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History and dynamics of the overexploitation of the blackspot sea bream (*Pagellus bogaraveo*) in the Bay of Biscay

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The blackspot sea bream (*Pagellus bogaraveo*) used to be a major species in the landings from the Bay of Biscay up to the early 1980s. Nowadays, it is only a minor bycatch. Up to the mid-1970s, more than 15 000 t of blackspot sea bream were landed annually in Spanish and French ports. Thereafter, catches declined sharply from 1975 to 1985 and have stayed at low levels ever since. Here, the full history of the fishery collapse is described, using time-series of landings dating back to the early 1900s. Fishing mortalities of the main demersal stocks (hake, anglerfish, sole) were in the range 0.2–0.5 during the last 30 years. It is likely that the blackspot sea bream stock was exploited at a similar level, which is shown here to be unsustainable. The blackspot sea bream is highly sensitive to overfishing because of its protandrous hermaphroditism, with late first maturity (8 years) as females and rather low productivity. According to a yield-per-recruit model, the biomass of fecund females (BFF) is reduced to <20% of virgin BFF for a fishing mortality around 0.2. A dynamic model assuming a simple stock–recruitment relationship fitted to the reconstructed landings explained the collapse, with estimated fishing mortalities never exceeding 0.5.

Keywords: deep water, management, sex change.

Introduction

The blackspot sea bream, *Pagellus bogaraveo* (Brünnich, 1768), also known as the red sea bream, stock in the Bay of Biscay collapsed during the period 1975–1985, and it has not been of significant fishery interest since. The decline of the stock was not anticipated. In the late 1960s, trawlers from La Rochelle, the main French port for landings of blackspot sea bream throughout the twentieth century, redirected more effort towards this species as a result of the declining catch rates for hake (Guichet *et al.*, 1971). Guichet *et al.* (1971) noted no sign of overexploitation and reported a large proportion of individuals aged 10 and older in the catch. Seven years later, a severe drop in landings was reported (Njock, 1978), and from the mid-1980s, it was clear that the stock had collapsed (Dardignac, 1988). Based on FAO landings data for the Northeast Atlantic for 1972–2002, blackspot sea bream was classified as a depleted species, and it is one of the few species whose landings had already declined to low levels by the early 1980s (Caddy and Surette, 2005).

From the 1950s to the 1970s, blackspot sea bream was exploited mainly by French and Spanish bottom offshore trawlers, by artisanal pelagic trawlers in the eastern Bay of Biscay (ICES Divisions VIIIa,b), and by Spanish longliners in the Cantabrian Sea (ICES Division VIIIc), with smaller contributions from other fisheries (Sánchez, 1983; Dardignac, 1988). Since the 1980s, it has been mainly a bycatch in France, and only a few small-scale handliners have been targeting the species.

Blackspot sea bream is found on the shelf and down to 700 m and on seamounts (Morato *et al.*, 2001), but breeding is in shallower waters. Juveniles occur at the coast, as shown by the catches of small individuals (<3 cm) from shrimp pushnets in the Bay of Biscay (Priol, 1932). Large fish are found deeper than juveniles, indicating an ontogenetic migration towards deeper waters (Olivier, 1928; Desbrosses, 1932; Morato *et al.*, 2001; Spedicato *et al.*, 2002). Nevertheless, large fish (>40 cm) have also been caught occasionally at the coast (Priol, 1932). In summer, the distribution of the population extends to the west of Scotland (Olivier, 1928; Desbrosses, 1932). The stock area is therefore considered to include ICES Subareas VI, VII, and VIII. Furthermore, tagging has shown that blackspot sea bream found in summer in the northern Bay of Biscay and Celtic Sea overwinter in the Cantabrian Sea (Guéguen, 1974; Sánchez, 1983).

Blackspot sea bream grow to at least 70 cm standard length (about 80 cm total length; Bauchot and Hureau, 1986) and up to 4 kg (Frimodt, 1995). In the Bay of Biscay, the biggest reported fish in the 1960s were 68 and 70 cm total length. Their scales, which were difficult to read, could have included 25–30 annual growth increments (Guéguen, 1969b).

The species is a typical protandric hermaphrodite (Buxton and Garratt, 1990), most individuals being first functional males and then developing into functional females. A fraction of the population never changes sex and is referred to as gonochoric. In fish-farming conditions, up to 40% of individuals are gonochoric females (Micale *et al.*, 2002), but the proportion of gonochoric females seems to be much lower in the wild (Krug, 1990). In the wild, the proportion of females per size class and their state of maturity over time may depend on population abundance, with more females at lower abundances (Krug, 1998). As a result, the proportion of females may increase as a result of fishing (ICES, 1996). In fish farms, food is supplied without limit, but in the wild, available food resources might increase at lower densities. For another protandric hermaphrodite, *Diplodus sargus*, a density-dependent effect is thought to account for the delayed sex change observed in one Marine Protected Area (Lenfant, 2003). In captivity, male blackspot sea bream first mature at a size of 28 cm total length and age 3; both gonochoric and secondary females first spawn at 29.5 cm total length and age 4 (Micale *et al.*, 2002). In the wild, the smallest observed mature female was 30 cm long and 5–8 years old (Sánchez, 1983; Krug, 1998). In the Strait of Gibraltar, Gil and Sobrino (2001) estimated the mean size at maturation of females as 35.7 cm total length.

Because of its particular biology, the blackspot sea bream may be especially sensitive to overfishing. This study attempted to revisit the history of the Bay of Biscay population collapse and to assess what would have been a possible sustainable exploitation level. Because landing levels were already high in the 1950s, landings were reconstructed starting in the 1900s. Other available data on abundance were also compiled. A yield-per-recruit simulation was used to assess the sensitivity of a blackspot sea bream population to fishing, and a dynamic model was used to estimate possible trends in historical fishing mortality. Based on these findings, the management implications for the current depleted stock are discussed.

Material and methods

Reconstructing landings

Several data sources were used to reconstruct the time-series of blackspot sea bream landings from the Bay of Biscay stock area for the period 1905–2008. The documented fishing countries were Spain, France, and the UK (Table 1). FAO catch statistics provided most of the data. FAO landings from the Northeast Atlantic (FAO Area 27, corresponding to the ICES Area) were extracted from the FAO website (http://www.fao.org/fishery/statistics/global-capture-production/en). FAO data are aggregated at the scale of the Northeast Atlantic and include Portuguese blackspot sea bream landings, but because in recent years, Portugal reported blackspot sea bream from ICES Subareas IX and X only (ICES, 2008), all Portuguese landings reported for the Northeast Atlantic from 1962 on in the FAO database were considered to come also from these areas and were not taken into account.

All Spanish landings from the Northeast Atlantic before the 1980s were allocated to the Bay of Biscay stock (Table 1). The current Spanish fishery in the Gulf of Cádiz only developed in the 1980s and from 1975 ICES data could be used to separate landings from the Bay of Biscay and the Gulf of Cádiz stocks (http://www.ices.dk/fish/statlant.asp). Landings before 1950 are certainly incomplete, because data were only found for 3 years.

