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What can exploratory modelling tell us about the ecobiology of European sea bass (*Dicentrarchus labrax*): a comprehensive overview

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Abstract – European sea bass, *Dicentrarchus labrax*, is a highly valuable species in Europe, both for aquaculture in the Mediterranean Sea and for commercial and recreational fisheries in the North East Atlantic Ocean. Subjected to increasing fishing pressure, the wild population has recently experienced significant recruitment fluctuation as well as a northward extension of its distribution area in the North Sea. While the nature of the ecological and/or physiological processes involved remains unresolved, ontogenetic habitat shifts and adult site fidelity could increase the species' vulnerability to climate change and overfishing. As managers look for expert information to propose management scenarios leading to sustainable exploitation, exploratory modelling appears to be a cost-efficient approach to enhance the understanding of recruitment dynamics and the spatio-temporal scales over which fish populations function. A conceptual modelling framework and its specific data requirements are discussed to tackle some sound ecological questions regarding this species. We consequently provide an updated review of current knowledge on bass population structure, biology and ecology. This paper will hence be particularly valuable to develop spatially-explicit models of European sea bass dynamics under environmental and anthropogenic forcing. Knowledge gaps requiring further research efforts are also reported.

Keywords: Population dynamics / essential habitats / connectivity / bioenergetic modeling / phenotypic plasticity / life cycle adaptation

1 Introduction

European sea bass, *Dicentrarchus labrax* (L. 1758) Moronidae (subsequently referred to as sea bass) is a highly valuable species in Europe whose production relies primarily on aquaculture but also on fishing. Commercial fisheries have been developing rapidly in the Northeast Atlantic (NEA) (Pawson et al. 2007), with landings increasing from 2000 t in the late 1970s to more than 9000 t in 2006. Landings have then stabilized around 7800 t (ICES 2012). Sea bass is also one of the most prized fish in Western Europe and the population has been subjected to increasing fishing pressures in recent years, both commercial and recreational.

Regarding stock assessment, the International Council for the Exploration of the Sea (ICES) currently considers four stocks. Only one stock (North Sea, eastern and western English Channel and Celtic Sea corresponding to ICES divisions IVb,c, VIIa,d-k) has been analytically assessed yet (ICES 2015). Over recent years, strongly declining recruitment and biomass have been reported, which led the European Com-

mission (EC) to implement emergency measures for this stock in 2015 (ban on pelagic trawling during the spawning season; European Commission 2015). The EC is also planning complementary measures to manage recreational fishing and limit catches in all commercial fisheries in order to “alleviate a serious threat to the conservation of sea bass”. The status of the three other sea bass stocks is still unclear as they are considered to lack sufficient data to perform an analytical assessment.

Assessing sea bass stocks and their dynamics is difficult because of dubious/fragmentary data concerning exploitation patterns and poor knowledge of the population structure as well as the life traits and spatio-temporal dynamics of the various components. Developing spatially-explicit models would be of great help for e.g. understanding life cycle dynamics and their key drivers, for studying population resilience/northward expansion in reaction to climate change or for assessing conservation strategies such as measures of spatial closure (Colman et al. 2008). However, such developments are rather challenging as sea bass exhibit varying degrees of mobility and sensitivity to environmental factors during an extended life cycle (Pawson et al. 2007; Reynolds et al. 2003).

The first step in the development of a modelling approach is the acquisition of knowledge about the system. This involves

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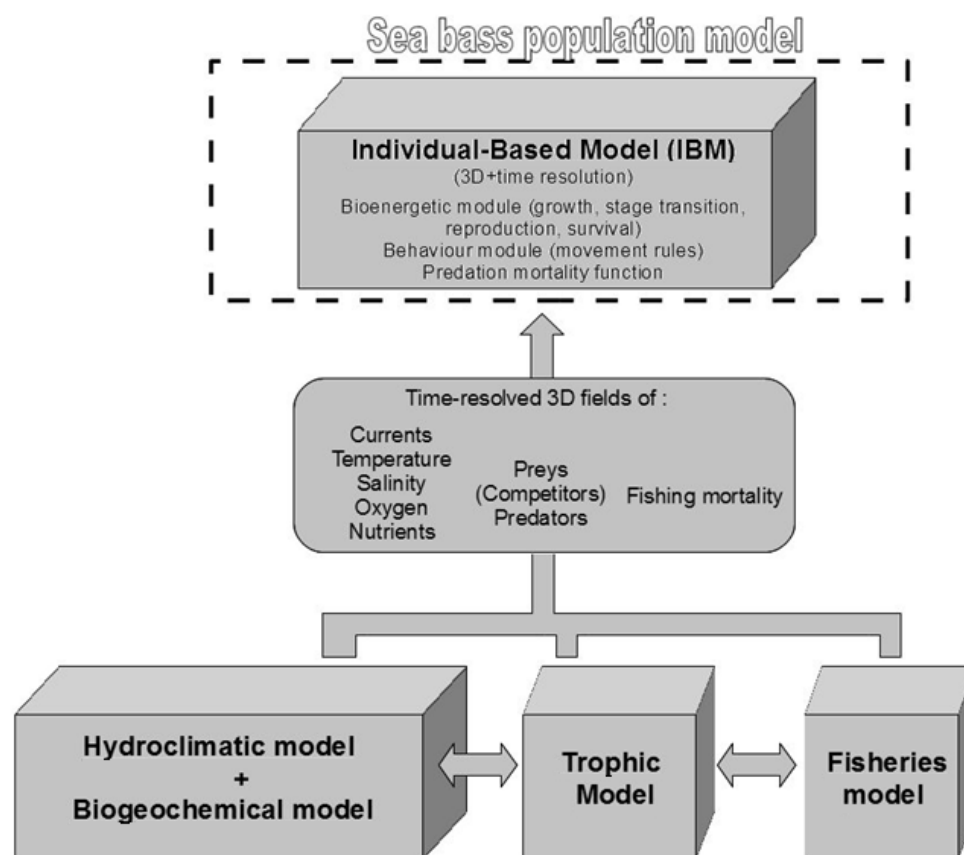


