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Are sex ratios in wild European sea bass (*Dicentrarchus labrax*) populations biased?

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Abstract – Sex ratios in farmed European sea bass are highly biased towards males (75 to 95%), which is problematic for aquaculture. In this mini-review, we re-analyse fisheries literature data about sex ratios in wild sea bass from 13 population samples, representing altogether 4889 individuals covering the major part of the distribution range of the species. We find that as a whole, the sex ratio of wild populations is biased towards females (59.4% females, $p < 0.001$), but that the sex ratio of the younger fish (<30 cm total length) is balanced (52.0% females, $p = 0.15$), while the sex ratio of the older fish is heavily biased towards females (69.5% females, $p < 0.01$). Possible causes of these differences (differential longevity, biased sampling) are discussed. When age-group sex ratios are available (three population samples out of 13), significant variation between age groups appears, part of which is most likely of environmental origin. This study shows that the excess of males in culture is not a characteristic of the species, but rather a consequence of the environments used in culture, interacting with a complex system where both environmental and genetic influences govern sex determination in sea bass.

Key words: Sex ratio / Genetics / Sex determination / Fish aquaculture / *Dicentrarchus labrax*

1 Introduction

The European sea bass (*Dicentrarchus labrax*) is a fish species that has been domesticated in the 1980's for aquaculture. Its production rose steadily since then, and it has become one of the major species of Mediterranean aquaculture, together with gilthead sea bream (*Sparus aurata*). It has been repeatedly observed that sex ratios in farmed populations were strongly biased towards males (75 to 95% Piferrer et al. 2005). This is not optimal for fish farming, as males may mature before commercial size, and then experience reduced growth. Moreover, at a similar age, females are larger than males (Saillant et al. 2001). Finally, as selective breeding of sea bass becomes a reality, with high potential gains in productivity (Vandeputte et al. 2009), a good balance between males and females in the populations is needed to allow efficient selection of both sexes.

There is a wide variation in sex determination systems in fish, where sex can be determined by environmental factors (mainly temperature), major genetic factors like sex chromosomes and

minor genetic factors, or a combination of those (see Baroiller et al. 2009 for a review).

In the European sea bass, sex is not yet determined at hatching, and temperature has been shown to play a major role in its determination, although its effect is not yet fully understood. The current hypothesis is that high temperatures early in development (before 100 days post-fertilization, dpf) lead to decreased female rates (Piferrer et al. 2005), probably through an inhibition of female differentiation (Navarro-Martin et al. 2009). However long-lasting low temperatures also produce an excess of males interpreted as caused by a low growth rate precluding female orientation (Navarro-Martin et al. 2009). Thus, the excess of males observed in culture would be due to the use of temperatures higher than in the wild. In addition to temperature effects, between-families variation of sex ratio shows that genotypic effects also exist (Saillant et al. 2002; Vandeputte et al. 2007), and the distribution of family sex ratios was shown to be compatible with a polygenic system, but not with a “classical” genotypic sex determination (GSD) system with sex chromosomes (Vandeputte et al. 2007). This type of sex determination system has seldom been evidenced in Vertebrates (McGaugh and Janzen 2011), and is believed to be

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evolutionarily unstable (Bulmer and Bull 1982; Rice 1986), as it should evolve in most cases towards a chromosomal system where sex is determined at conception. In some cases however, when the environment has differential effect on the fitness of both sexes (e.g., environment influences growth rate and females benefit more of a large size than males, as in *Menidia menidia* – Conover 1984), the polygenic system may in some rare cases be maintained or alternatively evolve towards a system where sex is determined by environmental factors only (Bulmer and Bull 1982).

The genetic component of sex ratio evidenced in culture conditions is a strong lever for natural selection to act and stabilize sex ratios at 1:1, as predicted by Fisher's theory of equal investment in both sexes (Fisher 1930). The rationale is simple: if there is more of one sex than of the other, then each individual of the more abundant sex will produce less offspring (and hence have a lower fitness) than individuals of the less abundant sex, which will then be favoured by natural selection. If the sex of an individual is governed by a system where there is a genetic variance for sex tendency (the propensity of an individual to differentiate as male or female), then frequency-dependent selection should stabilize the population at an even sex-ratio.

The environmental and genetic components of sea bass sex determination in farmed populations have been and remain subject to many investigations. However no reliable estimation of wild population sex ratios exists to date, although it is important to know if the excess of males is a characteristic of the species or is linked to farming conditions. The aim of the present study was to use published data from the fisheries literature to examine population sex ratios of the sea bass over its distribution range. When age class data were available, we also examined the possible variation of sex ratio between years, an indicator of environmental effects existing in the wild.

