

Life-history traits and population decline of the Atlantic mackerel *Scomber scombrus* in the Adriatic Sea

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This study investigated demographic structure and reproductive characteristics of the Atlantic mackerel *Scomber scombrus*, in relation to landing trends in the northern-central Adriatic Sea. Results highlighted the occurrence of only small-sized and young-age individuals, and a marked decline from the 1990s to the present in maximum age (from 8 to 3 years) and total length (L_T ; from 420 to 360 mm). Fecundity ranged between 40 000 and 190 000 eggs, and was related to female L_T . High levels of atresia implied lower values of actual fecundity. Sexual maturity was attained by 72.8% of individuals in their first year of life at 200 mm. The reduction in maximum L_T resulted in a marked decline in the population egg production, while the reduction in maximum age implied that females participated in fewer spawning events.

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Key words: age; fecundity; gonad; otolith; reproduction.

INTRODUCTION

The knowledge of biological characteristics of exploited species is critical to an understanding of the effects of fishing pressure on populations and for development of effective management strategies (Trippel, 1999). Estimating fecundity and sexual maturity of exploited stocks is therefore considered a staple of fishery science (Hunter *et al.*, 1992). Fecundity and its relationship with female size represent a key piece of information for population dynamics and for estimating spawning stock biomass (Hunter *et al.*, 1992; Witthames *et al.*, 2009). The size and age frequency distribution of a stock, delineating its population structure, may highlight, for instance, depletion of large and old individuals or juveniles, and therefore help in identifying management priorities.

Fishing pressure, selectively removing larger individuals, may drive evolutionary or phenotypic changes of life-history traits, with more heavily exploited stocks showing smaller size and younger age and attaining sexual maturity earlier than less-exploited ones (Rochet, 1998; Hamilton *et al.*, 2007; Hutchings & Fraser, 2008). The reduction in size of reproductively active females causes a decrease in egg production

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per individual, given the exponential relationship between fecundity and fish size (Jennings *et al.*, 2001; Evans *et al.*, 2008). Changes in demography may make a stock more vulnerable not only to exploitation but also to harsh environmental conditions. Species with a long life span and multiple spawning events and seasons may be able to cope better with unpredictable variations in environmental conditions than short-lived, semelparous species (Hutchings, 2002). Therefore, a reduction in the number of spawning occasions per female, as a consequence of a reduction in longevity, may have consequences for the overall reproductive success of a stock.

The Atlantic mackerel *Scomber scombrus* L. 1758 is a pelagic schooling species abundant in cold and temperate waters of the northern Atlantic Ocean and Mediterranean Sea (Froese & Pauly, 2012). *Scomber scombrus* is a valuable commercial species, targeted by purse seines, midwater trawls and longlines (FAO-FIGIS, 2005). The catch of this species declined in the Adriatic Sea at the beginning of the 1970s (Sinovčić, 2001; Azzurro *et al.*, 2011; Barausse *et al.*, 2011).

This study aimed to investigate the biology of *S. scombrus* from one of the most exploited Mediterranean areas, the northern-central Adriatic Sea, comparing the temporal development in (1) landings, (2) population structure in terms of size, sex and age, and (3) estimated reproductive traits, specifically size and age at sexual maturity, and fecundity.

MATERIALS AND METHODS

STUDY AREA

The Adriatic Sea (Fig. 1) is a small basin (800 km long; maximum width of 210 km) of the Mediterranean Sea, located between the Italian and Balkan Peninsulas, connected southwards with the Mediterranean Sea through the Otranto Channel (Russo & Artegiani, 1996). The northern part is characterized by shallow waters (average depth of 30 m), marked variability in salinity (35–38) and water temperature (5–27° C), a noteworthy river runoff, mainly represented by the Po River on the western side (Russo & Artegiani, 1996) and the highest levels of plankton biomass in the whole Mediterranean Sea (Fonda Umani, 1996). The general circulation of the northern-central Adriatic Sea is cyclonic, represented by a northward flow along the eastern coast, and a southern one, that runs on the opposite side of the basin (Artegiani *et al.*, 1997).

FISHERY DATA

Fishery data include official landing statistics of the Chioggia fishing fleet, the major fleet of the northern Adriatic Sea (Barausse *et al.*, 2011; CLODIA, 2013). Total fishing capacity (GRT, gross registered tonnage) of the Chioggia fishing fleet from 1951 to 2010 (from Barausse *et al.*, 2011 and CLODIA, 2013) was used as a proxy of fishing effort, as estimates of fishing effort were not available. Data on the fishing capacity of midwater trawls, the main fishing gear catching scombrids, were available from 1991. In fishery data, landings of *S. scombrus* and Atlantic chub mackerel *Scomber colias* Gmelin 1789 are pooled, as they were recorded together until 1997. On average, however, *S. scombrus* represents 89.2% of the total scombrid landings, justifying the assumption that total catches reflect *S. scombrus* catches [data from 1997 to 2010 (CLODIA, 2013)].

SAMPLE COLLECTION AND PROCESSING

Monthly samples were collected from two areas of the northern-central Adriatic Sea (Fig. 1). Fresh samples were collected directly from fishermen of the Chioggia and Ancona

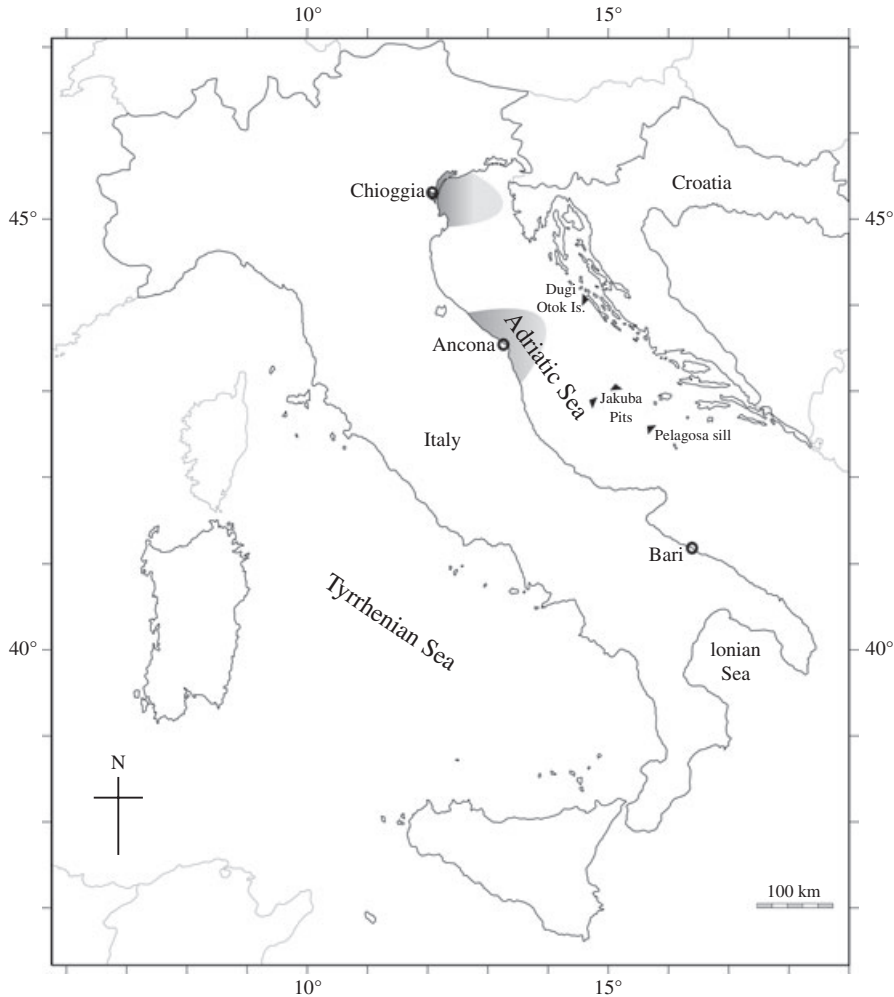


FIG. 1. Map of the Adriatic Sea showing the main fishing grounds ○ of fleets from harbours in Chioggia and Ancona (■).

fleets. Capture area and fishing technique were recorded during each sampling. A total of 1156 specimens were collected from the Chioggia fleet between September 2009 and December 2010 with longlines and trawling gears (otter and midwater trawls). Samples from Ancona ($n = 585$) were collected between January and December 2010 exclusively from otter trawls (about 20 m length, 82 t GRT). Owing to the ban on trawling in August, no samples from Ancona were available for this month.