Fig. 1. Conceptual modelling framework for sea bass dynamics.

gathering information concerning stage-specific distribution, life traits (growth, stage transition, etc.), ecophysiology and ethology, notably its sensitivity to specific environmental factors (e.g. environmental preferences, adaptive behaviour). We looked for both knowledge and long-term data sets from nursery samplings, tagging surveys, genetic studies as well as from experiments in controlled environments where the influence of distinctive forcing factors on sexed fish of known origin has been studied at the individual scale. Compared to other wild fish species, much is known on sea bass and a considerable number of papers have been published since the review of Pickett and Pawson (1994). Our work aims at updating and widening this review by gathering recent advances from both aquaculture and fisheries research. We first introduce a suitable exploratory modelling approach and its specific data requirements. This integrative modelling approach should ultimately help us to evaluate, over sea bass life cycle, which combination of factors make specific habitats essential (for a given life stage) and influence their inter-connectivity (Petitgas et al. 2013). Similarly, it would enable testing the influence of adaptive variation for behavioural and physiological traits (phenotypic plasticity). The review is structured by life stage following a short description of some of the main features of sea bass populations (distribution area, genetic structure, growth). We provide a synthesis of knowledge with a level of detail much higher than required to define the parameter values for a model of sea bass dynamics. This precision is useful for assessing the accuracy and uncertainty of parameters and hypotheses as-

sumed in the modelling process for quantifying the robustness of the model and investigate several realistic settings. The last section aims at identifying knowledge gaps which require dedicated research.

2 The modelling framework: a short overview

A spatially-explicit approach is particularly relevant to investigate key issues such as (i) for the egg and larval stages, the way environmental drivers influence the connectivity between offshore spawning grounds and coastal nurseries; (ii) for the juvenile stage, the relationship between nursery settlement and the recruitment to the fishery; and (iii) for the adult stage, the way behavioural processes under environmental control drive reproduction and stock structure (Fig. 1). To address the modelling of a fish population in a spatially heterogeneous environment, several methods could be considered, each one approaching the problem in a different way (Tyler and Rose 1994). In the reaction-diffusion models approach, the population is considered as a single entity, the distribution of which relies on the combination of variable diffusion and growth in different areas. The movements of “individuals” in the population are described by a random diffusion term. A good illustration of that approach is the “basin model” developed by MacCall (1990) in which some areas are considered more suitable than others and as a consequence are more attractive to the population. Population growth at a given location

is counteracted by population density: when the size of the population increases, the habitat becomes less suitable and the population diffuses into adjacent areas. A second type of approach is based on metapopulation models in which the population is split into a set of spatially distinct sub-populations, each one having its own internal dynamics. In such models, changes in population dynamics rely partly on variations in exchange rates between each sub-population (Hilborn 1990).

One of the limitations of those two classes of population models is that they do not represent explicitly the differences in terms of environmental “histories” between individuals, which may change in time and during the life cycle of the fish. On the contrary, the level of resolution of individual-based models (IBMs) allows formulating testable hypotheses regarding the role of (a) spatio-temporal variability of local interactions and movements (e.g. passive vs. active random/oriented displacement), (b) life-cycle and ontogenetic processes, (c) phenotypic variability and plasticity (including adaptive behaviour), and (d) demographic stochasticity and genetic variability (Grimm and Railsback 2013; Tyler and Rose 1994).

Bioenergetic models constitute suitable building blocks for IBMs (Fig. 1). In fact, they translate into individual performance traits (growth, survival and investment in reproduction) for the specific environmental conditions encountered by fish at a given location (determined by the IBM). Among existing bioenergetic models, the most popular and recommended one is the Dynamic Energy Budget (DEB) model (Kooijman 2010). Contrary to scope for growth (Winberg 1956) and net production models (Lika and Nisbet 2000), the DEB theory relies on a reduced number of equations and parameters to provide a mechanistic characterization of physiological processes over the full life-cycle (and complete size range) of an individual. Unlike models built under the metabolic theory of ecology (Brown et al. 2004), energy conservation rules are respected and the energy flow to reproduction is explicitly described. Solutions to DEB differential equations represent the life history of individuals in a variable¹ multi-factorial environment.

To perform the modelling development of dynamic environmental forcing for sea bass, it is necessary to reproduce, at the relevant spatio-temporal scale, the physical and trophic environmental features most relevant to the species.

For physical environmental features, Eulerian hydroclimatic models (e.g. Regional Oceanic Modelling Systems ROMs: Shchepetkin and McWilliams, 2005; MARS-3D: Lazure and Dumas 2008) under atmospheric and river forcing have become readily-accessible tools generating dynamic hydrodynamic (currents, turbulence, tides), temperature and salinity fields (Fig. 1). Yet, they may still require coupling to complementary modules in order to account for other abiotic features (e.g. oxygen, light environment: Chapelle et al. 1994; Mellor 1998). Because climate change has far-reaching ecological effects (Durant et al. 2007), IPCC climatic projections could be tested to force the hydroclimatic model (Stock et al. 2011).

