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Original Article

Atlantic mackerel daily spawning dynamics and implications for batch fecundity estimations

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The present study contributes to a better understanding of the daily spawning dynamics of southern NEA mackerel (*Scomber scombrus*) with implications for the estimation of batch fecundity. It shows that there is a time window during the day, mainly in the afternoon, during which the advanced oocyte mode in imminent spawners separates from the remaining, smaller oocytes. This synchronicity in the separation of the spawning batch amongst imminent spawners corroborates evidence for the existence of daily spawning synchronicity in the population. This is particularly important for applications of the daily egg production method, DEPM, because such pattern facilitates both the ageing of eggs for the estimation of the daily egg production at sea and the ageing of postovulatory follicles for the estimation of spawning frequency. For NEA mackerel, batch fecundity could only be measured when a clear hiatus was established between the spawning batch and the smaller oocytes. Hydrated females that do not show such hiatus would not be valid for batch fecundity measurements suggesting that the "hydrated oocytes method" is not fully applicable for this stock. Knowing the time of day at which the batch is separated, will facilitate the sampling of valid females for the estimation of batch fecundity.

Keywords: Atlantic mackerel, batch fecundity, daily egg production method, daily spawning dynamics

Introduction

The Atlantic mackerel (*Scomber scombrus*) is one of the most abundant and widely distributed fish species in the North Atlantic (Trenkel *et al.*, 2014), with the distribution extending from Morocco to Iceland and Norway (including the Black Sea, the Mediterranean, and the western Baltic Sea), and from North Carolina to Labrador (Scoles *et al.*, 1998). It supports one of the most important fisheries in the Northeast Atlantic (NEA), with estimated annual catches over one million tons since 2014 (ICES, 2017a). NEA mackerel is considered a single migratory stock that traditionally has been separated in three spawning components: the southern (ICES subdivisions 8.c and 9.a), the western (ICES divisions 6, 7, 5, 3.abde), and the North Sea (ICES divisions 3.a and 4) component (ICES, 2017a) with variable proportion of mixing between them. However, Jansen and Gislason (2013, and references therein), based on age structure and spawning activity, described the NEA mackerel population structure as a dynamic cline subjected to a straying process between all spawning areas (from South of Portugal to the North Sea). Moreover, in association with the increase of sea temperature (Jansen and Gislason, 2011), NEA mackerel started to expand its distribution west- and northwards in the mid-1990s (Astthorsson *et al.*, 2012), reaching waters of Iceland, Greenland and Svalbard in the mid-2000s (Berge *et al.*, 2015; Nøttestad *et al.*, 2016). This has resulted in the development of new NEA mackerel fisheries and new distribution of quotas.

A combination of multiple spawning components and a wide ranging and changing distribution have led to a complex assessment system. The assessment is based on data from commercial catches from several fleets, as well as data on abundance, recruitment and biology from national and international scientific surveys including acoustic, trawl, and egg survey data. Acoustic and

trawl data are used to estimate an abundance index while egg survey data are used to estimate the spawning stock biomass (SSB) based on egg production methods. There are two main types of such methods, the annual egg production method (AEPM) that has been developed for species with determinate fecundity, and the daily egg production method (DEPM) that is more suitable for indeterminate spawners; however, the latter can also be applied to determinate spawners (Stratoudakis *et al.*, 2006; Armstrong and Witthames, 2012).

The fecundity type of NEA mackerel is a controversial issue. Traditionally, NEA mackerel has been assumed to be a determinate spawner (Morse, 1980; Rickman *et al.*, 2000) and accordingly the AEPM has been used (Lockwood *et al.*, 1981) for SSB estimations. However, there is evidence that it employs a mixed strategy between determinate and indeterminate fecundity (Greer-Walker *et al.*, 1994) and some authors have recommended the use of DEPM to estimate SSB (Priede and Watson, 1993; Fitzhugh *et al.*, 2012). Even though the AEPM is the method of choice for the assessment of the NEA mackerel stock (ICES, 2017b), since 2013 the DEPM has also been applied to provide SSB estimates for the southern NEA component (ICES, 2012). Fish reproductive strategy is species-specific, but spawning stocks or components of the same species can show different tactics adapted to the habitat characteristics (Potts and Wootton, 1984). Considering results of Jansen and Gislason (2013), it is likely that NEA mackerel spawning components are not isolated contingents and might modulate their reproductive tactic according to environmental conditions.