French landings in 1926–1930 were reported in Desbrosses (1932) and official catch statistics per ICES Subarea were available for 1925–1956 (Table 1). Guéguen (1969a) compiled landings from the three main ports where blackspot sea bream was landed from 1955 to 1967 and specified that these landings represented 80–93% of the overall French blackspot sea bream landings from the Atlantic coast. These landings were therefore multiplied by 1.25 to estimate the total French landings in these years. Njock (1978) and Dardignac (1988) reported landings in the period 1967–1972 and landings statistics from Ofimer and Ifremer were used for 1973–2002.

Table 1. Sources of reconstructed landings data for blackspot sea bream from the Bay of Biscay (OF, official landings statistics).

Country	Reported years of landings	Data source	Years
International landings	1932–1938	Postuma (1978)	1932–1938
	1947–1973		1947–1973
	1950–2008	OF, ICES landings statistics	1974–2002
Spain	1925	Desbrosses (1932)	1925
	1928	OF, national landings statistics	1928
	1950–2002	OF, FAO landings statistics	1950–1959
	1960–1981	Sánchez (1982)	1960–1981
	1982–2001	OF, ICES landings statistics	1982–2001
UK	1905–1930	Desbrosses (1932)	1905–1929
	1930–1951	OF, yearly sea fisheries statistical tables, reported by the Ministry of agriculture and fisheries	1930–1951
	1950–2002	OF, FAO landings statistics	1950–2002
France	1926–1930	Desbrosses (1932)	1926–1930
	1931–1951	OF, yearly official landings statistics reported in Revue des Travaux de l'Office des Pêches Maritimes	1931–1947
	1948–1956	OF, yearly official landings statistics reported by the Directorate of Marine fisheries	1948–1954
	1955–1967	Guéguen (1969a)[a]	1955–1967
	1968–1969	Njock (1978)	1968–1969
	1970–1972	Dardignac (1988)	1970–1972
	1973–2002	OF, landings statistics from Ofimer and Ifremer	1973–2002

[a]Landings in the three main ports (La Rochelle, Lorient, and Concarneau) reported to produce 80% of total landings (see text).

UK catches were reported by Desbrosses (1932) for the period 1905–1930, with no data during the First World War (1914–1918) and extracted from official national landings statistics for the period 1930–1951, with no data during the Second World War (1939–1945) (Table 1).

The following rule was applied when several data sources were available for the same year and country: (i) if there were reasons to consider one dataseries more reliable, that series was used, (ii) otherwise, the highest figure was retained (last column in Table 1). As some landings data were aggregated up to the family level, species identification may be a problem. Nevertheless, historical scientific data show that the blackspot sea bream was much more abundant than other *Pagellus* species in the Bay of Biscay, and reported landings in catch statistics closely match best estimates reported in scientific papers (e.g.

Desbrosses, 1932; Guéguen, 1969a). This suggests that other species were probably only a minor component of landings reported as blackspot sea bream before the 1980s. Similarly, for Spain, landings reported by Sánchez (1982) were clearly ascribed to *P. bogaraveo* only. Misidentification may affect the small landings reported in recent decades more seriously, because other sea bream species did not undergo the same decline and may now be as common or more abundant than the blackspot sea bream.

Size composition of landings

No time-series of length frequency distributions of landings was found. In La Rochelle in the late 1960s, there were four commercial categories: (1) <250 g, (2) 250–500 g, (3) 500–1000 g, and (4) >1000 g. Landings statistics were not available for these four categories, but Guichet *et al.* (1971) reported that fish weighing <500 g (i.e. categories 1 and 2 combined) represented 20–24% of the landings in 1966–1968. To assess what might have been the size distribution of the landings, this value was converted into numbers using two simple assumptions. The mean weight of the four commercial categories was assumed to be 100, 375, 750, and 1500 g for categories 1–4 (i.e. the median of the given range for categories 2–4 and a crude assumption for category 1). For the first assumption, the proportion in weight of small fish in the landings was taken as the low end of the reported proportion (20%) and assumed to be only fish of category 2. For the second assumption, the proportion of small fish was taken as 24%; the additional 4% were assumed to be fish of category 1. Landed weights per category were converted to numbers based on the assumed mean weight per category. Landings in La Rochelle were assumed to be representative of international landings.

Landings per unit of effort

Estimated landings per unit of effort (lpue) were available for three short periods, 1937–1939, 1946, and 1966–1968, for offshore trawlers from La Rochelle (Letaconnoux, 1948; Guichet *et al.*, 1971). Landings and effort data from French fisheries statistics were used to estimate variations in lpue during 1972–1984 for the same category of trawlers from the same port. Available fishery statistics files including catch and effort for these times are limited and do not include vessel power. Because of this, aggregated lpue values were calculated as total annual catch divided by total number of days at sea for the fleet of offshore trawlers from La Rochelle. Offshore trawlers from La Rochelle were mainly side trawlers up to the late 1960s. Their number decreased in the late 1960s and they were mostly replaced by stern trawlers in the 1970s (Guichet *et al.*, 1971; Dardignac, 1988), so that fishing power changed over the time.

Surveys indices

Although there were no continuous time-series of fishery research surveys in the Bay of Biscay before the late 1980s (i.e. before the collapse of the blackspot sea bream stock), some surveys were carried out for different objectives and the archived data have been used here to calculate abundance indices of blackspot sea bream. One survey was carried out in 1959 mainly on the slope of the southern half of the Bay of Biscay (ICES Divisions VIIIb–c). Two surveys with protocols similar to the current western International Bottom Trawl Survey (IBTS) were carried out in November–December 1973 and April–May 1976. A quarterly survey was carried out from 1980 to 1984; it was followed by another quarterly survey with a different protocol and RV from 1985 to 1997. Densities were calculated at the time from the 1973 and 1976 surveys (Quéro *et al.*, 1989). Here, survey data from 1980–1984 and 1985–1997 were combined and the occurrence (proportion of tows where blackspot sea bream were caught) was calculated for this combined time-series and the 1959 survey. Because of the lack of a single time-series with a standardized protocol, accurate abundance estimates (e.g. swept-area densities) could not be derived.

Growth

Growth parameters were estimated by fitting the von Bertalanffy growth function to an age–length key based on reading growth rings on the scales of fish caught in the Bay of Biscay (Guéguen, 1969b). At the time, growth parameters were estimated using the graphical Walford method over ages 5–20 years and an additional fit for juveniles (Guéguen, 1969b). New estimates using non-linear least squares for all data reported in Guéguen (1969b) were derived using the software package R (R Development Core Team, 2008).

Yield-per-recruit model

The effect of fishing mortality on a blackspot sea bream stock was simulated using a yield-per-recruit model with mean size and weight-at-age from Guéguen (1969b) (Table 2) and sex- and maturity-at-length data from Krug (1998). Simulations were made with constant recruitment of 1000 individuals at age 1. The proportion of mature females per size class was introduced according to estimates for the year 1991 reported in Krug (1998):

$$P_{\mathrm{mat}} = \frac{e^{-25.6+0.794L_{\mathrm{F}}}}{1+e^{-25.6+0.794L_{\mathrm{F}}}}, \quad (1)$$

where L_{F} is the fork length and P_{mat} the proportion of females that are mature. The proportion of females P_{f} in the stock per size class

Table 2. Mean size and weight-at-age used as input parameters to the yield-per-recruit model.