Regarding the numeric description of the trophic environment, several options can be considered, from a static formu-

lation (e.g. reading values from an extended size-specific food density matrix) to a detailed mechanistic model (Whipple et al. 2000). The issue is to (1) represent the trophic environment of sea bass at the relevant resolution (spatial, temporal and size-specific scales), in order to (2) provide prey and predator fields of sea bass and to identify essential trophic linkages to its population dynamics under varying environmental conditions. Because of the reduced availability of long time-series of fine-scale basin-wide synoptic survey data, the trophic modelling approach appears to be the most appropriate solution (Fig. 1). Low trophic level models (e.g. ECOSMO: Daewel and Schrum, 2013; ERSEM: Edwards et al. 2012; NEMURO: Werner et al. 2007) would provide a suitably dynamic spatial field of size-structured plankton biomass available to sea bass post-larvae (Friedrichs et al. 2007). Yet, bio-geochemical models would fail to account for the distribution of prey consumed by later developmental stages. Hence, coupling to a high trophic level or using whole-system models (e.g. Ecopath with Ecosim EwE: Christensen and Walters 2004) would be necessary to generate bottom-up/top-down dynamic feedbacks between different life stages of sea bass and their potential prey, predators and competitors. Among available modelling platforms, OSMOSE² (Shin and Cury 2004) and bioenergetically-controlled APECOSM (Maury et al. 2007) are most appealing, as they are spatially-explicit and contain elaborate mechanisms for sensitivity analyses and interactive scenarios testing.

Fishing mortality is another field of predation that should be taken into account for a realistic description of sea bass survival (Fig. 1). Several fleet dynamics models can be considered, such as Random Utility Models (Vermard et al. 2008), which assume a maximisation of profit behaviour or the spatially-explicit fishery model ISIS-Fish (Mahévas and Pelletier 2004).

The calibration/validation of combined IBM-bioenergetic model requires detailed information on size/stage-specific nutritional requirements, timing of stage transitions, growth and reproductive performance of sea bass under monitored environmental conditions (e.g. temperature, salinity, oxygen, photoperiod, etc.). Such information would contribute to control the relative size of energy fluxes between metabolic functions. Together with stage-specific data on metabolic requirements and tolerance ranges to specific environmental factors, swimming performance, activity and exploration patterns are valuable data for building habitat selection models (Humston et al. 2004; Railsback et al. 1999).

3 Some main features of distribution area, genetic structure and growth

3.1 Spatial distribution and genetic structure

Sea bass is widely distributed in mid-latitudes (Fig. 2) from the Canary Islands (aquaculture escapees; Toledo Guedes et al. 2009) and the Atlantic coasts of Morocco to Scotland and Scandinavia (Colman et al. 2008), including the Azov, Black,

¹ Under constant development conditions, the growth equation simplifies and provides a physiological interpretation to Von Bertalanffy equations.

² Trophic interactions are formulated in a feeding opportunistic way, similar to sea bass feeding behaviour, based on spatio-temporal co-occurrence and size suitability between prey and predator.

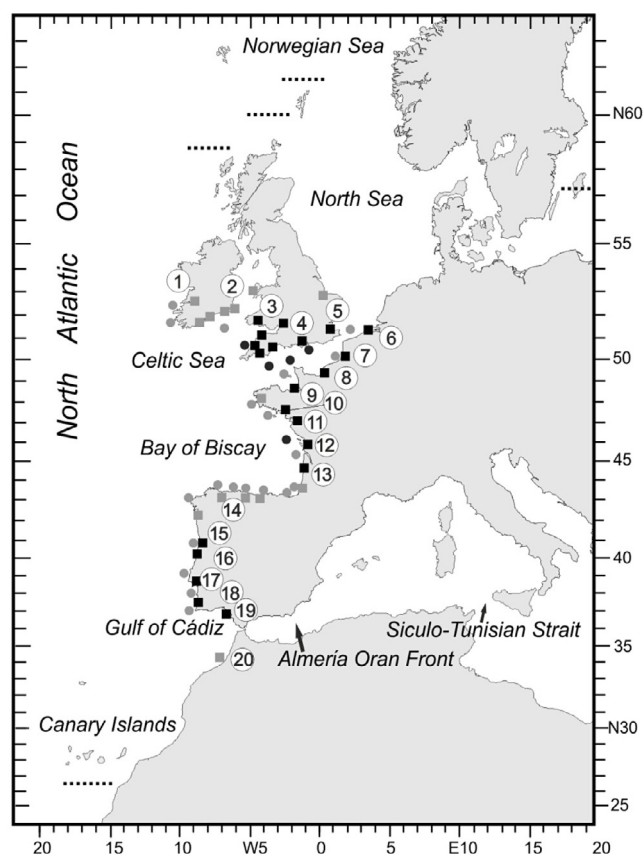


Fig. 2. Distribution range and functional habitats of European sea bass in the Northeast Atlantic. Nurseries: (1) Shannon, (2) South Irish Coast, (3) Severn & Bristol Channel, (4) Solent, (5) Thames, (6) Sheldt, (7) Somme, (8) Seine, (9) Normand-Breton Gulf, (10) Vilaine, (11) Loire, (12) Charente Sluices, (13) Arcachon Basin, (14) Cantabrian Coast, (15) Aveiro, (16) Mondego, (17) Tagus, (18) Mira, (19) Cádiz, (20) Kenitra. Nurseries and spawning areas are respectively represented by squares and circles. Identified and assumed nursery areas are represented in black and grey respectively. Information concerning assumed functional habitats comes from grey literature and empirical evidence.