Fish were measured (total length, L_T mm), weighed (to the nearest 0.01 g, M) and sexed through direct examination of the gonads after dissection. Macroscopic stages of sexual maturity were assigned according to Holden & Raitt (1974) (Table SI, Supporting Information) and standard ICES (2007) scales. The main results did not differ between these two scales, but only results from the Holden & Raitt (1974) scale are shown, as this scale allowed the maturation process to be followed in greater detail.

Gonads were excised and weighed (to the nearest 0.01 g, M_G), to calculate the gonadosomatic index ($I_G = 100 M_G M^{-1}$), and preserved in Dietrich solution (900 ml of distilled water, 450 ml of 95% ethanol, 150 ml of 40% formaldehyde and 30 ml of acetic acid) for

histological analyses. In the case of ripe ovaries, right and left gonads were excised, and separately weighed. One of these was then preserved in formaldehyde (7% in filtered sea water) for fecundity estimates, and the other one was stored in Dietrich solution for histological analyses. As oocyte numbers and size frequency distribution do not usually differ between left and right ovaries (Hunter *et al.*, 1985), the ovary used for fecundity estimates was chosen randomly. **Sagittal otoliths** were extracted, cleaned in alcohol (70%) and preserved dry for ageing.

Histological analyses were carried out on 113 samples (46 males and 67 females) to evaluate gonadal development throughout the year (minimum of three samples per sex and month) and to validate the macroscopic stage attribution. Histological analyses on ovaries used for fecundity estimates were aimed at evaluating the presence of post-ovulatory follicles and atretic oocytes (indicating the occurrence of a past spawning event). All samples, conserved in the fixative for at least 20 days, were embedded in paraplast, cut in transverse serial sections (7 µm) and mounted on slides. Slides were then stained with Harrys' haematoxylin and eosin (Pearse, 1985).

FECUNDITY

Fecundity (F) was estimated using 32 samples caught during the spawning season (11 females in January, 10 in February, seven in March and four in April; the sample was representative of the size range of ripe females available in each month), according to the gravimetric method (Hunter *et al.*, 1985), a standard procedure used also for scombrids (ICES, 2010). After at least 20 days of fixation in formaldehyde, a sub-sample of each ovary (100–131 mg), representing 1–2% of the total gonad mass, was weighed and immersed in commercial sodium hypochlorite [30% in filtered sea water (Choy, 1985)] for 3 min to facilitate the disintegration of ovarian lamellae, and then immersed in filtered sea water in a Petri dish. Oocytes were manually separated and photographed with a Leica DFC 420 camera (www.leica-microsystems.com), keeping the camera settings standard for all images. Oocyte diameter was taken semi-automatically with the National Instruments IMAQ Vision Builder 6 software (www.ni.com). The software counts and measures all objects above a specific threshold size that can be set by the operator. The operator can manually modify or delete objects on the image, if they represent background noise. The reliability of measurements was validated by comparing the diameters of a sphere of known size, photographed at various magnifications ($n = 11$). Repeatability of measurements taken with Image Q was tested according to the method of Becker (1984), performing three repeated measurements on a sub-sample of 62 eggs. The treatment with sodium hypochlorite was validated by measuring 100 oocytes before and after the treatment. Finally, a comparison between the numbers of oocytes from different parts of the ovary was performed using four ovaries. As found in other species, no consistent trend was present in oocyte number or size across the ovary (Witthames *et al.*, 2009); therefore, in the other samples the portion of ovary used for the analyses was randomly chosen. Pre-vitellogenic oocytes were excluded from the counts. A threshold size of 123 µm was set as the minimum size of vitellogenic oocytes, based on direct measurements and in accordance with the minimum diameter of vitellogenic oocytes reported for *S. scombrus* in the Atlantic Ocean (Greer Walker *et al.*, 1994). The number of vitellogenic oocytes per female (N) was estimated as: $N = n M_{\text{sub}}^{-1} M_G$, with n = number of oocytes counted in the sub-sample and M_{sub} = mass of the sub-sample. The number of vitellogenic oocytes was calculated correcting for the change in mass due to fixation of the gonads.

AGE

Age was estimated by counting growth zones (annuli) on both sagittal otoliths of a random sub-sample from 1165 samples (**684 specimens from Chioggia** and **481 specimens** from Ancona). The annular pattern was observed under reflected light against a dark background at $\times 10$ – 25 magnification, with otoliths immersed in ethanol (70%), generally with the sulcus acusticus face down. Each year of age (annulus) was assigned by counting the hyaline zones. In order to confirm the annual deposition of the first annulus, micro-increment counts were conducted on a sub-sample of 17 young-of-the-year (age 0+ years) *S. scombrus*, assuming

daily periodicity of micro-increments validated elsewhere (Mendiola & Alvarez, 2008). Moreover, periodicity in the deposition of hyaline and opaque zones was analysed by calculating the monthly percentage of the hyaline and opaque edge throughout the year. The first year was assigned to the central opaque nucleus and the first hyaline zone immediately adjacent to it. When discontinuities in the hyaline zones were present along the perimeter of the otolith, as the otolith accretion is higher along the antero-posterior axis, the reading was done through the rostral and postrostral axes. For each otolith, two blind readings (*i.e.* without any additional information on, for example, L_T and date of capture) were made separately by two different readers. When agreement was not reached between the readers, a third blind reading was done. The index of average per cent error (I_{APE}) (Beamish & Fournier, 1981) and the mean c.v. (Chang, 1982) were calculated to estimate the relative precision between readings.

DATA ANALYSIS

Parametric or non-parametric tests were used according to data distribution and test assumptions. Statistical analyses were performed using STATISTICA 10 software (www.statsoft.com).

Minimum L_T and age at sexual maturity for each sex were estimated as the smallest or youngest female or male at stages 3 (ripening), 4 (ripe) or 5 (spent) during the breeding season. It was not possible to estimate the L_T and age at which 50% of individuals were sexually mature (L_{T50} , A_{50}) because very few small specimens were available, and most of the individuals were at stages 3–5 during the breeding season.

The number of oocytes was estimated as total number of oocytes and number of oocytes per single mode. Relative fecundity per female was then calculated as the number of oocytes g^{-1} body mass (without gonads) (Hunter *et al.*, 1992). To assess the type of fecundity, determined (no pre-vitellogenic oocytes start vitellogenesis during the spawning season and potential annual fecundity is determined prior to spawning) or undetermined [pre-vitellogenic oocytes are also recruited after the beginning of the breeding season (Murua & Saborido-Rey, 2003)], variation in the number of vitellogenic oocytes (ln transformed) was analysed using ANCOVA, with female L_T (ln transformed) as covariate and month (January to March) as fixed factor. Some ovaries collected in April still contained large numbers of small vitellogenic oocytes. In these ovaries, it can be reasonably assumed that oocytes in early stages of vitellogenesis will be reabsorbed as the vitellogenesis period is rather long [140–154 days (Greer Walker *et al.*, 1994)], and the spawning season was almost over, as most females were spent. Two estimates of relative fecundity were calculated: potential fecundity and actual (*i.e.* realized) fecundity. Relative potential annual fecundity was estimated as the number of vitellogenic oocytes at the beginning of the breeding season (January samples) uncorrected for atretic losses (Hunter *et al.*, 1992). One female with post-ovulatory follicles (proof of a recent spawning) was excluded from the analysis (ICES, 2006). Relative actual fecundity was estimated by subtracting the mean relative number of oocytes in early vitellogenesis of samples collected in April (assumed to be reabsorbed), from the mean relative number of oocytes estimated from January samples (at the beginning of the breeding season). The rate of atresia was estimated as the ratio between these two values. Potential annual fecundity and actual fecundity were then estimated by multiplying the relative fecundity with the mass ($M - M_G$) of mature females sampled during the breeding season. The power function of the L_T and fecundity relationship (Jennings *et al.*, 2001) was then calculated.