The main advantage of DEPM over AEPM is that it requires only a single egg survey, which is carried out during peak spawning. This gives significant savings on both survey costs and labour. On the other hand, DEPM requires the estimation of more complex reproduction parameters such as batch fecundity and spawning fraction, the latter still constituting the Achille's heel of these applications (Ganias, 2012). The successful application of the DEPM is facilitated by the daily synchronous spawning behaviour of the assessed species (Armstrong and Witthames, 2012) because synchronicity of spawning and estimation of mean spawning time are very helpful both for the ageing of postovulatory follicles (POFs) and the ageing of eggs for subsequent estimations of spawning fraction and daily egg production, respectively (Stratoudakis *et al.*, 2006). In species with daily spawning synchronicity, fish sampled at a given time of the day have distinct cohorts of POFs belonging to current (day-0) or preceding night's spawning events (day-1, day-2, etc.) instead of the continuum of POF degeneration stages that is typically observed when there is not synchronicity (Armstrong and Witthames, 2012).

Batch fecundity is usually estimated from ovaries that contain hydrated eggs (hydrated oocyte method; Hunter *et al.*, 1985), but in the case of NEA mackerel, fish at the hydration stage are difficult to obtain. It would thus be helpful if batch fecundity could also be estimated from non-hydrated females, e.g. based on germinal vesicle migration oocytes (Armstrong and Witthames, 2012). An alternative way to estimate batch fecundity in non-hydrated specimens could be the analysis of oocyte size frequency distribution to detect the hiatus located between the advanced batch and the less developed oocytes (Ganias *et al.*, 2010).

Studies on daily spawning pattern, based on both back-calculation of spawning time from plankton samples and captivity experiments (Ferraro, 1980; Walsh and Johnstone, 1992; Nichols and Warnes, 1993), suggest that spawning of Western

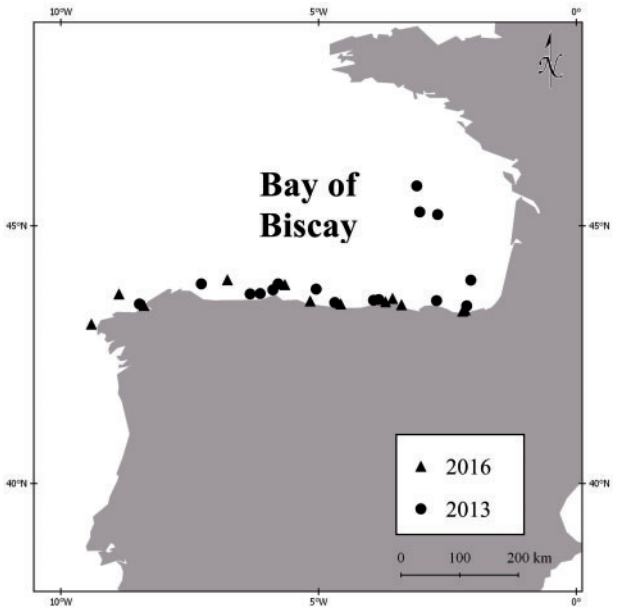

Figure 1. Map of the survey area showing the sampling locations of adult Atlantic mackerel samples for 2013 and 2016.

NEA mackerel is not synchronized and individuals can spawn at any time of day or night. This contrasts with the Japanese chub mackerel (*S. japonicus*) caught off the Izu islands (34o 20'–34o 40' N), which exhibits daily synchronicity, spawning from 22.00 to 24.00 h (Yamada *et al.*, 1998). The present study focuses on elucidating daily spawning dynamics in the southern NEA mackerel and attempts to describe its implications for batch fecundity estimations. This is done through the analysis of the daily pattern in the formation of the spawning batch in imminent spawning stages. Results are discussed within the framework of promoting the use of the DEPM in future assessments of the SSB of NEA mackerel.

Material and methods

Adult mackerel samples were collected in 2013 and 2016 in the Bay of Biscay during the spring acoustic survey for pelagic commercial species assessment (PELACUS) carried out by the Spanish Institute of Oceanography (IEO) (Figure 1). Sampling was performed during the peak of Atlantic mackerel spawning season in the Northwest Iberian Peninsula (March–April; Villamor *et al.* (1997) and references therein) within the framework of the triennial estimation of its SSB. Samples were collected both by research vessel and from the commercial fishery (Figure 1). In the research vessel, samples were processed onboard immediately after capture according to the protocols of the ICES Working Group on Mackerel and Horse Mackerel Egg Surveys (WGMEGGS; ICES, 2016a) while commercial samples were initially placed on ice and were processed as soon as possible after being landed at the harbour. Both, research and commercial samples, were processed in the same manner; specimens were measured for total length, TL (cm), eviscerated weight, W_{EV} (g), and were sexed. Ovaries were removed and fixed in flasks with 3.6% neutral buffered formaldehyde (NBF) and were then transferred at IEO where they were weighed (W_G; 0.01 g) and stored either in NBF or in 70% EtOH.