Age group	Mean size (total length, cm)	Mean weight (g)	Proportion of females mature
0			0
1	11.2	18	0
2	17.6	72	0
3	22.3	149	0
4	26	239	0
5	29.2	342	0
6	31.9	449	0.007
7	34.3	562	0.05
8	36.1	658	0.15
9	37.9	765	0.31
10	39.5	870	0.45
11	40.9	969	0.54
12	42.3	1076	0.62
13	43.7	1190	0.68
14	44.8	1285	0.73
15	45.9	1386	0.77
16	46.7	1462	0.80
17	47.8	1572	0.83
18	49.2	1719	0.86
19	49.9	1796	0.88
20	50.2	1830	0.89

Data derived from Guéguen (1969b) and Krug (1998).

was simulated as

$$P_{\mathrm{f}} = \frac{e^{-7.55+0.215L_F}}{1+e^{-7.55+0.215L_F}}. \qquad (2)$$

The proportion of mature females in the stock per size is then $P_{\mathrm{f}} \times P_{\mathrm{mat}}$. These equations were applied to the mean size-at-age from Guéguen (1969b) to estimate the proportion of mature females per age group.

Fecundity, the number of oocytes spawned per female, was expressed as a function of mean length-at-age:

$$F = 1028.44e^{0.15L_F}. \qquad (3)$$

When necessary, fork length was converted to total length using the relationship from Krug (1989):

$$L_{\mathrm{T}} = 1.13L_{\mathrm{F}} - 0.04. \qquad (4)$$

Yield-per-recruit simulations were made, assuming a natural mortality of 0.2. This estimate of M was derived from the presumed longevity in the population. Hewitt and Hoenig (2005) compared two such approaches and recommended the rule $M = 4.22/t_{\max}$, where $t_{\max}$ is the maximum age in the population derived from data from many populations. The oldest fish observed by Guéguen (1969b) was 20 years old, which, taken as maximum age, corresponds to $M = 0.211$. Setting $M = 0.2$ implies that 1% of the population survives to 23 years, which matches with the observations from Guéguen (1969b) of a few older fish from auction markets. The same natural mortality was used for exploratory assessments in recent years of stocks in the Azores and the Gulf of Cádiz (ICES, 2006).

The simulated exploitation pattern assumed the same fishing mortality at all ages after recruitment to the fishery and no fishing mortality before (i.e. a knife-edge recruitment). Simulations were carried out for four different ages at recruitment to the fishery: 1, 4, 8, and 12 years old. Recruitment-at-age 1 simulates the situation where juveniles are exploited with the same intensity as adults. Recruitment-at-age 4, corresponding to around 27 cm total length, is a knife-edge proxy for an exploitation pattern including younger fish, as indeed was the case (Priol, 1932). Simulations of recruitment to the fishery at ages 8 and 12 explore the possible state of the stock when fish are not exploited before the age at which most of the population has changed to reproductive females. Using the parameter values and assumptions just described, equilibrium catches, biomass of fecund females (BFF), and fecundity per recruit were simulated. Computations were carried out using *R*.

Dynamic population model

To explore the temporal changes in fishing mortality that could explain the observed landings pattern, two age-structured models were fitted to the reconstructed time-series of landings. The models differed in how recruitment (age 0) was handled. As no data for fitting a stock–recruit function were available for blackspot sea bream, two extreme one-parameter stock–recruit functions were investigated. In model 1, recruitment was assumed constant, and thus independent of stock size. In model 2, recruitment was first constant, then from a certain point in time on assumed to be proportional to BFF to model a negative effect of decreasing BFF on recruitment.

The basic population dynamics were in both cases

$$N_{y,a} = N_{y-1,a-1}\exp(M - s_aF_y) \quad 0 < a, \qquad (5)$$

$$B_{y,a} = w_aN_{y,a}, \qquad (6)$$

where $N_{y,a}$ is numbers-at-age a in year y, M the natural mortality (constant across ages and time), F_y the fishing mortality in year y, and s_a the selectivity at age. Therefore, fishing mortality was assumed to be separable into a selectivity component and an annual component. Biomass-at-age, $B_{y,a}$, was obtained by multiplying numbers-at-age by mean weight-at-age w_a from Guéguen (1969b), which was assumed constant for all years.

BFF is calculated from

$$\mathrm{BFF}_y = \sum_a w_a\, p_a N_{y,a}, \qquad (7)$$

where p_a is the proportion of mature females at age a as defined for the yield-per-recruit model.

In model 1, recruitment-at-age 1 was assumed to be constant during the study period (1950–2001), but also before:

$$N_{y,1} = \frac{B_0}{w_1}, \qquad (8)$$

where B_0 is the constant recruitment biomass at age 1. In model 2, recruitment was assumed constant up to 1966 and proportional to BFF thereafter, similar to a hockey-stick recruit function, though in time rather than as a function of BFF:

$$N_{y,1} = \frac{B_0}{w_1} \quad \text{for } y < 1967, \qquad (9a)$$

$$N_{y,1} = \frac{r\mathrm{BFF}_y}{w_1} \quad \text{for } y \geq 1967, \qquad (9b)$$

where r is an unknown proportionality constant.

The numbers-at-age in the initial year, $N_{1,a}$, were obtained by assuming a constant fishing mortality F_0 for all years before 1950 and the same constant recruitment B_0/w_1:

$$N_{1,a} = \frac{B_0}{w_1}\prod_{1}^{a-1}\exp(-(M + s_aF_0)), \qquad (10)$$

$$N_{1,a} = \frac{B_0}{w_a}\exp(-(M + s_aF_0)a). \qquad (11)$$

Using the traditional catch equation and no discards, the landings in weight corresponding to the model [Equations (5) and (6)] are

$$L_{y,a} = \frac{s_aF_y}{M + s_aF_y}(1 - \exp(-M - s_aF_y))B_{y,a}. \qquad (12)$$

Assuming lognormal observation errors, the observation model for recorded landings $l_{y,a}$ (in weight) is then

$$l_y, a \sim N(\log(L_{y,a}), \sigma^2), \quad (13)$$

where σ^2 is the variance on the normal scale.

A constant coefficient of variation (CV) was assumed for all years and transformed using the well-known result for the lognormal distribution (Aitchison and Brown, 1957):

$$\sigma^2 = \log(CV^2 + 1).$$

The data used for fitting the two models were reconstructed annual landings for the period 1950–2001, average weight-at-age, and the average proportion of mature females per age class as described for the yield-per-recruit model (Table 2). The CV of landings was (arbitrarily) set to 3%. Knife-edge selection from age 4 was assumed, which seemed to be a realistic assumption based on the yield-per-recruit and size distributions of the landings investigations. Thus, selectivity-at-age was

$$s_a = 0 \quad \text{for } a < 4,$$

$$s_a = 1 \quad \text{for } a \geq 4.$$

To reduce the number of parameters to be estimated, some parameters were fixed. Natural mortality was set to $M = 0.2$. Considering the available landings data (Figure 1), fisheries exploitation was assumed to have been constant at moderate levels up to 1950, changing between 1951 and 1996, and constant again from 1997 on. Consequently, the following constraints were imposed on fishing mortality estimates: $F_{1950} = F_0$ and $F_{1997} = F_{1998} = F_{1999} = F_{2000} = F_{2001}$. The parameters to be estimated for both models were F_0, B_0, and 45 annual fishing mortalities using the 52 datapoints, giving the models rather too many parameters given the number of observations. For model 2 with varying recruitment [Equation (9)], the parameter r was also estimated. It turned out that in that case F_0 was not estimable, so it was set to $F_0 = 0.2$.