RESULTS

FISHERY DATA

Fishery data from 1951 to 2010 showed a massive decline in *S. scombrus* landings (corrected by fishing capacity) by the beginning of the 1970s, a slight recovery from

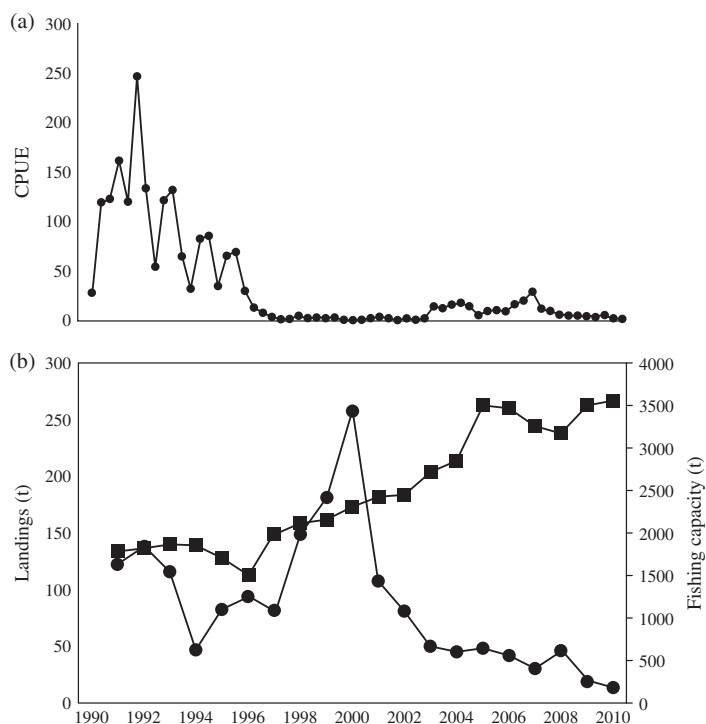


FIG. 2. Time series of landings of *Scomber scombrus* from the Chioggia fishing fleet. (a) Catch per unit of effort (CPUE) from 1951 to 2010, landing data have been corrected for total fishing capacity. (b) Landings (●) and fishing capacity (■) of midwater trawls from 1991 to 2010.

1990 to 2000 and then a new decline from 2001 onwards (Fig. 2). From 1996, total fishing capacity of midwater trawls increased [Fig. 2(b)].

POPULATION STRUCTURE

Scomber scombrus ranged from 134 to 358 mm L_T (Fig. 3), with no differences between sampling sites (independent samples t test, $t_{1739} = 0.75$, $P > 0.05$); therefore, all data were pooled for the analyses. Small-sized fish were scarcely represented in the whole sample, because of the minimum landing size of 180 mm L_T allowed in the Adriatic Sea.

Sex was assigned macroscopically to 1649 individuals, 927 females and 722 males, with a sex ratio significantly skewed towards females (sex ratio females: $\chi^2_1 = 25.48$, $P < 0.001$). Mean \pm S.D. L_T did not differ between sexes (males: 258.1 ± 27.4 mm; females: 256.8 ± 32.3 mm; Mann–Whitney U -test, $U = 328011.5$, $N_m = 722$, $N_f = 927$, $P > 0.05$). Sex was not determined in 90 specimens ($L_T = 183.4 \pm 40.2$ mm).

GONADO-SOMATIC INDEX AND MATURITY STAGES

I_G ranged from 0.01 to 9.20 in females (mean \pm S.D. = 256.8 ± 32.3 mm L_T , $n = 924$) and from < 0.01 to 8.58 in males (mean \pm S.D. = 258.1 ± 27.4 mm L_T ,

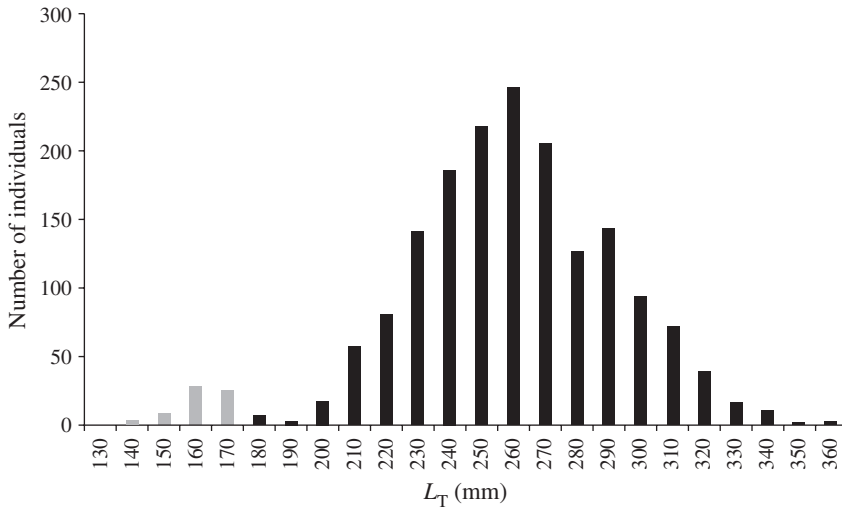


FIG. 3. Total length (L_T) frequency distribution of *Scomber scombrus* collected from the northern-central Adriatic Sea (■, individuals smaller than the minimum landing L_T ; ■, individuals \geq than the minimum landing size).

$n = 722$). In both sexes, I_G increased from November, reached the highest values in January and then decreased until March. Considering specimens collected from January to March, male and female I_G were higher in Ancona than in Chioggia (Fig. 4), and the difference was significant for females (Mann Whitney U -test, $U = 1319.0$, $N_A = 130$, $N_C = 39$, $P < 0.001$), and close to but not significant for males (Mann Whitney U -test, $U = 1597.0$, $N_A = 116$, $N_C = 35$, $P > 0.05$). Considering only samples from Ancona (as specimens caught in this area were almost exclusively ripe), I_G decreased significantly during the breeding season in both females ($F_{2,129} = 19.33$, $P < 0.001$) and males (Kruskal–Wallis test, $H_2 = 39.96$, $P < 0.001$). I_G did not correlate with L_T (Pearson correlation, males: $r = -0.07$, $n = 151$, $P > 0.05$; females: $r = -0.06$, $n = 169$, $P > 0.05$).

Maturity stages of gonads were assigned to 762 females and 617 males. Ripe gonads were observed mainly from January to March (Fig. S1, Supporting Information), and more frequently in samples from Ancona (in samples from January to March: 38% of males and 41% of females were ripe) than from Chioggia (11% of males and 23% of females were ripe), where fish gonads were mainly at stage 2 (maturing, $n = 36$) or 3 (ripening, $n = 22$). In April, most individuals were spent, indicating the end of the breeding season.

Considering the L_T frequency distribution and the maturity stages of individuals sampled during the spawning season, the minimum L_T of sexual maturity was 200 mm for both males and females.

HISTOLOGICAL ANALYSES

Females had asynchronous ovaries (Nagahama, 1983), with different stages of vitellogenic oocytes during the breeding season [Fig. 5(e)]. Atretic oocytes [Fig. 5(g)] were observed in five individuals caught in March, two in May and in all

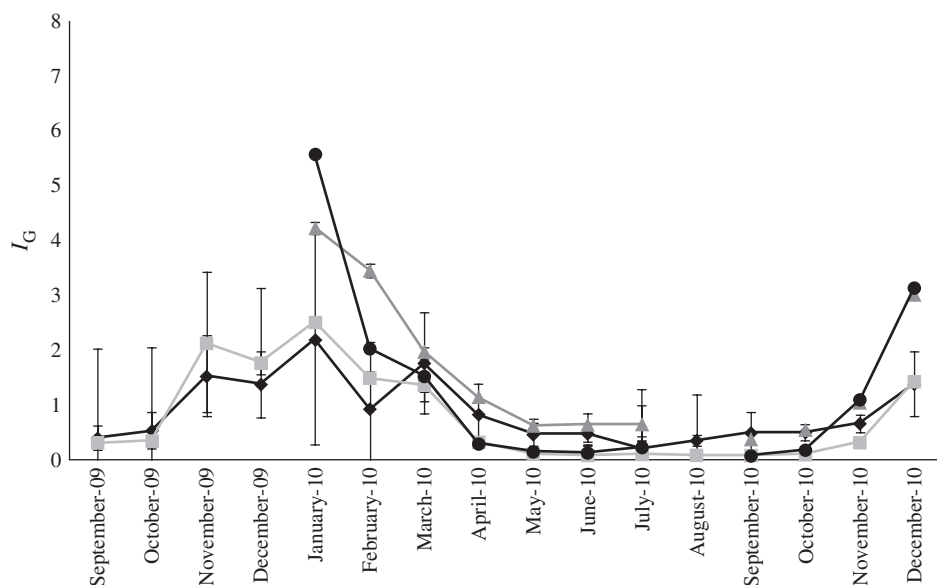


FIG. 4. Monthly values (mean \pm S.D.) of the gonado-somatic index (I_G) estimated for *Scomber scombrus* from Ancona (▲, females; ●, males) and Chioggia (◆, females; ■, males).

samples in April. Post-ovulatory follicles [Fig. 5(g)] were observed throughout the breeding season (January: $n = 2$; February: $n = 1$; March: $n = 1$), particularly in samples caught in April ($n = 7$). From May onwards, only pre-vitellogenic oocytes were present in ovaries [Fig. 5(a)], except in two samples in which remnant signs of atresia were still present. The vitellogenesis process was observed to start again in November [Fig. 5(c)].