2 Material and methods

2.1 Data sets

We used data from nine publications, covering the major part of the natural range of the species, with data from the Atlantic Ocean (Ireland, UK, Spain), the West of the Mediterranean Sea (France, Algeria), and the East of the Mediterranean Sea (Egypt, Turkey). These samples encompass the major populations (Atlantic, East and West Mediterranean) identified by population genetics (Bahri-Sfar et al. 2000; Naciri et al. 1999). In those papers, sex ratio was not the parameter studied, but the sex of the fish was recorded, creating a valuable data base for our purpose.

2.2 Statistical methods

Observed numbers of males and females in each population were compared to the expected numbers under an even sex ratio hypothesis with a chi-square test. A significant difference

indicated that the observed sex-ratio departed from the expected 1:1. Such tests were also performed on population sub-samples comprising only younger fish (<30 cm body length) or older fish (>40 cm body length). Body size limits were chosen as a surrogate for age, which was available in three populations only, but remain imperfect as their relation to age may be influenced by sex and water temperature.

3 Results

3.1 Population sex ratios

Nine publications concerning thirteen population samples were examined (Table 1), with altogether 4889 wild sea bass sexed. The gross proportion of females across all population samples was 59.6%, which is higher than an expected 50% ($\chi^2 = 180$, 1 df, $p < 0.001$). Some variation of sex ratios was seen between population samples (50.0 to 73.6% of females), and twelve samples out of thirteen had an excess of females, although it was significant in eight samples only. It should be noted that eight of the nine samples from the north Atlantic had a significant excess of females, while this was the case for only two of the five South Atlantic / Mediterranean samples.

When considering only 1314 young fish (<30 cm), the proportion of females was 52.0%, not different from 50% ($\chi^2 = 2.05$, 1 df, $p = 0.15$). None of the population samples, taken individually, did significantly depart from 1:1 ($p > 0.05$, with observed sex ratios varying from 49.1% to 57.0%). So, the primary sex ratio can be considered to be even. On the contrary, the largest fish were mostly females (69.5% in 1811 fish > 40 cm, $p < 0.001$). In this case, eight of the 10 population samples with available data significantly departed from 1:1 (observed sex ratios 58.2% to 95.6%), while two did not due to small sample size, although observed sex ratios were high (61 and 67% females, see Table 1).

3.2 Age class/age group sex ratios

In the study on Irish bass, age-class sex ratios were available, and three “good” brood years with a high contribution to the population were identified (Kennedy and Fitzmaurice 1972). Among the 126 fish sampled from 13 year classes, 82 (65%) were born in those three years, and among those 65.9% were female vs. 45.5% in the other 10 year classes, a significant difference ($\chi^2 = 4.92$, 1 df, $p = 0.03$).

Age group sex ratios were available in the Egypt study (Wassef and El Emary 1989), but no “good” brood years could be identified there, as the number of fish per age group was an essentially monotonous decreasing function of age. Of the 11 age groups with more than 10 fish (age groups X to XV were merged to obtain sufficient numbers of fish), six were balanced (46 to 61% females, $p(\chi^2) > 0.05$), three had an excess of females (88% in age group VII, $p < 0.001$, 100% in age groups IX and X to XV, $p < 0.01$) and one was lacking females (26% in age

Table 1. Numbers and proportions of male and female European sea bass sampled in 9 locations. Ref = reference; Nm = number of males; Nf = number of females. Chi-square (χ^2) test for H_0 : equal proportions of males and females (significant results are highlighted with italics). NA: not available.