All parameter estimations were carried out by maximum likelihood. To obtain reasonably smooth time-series of estimated F_y, interannual variations of fishing mortality were constrained during the estimation to $F_y = F_{y-1} \pm 0.5$. Model fit was investigated by visual inspection of residuals and only results from converged runs were used (convergence criterion maximum gradient $<10^{-4}$).

Results

Reconstructed time-series of landings

The reconstructed time-series of landings is complete from 1950 and patchy from 1905 to 1950 (Figure 1). International annual catches of about 10 000 t were landed in the 1950s, increasing to a level of 15 000 t in the early 1960s; they then levelled off to 20 000 t from the mid-1960s, started to decrease from the 1970s, and collapsed to <1000 t in the 1990s. The historical situation in the first half of the twentieth century is less clear. Landings from Spain, which was the main fishing country after 1950, were only found for the years 1921, 1925, and 1928 in the scientific literature. International landings from these few years suggest that more than 10 000 t of blackspot sea bream were landed, at least from the 1920s (Figure 1).

The contribution of different countries to the landings changed over time, with the UK landing significant quantities until the late 1940s (Figure 1). The UK may have been the main country exploiting the species in the early twentieth century. It is not known why UK landings decreased before French and Spanish landings, in particular because catches by ICES Subarea do not indicate an earlier reduction in the catches in northern areas than farther south. Since the 1960s, landings have been roughly 2/3 Spanish and 1/3 French.

The overall annual landings in the ICES data are smaller than in the above reconstructed time-series because not all landings were reported to ICES. Nevertheless, the temporal pattern is similar. In the 1950s and 1960s, landings of blackspot sea bream were highest from Subarea VIII, but the species was also caught in significant quantities in Subareas VII and VI. Landings seem to have declined

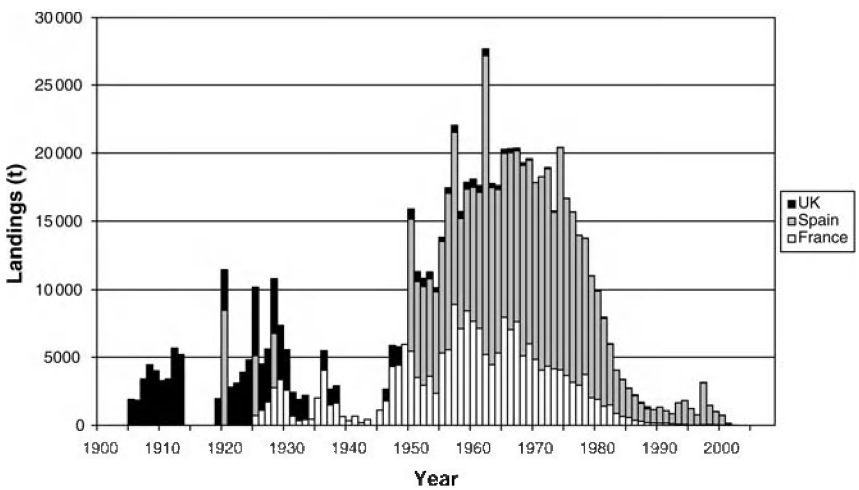

Figure 1. Reconstructed time-series of landings of red sea bream by country from the Bay of Biscay population (catch from ICES Subareas VI, VII, and VIII).

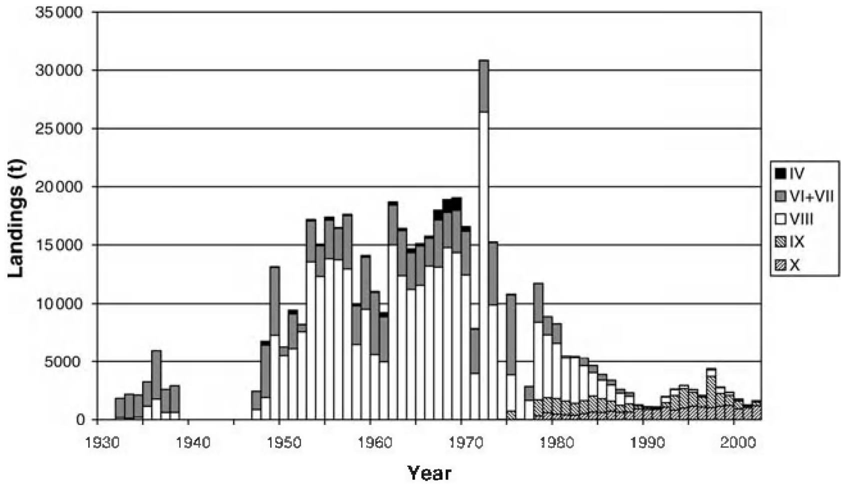

Figure 2. Landings of red sea bream by ICES Subarea (source: ICES statistical bulletin and ICES database).

Table 3. Reconstructed landings, effort, and lpue for blackspot sea bream and hake of high-sea trawlers from La Rochelle for the period 1937–1984.

Year	Landings (t)	Effort (days fishing)	Red sea bream lpue	Hake lpue	Source
1937–1939	–	–	81	804	–
1946	–	–	279	1 948	Letaconnoux (1948)
1966	–	15 900	130	419	–
1967	–	12 100	175	519	Guichet *et al.* (1971)
1968	–	10 818	206	503	–
1972	2 409	6 401	376	535	–
1973	3 845	13 170	291	778	–
1974	4 436	13 425	330	630	–
1975	3 350	11 179	299	669	–
1976	1 634	8 972	182	571	–
1977	1 489	7 559	196	524	–
1978	NA	4 037	NA	NA	This study
1979	NA	4 482	NA	NA	–
1980	NA	3 359	NA	NA	–
1981	NA	3 295	NA	NA	–
1982	174	2 531	69	332	–
1983	88	2 324	37	264	–
1984	106	1 690	62	456	–

NA, not available.

in Subareas VI, VII, and VIII at the same time (Figure 2). Nevertheless, low catches in recent years came mainly from ICES Division VIIIc.

There were changes in fishing gears over time. Until the 1970s, 95% of French landings were from bottom otter trawlers, but, pelagic trawlers caught 18% of the landings of the species in 1984 (Dardignac, 1988). French landings reported in the 1990s and early 2000s were mainly from artisanal longliners from one port in western Brittany (Audierne).