Testes are of the unrestricted spermatogonial type described by Grier (1981), with spermatogonia distributed in the germinal epithelium along the whole testis length [Fig. 5(b), (d)]. Spermatogenesis started in July [Fig. 5(b), (d)] and during the breeding season few spermatocytes and spermatids could be recognized in the germinal epithelium, while lobule lumina and ducts were completely filled with sperm [Fig. 5(f), (h)]. Main testicular ducts and sperm ducts were multi-chambered, with walls comprising connective tissue and a single-layered flat epithelium.

Microscopic analyses confirmed the macroscopic attribution of the maturity stage in 46 out of 67 females and in 32 out of 46 males analysed. Conflicting results were found between stages 1 and 2, 2 and 3, and 5 and 2, outside the breeding season, and between 4 and 5 at the end of the breeding season.

FECUNDITY

Oocyte measurements were reliable (mean \pm S.E. = $1.08 \pm 3.28\%$) and highly repeatable ($r = 0.99 \pm 0.00$). No significant differences were found when measuring 100 oocytes before and after the treatment with sodium hypochlorite (t -test for paired comparison: $t_{99} = 0.90$, $P > 0.05$). Oocyte size frequency distribution showed two, more or less overlapping modes in all samples, corresponding respectively to oocytes in early (diameter = 123–600 μm) and late vitellogenesis (diameter = 600–

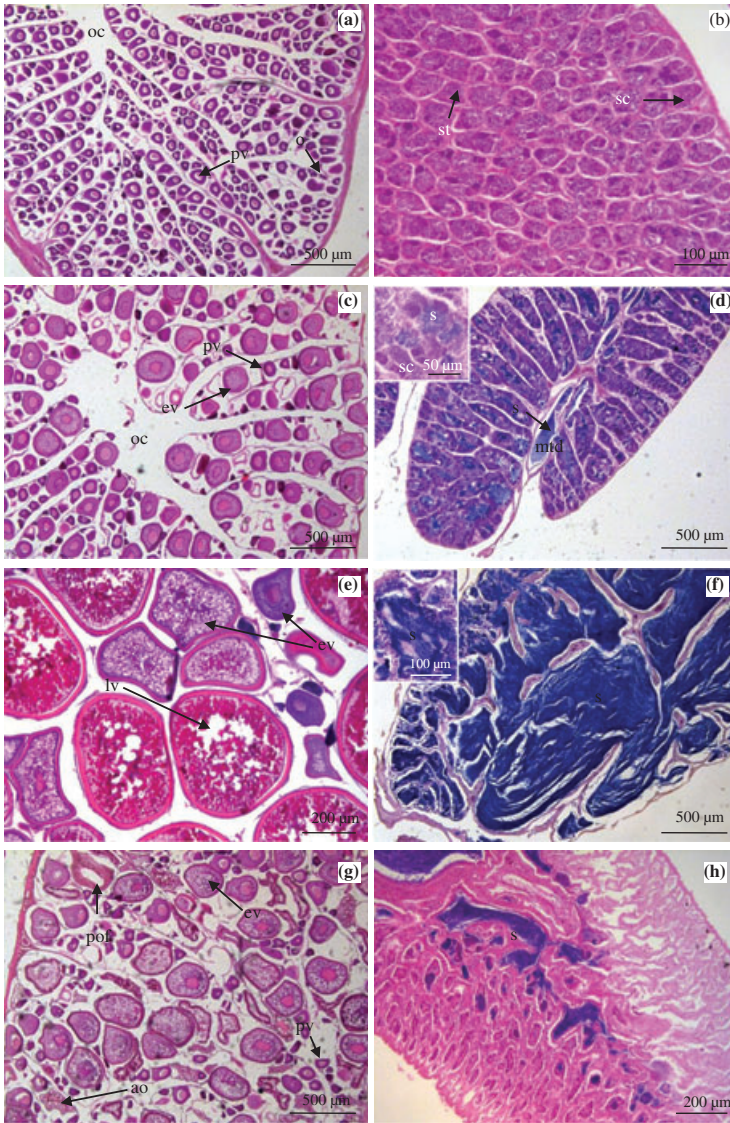


FIG. 5. Transverse histological sections of gonads of *Scomber scombrus*: (a) maturing ovary (total length, L_T , = 301 mm, June) showing only oocytogenesis and previtellogenic oocytes; (b) maturing testis (L_T = 309 mm, July) with spermatocytes and some spermatids in lobule epithelium; (c) ripening ovary (L_T = 215 mm, December) with pre-vitellogenic and early vitellogenic oocytes; (d) ripening testis (L_T = 206 mm, December) with sperm in lobule lumina and main testicular duct, and different stages of spermatogenesis in lobule epithelium, an enlargement of lobules is shown in the insert; (e) ripe ovary (L_T = 232 mm, January) with early and late-vitellogenic oocytes; (f) ripe testis (L_T = 237 mm, January) with lobule lumina and main testicular ducts completely filled with sperm, and few earlier stages of spermatogenesis in lobule epithelium, an enlargement of lobules is shown in the insert; (g) spent ovary (L_T = 278 mm, April) with still some early vitellogenic oocytes, post-ovulatory follicles, atretic oocytes and previtellogenic oocytes; (h) spent testis (L_T = 230 mm, April) with sperm still in the main testicular ducts and lobule lumina. Ao, atretic oocytes; ev, early vitellogenic oocytes; lv, late vitellogenic oocytes; mtd, main testicular duct; o, oocytogenesis; oc, ovarian cavity; pof, post-ovulatory follicles; pv, pre-vitellogenic oocytes; s, sperm; sc, spermatocytes; st, spermatids.

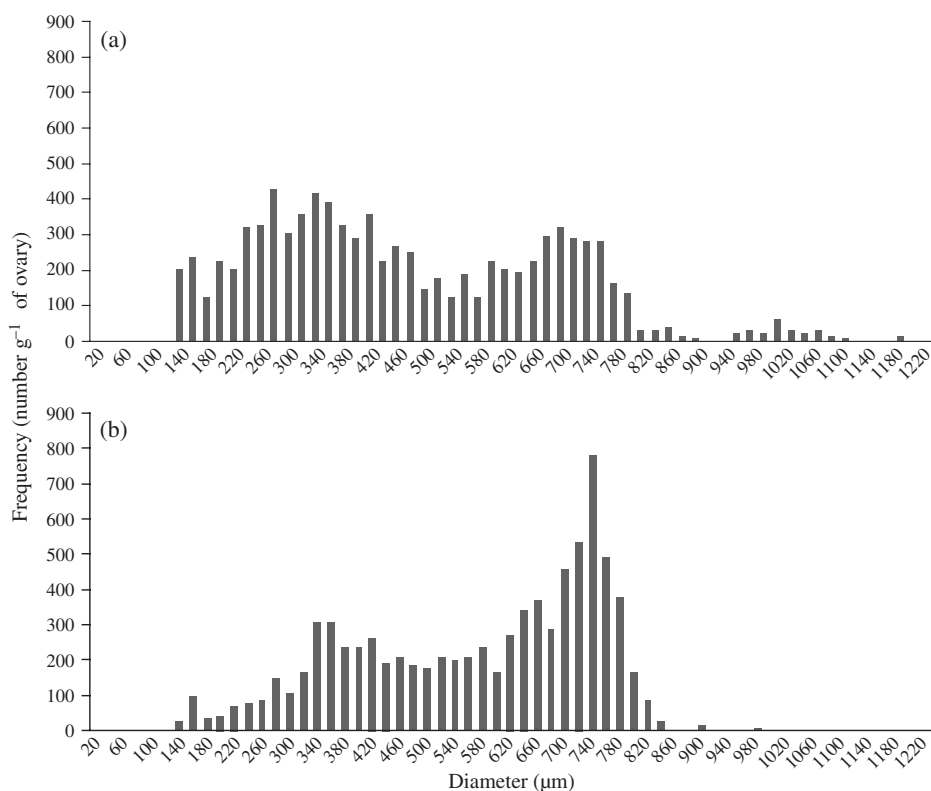


FIG. 6. Relative frequency distribution of oocyte diameters of females of *Scomber scombrus* sampled in (a) February (total length, L_T = 265 mm) and (b) April (L_T = 255 mm).