Mediterranean and southern Baltic seas (Bagdonas et al. 2011; Quéré et al. 2012). The NEA is considered home to a distinctive population unit from Western and Eastern Mediterranean populations (Bahri-Sfar et al. 2000; Naciri et al. 1999; Tine et al. 2014), transition zones being respectively the Almería-Orán front and in the Siculo-Tunisian strait (Quéré et al. 2012). Sea bass in the Adriatic Sea also constitutes an independent population (Souche et al. 2015). Subpopulation structure has been suggested in the Eastern Mediterranean in relation to the diverse sea basins (e.g. Bahri-Sfar et al. 2000). The Atlantic population has been generally perceived as an homogeneous one (e.g. Coscia et al. 2012), despite subpopulation structure being suggested between the North Sea and the Bay of Biscay (Quéré et al. 2012) as well as off the Irish coasts (Fritsch et al. 2007). As a contact zone between Atlantic and Western Mediterranean fish, Southwestern Iberian and Moroccan Atlantic waters could potentially harbour a distinctive population (Souche et al. 2015). Interestingly, sea bass distribution range presents a significant degree of overlap with

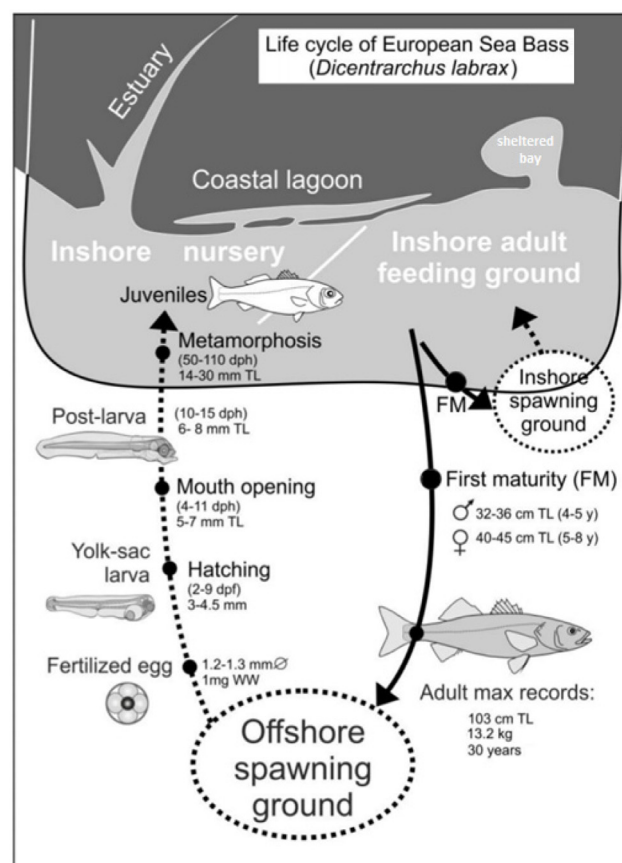


Fig. 3. Typical life cycle of European sea bass and movements/migrations between essential habitats.

the related species spotted sea bass *Dicentrarchus punctatus* (Bloch 1792), yet little is known of their functional inter-relationships if any.

The distribution and life cycle of sea bass encompass environmentally-contrasted habitats. As various life cycle strategies have been identified (Fig. 3), enhanced understanding of the patterns of local adaptation in this species would generate a better identification of marine population units. In Mediterranean populations, it has been suggested that adults inhabiting coastal lagoons would genetically diverge through an adaptive selection process from those inhabiting offshore areas (Allegrucci et al. 1997; Lemaire et al. 2000; Tine et al. 2014). Finally, there is growing evidence of genetic interaction between wild populations and escapees from aquaculture (e.g. Bahri-Sfar et al. 2000; Coscia et al. 2012) and more studies are required to assess the extent of hybridization between wild and farmed fish and the impacts that aquaculture may have on wild populations.

3.2 Growth and longevity

Maximum morphometric records for NEA sea bass report individuals reaching 103 cm total length (TL) and over 12 kg wet weight³. Sexual dimorphism in growth (Fig. 4)

³ Froese R., Pauly D., 2014. FishBase [WWW Document]. FishBase.

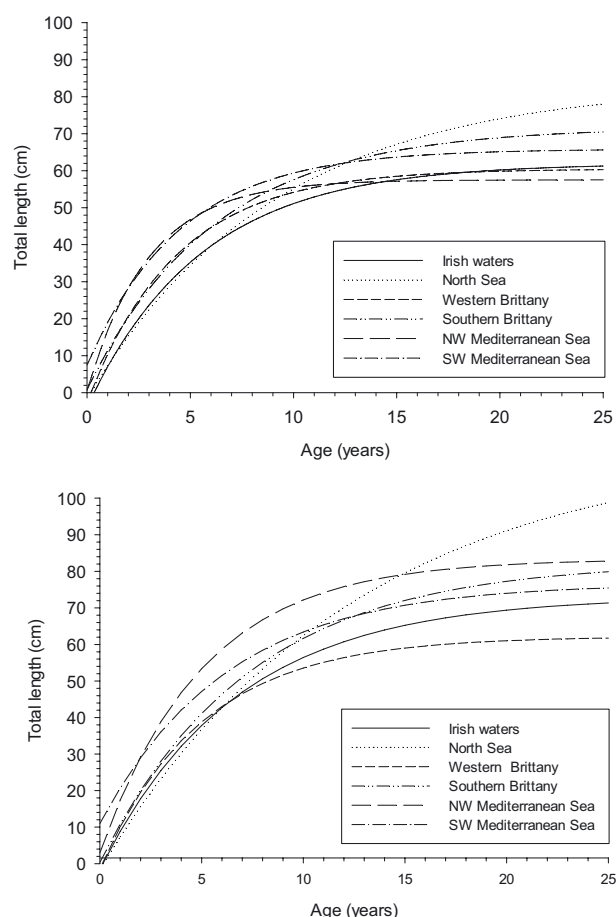


Fig. 4. Von Bertalanffy growth models estimated throughout sea bass distribution area for both male (top) and female (bottom). References: North Sea (Cardoso et al. 2015), Irish waters (Bou Ain 1977 after Kennedy and Fitzmaurice 1972), Western Brittany waters (Bou Ain, 1977 after Boulineau-Coatanea 1969), South Brittany waters (Bertignac 1987), NW Mediterranean Sea (Barnabé 1976).