Effort and lpue of offshore trawlers from La Rochelle

The reconstructed time-series of effort and lpue data for offshore trawlers from La Rochelle are shown in Table 3. In a comparison of catch rates before and after the Second World War, the average blackspot sea bream landings for an offshore trawler from La Rochelle during a 12-d sea trip were estimated at 976 kg in 1937–1939 and 3343 kg in 1946 (Letaconnoux, 1948). These results were based on data from 552 sea trips carried out in 1937–1939 and 117 in 1946. They showed a 2.4-fold increase in lpue after the War compared with before the War; the increase was the highest (3.4-fold) for blackspot sea bream. Converting these results to catch per day at sea provides lpue estimates of 81 and 279 kg d^{-1} for years before and after the War (Table 3). Lpues of La Rochelle offshore trawlers in the late 1960s were about 23 kg per 100 hp d^{-1}. The mean power of the fleet then was about 700 hp (Guichet *et al.*, 1971), resulting in lpue values of about 161 kg d^{-1} (Table 3). Lpue values calculated based on data for 1972–1984 showed high levels in the early 1970s, started to decline in 1976–1977, and reached much lower levels by 1982–1984 (Table 3). Unfortunately, data for 1978–1981 were not available for the port of La Rochelle separately. Lpue values were not calculated after 1984 because of the low fishing effort by this fleet.

Size composition of landings

Depending on the assumption used for converting weight by commercial categories into numbers, fish of 250–1000 g might have represented 60–80% of the total landings in numbers (Table 4).

Table 4. Assumed contribution to the landings in numbers and weight of the commercial category of red sea bream landed in La Rochelle in the late 1960s.

			Assumed contribution to the landings (%)			
			Hypothesis 1		Hypothesis 2	
Commercial category	Weight range (g)	Median weight (g)	In weight	In number	In weight	In number
1	<250	100	0	–	4	24
2	250–500	375	20	40	20	32
3	500–1000	750	40	40	37.5	30
4	>1000	1 500	40	20	37.5	15

Based on data in Guichet *et al.* (1971).

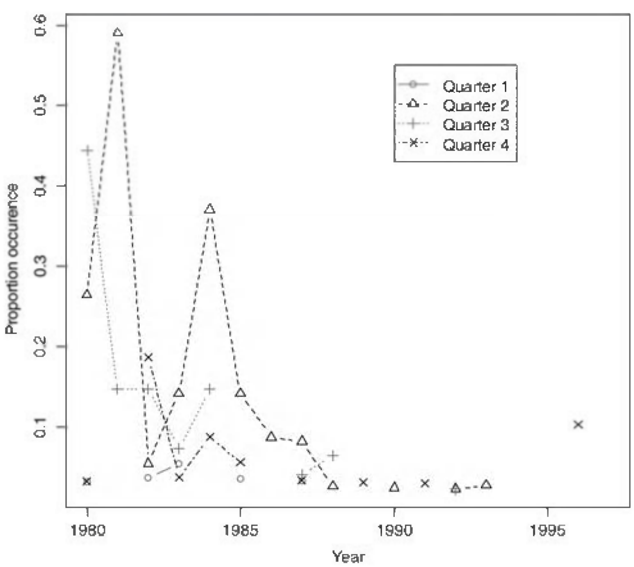

Figure 3. Time-series of the proportion of tows where red sea bream was caught in surveys from 1980 to 1997 in the Bay of Biscay.

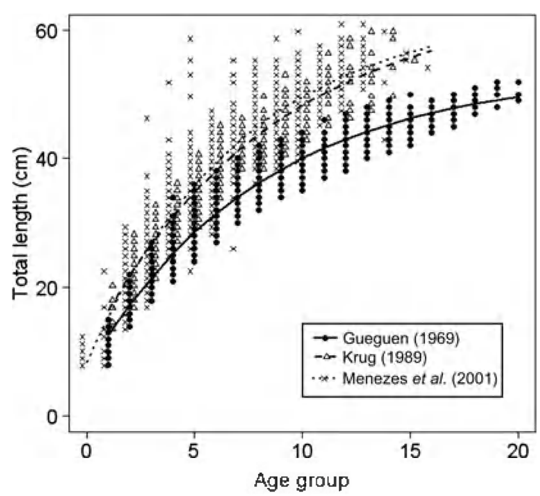

Figure 4. Age–length keys and von Bertalanffy growth curve estimates for blackspot sea bream in the Bay of Biscay, based on data from Guéguen (1969a) and Azorean waters based on data from Krug (1989) and Menezes *et al.* (2001).

Big fish of >1 kg may not have made up more than 20% of the landings in numbers and smaller fish of <250 g may have represented up to 25% of the landings in numbers. For an estimated mean weight of 239 g at age 4 (Guéguen, 1969b), these results suggest that knife-edge selectivity at age 4 appears plausible.

Survey indices

The survey carried out in 1959 caught blackspot sea bream in 31 of 52 hauls. Blackspot sea bream was often caught in the surveys carried out in 1972 and 1976. Catch rates of more than 100 fish per hour were observed locally and catch rates of 10–100 fish per hour were estimated for large areas of the Bay of Biscay in April–May 1976 (Quéro *et al.*, 1989). The occurrence of blackspot sea bream in hauls calculated combining the time-series from 1980 to 1984 and 1985 to 1997 showed both a seasonal pattern with higher abundances in Quarters 2 and 3 and a general decline over the period (Figure 3). Since 1987, catches in the western IBTS survey have been only occasional. In most years, no blackspot sea bream were caught.

Growth

The new fit of the von Bertalanffy growth model to the historical length-at-age data in the Bay of Biscay was good (Figure 4, Table 5). Available length-at-age and growth parameters from the Azores suggest faster growth there. In the Azores, estimated maximum ages were also younger, reaching only 15 or 16 years compared with 20 years in the Bay of Biscay.

Spawning-stock biomass and fecundity

Using parameters estimated in the Azores for 1991 (Krug, 1998), the size at 50% maturity of females is about 36 cm, corresponding to 8-year-old fish (Figure 5a). At that size, the proportion of females in the population is still below 50% (Figure 5b). Combining these two functions, the proportion of mature females per size class is estimated to reach 50% at 40 cm, corresponding to age 10 (Figure 5c, Table 2). Lastly, because of increasing weight, fecundity beyond 40 cm total length increases strongly (Figure 5d) so that in this species, large fish may make a major contribution to the production of female gametes.

Yield-per-recruit model

In the yield-per-recruit model, equilibrium catches in number were highest for a high fishing mortality applied to young ages, catches in weight levelling off at an F level that depended on the assumed age at recruitment to the fishery (Figure 6a). With fishing mortality applied from age 1, catch in weight peaked for $F \approx 0.15$, then decreased (Figure 6b). With fishing mortality starting later (4–8 years), higher catches in weight were obtained with a fishing mortality between 0.2 and 0.4.

Table 5. von Bertalanffy growth coefficient for *P. bogaraveo* for the Bay of Biscay and Azorean stocks.

k	L_∞	t_0	*N*	ICES Area	Method and reference
0.092	56.8	−2.92	–	VIII	Walford method from Guéguen (1969b)
0.162	48.3	−0.72	10 186[a]	VIII	New fit using data from Guéguen (1969b)
0.137	51.4	−0.97	20[b]	VIII	New fit to mean length at ages from Guéguen (1969b)
0.209	51.56	−0.53	530	VIIIc	Sánchez (1983)
0.174	53.9	−0.66	–	VIIIc	Ramos and Cendrero (1967)
0.196	48.06	−0.47	–	VIIIc	Alcazar *et al.* (1987)
0.174	54.2	−0.66	–	VIIIb,c	Castro Uranga (1990)
0.117	58.50	−1.55	659	X	Krug (1989)
0.136	63.8	−1.04	1 375	X	Menezes *et al.* (2001)[c]

[a]Size at age derived from back calculation (Guéguen, 1969b).
[b]Number of age groups.
[c]Recalculated fit to the data from Menezes *et al.* (2001) converted to total length using the relationship $L_T = 1.13L_F - 0.04$ (Krug, 1989).