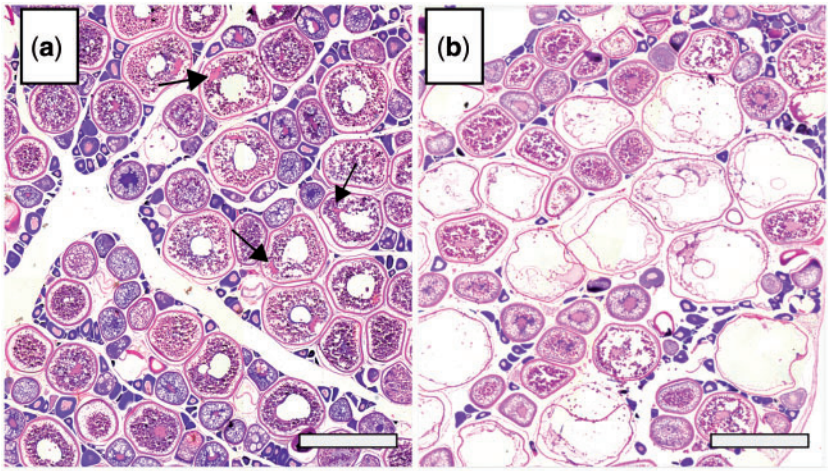

Figure 2. Photomicrographs of southern NEA mackerel ovary slides, showing germinal vesicle migration (a) and hydrated stages (b). Arrows indicate the position of the germinal vesicle. Scale bar= 1 mm.

Table 1. Daily distribution of Atlantic mackerel ovarian samples from both commercial and research surveys in 2013 and 2016.

	2013		2016		
Time	**Commercial**	**Research**	**Commercial**	**Research**	**Total**
1–2	3	–	–	–	3
2–3	–	–	4	–	4
6–7	–	–	6	–	6
7–8	–		–	3	3
8–9	–	28	–	3	31
9–10	–	2	–	6	8
10–11	–	–	4	–	4
11–12	–	–	–	4	4
12–13	–	18	–	–	18
13–14	–	14	–	–	14
14–15	–	1	–	–	1
15–16	–	–	–	6	6
16–17	–	3	–	–	3
19–20	20	–	–	–	20
23–24	6	–	–	–	6
Total	29	66	14	22	131

In the laboratory, the ovaries were initially processed histologically, using standard procedures (paraffin embedding; 4 µm sections; haematoxylin/eosin staining). Histological slides were examined and scored for the most advanced stage of oocytes present in the ovary. Our analysis was focused on imminent spawners from the stage of germinal vesicle migration (GVM; Figure 2a) to hydration (HYD; Figure 2b). A total of 131 specimens (95 from 2013 and 36 from 2016) were selected in such a way as to cover both histological stages (43 GVM and 83 HYD ovaries) and the widest possible range of sampling hours (Table 1). Concerning the preservation medium, 14 ovaries from 2013 and all ovaries from 2016 had been stored in in NBF while the remaining ovaries from 2013 ($n = 81$) had been stored in 70% EtOH.

At later stage, ovaries were processed gravimetrically using whole mount procedures. Whole mount processing was performed according to ICES (2016a) protocol and briefly consisted of: (i) dissecting a small portion of ovarian tissue and weighing it (W_{SS}; 0.001 g), (ii) washing the subsample into a 400 µm mesh sieve to discard pre-vitellogenic and smaller vitellogenic oocytes that would be redundant for the analysis, (iii) processing the tissue under a stereo-microscope (Nikon SMZ 1500) to separate oocytes and spread them in a mono-layer, and (iv) capturing the whole mount at 8x magnification with a camera (Nikon DXM 1200 F) fitted to the stereo-microscope. In each image, the diameter of the oocytes was measured according to Thorsen and Kjesbu (2001). Oocyte size frequency distributions were analysed to define distinct normally distributed groups within the multimodal size distributions (Figure 3). For all specimens, the analysis revealed the existence of an advanced oocyte mode (AM), which could largely or partially overlap (Figure 3a) or be completely separated (Figure 3b) from the oocytes of the subsequent mode. A hiatus was considered to occur when the upper and lower tails of the two adjacent density curves did not overlap (Figure 3b). In cases of overlap, the number (N_{AM}) and the modal size (OD_{AM}) of oocytes from the most advanced mode were estimated through the Bhattacharya's method (Bhattacharya, 1967), which resolved separate normally distributed groups within the multimodal size distributions (for more details on this analysis see Ganias *et al.* 2010). The maximum oocyte size was also calculated.