has long been reported in favour of females together with greater longevity leading to higher absolute size and mass than those observed in males (Pickett and Pawson 1994). The three metapopulations (Atlantic, western and eastern Mediterranean) have distinct phenotypic characteristics including growth as found experimentally in controlled conditions (Costa et al. 2010; Gorshkov et al. 2004). Yet, a recent multi-sites experiment of the rearing performances of 5 wild populations indicated that the genotype by environment interaction for growth rate was limited between populations but strong within populations (Vandeputte et al. 2014). Sampled in the wild, populations also showed noticeable differences as reported in Table 1. Yet, it should be noted that a number of estimates were inferred despite methodological limitations (e.g. truncated age distribution, range of mean size at age without dispersion statistics) and growth parameters in the wild require updating. Some sex-specific Von Bertalanffy growth models are displayed on Figure 4, while Table 2 provides some length-mass relationships obtained from different regions. Despite mean length-at-age data being available for both sexes in British waters (Kelley, 1988; DAAF unpubl. cited by Pickett

and Pawson 1994), no sex-specific von Bertalanffy growth equation was estimated. Maximum longevity has been reported to be 30 years (Pickett and Pawson 1994).

4 Eggs and larval stages

4.1 Distribution and behaviour

Very little is known regarding egg distribution in the wild. Nearly-neutrally buoyant eggs are assumed to occur in mid-water (top-20 m) and undergo passive vertical ascent until their density increases just before hatching (Boulineau-Coatanea 1969). To our knowledge, there is no recent paper reporting on the variability of the horizontal distribution of sea bass eggs (but see Thompson and Harrop 1987; Jennings and Pawson 1992). Such a distribution is the result of the interplay between spawning pattern and local hydrodynamics.

Sea bass post-larvae (5–11 mm notochord length, 15–55 days post-fertilization dpf) feed and grow for at least one month in unstratified waters in the English Channel (Jennings and Pawson 1992). In addition to positive phototropism (Barnabé 1976), they exhibit positive rheotaxis and increase their swimming performance between 10 and 20 days-post-hatch (dph) (Georgalas et al. 2007; Leis et al. 2012). Yet, they are unable to overcome strong currents, suggesting that, during this period, movements are mostly driven by hydrodynamics. Still, sea bass larvae are able to perform vertical movements (Barnabé 1990) that could enable them to avoid or take advantage of wind-induced or tidal currents.

Active horizontal movements (0.3–0.7 km/h) are assumed to occur in synchrony with notochord flexion (9.8–11.5 mm TL, 28–50 dpf at 20–13 °C: Alami-Durante et al. 2006) and caudal fin formation (12 mm standard length (SL); Leis et al. 2012). Smallest individuals observed in coastal nurseries measure ca. 12–15 mm TL (e.g. Jennings and Pawson 1992). It has been suggested that, provided they have orientation capabilities, post-larvae could respond to environment signals to perform migrations towards coastal nurseries (Leis et al. 2012). River drainage could control both sea bass small-scale movements and nursery settlement (Vinagre et al. 2009). Similarly, a significant relationship was identified between temperature and nursery settlement (Reynolds et al. 2003).

Across the NEA, nursery settlement, penetrating sometimes several kilometers into estuaries, occurs between April and September (Iberian Peninsula: Martinho et al. 2008; UK waters: Jennings and Pawson 1992; Kelley 1986; Mediterranean: Dufour et al. 2009), by which time major concentrations are reported in the UK (Pickett and Pawson 1994). The elapsed time between hatching and nursery settlement is for instance 2 to 3 months in the Bristol Channel Reynolds et al. 2003).

4.2 Development and growth

Sea bass egg and larval development has been described in Barnabé et al. (1976), Jennings and Pawson (1991) and Cucchi et al. (2012). Salinity influences hatching rate while temperature controls incubation duration, embryo metabolism and

Table 1. Parameters of the von Bertalanffy growth models estimated throughout the European sea bass distribution area. With L_{∞} (cm), K (year^{-1}), t_0 (year). Growth performance index is obtained by $= \log 10 K + 2 \times \log 10 L_{\infty}$. Regions for which putative methodological issues cast doubt upon parameter equations are indicated by an *.

Area	Reference	Sex	N	Age range	L_{∞}	CI L_{∞}	K	CI K	t_0	Growth performance
North Sea	Cardoso et al. 2015	M	156	1–11	83.5	70.8–101.8	0.11	0.09–0.14	0.16	2.88
		F	151	1–11	114.6	95.1–146.6	0.08	0.06–0.10	0.16	3.02
		Sex-combined	335	1–11	102.4	90.6–121.3	0.09	0.07–0.11	0.16	2.97
Ireland*	Bou Ain, 1977 from Kennedy and Fitzmaurice, 1972	M	281	1–16	62		0.18		0.33	2.84
		F			73.1		0.15		0.14	2.90
British waters	ICES, 2015	Sex-combined	>90 000	1–28	84.55		0.09699		–0.73	2.84
Western Brittany *	Bou Ain, 1977 from Boulineau, 1969	M	199	1–11	60.5		0.23		0.18	2.93
		F		1–11	62.2		0.2		0.11	2.89
Southern Brittany	Bertignac, 1987	M	103	4–18	71.77	70.59–72.95	0.161	0.148–0.174	–0.079	2.92
		F	89	4–17	82.59	80.49–84.69	0.137	0.127–0.147	–0.033	2.97
		Sex-combined	192		80.36	77.31–83.40	0.13	0.119–0.141	–0.073	2.92
Central Bay of Biscay	Bou Ain, 1977 from Hoai Thong, 1970	Sex-combined	462	1–8	103.5		0.11		0.08	3.07
Cádiz Gulf	Arias, 1980	Sex-combined	1013	1–7	99.33		0.14		–0.462	3.14
Atlantic coast of Morocco*	Bou Ain, 1977 from Gravier, 1961	Sex-combined	203	1–13	80.3		0.12		–0.59	2.89
NW Mediterranean	Barnabé, 1976	M	106	0–6	57.54		0.334		–0.0351	3.04
		F	166	0–6	83.4		0.197		–0.187	3.14
		Sex-combined	1330	0–7	85.51		0.1818		–0.223	3.12
SW Mediterranean	Kara and Chaoui, 1998	M			65.85		0.22		–0.55	2.98
		F			76.7		0.16		–0.97	2.98
		Sex-combined			68.35		0.2		–0.83	2.97
SE Mediterranean	Mehanna et al., 2010	Sex-combined	1479	1–8	76.36		0.29		–0.19	3.23

Table 2. Parameters of length-mass relationships ($W(g) = aL(\text{cm})^b$) estimated for European sea bass in various areas.