Area of capture	Ref ^c	All fish				Fish < 30 cm total length				Fish > 40 cm total length			
		Nm	Nf	Female ratio (%)	$p < \chi^2$	Nm	Nf	Female ratio (%)	$p < \chi^2$	Nm	Nf	Female ratio (%)	$p < \chi^2$
Ireland	1	52 ^a	91	63.6	<i>0.001</i>	NA	NA	NA	NA	NA	NA	NA	NA
Yealm & Blackwater, UK	2	30	30	50.0	1.00	30	30	50.0	1.00	NA	NA	NA	NA
Northern UK	3	169	309	64.6	<i><0.001</i>	43	53	55.2	0.31	72	175	70.9	<i><0.001</i>
Central UK	3	241	339	58.4	<i><0.001</i>	81	85	51.2	0.76	85	185	68.5	<i><0.001</i>
Southern UK	3	256	320	55.6	<i>0.008</i>	51	60	54.1	0.39	151	210	58.2	<i>0.002</i>
Western UK	4	259 ^b	428 ^b	62.3	<i><0.001</i>	81 ^b	85 ^b	56.0	0.30	116 ^b	258 ^b	69.0	<i><0.001</i>
Southern UK	4	96 ^b	256 ^b	72.7	<i><0.001</i>	15 ^b	19 ^b	55.9	0.49	50 ^b	194 ^b	79.5	<i><0.001</i>
South-eastern UK	4	34 ^b	95 ^b	73.6	<i><0.001</i>	NA	NA	NA	NA	34	95	73.6	<i><0.001</i>
Cadiz, Spain	5	170	189	52.6	0.31	NA	NA	NA	NA	NA	NA	NA	NA
Sète, Gulf of Lion, France	6	74	136	64.8	<i><0.001</i>	44	43	49.4	0.92	17	56	76.7	<i><0.001</i>
Gulf of Annaba, Algeria	7	227	300	56.9	<i>0.001</i>	74	98	57.0	0.07	17	27	61.4	0.13
Goksu Delta, Turkey	8	136	158	53.7	0.20	88	87	49.7	0.94	8	16	66.7	0.1025
Alexandria, Egypt	9	232	262	53.0	0.18	172	166	49.1	0.74	2	43	95.6	<i><0.001</i>
TOTAL		1976	2913	59.6	<i><0.001</i>	631	683	52.0	0.15	552	1259	69.5	<i><0.001</i>

^a data from 1967 and 1968 captures (Table 7, p. 579)

^b Numbers of males and females from Kelley (1988) were estimated from the total numbers recorded and the proportions of males in each size class deduced from Figure 10 of the article. In this case also, fork length was used instead of total length to classify fish.

^c References: (1) Kennedy and Fitzmaurice 1972, (2) Pawson et al. 2000, (3) Pawson and Pickett 1996, (4) Kelley 1988, (5) Arias 1980, (6) Barnabé 1973, (7) Kara 1997, (8) Ergene 1999, (9) Wassef and El Emary 1989.

group VI, $p < 0.01$). In the Turkish population where age-group sex ratios were also available (Ergene 1999), none of the six age groups with more than 10 fish significantly departed from the expected 50:50 sex ratio ($p > 0.05$).

4 Discussion

Our analysis of the sea bass fisheries literature allowed to show that wild sea bass populations taken as a whole exhibited a slight but significant excess of females (59.6% females on average), and thus differed from the cultured populations where a large excess of males (75 to 95%) is the rule (Piferrer et al. 2005). The first question that comes is the representativeness of samplings, as sex ratios can vary between locations and times of the year (Pawson and Pickett 1996). Most of the studies were done with repeated sampling all along the year, and sometimes over several years, thus eliminating the “time of the year” bias. Capture methods were diverse and included commercial fisheries (Arias 1980; Wassef and El Emary 1989; Pawson and Pickett 1996), research vessels surveys (Pawson and Pickett 1996), rod and line (Kelley 1988; Kennedy and Fitzmaurice 1972; Pawson and Pickett 1996), spear fishing (Barnabé 1973; Kara 1997), gill netting (Kara 1997; Ergene 1999) and fyke

netting (Ergene 1999). The homogeneity of the observed results would however rule out a large effect of capture method on the sex ratio. One more important point is that most of the captures were done in coastal or lagoon areas, and that offshore catches were little represented. Kelley (1988) suggested that large males might be more numerous in offshore areas – therefore one cannot exclude that at least some of the distortion of sex ratios in favour of females would be due to insufficient sampling in offshore areas.

Females tended to grow faster than males in some cases (Kelley 1988; Pawson and Pickett 1996), but also sometimes had the same size at age (Ergene 1999; Wassef and El Emary 1989). In general however, wild sea bass females tend to be slightly larger than males of the same age class (reviewed by Pickett and Pawson 1994). The observed predominance of females in large fish could then partly be due to a faster growth of females, but this effect is expected to be limited as the body length of males and females of the same age differ by less than 5% on average (average of 5 populations reviewed by Pickett and Pawson 1994). Another possible bias is that using size limits as a surrogate for age implies that the age limits of the size categories will differ among populations, depending on the growth conditions encountered. However when age-group data are

available, it is also apparent that there are usually more females in older fish (Kennedy and Fitzmaurice 1972; Wassef and El Emary 1989), which has been attributed to a higher longevity of females (Kelley 1988).