The gravimetric method was then used to estimate the fecundity (F_{AM}) and relative fecundity (RF_{AM}) for the advanced mode through the formulas:

$$F_{AM} = N_{AM} \times \ W_G / W_{SS} \quad (1)$$

and

$$RF_{AM} = F_{AM} / W_{EV}. \quad (2)$$

The daily spawning pattern of NEA mackerel was examined through analysing (i) the daily prevalence of hiatus amongst imminent spawners and (ii) variability in OD_{AM} in females exhibiting hiatus. The daily prevalence of hiatus was analysed through modelling its dichotomous presence/absence data as an anisotropic bivariate function (f(.)) of sampling time, using generalized additive models (GAMs) with a binomial error distribution and a logit link (Wood, 2003). Variability in OD_{AM} was analysed with sampling time as a smooth term again by means GAMs

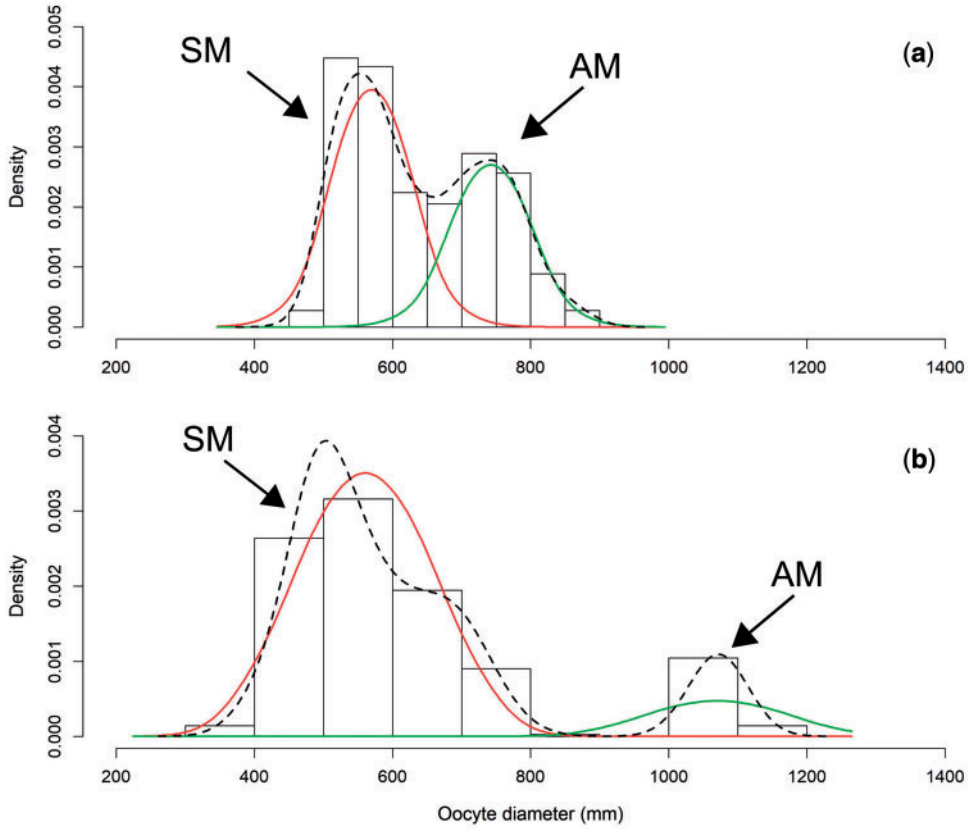

Figure 3. Illustrated criteria for the absence (a) and presence (b) of size hiatus in the oocyte size frequency distribution of Atlantic mackerel. The dashed line is the nonparametric density estimate while the red and green solid curves correspond to the individual Gaussian density components of the subsequent (SM) and the advanced (AM) oocyte modes, respectively.

using TL, RF_{AM} (linear terms), and preservation medium and type of fishery (factorial terms) as covariates. In both models, sampling time was included in the model using a penalized cyclic regression spline (CC) smoother limited to 12 knots ($k = 12$).

Results

A hiatus in the oocyte size distribution was established between the advanced mode and the remaining oocyte modes at 850–900 μm (Figure 4). The hiatus became wider as the advanced mode was gaining size while the subsequent oocyte mode was almost always smaller than 900 μm. The hiatus was mostly prominent at the HYD stage, occurring in 61 out of the 88 hydrated females (70%). However, there was also a number of GVM stage females (8 out of 42; 19%) showing a hiatus in their oocyte size frequency distribution. There were also four GMV females where the proportion of >900 μm oocytes in the whole mount was very small (<1%). Consequently, these oocytes were either scarce or even completely absent in histological sections and it was impossible to determine whether they were hydrated, ovulated or atretic. Even if these specimens appear in the upper bound of the size frequency distribution plot amongst those exhibiting hiatus (Figure 4) they were marked as not having hiatus.