860 μm). In 27 out of 32 samples, a third mode (diameter > 860 μm) consisting of hydrated oocytes was recognizable (Fig. 6a). The maximum size of hydrated oocytes was 1480 μm .

The total number of vitellogenic oocytes varied significantly in relation to both L_T ($F_{1,24} = 28.79$, $P < 0.001$) and spawning months ($F_{2,24} = 4.23$, $P < 0.05$), with larger females having a higher total number of oocytes, and a decrease in the number of oocytes during the breeding season (Table I). The number of oocytes in early vitellogenesis was related to female size ($F_{1,24} = 25.95$, $P < 0.001$), but did not significantly vary among breeding months ($F_{2,24} = 3.08$, $P > 0.05$). Conversely, oocytes in late vitellogenesis were found to be unrelated to female size ($F_{1,24} = 2.51$, $P > 0.05$) and still did not vary among months ($F_{2,24} = 1.14$, $P > 0.05$). The number of hydrated oocytes varied greatly among females, being between 29 and 3116 oocytes per ovary, and was not related to female L_T (Spearman rank correlation, $r_s = -0.269$, $n = 25$, $P > 0.05$), preventing any estimate of batch fecundity.

Samples from April varied in the number of vitellogenic oocytes (Table I), with two females caught in the northern Adriatic Sea having a total number of oocytes at early stages of vitellogenesis similar to those collected in January [Fig. 6(b)].

The estimated mean \pm s.d. relative potential annual fecundity was 826.2 ± 173.9 oocytes g^{-1} per female (Table I), while the relative actual fecundity was 414.6

TABLE I. Relative number of oocytes (mean \pm s.d.) within three size groups of female *Scomber scombrus* collected from January to April. Number of females (n) is reported in parentheses

Oocyte diameter (ϕ , μm)	January ($n = 11$)	February ($n = 10$)	March ($n = 7$)	April ($n = 4$)
$\phi < 123$	839 ± 171	670 ± 164	572 ± 148	643 ± 185
$123 \leq \phi \leq 600$	691 ± 168	556 ± 127	488 ± 120	458 ± 180
$600 < \phi \leq 860$	148 ± 81	99 ± 75	72 ± 35	183 ± 185

oocytes g^{-1} per female, with a maximum estimated rate of atresia of 49.8%. For females with L_T ranging from 199 to 217 mm, potential estimated mean \pm s.d. annual fecundity was $96\,675 \pm 35\,943$ (range = 40 406–189 852), while mean \pm s.d. actual fecundity was $48\,513 \pm 18\,037$ (range = 20 276–95 271), related to female size by the equation $F = 0.25 L_T^{2.28}$; $r^2 = 0.47$.

AGE

The c.v. and average percentage errors (APE) between the two readers indicated a great precision (Ancona: c.v. = 2.84%, APE = 2.77%; Chioggia: c.v. = 4.00%, APE = 2.83%). Micro-increment counts were carried out on a sub-sample of *S. scombrus* measuring between 134 and 177 mm L_T . Age estimates ranged from 152 to 219 days. Hence, micro-increment counts validated the first annulus formation, by assigning an age of c. 5–7 months to individuals aged 0+ years by counting annuli (as they did not exhibit hyaline zones in their otoliths). Periodicity of opaque and hyaline zone deposition followed the typical sinusoidal trend, with a higher percentage of hyaline edge in autumn–winter and opaque edge in spring–summer, validating the annular pattern of the sagittal otoliths.

The maximum estimated age was 3 years, although most of the fish were age 0 or 1 year-old specimens (83%). Specimen sizes within each age class were significantly different (Kruskal-Wallis test, $H_3 = 399.86$, $P < 0.001$), although a considerable overlap in sizes among age classes was evident in the age–length key (Table SII, Supporting Information). Sexual maturity was reached by 72.8% of individuals in their first year of life.

DISCUSSION

The results of this study confirmed and extended previous data on the decline in landings of *S. scombrus* in the Adriatic Sea (Sinovčić, 2001; Azzurro *et al.*, 2011; Barausse *et al.*, 2011). The consistency of fishery data from different Adriatic areas makes this decline in catch a clear sign of population collapse in the Adriatic Sea, which constitutes one of the most fished areas of the Mediterranean Sea (Caddy *et al.*, 1995; Barausse *et al.*, 2009; Fortibuoni *et al.*, 2010). The decline in abundance of *S. scombrus* may have several causes that may act synergistically including overexploitation, interspecific trophic interactions and variations in environmental factors

such as seawater temperature, river inflow and nutrients. Environmental factors and fishing have played a role in changes to landings and community composition in the northern and central Adriatic Sea (Coll *et al.*, 2010; Barausse *et al.*, 2011). Considering that *S. scombrus* is a cold-water species, the increase in seawater temperature observed in the Adriatic Sea (Barausse *et al.*, 2011) could have contributed to the decline, but the specific contributions of the different factors determining population changes deserve further investigation.

The results of this study indicate that in the northern and western-central Adriatic Sea the population of *S. scombrus* is composed of relatively small individuals, having a short life span, with a maximum of 3 years attained by very few individuals. Maximum size and age recorded here are considerably smaller than those observed in the Atlantic Ocean, where the species can grow to 500 mm L_T and attain *c.* 20 years of age (Villamor, 1997; Studholme *et al.*, 1999; Villamor *et al.*, 2004), in the southern Adriatic Sea, where specimens up to 400 mm L_T were sampled by Bottari *et al.* (2004), and in the eastern-central Adriatic Sea (Sinovčić, 2001).

Sex ratio was significantly skewed towards females, in agreement with the findings of Bottari *et al.* (2004) in the southern Adriatic Sea. In samples from the fishery, skewed sex ratios may reflect a real difference in the number of males and females in the population or a sampling bias. In gonochoristic species, such as *S. scombrus*, skewed sex ratios are uncommon and may reflect, for instance, a differential mortality between sexes. On the other hand, sampling bias could be the result of different catchabilities of the two sexes or sex-related spatial segregation. None of these hypotheses can be excluded in this study.

On the basis of the maximum values of I_G and the presence of ripe individuals, breeding of *S. scombrus* has been shown to occur in winter (mainly from January to March). The breeding season has been shown, however, to vary with temperature in the North Sea (Jansen & Gislason, 2011), indicating that some interannual variation may occur. From January, with the beginning of the breeding season, and continuing during all the spawning months, *S. scombrus* almost disappears from the northern waters of the Adriatic Sea (Papetti *et al.*, 2013), and the few individuals that have been caught in this area in winter had low I_G values, and in most cases maturing gonads. Conversely, individuals caught off Ancona (central Adriatic Sea) were in the mature–ripe stage and exhibited the highest I_G values. These data strongly suggest the migration of spawners to spawning grounds, located in an area not far from Ancona, as suggested by seasonal fishery data, along the western coast of the Adriatic Sea (Papetti *et al.*, 2013). In the Atlantic Ocean, this species is known to migrate to different depths and areas according to seasonal water temperature variations and for reproduction (Castonguay *et al.*, 1992; D'Amours & Castonguay, 1992; Studholme *et al.*, 1999; Punzón & Villamor, 2009), with long journeys (>1110 km, 600 nautical miles) between feeding and spawning grounds (Iversen & Ljøen, 1985; Overholtz *et al.*, 1991; Uriarte & Lucio, 2001). No direct information is available on the migration patterns in the Mediterranean Sea, but contrary to its congener, *S. colias*, this species shows genetic differentiation along the east–west axis of the Mediterranean Sea basin (Zardoya *et al.*, 2004), suggesting limited migrations within the Mediterranean Sea. Migrations appear limited within the Adriatic Sea, given that genetic data suggest the occurrence of a single panmictic population in the northern-central Adriatic Sea (Papetti *et al.*, 2013), distinct from

the *S. scombrus* of the southern Adriatic Sea (Zardoya *et al.*, 2004; Papetti *et al.*, 2013).