Finally, the sex ratio of the younger fish (<30 cm) was balanced between males and females, and then conformed to Fisher's theory. More females were present in older fish presumably because (1) males are shorter-lived than females and (2) biased sampling may occur if large males tend to live more offshore, as discussed before. This observation of unbiased sex ratio in the wild shows that the excess of males observed in cultured populations is not linked to an intrinsic characteristic of the species to show male biased sex ratios. Previous experimental evidence showed that temperatures higher than 17 °C in the larval rearing phase, which are typically used by the industry, have a male biasing effect (reviews by Piferrer 2005; Navarro-Martin et al. 2009). It can be then reasonably postulated that the excess of males in farmed populations is actually linked to the environmental conditions during larval rearing.

Additional information was obtained from Irish data, in which “good” brood years were correlated with warm summers or springs, and contributed a high proportion of the catches (Kennedy and Fitzmaurice 1972). It appeared that in those good brood years, sex ratio was biased towards females. The 1959 year class, which was specially numerous, had 67.2% females. The same year class was also found to be very abundant in the UK by Kelley (1988), who also found a predominance of females (71.2%). One of the major issues to explain the abundance of females in good brood years in these Irish and UK data is to know whether the fish in the good years are (1) issued from local spawns or (2) originating from Biscay and migrating North, as hypothesized by Kelley (1988). In the first case, the source of the higher female ratio would be linked to local environmental conditions, while in the second case it could also include genetic effects if the fish come from a different population. The general picture of sea bass population genetics is a genetic homogeneity of populations within the Atlantic (Fritsch et al. 2007; Naciri et al. 1999), although some local differences may occur. Then, even if fish were massively migrating it seems quite unlikely that genetic differences would impact on sex ratios. This is further supported by the remarkable homogeneity found in the present study among population level sex ratios in young fish. Therefore, the environmental cause for excess of females in some years seems more plausible than the genetic one. It has to be noted that in the Mediterranean, we could not identify “good” years (specially abundant year classes) in the published data from Egypt (Wassef and El Emary 1989) and Turkey (Ergene 1999), though variation in age-group sex ratios was evidenced in Egypt. In this latter case however, three cases of unbalanced age group sex ratios reflected excess of females in old age groups (>VIII), which can be explained by the higher longevity of females, as seen before. Still, the very low female ratio in age group VI (26.4%) cannot be explained by differential longevity between the sexes and is likely to be the result of environmental variation between years.

There is little doubt that the variation in sex-ratio between age classes, when it cannot be explained by differences in longevity or a sampling bias between sexes, is of environmental origin. However, the available data do not allow the determination of the time at which the differences appear and of the mechanism involved. Still, as temperature in early life has been shown to influence sex-ratios, and temperature is highly variable between years, the fact that variation in natural temperature may also induce variations in sex ratio seems plausible. The European sea bass has a polygenic sex determination system, with an estimated heritability of 0.62 ± 0.12 for sex tendency (Vandeputte et al. 2007). In such a system, when environmental variation induces different sex-ratios in different years, evolution should drive the system towards chromosomal sex determination, or environmental sex determination if environment variations have different effects on the fitness of males and females (Bulmer and Bull 1982; Charnov and Bull 1977). As chromosomal sex determination has been excluded (Blazquez et al. 1999; Vandeputte et al. 2007), as well as purely environmental sex determination (Vandeputte et al. 2007), the only possibility remaining is polygenic (or at least oligogenic) sex determination, but this is expected to be only a transient state, as in most conditions it is evolutionary unstable (Bulmer and Bull 1982; Hatcher and Tofts 1995; Rice 1986). As environmental conditions are expected to be quite variable in the Atlantic, the West Mediterranean Sea and the East Mediterranean Sea, it is likely that this system combining genetic variation and environmental influences on sex ratios could have reached different equilibrium states in the main wild sea bass populations, as has been observed in the Atlantic silverside *Menidia menidia*, where the relative influence of genetics and temperature on sex ratios differs along a latitudinal gradient (Lagomarsino and Conover 1993), or in the lizard *Niveoscincus ocellatus* in which highland populations show genotypic sex determination and lowland populations show temperature-dependent sex determination (Pen et al. 2010). Therefore, exploring the between population variation in sex determination patterns might be of great help to better control sex ratios in sea bass aquaculture, and to further increase our knowledge of the evolution of sex-determining mechanisms.

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