Generalized additive model analysis showed that sampling time was a significant ($p < 0.001$) predictor of the occurrence of size hiatus (P_{HIATUS}) in the size frequency distribution (Figure 5), even if the percentage of deviance explained in the model was rather small (15.3%). The smoothed curve of the additive sampling time on predicted P_{HIATUS} showed that the probability steadily increased from almost zero at midnight to a maximum value of ca. 80% at early afternoon (13:00–15:00) and then it dropped again towards midnight (Figure 5).

In females showing hiatus there was no significant relationship between the relative fecundity of the advanced mode (RF_{AM}) and sampling time (Figure 6). This consistency clearly suggested that the advanced mode in these females corresponded to the spawning batch, i.e. the oocytes to be released during the next spawning episode. Thus, RF_{AM} in these females was considered to reflect relative batch fecundity (RF_B). Mean RF_B was 49.6 oocytes/g (SE±: 3.5) and did not differ significantly between HYD and GVM stage females ($p > 0.1$). On the other hand, "non-hiatus" females exhibited higher RF_{AM} values (mean = 204.7 oocytes/g, SE±: 22.2). As shown in Figure 6, these values showed an hourly pattern which was concomitant to the daily prevalence of hiatus described in the previous paragraph. Specifically, RF_{AM} in these individuals steadily decreased towards noon and increased back towards midnight.

Given that the spawning batch is fixed in females with hiatus, it was tested whether mean diameter of the spawning batch oocytes (OD_{AM}) in these females also exhibited a pattern with sampling time. GAM analysis showed that sampling time was a significant predictor of OD_{AM} ($p < 0.001$) (Figure 7). However, given the limited number of evening samples this result was not robust. In addition, OD_{AM} in commercial samples was

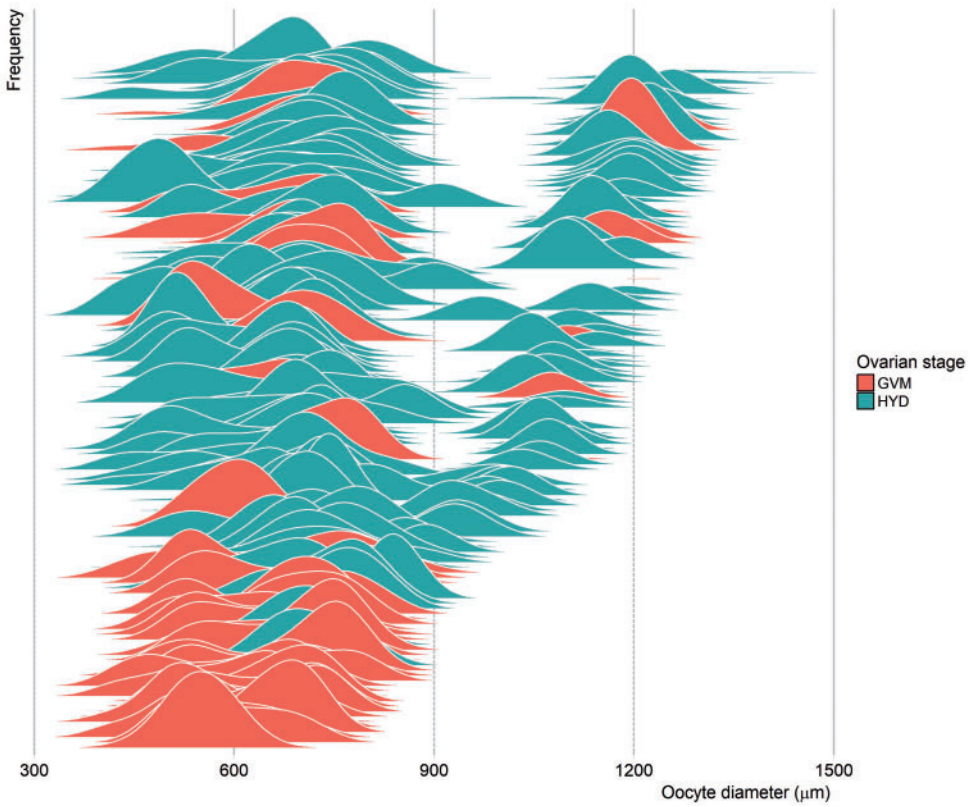

Figure 4. Oocyte size frequency distributions from 131 mackerels in ascending maximum oocyte size for germinal vesicle migration (GVM) and hydrated (HYD) ovaries.