Area	Reference	Sex	N	L Range	$a \times 10^3$	b
Bristol and Western English Channel	Pickett and Pawson 1994	Sex-combined	592	9.4–78.1 cm	12.96	2.969
English Channel	Dorel 1986	Sex-combined	498	2–69 cm	12.44	2.953
Normand-Breton Gulf	Le Mao 1985	Sex-combined	100	8.8–40.7 cm FL	7.9	3.062
Bay of Biscay	Dorel 1986	Sex-combined	1590	6.5–84.5 cm	12.31	2.954
Central Bay of Biscay	Hoai Thong 1970	Sex-combined	462	2.26–77.88 cm FL	11.83	3.04
Cádiz	Arias 1980	Sex-combined	837	2.6–66 cm	4.7	3.14
NW Mediterranean (France)	Barnabé 1976	M	74		12.71	2.9377
		F	203		8	3.048
		Sex-combined	277	9–75 cm	9.6	3.02
SE Mediterranean (Egypt)	Ahmed 2011	Sex-combined	1688	18.2–64.7 cm	14	2.883

ontogeny (Marangos et al. 1986). Best hatching performance is reported at intermediate temperatures (12–20 °C) and low salinities (15–25 PSU) (Conides and Glamuzina 2002). Photoperiod does not seem to affect egg quality. Incubation time measured at different temperatures constitute a valuable source of information to control the sensitivity of eggs to thermal forcing (e.g. for NEA and Mediterranean strains respectively: Jennings and Pawson, 1991; Marangos et al. 1986).

Hatching occurs from 3 to 9 dpf at 17 and 9 °C respectively (Jennings and Pawson 1991). Hatching length ranges from 3.05 to 4.5 mm (Kennedy and Fitzmaurice 1972; Regner and Dulčić 1994) and is positively correlated with incubation temperature and egg diameter (Alami-Durante et al. 2006; Koumoundouros et al. 2001). Environmentally-modulated maternal (Cerdá et al. 1994a, 1994b) and paternal factors (Saillant et al. 2001) interact with egg size, hatching rate, larval de-

velopment and survival up to 3 months post-hatch (García de León et al. 1998).

Mouth opening is a major ontogenetic event which occurs at 4–14 dph at 19–9 °C respectively (Barnabé et al. 1976; Rønnestad et al. 1998). Exogenous feeding then begins at a size of 4.5–5 mm (Alami-Durante et al. 2006). Exotrophy becomes complete with yolk sac and lipid globule resorption (7–8 and 10–16 dph respectively; Regner and Dulčić 1994; Rønnestad et al. 1998). Growth resumes with consumption of external food up to 19 mm TL (Alami-Durante et al. 2006). Valuable data on larval growth with respect to temperature influence are provided by Ayala et al. (2001) and Mylonas et al. (2005) for NEA and Mediterranean strains respectively. The relationship between growth and feeding rations can be found in e.g. Girin (1975). In experimental conditions, survival and growth of larvae are enhanced

at 15 °C (Koumoundouros et al. 2001). Developmental processes are sped up and occur at smaller sizes with rising temperatures up to an optimum (phenotypic plasticity: Ayala et al. 2003). Yet, the relative elapsed time between ontogenetic events up to metamorphosis is maintained (Koumoundouros et al. 2001). At temperatures below 17 °C and under optimal food conditions, larval and early juvenile food conversion efficiency (FCE) and growth are enhanced at low salinities (11–15) (Saillant et al. 2003b). Exhibiting high tolerance to low salinities, larvae gradually increase their tolerance to high salinities during development (Varsamos et al. 2001). Early development of salinity tolerance could provide flexibility to synchronise migration towards low salinity habitats, where survival is enhanced (Johnson and Katavić 1986). Larval growth and day length are positively correlated (14–16 h optimum photophase: Villamizar et al. 2009) because of enhanced FCE (Azzaydi et al. 2000) and/or improved foraging success. Digestive development delay and long-term growth depression follow chronic moderate exposure of sea bass larvae to hypoxia (Vanderplancke et al. 2014).

There is no consensus regarding the criteria determining the metamorphosis period. Between 13 and 17 mm TL, sea bass larvae grow teeth and acquire pigmentation as well as most adult fin meristic characteristics (33–87 dph at 20–13 °C; Alami-Durante et al. 2006; Barnabé et al. 1976). Fish scale development and acquisition of adult body proportions have also been used as metamorphosis landmarks, occurring in synchrony with a shift from a pelagic to a demersal life (20–30 mm TL, 52–110 dph at 19–15 °C; e.g. Barnabé 1990). Based on growth rate analysis, Regner and Dulčić 1994 set the end of metamorphosis at ca. 14 mm SL (50–55 dph) while Koumoundouros et al. (2001), assuming a dual post-larval growth phase, established it concluded at 24 mm TL (~80–110 dph). Finally, Georgakopoulou et al. (2007) associated metamorphosis end with lateral line delineation and acquisition of silvery colour (ca. 38.1 ± 4 mm SL).