From January onwards, most males had testes filled with sperm, with few cysts of spermatids or spermatocytes, indicating that spermatogenesis was almost complete at the beginning of the breeding season. Testis mass decreased during the breeding season, indicating that sperm, stored in testes, main testicular ducts and sperm ducts are used and not re-established during the breeding months. A similar pattern of gametogenesis has been observed in other species performing more or less extensive migrations to spawning grounds, for instance the bluefin tuna *Thunnus thynnus* (L. 1758) (Abascal *et al.*, 2004), the plainfin midshipman *Porichthys notatus* Girard 1854 (Barni *et al.*, 2001) and the rosy lip sculpin *Ascelichthys rhodorus* Jordan & Gilbert 1880 (Petersen *et al.*, 2004).

In females, the decrease in the number of oocytes during the breeding season supports a determinate fecundity for this species, in agreement with Greer Walker *et al.* (1994). Not all the characteristics of the ovaries completely match the criteria for a determinate fecundity, however, and indeterminate fecundity has been suggested as a possibility by Hunter & Macewicz (1985) and Hunter *et al.* (1985). Moreover, it has recently been suggested that the type of fecundity may change with food availability, with females continuing to recruit new pre-vitellogenic oocytes in the vitellogenic process when food conditions are favourable (ICES, 2011). In species with a determinate fecundity, a gap in size between the stock of vitellogenic and pre-vitellogenic oocytes is expected (Hunter & Macewicz, 1985) and phenomena of atresia occur throughout the breeding season (West, 1990; Greer Walker *et al.*, 1994). Conversely, a gap in size was not found in this study and atresia was evident only in females at the end of the breeding season. *Scomber scombrus* may, however, feed extensively during the breeding season (Greer Walker & Nichols, 1993), and it has been suggested that atresia may be linked to food availability (Greer Walker *et al.*, 1994). Females could therefore resorb oocytes at the end of the breeding season if they did not get enough food to complete the vitellogenesis and according to other environmental conditions. In *S. scombrus*, the breeding season is quite short, compared with an estimated duration of vitellogenesis of *c.* 5 months (Greer Walker *et al.*, 1994). Therefore, it is unlikely that pre-vitellogenic oocytes, if recruited in the vitellogenic stock during the breeding season, could actually complete the vitellogenesis process within the same season. The estimated actual fecundity, for the Adriatic population of *S. scombrus* is much lower than the potential, with a high value of maximum atresia (50%), which even if estimated using only few females at the end of the breeding season, is in agreement with that estimated in the North Sea (Greer Walker *et al.*, 1994, ICES, 2009). If the rate of atresia depends on food availability and environmental conditions experienced individually (Greer Walker *et al.*, 1994), it may change annually, as found in Atlantic stocks (ICES, 2006, 2009), or among females.

The estimate of relative fecundity of *S. scombrus* in the Adriatic Sea was among the lowest values reported for the Atlantic Ocean (ICES, 2011). Likewise, absolute fecundity estimated for the largest females collected in the Adriatic Sea (317 mm L_T , fecundity = 190 000 eggs) is similar to the lowest values obtained for Atlantic individuals of comparable length (ICES, 2011). Relative and consequently absolute fecundity, batch fecundity and rates of atresia, however, vary widely between years in the Atlantic Ocean (Watson *et al.*, 1992; Priede & Watson, 1993;

Greer Walker *et al.*, 1994; ICES, 2006, 2009, 2011). Hence, both potential and actual fecundity estimated for the Adriatic population can give only a temporarily defined picture of this reproductive trait, and definitely deserves longer temporal investigations.

The majority of females and males of *S. scombrus* attain sexual maturity during their first year of life, with a minimum size at sexual maturity of *c.* 200 mm L_T . This estimate must be considered conservative, however, as it was not possible to sample small-sized individuals during the breeding season. It agrees with the minimum size at sexual maturity reported from the southern Adriatic Sea (Bottari *et al.*, 2004). In comparison with the Adriatic population, *S. scombrus* from other areas attain sexual maturity later, maturing mainly between 2 and 3 years at sizes of 260–300 mm (Studholme *et al.*, 1999), and only *c.* 8% of specimens has been reported to mature at 1 year in the western Atlantic Ocean (ICES, 2012). Such differences probably reflect geographic variability in these parameters, as observed in other species [*e.g.* horse mackerel *Trachurus trachurus* (L. 1758) (Abaunza *et al.*, 2003) and pilchard *Sardina pilchardus* (Walbaum 1792) (Silva *et al.*, 2006)], consistent with the smaller age and sizes attained by the Adriatic population in comparison with the Atlantic population. A reduction in age and size at maturity has been highlighted, for instance, for the western Atlantic stock of *S. scombrus* (Studholme *et al.*, 1999), but since no historical data are available on the size and age at sexual maturity from the Adriatic Sea, temporal variation in these traits could not be verified.

The population of *S. scombrus* from the northern-central Adriatic Sea shows clear signs of overexploitation. While the decline in catches has been highlighted by several authors (Sinovčić, 2001; Azzurro *et al.*, 2011; Barausse *et al.*, 2011), this study highlights for the first time a probable decrease of maximum age and L_T in the last two decades. Indeed, a maximum age of 8 years and a maximum L_T of 419 mm were recorded in eastern-central Adriatic individuals sampled during 1991–1993 (Sinovčić, 2001), before the most recent decline in landings, in comparison with the maximum age of 3 years and maximum L_T of 358 mm found in this study (Table SIII and Fig. S2, Supporting Information). Such differences are not related to the sampling of different populations, considering that *S. scombrus* belongs to a single panmictic population in the northern-central Adriatic Sea (Papetti *et al.*, 2013). Samples from 1991 to 1993 were collected using purse seines, a fishing technique not employed in this study, but several techniques were indeed employed in this study, making a bias in catchability unlikely. Moreover, in the central-western Adriatic Sea, the use of large otter trawls should reduce any bias in maximum size. Alternatively, it could be hypothesized that while *S. scombrus* up to 3 years of age move freely in the northern-central Adriatic Sea, larger and older *S. scombrus* remain all year around in the eastern-central Adriatic Sea. Although this hypothesis cannot be completely ruled out, the size of samples of *S. scombrus* collected from Croatian waters in 2005 (Zorica *et al.*, 2010) and 2010 (Papetti *et al.*, 2013) had maximum sizes smaller than the maximum size reported during 1991–1993. Therefore, the most reasonable explanation is that the observed variability in size actually reflects the current loss of the largest and oldest individuals from the population. Considering that a decline in landings was observed from the 2000s, after a slight recovery of catches from 1990s, and that the fishing capacity of midwater trawls increased from 1996 onwards, fishing pressure is

probably the main cause of this strong reduction in maximum age and size, as widely documented in other species (Rochet, 1998; Hamilton *et al.*, 2007; Hutchings & Fraser, 2008).

The largest females sampled in the 1990s would contribute 10 times the egg production of the smallest ones. As a consequence, such a reduction in size and age has negative consequences for the reproductive potential of the population. Moreover, a shorter life span implies a lower number (in most cases just one) of reproductive seasons per female, making the population more vulnerable to unpredictable variations in environmental conditions (Hutchings, 2002).

Considering all the available information, the status of the population of *S. scombrus* in the northern-central Adriatic Sea appears to be critical. Besides fishing pressure, two additional factors possibly contribute to its depletion: (1) it appears genetically distinct from *S. scombrus* inhabiting the southern Adriatic Sea (Papetti *et al.*, 2013), suggesting a low potential of recruitment from other populations and sites and (2) in a scenario of climate change, typical cold-water species, such as *S. scombrus*, are particularly vulnerable to the effect of global warming (Pörtner & Knust, 2007). The management of *S. scombrus* in the Adriatic Sea is currently limited to a minimum landing size. Although this size appears adequate, being smaller than the size at sexual maturity, its efficacy highly depends on the catch rate of undersized individuals and their survival once released back into the sea. These data are currently unavailable. Considering the catch trends, more adequate management actions, possibly including the protection of spawning grounds and of the large-sized individuals that contribute most to the reproductive potential of the species, are urgently needed.