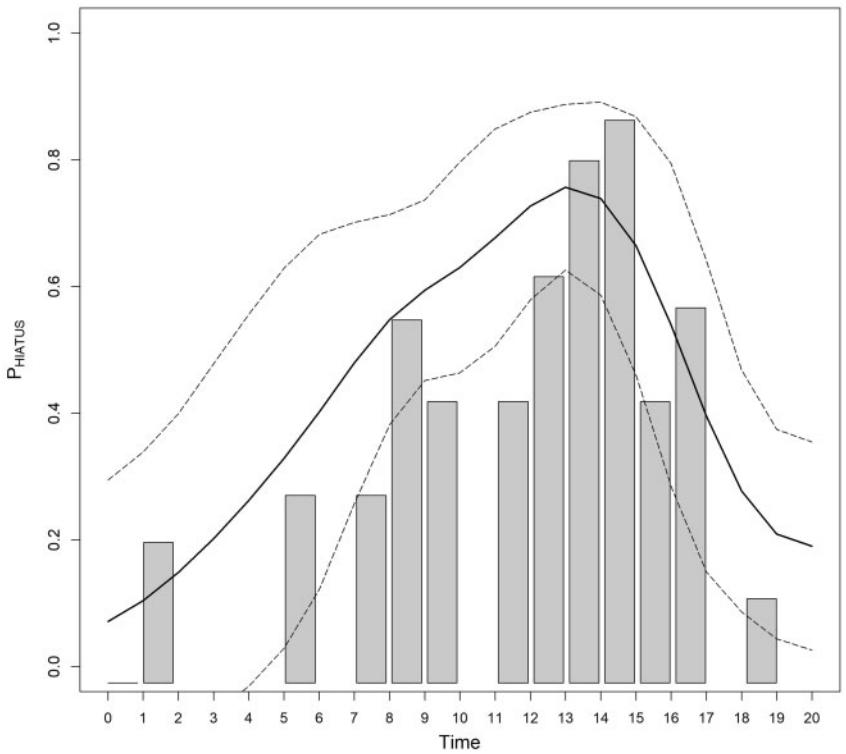

Figure 5. Generalized Additive Model (GAM) predicted probability of hiatus (P_{HIATUS}) between the advanced mode and the remaining oocytes with sampling time. Barplot shows the realized fractions. Confidence intervals (dotted lines) are also provided.

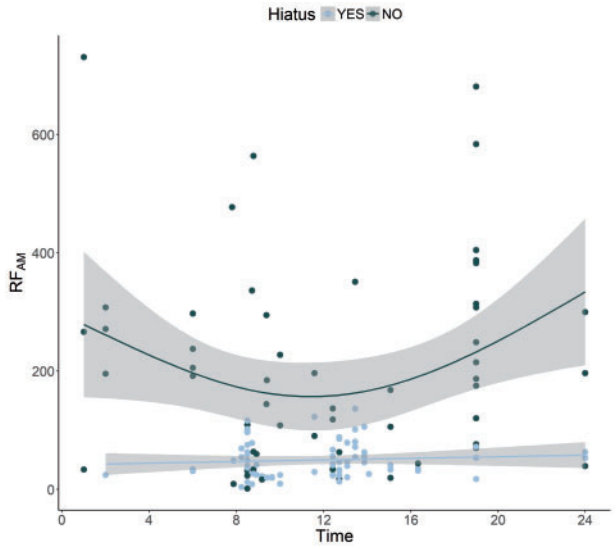

Figure 6. Hourly variation of relative fecundity of the advanced mode of oocytes (RF_{AM}) in females with and without hiatus between the advanced batch and the remaining oocytes. Smoothed conditional means lines [and 95% confidence intervals (shaded)] are also shown for both relationships.