4.3 Diet and nutritional physiology

Eggs and yolk-sac larvae are non-feeding stages, whose development is controlled by the quantity and quality of yolk reserves (Rønnestad et al. 1998). Assuming a standard chemical composition (Cerdá et al. 1994b; Devauchelle and Coves 1988), the energetic value of a sea bass egg is ~3 J. Together with free amino acids, lipids provide most of the energy invested in organogenesis and swimming before feeding onset (Rønnestad et al. 1998). Older yolk-sac larvae use yolk proteins as a primary energy source for tissue synthesis and aerobic metabolism (Rønnestad et al. 1998).

Larvae can ingest more than 100% of their own mass but feeding rate and mass-specific food consumption decrease as fish grow and become more efficient predators (Barnabé 1990). Besides, turbulence would be detrimental to large post-larvae foraging (Mahjoub et al. 2012). Sea bass stomach is assumed to be fully functional by 25–39 dph (19 °C; Cahu and Zambonino 2007). Larval nutritional needs for proteins and lipids have been estimated to be respectively 50–60% and 7–17% of food dry weight (Cahu and Zambonino 2007). Despite negative effects of suboptimal feeding on larval growth

and muscular ontogeny, first-feeding bass larvae can handle several days of starvation without incurring severe mortality (ca. 2 weeks at 19 °C; Catalán et al. 2015).

In the wild, sea bass larvae feed on copepods (e.g. *Eurytemora affinis*, rarely harpacticoids) but can also ingest mysids (e.g. *Neomysis integer*) and algal cells (Pickett and Pawson 1994). In experimental conditions (17.5–20 °C), a 1-month sea bass (12 mm TL) was estimated to consume a total of 1600–2000 rotifers, 2500–3000 *Artemia* spp. nauplii and 135–150 metanauplii (Girin 1975). At feeding onset, prey selection by sea bass is chiefly constrained by the prey-to-predator size ratio (50–125 µm prey, Barnabé 1990; Iizawa 1983). Growing larvae then quickly increase capture efficiency, size spectrum and ingestion (e.g. 200–400 µm between 15–40 dph and 400–600 µm afterwards: Barnabé 1990; Georgalas et al. 2007). Dietary energy content and composition (notably phospholipids), data seldom available in the wild, are considered major factors controlling food intake (e.g. Aranda et al. 2001; Rubio et al. 2005) and the maturation of digestive enzymes (Zambonino Infante and Cahu 1999). Post-larval diet is typically made of fatty acid- and protein-rich zooplankton species.

4.4 Sexual physiology

Sex determination is under the influence of genotype-environment interactions, potentially reflecting both different genetic make-up and distinctive parental sensitivities to the environment (Vandeputte et al. 2007). Common garden experiments found significant sex ratio differences among fishes of different origin (stronger masculinizing effect of high temperature in SE Mediterranean fish; Mylonas et al. 2005).

Environmental conditions experienced by fish during a period spanning until ca. 160 dpf (juvenile stage) can impact sex determination. Sea bass yolk larvae are particularly sensitive to temperature effects, which can be observed until 137 dpf (Mylonas et al. 2005; Pavlidis et al. 2000). High temperatures (>17 °C) exert a masculinising effect (female genotype inhibition) while exposure to low temperatures (<15 °C for a duration between 46–100 days) tends to favour females (Navarro-Martín et al. 2009). Long-term rearing at low temperatures would prevent the expression of female phenotype by negatively impacting growth (critical body size at the onset of sex differentiation for females; Mylonas et al. 2005). Steroid hormones are effective beyond 100 dpf (Blázquez et al. 2001). No effect of density or social status on sex ratio has been detected. In the wild, sex ratios are seemingly balanced in early age classes before being skewed in favour of females in older fish (Vandeputte et al. 2012).

5 Juvenile stage

5.1 Distribution and behaviour

From their first summer up to age 2 to 5 depending on habitat characteristics, immature sea bass inhabit coastal nursery areas (e.g. sheltered bays, coastal lagoons, estuaries: Arias 1980; Kelley 1986; Pawson et al. 1987). Major nurseries along

the British coasts, where sea bass frequently constitutes the second most abundant species (Pickett and Pawson 1994), are well identified (Fig. 2). Such precise knowledge does not exist along the French, Spanish and Portuguese coasts although the species is abundant in these regions.

Initially concentrated at the upper salt wedge (up to <1 PSU) of estuaries, 0+ juveniles perform a gradual downstream migration (Jennings et al. 1991). The thermal gradient between estuarine nurseries and adjacent coastal waters could, at least partly, drive immature sea bass distribution (Cabral and Costa, 2001; Jennings et al. 1991). In late autumn, the decrease of temperature below 10 °C triggers migration towards deeper waters (Kelley, 1986), older and larger fish preceding younger ones. Return migration takes place from March onwards (Pawson et al. 1987). First winter is a critical period for sea bass, and >60 mm TL fish may be less vulnerable to overwintering mortality (Kelley, 2002). Juvenile movements in the UK exhibit low connectivity between nursery complexes, most fish remaining within 16 km of their tagging site (Pawson et al. 1987). As they approach maturity, sea bass exhibit increasing mobility, sometimes achieving significant recruitment to distant fishery areas (Pawson et al. 1987; Pickett et al. 2004).