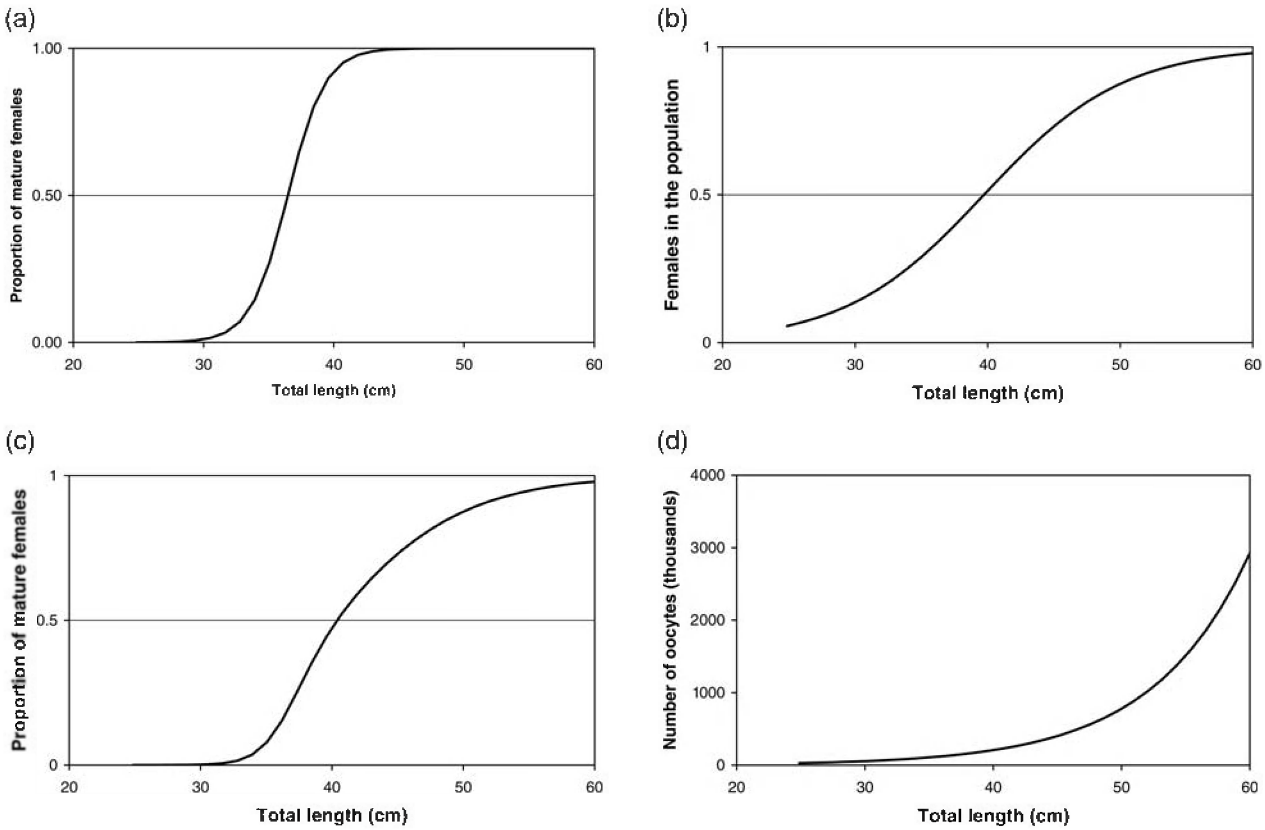

Figure 5. Maturity and fecundity according to size, using parameters from Krug (1998). (a) Proportion of mature females in the female population; (b) proportion of females in the total population; (c) proportion of mature females in the total population; and (d) fecundity at length.

Lower catches in weight were obtained with fishing mortality starting at age 12, even at high *F* levels. Total numbers in the stock were strongly reduced for moderate fishing mortality applied from age 1 and remained close to unexploited levels if there was no fishing mortality before age 8 (Figure 6c). Total biomass was reduced to <50% of the unexploited level with fishing mortalities of about 0.1 and 0.2, assuming fishing mortality was applied from ages 1 and 4, respectively (Figure 6d). Female spawning-stock biomass was much more sensitive to exploitation and was reduced to <50% of the unexploited level for $F < 0.1$, assuming fishing mortality started at age 1 or 4. If fishing mortality started only from age 8, the BFF was reduced to 50% of the unexploited level for $F \approx 0.2$ (Figure 6e). The sensitivity to exploitation was stronger for fecundity, which was reduced to 50% virgin stock levels for $F \approx 0.05$, 0.07, 0.14, and 0.6 when fishing mortality started at ages 1, 4, 8, and 12, respectively (Figure 6f).

Dynamic modelling

Model predictions for both the constant recruitment and varying recruitment models are shown in Figure 7. If constant recruitment was assumed during and before the study period, fishing mortality had to increase to a value >2 in the 1990s to explain the observed decline in landings (continuous line in Figure 7c). Initially, fishing mortality was estimated to decrease for some years, which led to an increase in total biomass and BFF (Figure 7b). Assuming