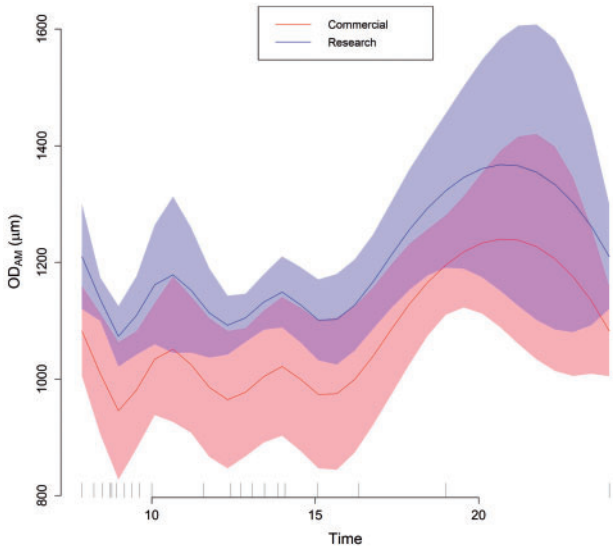

Figure 7. GAM predicted advanced oocyte mode size (OD_{AM}) with sampling time for commercial and research vessel samples. Shades areas = 95% confidence intervals.

significantly lower to research samples ($p < 0.05$) (Figure 6). None of the remaining factors analysed in the GAM, i.e. preservation medium, total fish length, and RF_B affected OD_{AM} significantly (p values were higher than 0.1 in all cases) and were subsequently dropped from the model. The deviance explained by the final model, only including the effects of sampling time and fishery type, was 24%.

Discussion

The present study examines daily spawning dynamics in field collected NEA mackerel, *Scomber scombrus*, focusing on ovarian stages beyond the onset of final oocyte maturation (FOM), i.e. from early germinal vesicle migration (GVM) to hydration (HYD). Under experimental conditions, FOM for captive chub mackerel, *Scomber japonicus*, at 18–19°C lasts about 12–18 h (Shiraishi *et al.*, 2009). Given that the temperatures in the present study ranged between 12 and 14°C (unpublished data), even after accounting for the fact that FOM varies with temperature [decreasing by about 30% for every 10°C (Kurita *et al.*, 2011)], it is likely that duration of the developmental stages used in the present study did not exceed 1 day. Hence, as samples were collected over a 24-h cycle, if present, diel patterns in relation to spawning should be detectable.

The advanced mode of oocytes was shown to separate in size from the bulk of smaller oocytes at the transition between the GVM stage and hydration. This separation took place at 850–900 μm with the diameter of the advanced mode reaching up to 1 200 μm. The hiatus position is similar to that reported for the hydration stage of the Adriatic population of *S. scombrus* by Meneghesso *et al.* (2013) where a mode with diameter larger than 860 μm was recognizable in hydrated ovaries. However, in the present study the presence of hiatus was not an exclusive, neither distinctive, feature of the hydration stage. Amongst our specimens there were both hydrated females without a hiatus and few GVM females exhibiting hiatus. A widest size gap between the advanced mode and smaller oocytes, leading to clearer differences between hydration and previous stages, is reported by Shiraishi *et al.* (2005) for chub mackerel where the hiatus is formulated at a quite smaller size range (~650 μm). Such differences in the structure of the oocyte size frequency distribution might reflect differences in the factors shaping spawning dynamics such as spawning interval and oocyte growth rate (Ganias *et al.*, 2015). Indeed, chub mackerel off Kyushu, Japan spawns almost every 6 days (Shiraishi *et al.*, 2009), while NEA mackerel seems to spawn more frequently, even at daily intervals (Priede and Watson 1993). Such implications are of direct importance to an ongoing collaborative work within the framework of the ICES WGALES working group, which intends to improve estimates of spawning frequency in fish stocks—including the NEA mackerel stock—assessed by means of egg production methods (ICES, 2016b).

The relative fecundity of the advanced mode, RF_{AM}, in females where a hiatus was present did not vary significantly with sampling time and was equal to 49, 6 oocytes/g (SE±: 3.5). This value is similar to the pooled estimate of 53.05 oocytes/g of relative batch fecundity reported by Watson *et al.* (1992) for the western component (51–55° North) of NEA mackerel stock. Therefore, we can safely conclude that the advanced oocyte mode in females with hiatus corresponds to the spawning batch, i.e. the oocytes to be spawned in the next spawning event. On the other hand, RF_{AM} in females without hiatus, even when these were at the hydration stage, was higher by orders of magnitude, surpassing in some cases the value of 400 oocytes/g. Obviously, this is due to a higher number of coexisting batches inside the advanced mode. RF_{AM} values in these females showed an hourly pattern, which was concomitant to the daily prevalence of hiatus. Specifically, RF_{AM} in these specimens steadily decreased towards noon and increased back towards midnight showing that there is a time window during the 24-h cycle that the advanced mode tends to separate from the smaller oocytes, to formulate the spawning batch.

