked to sea water temperature. It moves almost exclusively in surface waters above the thermocline (Sepulveda et al., 2011; Widodo et al., 2012) in waters with temperatures between 10 and 30ºC, but mainly (98% of its time) above 22ºC (Sepulveda et al., 2011; Gao et al., 2020; Madigan et al., 2021). As temperature increases in subtropical waters with the seasons, there is a shift of wahoo from equatorial tropical Atlantic waters, where it is observed year-round (Kindong et al., 2022), to higher latitudes in the central eastern-central Atlantic. In this regard, it is worth noting that temperature is one of the main factors in seasonal migrations of large marine pelagic fishes (Pauly and Keskin, 2017; Pauly, 2019; Relano and Pauly, 2022) and plays an important role in their global distribution patterns (Boyce et al., 2008; Relano and Pauly, 2022).

Understanding the movements of large marine pelagic fishes is key to sustainability. Relano and Pauly (2022) proposed the concept of philopatry, the natural tendency of wahoo to return to their natal breeding grounds, as the key to understanding seasonal migration. This concept implies that wahoo migrations involve an annual seasonal loop for most individuals. In

the eastern-central Atlantic, the wahoo stock is probably composed of a mixture of individuals breeding in the Equatorial and South Atlantic during the austral summer and others breeding in the Northern Hemisphere during the summer. Wahoo migrate from the south towards subtropical waters of the eastern Atlantic off the Cape Verde, Canary, Madeira, and Azores archipelagos (Wirtz, 1998), even reaching into the Mediterranean (Romeo et al., 2005). For the Pacific Ocean, Relano and Pauly (2022) also indicated two phenotypic populations with distinct spawning grounds. Long-distance seasonal movements of over 1,000 km have been recorded for wahoo (Franks, 1998; Oxenford et al., 2003; Theisen and Baldwin, 2012). Together with their wide larval drift capacity, this proposed migratory pattern would explain the absence of genetic differences in the Atlantic population comparing the central equatorial and south Atlantic observed by Ollé et al. (2020). Furthermore, like many other large pelagic marine fishes, the homogeneity observed in the Atlantic population of wahoo may be due to a high dispersal capacity of floating eggs spawned in open ocean currents (Brown-Peterson et al., 2000; Theisen et al., 2008; Theisen and Baldwin, 2012).

CRediT authorship contribution statement

Raül Triay-Portella: Coordinated the reproductive study, Processed and analysed the tissues, Analysed the data, Wrote the original submitted version. **José A. González:** Obtained and sampled the animals, Analysed the data, Correia administered the project, Obtained the funding. **José M. Lorenzo:** Obtained and sampled the animals, Processed and analysed the tissues, Analysed the data, Obtained the funding. **Sandra Correia:** Obtained and sampled the animals, Correia administered the project. **José G. Pajuelo:** Coordinated the reproductive study, Wrote the original submitted version, Obtained the funding.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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