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Supporting Information

Supporting Information may be found in the online version of this paper:

Figure SI. Relative frequency per month of gonad maturity stages (macroscopic analyses, according to Holden & Raitt, 1974, corrected when necessary with microscopic analyses) of *Scomber scombrus*. Females and males from Chioggia and Ancona are represented separately. Stage 1, immature; stage 2, maturing; stage 3, ripening; stage 4, ripe; stage 5, spent.

Figure SII. Age frequency distribution of *Scomber scombrus* samples from 1991–1993, eastern-central Adriatic Sea (Sinovčić, 2001), and from 2009–2010, northern and central-western Adriatic Sea (this study).

Table SI. Description of macroscopic stages of gonad maturity of *Scomber scombrus*, according to Holden & Raitt (1974). No photographs are available for stage 1

Table SII. Age–length key of population of *Scomber scombrus* from the northern-central Adriatic Sea. L_T , total length; N, number of specimens

Table SIII. Mean size at age (L_T , mm) of *Scomber scombrus* for samples in 1991–1993 from eastern-central Adriatic Sea (Sinovčić, 2001) and in 2009–2010 from northern and central-western Adriatic Sea (this study)

References

- Abaunza, P., Gordo, L., Karlou-Riga, C., Murta, A., Eltink, A. T. G. W., García Santamaría, M. T., Zimmermann, C., Hammer, C., Lucio, P., Iversen, S. A., Molloy, J. & Gallo, E. (2003). Growth and reproduction of horse mackerel, *Trachurus trachurus* (Carangidae). *Reviews in Fish Biology and Fisheries* **13**, 27–61. doi: 10.1023/A:1026334532390
- Abascal, F. J., Megina, C. & Medina, A. (2004). Testicular development in migrant and spawning bluefin tuna (*Thunnus thynnus* (L.)) from the eastern Atlantic and Mediterranean. *Fishery Bulletin* **102**, 407–417.
- Artegiani, A., Bregant, D., Paschini, E., Pinardi, N., Raicich, F. & Russo, A. (1997). The Adriatic Sea general circulation. Part II: Baroclinic circulation structure. *Journal of Physical Oceanography* **27**, 1515–1532.
- Azzurro, E., Moschella, P. & Maynou, F. (2011). Tracking signals of change in Mediterranean fish diversity based on local ecological knowledge. *PLoS One* **6**, e24885. doi: 10.1371/journal.pone.0024885
- Barausse, A., Duci, A., Mazzoldi, C., Artioli, Y. & Palmeri, L. (2009). Trophic network model of the Northern Adriatic Sea: analysis of an exploited and eutrophic ecosystem. *Estuarine, Coastal and Shelf Science* **83**, 577–590. doi: 10.1016/j.ecss.2009.05.003
- Barausse, A., Michieli, A., Riginella, E., Palmeri, L. & Mazzoldi, C. (2011). Long-term changes in community composition and life-history traits in a highly exploited basin (northern Adriatic Sea): the role of environment and anthropogenic pressures. *Journal of Fish Biology* **79**, 1453–1486. doi: 10.1111/j.1095-8649.2011.03139.x
- Barni, A., Mazzoldi, C. & Rasotto, M. B. (2001). Reproductive apparatus and male accessory structures in two batrachoid species (Teleostei, Batrachoididae). *Journal of Fish Biology* **58**, 1557–1569. doi: 10.1006/jfbi.2001.1560
- Beamish, R. J. & Fournier, D. A. (1981). A method of comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 982–983. doi: 10.1139/f81-132
- Becker, W. A. (1984). *A Manual of Quantitative Genetics*. Washington DC: Pullman Academic Enterprises.
- Bottari, T., Rinelli, P., Giordano, D. & Greco, S. (2004). Length–weight relationship and maturity of the Atlantic mackerel, *Scomber scombrus*, from the Adriatic Sea (Eastern Mediterranean). *Cahiers de Biologie Marine* **45**, 49–53.
- Caddy, J. F., Refk, R. & Do-Chi, T. (1995). Productivity estimates for the Mediterranean: evidence of accelerating ecological change. *Ocean and Coastal Management* **26**, 1–18. doi: 10.1016/0964-5691(95)00015-T
- Castonguay, M., Rose, G. A. & Leggett, W. C. (1992). Onshore movements of Atlantic mackerel (*Scomber scombrus*) in the Northern Gulf of St. Lawrence: associations with wind-forced advections of warmed surface waters. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2232–2241. doi: 10.1139/f92-244
- Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1208–1210. doi: 10.1139/f82-158
- Choy, S. C. (1985). A rapid method for removing and counting eggs from fresh and preserved decapod crustaceans. *Aquaculture* **48**, 369–372.
- Coll, M., Santojanni, A., Palomera, I. & Arneri, E. (2010). Ecosystem assessment of the north-central Adriatic Sea: towards a multivariate reference framework. *Marine Ecology Progress Series* **417**, 193–210.
- D'Amours, D. & Castonguay, M. (1992). Spring migration of Atlantic mackerel, *Scomber scombrus*, in relation to water temperature through Cabot Strait (Gulf of St. Lawrence). *Environmental Biology of Fishes* **34**, 393–399.
- Evans, R. D., Russ, G. R. & Kritzer, J. P. (2008). Batch fecundity of *Lutjanus carponotatus* (Lutjanidae) and implications of no-take marine reserves on the Great Barrier Reef, Australia. *Coral Reefs* **27**, 179–189. doi: 10.1007/s00338-007-0309-8
- Fonda Umani, S. (1996). Pelagic production and biomass in the Adriatic Sea. *Scientia Marina* **60**, 65–77.

- Fortibuoni, T., Libralato, S., Raicevich, S., Giovanardi, O. & Solidoro, C. (2010). Coding early naturalists' accounts into long-term fish community changes in the Adriatic Sea (1800–2000). *PLoS One* **5**, e15502. doi: 10.1371/journal.pone.0015502
- Greer Walker, M. & Nichols, J. H. (1993). Predation on *Benthoosema glaciale* (Myctophidae) by spawning mackerel. *Journal of Fish Biology* **42**, 618–620.
- Greer Walker, M., Withames, P. R. & Bautista de los Santos, I. (1994). Is the fecundity of the Atlantic mackerel (*Scomber scombrus*: Scombridae) determinate? *Sarsia* **79**, 13–26.
- Grier, H. J. (1981). Cellular organization of the testis and spermatogenesis in fishes. *American Zoologist* **21**, 345–357.
- Hamilton, S. L., Caselle, J. E., Standish, J. D., Schroeder, D. M., Love, M. S., Rosales-Casian, J. A. & Sosa-Nishizaki, O. (2007). Size-selective harvesting alters life histories of a temperate sex-changing fish. *Ecological Society of America* **17**, 2268–2280. doi: 10.1890/06-1930.1
- Holden, M. J. & Raitt, D. F. S. (1974). Manual of fisheries science. Part II: Method of resource investigation and their application. *FAO Fisheries Technical Paper* **115** (Rev 1).
- Hunter, J. R. & Macewicz, B. J. (1985). Measurement of spawning frequency in multiple spawning fishes. In *An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy*, Engraulis mordax (Lasker, R., ed.), pp. 79–94. *NOAA Technical Report NMFS* **36**.
- Hunter, J. R., Lo, N. C. H. & Leong, R. J. H. (1985). Batch fecundity in multiple spawning fishes. In *An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy*, Engraulis mordax (Lasker, R., ed.), pp. 67–77. *NOAA Technical Report NMFS* **36**.
- Hunter, J. R., Macewicz, B. J., Lo, N. C. H. & Kimbrell, C. A. (1992). Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fishery Bulletin* **90**, 101–128.
- Hutchings, J. A. (2002). Life histories of fish. In *Handbook of Fish Biology and Fisheries*, Vol. 1 (Hart, P. J. B. & Reynolds, J. D., eds), pp. 149–174. Oxford: Blackwell Publishing.
- Hutchings, J. A. & Fraser, D. J. (2008). The nature of fisheries- and farming-induced evolution. *Molecular Ecology* **17**, 294–313. doi: 10.1111/j.1365-294X.2007.03485.x
- Jansen, T. & Gislason, H. (2011). Temperature affects the timing of spawning and migration of North Sea mackerel. *Continental Shelf Research* **31**, 64–72.
- Jennings, S., Kaiser, M. J. & Reynolds, J. D. (2001). *Marine Fisheries Ecology*. Oxford: Blackwell.
- Mendiola, D. & Alvarez, P. (2008). Validation of daily increments in the otolith microstructure of Northeast Atlantic mackerel fish larvae. *Fisheries Research* **89**, 300–304.
- Murua, H. & Saborido-Rey, F. (2003). Female reproductive strategies of marine fishes of the North Atlantic. *Journal of Northwest Atlantic Fishery Science* **33**, 23–31.
- Nagahama, Y. (1983). The functional morphology of teleost gonads. In *Fish Physiology*, Vol. IX (Hoar, W. S., Randall, D. J. & Donaldson, E. M., eds), pp. 223–275. New York, NY: Academic Press.
- Overholtz, W. J., Armstrong, R. S., Mountain, D. G. & Tercerio, M. (1991). Factors influencing spring distribution, availability and recreational catch of Atlantic mackerel (*Scomber scombrus*) in the Middle Atlantic and southern New England regions. *NOAA Technical Memorandum NMFS-F/NEC-85*.
- Papetti, C., Di Franco, A., Zane, L., Guidetti, P., De Simone, V., Spizzottin, M., Zorica, B., Čikeš Keč, V. & Mazzoldi, C. (2013). Single population and common natal origin for Adriatic *Scomber scombrus* stocks: evidence from an integrated approach. *ICES Journal of Marine Science* **70**, 387–398. doi: 10.1093/icesjms/fss201
- Pearse, A. G. E. (1985). *Histochemistry, Theoretical and Applied Analytical Technology*. Edinburgh: Churchill Livingstone.
- Petersen, C. W., Zarrella, K. A., Ruben, C. A. & Mazzoldi, C. (2004). Reproductive biology of rosy lip sculpin, an intertidal spawner. *Journal of Fish Biology* **64**, 863–875. doi: 10.1111/j.1095-8649.2004.00355.x
- Pörtner, H. O. & Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**, 95–97. doi: 10.1126/science.1135471