We thus conclude that batch fecundity in NEA mackerel cannot be estimated in females with no well-established hiatus between the spawning batch and the remaining oocytes even if these are at the

hydration stage. A similar analysis in Atlantic horse mackerel, *Trachurus trachurus*, showed that non-hydrated females cannot be used to estimate batch fecundity (Ganias *et al.*, 2017). However, differently from NEA mackerel, in A. horse mackerel the spawning batch is well separated in all hydrated females, suggesting that the hydrated oocyte method (Hunter *et al.* 1985) can be safely applied. In other batch spawning fish, with more discrete oocyte size frequency distributions, like sardines (Ganias *et al.*, 2010) and anchovies (Ferreri *et al.*, 2016), the spawning batch can be identified and enumerated even at previous developmental stages, e.g. since mid-vitellogenesis.

Even though specimens with a hiatus almost occurred throughout the day, there was an increase in their prevalence at noon and late afternoon showing a clear diel pattern. In that respect, the separation of the spawning mode from the diverse cohorts of smaller oocytes was synchronized amongst imminent spawners. Synchronicity in preovulatory oocyte growth provides evidence for the existence of daily spawning synchronicity in southern NEA mackerel, which contrasts to findings for the western component of the same stock. In particular, Walsh and Johnstone (1992) report that spawning by captive Atlantic mackerel—kept under the same ambient conditions (photoperiod, temperature) to wild populations at latitude 50–60° North—can occur at any time of day or night and is not synchronized. Moreover, analysis of ages of eggs in the central spawning area (51–55° North) (Nichols and Warnes, 1993) indicated that spawning occurred throughout the 24-h cycle but with a slight bias towards daytime. These differences might be attributed to respective differences in ambient light regime encountered by mackerel in the northern range of NEA mackerel distribution against light regime in the present survey area (43–45° North), which represents its southernmost range. The pattern of spawning at any time of day is usual for northern demersal fish [see Walsh and Johnstone (1992) and references therein] while most temperate and sub-tropical pelagic fish are crepuscular spawners with limited daily spawning periods (Ganias *et al.*, 2014). It could thus be hypothesized that the observed shift in NEA mackerel diel spawning pattern between the two areas is due to latitudinal clines in photoperiod. Specifically, the larger deviations of L:D ratios exhibited at higher latitudes (longer duration of both day and night) offer wider environmental windows of appropriate light cues for oocyte recruitment to FOM, resulting in lack of synchronicity of spawning at the northern range of NEA mackerel distribution.

The modal oocyte diameter of the spawning batch, OD_{AM}, exhibited a similar pattern with sampling time to the one described for the hiatus, but the relationship was less robust. Hourly pattern in the OD_{AM} of imminent spawners has been described for fishes with daily spawning synchronicity like the Atlantic sardine (Ganias *et al.*, 2011) or the Atlantic horse mackerel (Mouchlianitis *et al.*, 2018), corroborating evidence that NEA mackerel also exhibits daily spawning synchronicity. Diel variability of OD_{AM} in mackerel was less prominent maybe because its spawning act is less synchronized in the population compared to sardines, which form ephemeral spawning aggregations (Ganias *et al.*, 2014). Additional sources of variability in OD_{AM} such as the observed differences in the preservation protocol between commercial and research samples or/and seasonal effects on oocyte size might have further mitigated its pattern with sampling time. For example, Greer-Walker *et al.* (1994) report that the diameter of migratory nucleus oocytes in A. mackerel decreases with the increasing portion of the pre-spawning standing stock of vitellogenic oocytes spawned, suggesting seasonal decline in oocyte size with the progress of spawning. Such pattern, has also been described for laboratory reared Atlantic cod (*Gadus morhua*; Kjesbu 1989).

The present study contributes to a better understanding of the daily spawning dynamics of southern NEA mackerel with implications for the estimation of batch fecundity. Our findings are anticipated to facilitate future applications of the DEPM, which is advantageous over the AEPM—i.e. the method that is currently applied for the assessment of the NEA mackerel stock (ICES, 2017b)—since it requires only single egg surveys thus decreasing a lot both survey costs and labour. Although some differences in reproductive tactics related to environmental conditions might exist among the different NEA mackerel spawning components (e.g. oocyte growth rates, spawning frequency, and energetics), the results of this study can be extrapolated and compared to the rest of spawning areas.

Even if the present study suggests daily synchronicity of spawning for southern NEA mackerel it does not explore the realized daily spawning activity of the population. For example, it does not provide an estimate of the mean and range of daily spawning time. Optimally this is done through testing the temporal pattern of preovulatory, running, and early postovulatory stages (e.g. Basilone *et al.*, 2015). Therefore, to go on with this estimation, a good assessment of early POF stages and an intensification of sampling during the period of the day when spawning is postulated to occur (noon to early morning) is strongly recommended.

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