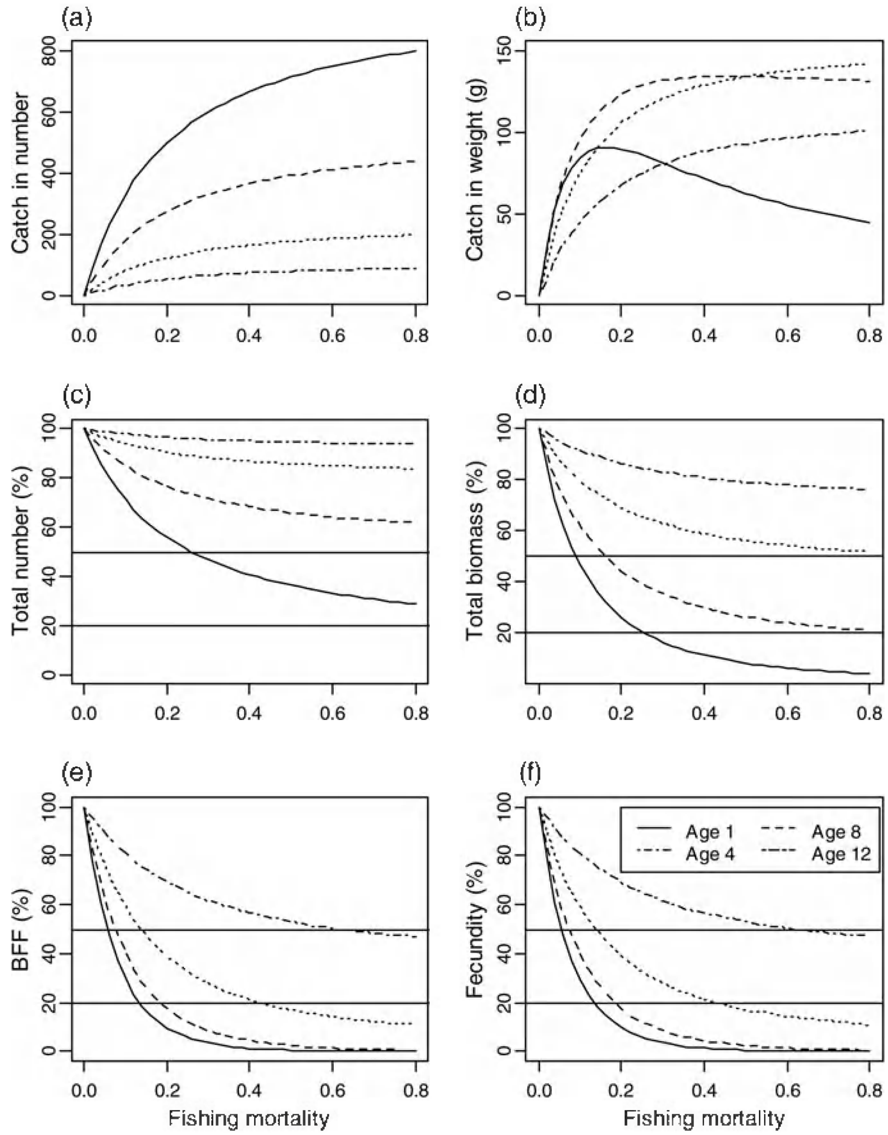

Figure 6. Results of the yield-per-recruit model. Catch in (a) numbers and (b) weight for 1000 recruits. (c) Total stock numbers, (d) total-stock biomass, (e) BFF, and (f) fecundity as a percentage of an unexploited red sea bream stock with $M = 0.2$, $F = 0.2$, and fishing mortality starting from ages 1, 4, 8, and 12.

recruitment proportional to BFF from 1967 (dashed lines in Figure 7) leads to a similar decline in BFF but an earlier decline in total biomass. The biggest difference, however, was in the estimated fishing mortalities. Under this scenario, fishing mortality never exceeded 1 and generally fluctuated around 0.5 to bring about the observed collapse of blackspot sea bream landings. Note that both models fitted the observed landings rather well (Figure 7d), which led to generally small standardized residuals, except for the final years because of the assumption of constant fishing mortality (results not shown). This is not surprising given that both models had many parameters. Therefore, the results should be taken as indicative rather than factual.

Discussion

Notwithstanding the poor quality of reconstructed landings data, the blackspot sea bream was a major fishery resource in ICES Subareas VI, VII, and VIII until the mid-1970s. Thereafter, landings decreased to a low level in about 10 years. Catches have always been higher in Subarea VIII, but landings from areas farther north also occurred in the past. French landings were mainly caught by offshore trawlers in the Bay of Biscay (ICES Subarea VIII), and the main landing port was La Rochelle. In the late 1960s, about half the total blackspot sea bream catches of offshore trawlers from La Rochelle were from ICES Division VIIIc (Cantabrian Sea). The other main fishing areas were ICES Divisions VIIIa,b and to a lesser extent VIIj,h (Guichet *et al.*, 1971). The fishing areas in the 1930s and 1940s could not be identified.

Anecdotal reports suggest that the species' catchability varied from year to year, as fishers were able to "find" fish or not. For adult fish, this cannot be to the result of variations in abundance because several age classes were exploited. It is unknown whether these changes in catchability can explain the large year-to-year variations in landings, with much higher landings in a few years

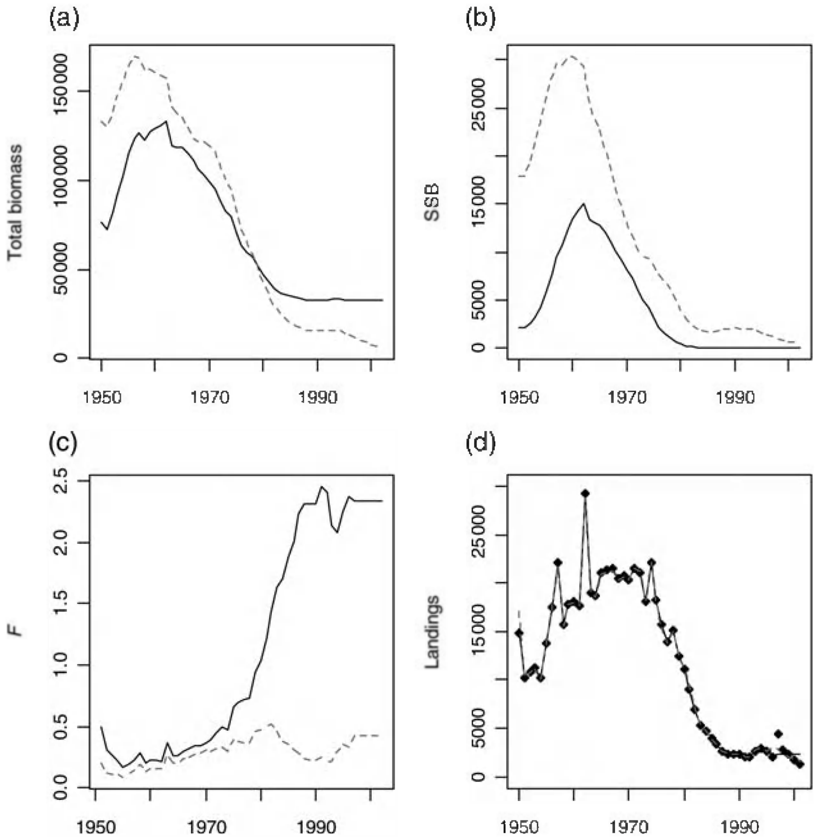

Figure 7. Dynamic model estimates for (a) total biomass, (b) spawning-stock biomass (SSB), (c) fishing mortality (F), and (d) landings. Model with constant recruitment (continuous line); recruitment fixed before 1967 and proportional to BFF thereafter (dashed lines). Points in (d) are observed landings (as in Figure 1).

(Figure 1), or if these variations were the result of poor data quality.

Data quality is a problem for the older landings statistics. For example, for 1955 and 1956, French landings from Guéguen (1969a) are 30–40% higher than official landings. The data compiled about 10 years thereafter by Guéguen were considered to be more reliable. Likewise, landings given by Dardignac (1988) for the year 1950, 8370 t, are about twice those given by the national landings statistics of the ministry, 4366 t. In this study, the national landings statistics figure was kept as Dardignac (1988) reported landings from 1 year only, without specifying how the 8370 t figure was obtained. Nevertheless, this shows the magnitude of uncertainty of past landings.