- Priede, I. G. & Watson, J. J. (1993). An evaluation of the daily egg production method for estimating biomass of Atlantic mackerel (*Scomber scombrus*). *Bulletin of Marine Science* **53**, 891–911.
- Punzón, A. & Villamor, B. (2009). Does the timing of the spawning migration change for the southern component of the Northeast Atlantic Mackerel (*Scomber scombrus*, L.1758)? An approximation using fishery analyses. *Continental Shelf Research* **29**, 1195–1204. doi: 10.1016/j.csr.2008.12.024
- Rochet, M. J. (1998). Short-term effects of fishing on life history traits of fishes. *ICES Journal of Marine Science* **55**, 371–391. doi: 10.1006/jmsc.1997.0324
- Russo, A. & Artegiani, A. (1996). Adriatic sea hydrography. *Scientia Marina* **60**, 33–43.
- Silva, A., Santos, M. B., Caneco, B., Pestana, G., Porteiro, C., Carrera, P. & Stratoudakis, Y. (2006). Temporal and geographic variability of sardine maturity at length in the northeastern Atlantic and the western Mediterranean. *ICES Journal of Marine Science* **63**, 663–676. doi: 10.1016/j.icesjms.2006.01.005
- Sinovčić, G. (2001). Population structure, reproduction, age and growth of Atlantic mackerel, *Scomber scombrus* L. in the Adriatic Sea. *Acta Adriatica* **42**, 85–92.
- Studholme, A. L., Packer, D. B., Berrien, P. L., Johnson, D. L., Zetlin, C. A. & Morse, W. W. (1999). Essential fish habitat source document: Atlantic mackerel, *Scomber scombrus*, life history and habitat characteristics. *NOAA Technical Memorandum NMFS NE* **141**.
- Trippel, E. A. (1999). Estimation of stock reproductive potential: history and challenges for Canadian Atlantic gadoid stock assessment. *Journal of Northwest Atlantic Fishery Science* **25**, 61–81.
- Uriarte, A. & Lucio, P. (2001). Migration of adult mackerel along the Atlantic European shelf edge from a tagging experiment in the south of the Bay of Biscay in 1994. *Fisheries Research* **50**, 129–139.
- Villamor, B. (1997). Distribution and age structure of mackerel (*Scomber scombrus*, L.) and horse mackerel (*Trachurus trachurus*, L.) in the northern coast of Spain, 1989–1994. *Scientia Marina* **61**, 345–366.
- Villamor, B., Abaunza, P. & Fariña, A. C. (2004). Growth variability of mackerel (*Scomber scombrus*) off north and northwest Spain and a comparative review of the growth patterns in the northeast Atlantic. *Fisheries Research* **69**, 107–112. doi: 10.1016/j.fishres.2004.02.005
- Watson, J. J., Priede, I. G., Witthames, P. R. & Owori-Wadunde, A. (1992). Batch fecundity of Atlantic mackerel, *Scomber scombrus*. *Journal of Fish Biology* **40**, 591–598. doi: 10.1111/j.1095-8649.1992.tb02608.x
- West, G. (1990). Methods of assessing ovarian development in fishes: a review. *Australian Journal of Marine and Freshwater Research* **41**, 199–222.
- Witthames, P. R., Thorsen, A., Murua, H., Saborido-Rey, F., Greenwood, L., Domingues, R., Korta, M. & Kjesbu, O. S. (2009). Advances in methods for determining fecundity: application of the new methods to some marine fishes. *Fishery Bulletin* **107**, 148–164.
- Zardoya, R., Castilho, R., Grande, C., Favre-Krey, L., Caetano, S., Marcato, S., Krey, G. & Patarnello, T. (2004). Differential population structuring of two closely related fish species, the mackerel (*Scomber scombrus*) and the chub mackerel (*Scomber japonicus*), in the Mediterranean Sea. *Molecular Ecology* **13**, 1785–1798. doi: 10.1111/j.1365-294X.2004.02198.x
- Zorica, B., Sinovčić, G. & Čikeš Keč, V. (2010). Preliminary data on the study of otolith morphology of five pelagic fish species from the Adriatic Sea (Croatia). *Acta Adriatica* **51**, 89–96.

Electronic References

- CLODIA (2013). *Database of Fishery Data from Chioggia, Northern Adriatic Sea*. Available at http://chioggia.scienze.unipd.it/Inglese/Database_landing.html
- FAO-FIGIS (2005). A world overview of species of interest to fisheries. Chapter: *Scomber scombrus*. *FIGIS Species Fact Sheets. Species Identification and Data Programme-SIDP, FAO-FIGIS*. Available at www.fao.org/figis/servlet/species?fid=2473.

- Froese, R. & Pauly, D. (2012). *FishBase*. Available at www.fishbase.org (last accessed 20 October 2012).
- ICES (2006). Report of the working group on mackerel and horse mackerel egg surveys (WGMEGS). *ICES CM 2006/LRC 09*. Available at <http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/lrc/2006/wgmeGS/wgmeGS06.pdf> (last accessed 17 February 2012).
- ICES (2007). Report of the workshop on sexual maturity staging of mackerel and horse mackerel (WKMSMAC). *ICES CM 2007/ACFM 26*. Available at http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2007/WKMSMAC/wkmsmac_final.pdf (last accessed 1 December 2009).
- ICES (2009). Report of the working group on mackerel and horse mackerel egg surveys (WGMEGS). *ICES CM 2009/LRC 09*. Available at <http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/SSGESST/2009/WGMEGS/WGMEGS09.pdf> (last accessed 18 June 2012).
- ICES (2010). Report of the working group on mackerel and horse mackerel egg surveys (WGMEGS). *ICES CM 2010/SSGESST 02*. Available at <http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/SSGESST/2010/WGMEGS10.pdf> (last accessed 18 June 2012).
- ICES (2011). Report of the working group on mackerel and horse mackerel egg surveys (WGMEGS). *ICES CM 2011/SSGESST 07*. Available at <http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/SSGESST/2011/WGMEGS11.pdf> (last accessed 5 February 2013).
- ICES (2012). Report of the working group on widely distributed stocks (WGWIDE). *ICES CM 2012/ACOM 16*, pp. 36–161. Available at <http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2012/WGWIDE/WGWIDE%202012.pdf> (last accessed 21 January 2013).
- Iversen, S. A. & Ljøen, R. (1985). The spawning and distribution of mackerel eggs in the North Sea related to the hydrography. *ICES CM 1985/H 37*. Available at http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/Pelagic%20Fish%20Committee/1985/1985_H7.pdf (last accessed 17 February 2012).