Lpue values were reconstructed for La Rochelle trawlers, the only trawler fleet sufficiently documented, and it decreased sharply from the mid-1970s. Relating these lpues to fishing effort, from 1950 to 1980, French fishing effort in the Bay of Biscay and elsewhere strongly increased. Effort of French trawlers from the Atlantic coast increased by 74% from 1961 to 1975 (Guillou and Njock, 1978). The total engine power of the French fishing fleet continued to increase during the 1980s (Mesnil, 2008). This increase does not account for technological creep, and some technological developments were reported to be targeted at blackspot sea bream (Maucorps, 1970; Guichet *et al.*, 1971). Therefore, the increase in lpue reported for 1966–1968 (Guichet *et al.*, 1971, Table 3), and the high lpues sustained in the early 1970s might have resulted from increasing fishing efficiency. This may have completely masked the actual stock trend. As a result of this likely change in fishing power and the paucity of historical data, lpue figures computed here for the La Rochelle offshore trawlers are unlikely to track the stock trend. Blackspot sea bream lpues for this fleet were considered uninterpretable by Njock (1978), but as they start in the late 1930s, they may still convey some information.

Age-at-length values from Guéguen (1969b) were similar to older estimates from the Bay of Biscay and the coast of Morocco (Guéguen, 1969b), but seemed smaller than age-at-length values from the Azores. It was not possible to assess whether the difference is real or the result of sampling bias, because the material for age estimation was not the same (scales in the Bay of Biscay and whole otoliths in the Azores) and there was no intercalibration. It may be either that scales include check rings or that growth increments of older fish are difficult to identify from whole otoliths. Data used for the yield per recruit and the dynamic models were length- and weight-at-age from Guéguen (1969b) and maturity from Krug (1998). The yield-per-recruit model provided a static view of exploitation levels that a blackspot sea bream stock may sustain, depending on which age groups are exploited. Sustainable F levels are low because the BFF is strongly reduced by exploitation. Even with a fishing mortality starting at age 8 only, the BFF and the fecundity of the stock are reduced to <50% of the unexploited level for $F \approx 0.2$. With fishing mortality starting at younger ages, levels below 20% of unexploited levels are obtained for the same fishing mortality of 0.2. From this, blackspot sea bream stocks are understood as only able to sustain low fishing mortality. As fishing mortalities of the main

Table 6. Average fishing mortalities for the main demersal stocks in the Bay of Biscay and Celtic Sea (source: ICES).

Stock	*F*	Years
Northern hake (*Merluccius merluccius*)	>0.25	1990–2005
Monkfish (*Lophius piscatorius* and *L. budegassa*) from the Celtic Sea and Bay of Biscay	Around 0.23	1990–2005
Megrim (*Lepidorhombus whiffiagonis*) from the Celtic Sea and Bay of Biscay	>0.3 in most years	1990–2005
Whiting (*Merlangius merlangus*) from the Celtic Sea	0.1–0.5	1985–2005
Sole (*Solea solea*) Bay of Biscay	0.4–0.6	1985–2005

demersal stocks (hake, anglerfish, sole) in the Bay of Biscay have been typically in the range 0.2–0.5 over the past 30 years (Table 6), blackspot sea bream is likely to have been exploited at *F* well above 0.2, at least in the late 1970s.

The yield-per-recruit model does not account for density-dependent compensation of the age of sex change and maturation because there are no data about the extent to which this might occur in the wild. Sex change may, however, be plastic in blackspot sea bream and reduced population abundance might therefore induce an increased fecundity, with males changing to females earlier and possibly faster growth. The growth, sex ratios, and maturation observed in captivity (Micale *et al.*, 2002) are unlikely to happen in the wild, where food is never unlimited and inter-specific competition is maintained. Nevertheless, some year-to-year variations of sex change and maturation were observed in the Azores (Krug, 1998).

A dynamic model accounting for flexibility in sex change has been proposed (Molloy *et al.*, 2007). It predicts that flexibility in sex change increases the resilience to fishing of male first sex changers. The collapse of the blackspot sea bream stock in the Bay of Biscay indicates that such flexibility, if it occurred, was insufficient to cope with past levels of fishing mortality.

The dynamic model with constant recruitment estimated high fishing mortalities to fit the low landings from the 1980s. Assuming a simple stock–recruitment relationship, the model estimated fishing mortalities not exceeding 0.5 in most years. None of the models represents the true history of the blackspot sea bream stock, but despite the different assumptions, some common patterns emerged. For both models, the estimated decline in BFF preceded that of landings, suggesting that for such a stock with delayed maturity, the effect of fishing might remain unnoticed for a while. In the real world, the probable increasing fishing efficiency in the early 1970s (see above) contributed to the lack of any warning about the collapse. At that time, there was little experience of stock collapse and management was not designed to prevent them. Indeed, no management was implemented until about 20 years later.

It was only in 2003 that a total allowable catch (TAC) was introduced by the EU [Council Regulation (EC) No. 2340/2002 of 16 December 2002]. This TAC was further reduced in 2005 and 2009. A minimum landing size was also set by Council Regulation (EC) No. 1359/2008 of 28 November 2008 to 30 cm in 2009 and 35 cm in 2010. These management measures seem appropriate to allow the stock to rebuild. The exploitation of small blackspot sea bream in the past is confirmed by Priol (1932) and by the existence of a commercial category for small fish in La Rochelle (Guichet *et al.*, 1971). In more recent years, 1-year-old blackspot sea bream were exploited in the Strait of Gibraltar (Erzini *et al.*, 2006). As there was no management of the landings before 2003, it may well be that any small amount of fish appearing somewhere was quickly fished out, preventing any rebuilding.

The potential for the stock to rebuild to past levels is unknown, but the increase in lpue after the War suggests that a 5-year reduction in fishing mortality allowed for a strong increase in the stock, which was then much bigger. The continuation of small landings in the 1990s and 2000s indicates that the residual stock has not died out. It is not known if the carrying capacity of the ecosystem for this species has remained the same, but there is no known ecosystem change that would be deleterious to this species. Observed hydrological changes (Michel *et al.*, 2009) have not made the Bay of Biscay significantly divergent from the range of conditions sought by blackspot sea bream. The effect of the fishery since the 1960s is enough to explain the stock collapse, and catch levels during the past 20 years seem a sufficient explanation for its low level. Although currently many studies focus on global stock depletion and fisheries collapse, there are some good examples of commercial stock rebuilding as well as of rebuilding of threatened populations of birds, mammals, and other species when mortality or threats are lifted. Reducing the fishing mortality of the small residual stock will probably allow an increase in abundance, but because management has only recently been introduced, it may take some years for the effects to become visible. Blackspot sea bream mature late, so the reduction of mortality in small fish will take time to generate an increase in spawning stock.

In addition to managing the commercial fishery, it would be useful to regulate recreational fishing because juvenile blackspot sea bream are coastal during summer and thus susceptible to being caught by recreational anglers, or released with damage. In the past, the coastal distribution of juveniles and their high catchability made them an easy catch for recreational and subsistence fisheries (Priol, 1932). Small blackspot sea bream (<20 cm total length) were sold commercially under vernacular names such as "pirono" and "pelon" in Brittany (Priol, 1932). Wounds to the mouth have been observed and attributed to hooks, and significant mortality of small fish damaged by hooks has been assumed (Desbrosses, 1931).

A recovery of the stock should be detectable well before full replenishment by the ongoing western IBTS survey. When the stock was abundant, the species was caught during most surveys in the Bay of Biscay and it was still caught up to the mid-1980s when the stock was already low.

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