Juvenile and adult sea bass display a diel pattern of activity, flexible with physiological status and seasonal variation of food availability (Bégout Anras 1995; Sánchez-Vázquez et al. 1998). Highest vertical movement amplitude is observed in winter for juveniles (Bégout Anras et al. 1997). Sea bass activity is also modulated by temperature (reduced activity outside the range 12–22 °C; Pickett and Pawson 1994), wind regime and atmospheric pressure (Bégout Anras 1995). Rainfalls stimulate sea bass activity in lagoons (Bégout Anras 1995). Hypoxia triggers an inversion of activity and impairs daily vertical migration, possibly to optimize aerobic metabolic capacity (Schurmann et al. 1998). Finally, social context and fish personality are also important (Millot 2008). Starting at 3–4 cm TL, shoaling is observed diurnally in juvenile sea bass of similar size (Boulineau-Coatanea 1969). Shoaling has significant implications in terms of predation vulnerability, food intake and energy saving (Herskin and Steffensen 1998). Although mainly within captive populations, moderate density-dependent agonistic behaviours (territorial competition, cannibalism) have been reported in sea bass (e.g. Henderson and Corps 1997; size-dependent homerange segregation in the wild: Ilestad et al. 2012).

Swimming performances are often reported in terms of critical swimming speed⁴. Up to 3 cm TL, sea bass critical speed is <1.5 km/h (Leis et al. 2012) but rapidly increases with fish age/size (3–4 km/h in 15–30 cm TL fish respectively; Leis et al. 2012; Luna-Acosta et al. 2011). Ranging from 1.15–2.5 km/h, optimum speeds are temperature-dependent and represent ca.44.5% of the fish active metabolic rate (Claireaux et al. 2006). Temperature impacts swimming performance through its influence on: (i) water density (Johnson et al. 1998), (ii) biochemical reaction rates and energy fluxes (Claireaux et al. 2006), and (iii) fish development (Koumoundouros et al. 2001), most notably muscular ontogeny (e.g. Ayala et al. 2003). While temperature

does not influence swimming costs at a given submaximal speed (Claireaux et al. 2006), temperature-related changes in cardio-respiratory performance and hence in scope for activity (the difference between active and standard metabolic rates) account for the seasonal changes in maximum swimming performance of sea bass. Scope for activity and maximum swimming speed⁵ increase with temperature up to 22–25 °C in sea bass juveniles and young adults (Claireaux et al. 2006; Koumoundouros et al. 2002). Interestingly, fish are able to maintain swimming speed at more than 90% of its maximum value over a 10 °C-range (between 19.3–29.6 °C; Koumoundouros et al. 2002). Despite larger fish having a higher scope for activity (higher standard metabolic rate too), smaller juveniles present a more efficient oxygen consumption at any given speed (Zupa et al. 2015).

In hypoxic conditions, sea bass adjust their swimming activity as well as their energetic demands and metabolic expenditures (Pichavant et al. 2001). Individual oxygen consumption increases exponentially with swimming speed while tail beat frequency increases linearly with speed, with significant differences in energetic allocation existing between wild and domesticated fish (Luna-Acosta et al. 2011). A dichotomy may exist between cruising specialists (high aerobic performance, quick recovery but low burst speeds) and sprinting specialists (higher max. burst speeds, lower aerobic performance and slow recovery) (Marras et al. 2010). Finally, food quality, notably fatty acid content, influences swimming performance and respiratory metabolism (Marras et al. 2010).

5.2 Development and growth

Being mostly investigated in experimental conditions, juvenile growth has been described with curvilinear and sigmoid models (Gardeur et al. 2001). Several studies measured thermally-induced variability of metabolic rates (e.g. Claireaux and Lagardère 1999; Lupatsch et al. 2001; Person-Le Ruyet et al. 2004). When food is non-limiting, juvenile growth is enhanced between 22–24.5 °C, 2 and 32 °C being respectively the lower and upper lethal limits for sea bass (Barnabé 1990; Vinagre et al. 2012). Juvenile sea bass are able to tolerate a large salinity range (0–60 PSU; Varsamos et al. 2001), provided they are not food-restricted (otherwise osmoregulatory capacity is impaired <20 PSU; Sinha et al. 2015). Long photoperiod has a positive effect on both somatic and gonadic growth in juveniles (Yildirim and Vardar 2015). Russell et al. (1996) and Thetmeyer et al. (1999) provided models relating mass growth and food intake. Conversion of mass growth from a dry to a wet weight basis has been detailed in e.g. Person-Le Ruyet et al. (2004) and Stirling (1976).

Different growth capacities are modulated by inter-individual variations in food intake related to fish physiology, environmental conditions and social interactions (e.g. Thetmeyer et al. 1999). Compensatory growth may occur up to 300 dph if adverse growth conditions are experienced during the larval phase (up to 70 dph; Pavlidis et al. 2000) but not during the early nursery phase (Mylonas et al. 2005). Growth

⁴ Speed at which a fish is unable to remove itself from the back grid of a swim chamber.

⁵ Max speed is slightly lower than critical speed and corresponds to a change from sustained to burst-and-glide swimming.

dimorphism in favour of females appears at this time (Ferrari et al. 2014) and increases at high temperatures (Saillant et al. 2003a). Mass dimorphism varies with fish age, reaching 67% at 10 months old before decreasing and stabilizing around 25% in 2 year old fish (Navarro-Martín et al. 2009; Saillant et al. 2001). Together with careful monitoring of the daily energetic ration ingested, early sexing of individuals should be a more common practice in growth experiments: whether growth dimorphism is accounted for by distinctive physiological and/or feeding behavioural traits would condition the structure of sex-specific models.

5.3 Diet and nutritional physiology

Around metamorphosis (2.5–3 cm TL), sea bass start feeding on fish, including smaller conspecifics (Katavić et al. 1989). A shift from planktonic to larger epibenthic and benthic preys is observed between 3 and 6 cm TL (Barnabé 1990). Juvenile sea bass mostly consume small crustaceans, particularly mysids, calanoid copepods, amphipods, isopods and small decapods (Arias 1980; Cabral and Costa 2001; Kelley 2002). Polychaetes and bivalves can constitute significant secondary preys (Laffaille et al. 2001; Martinho et al. 2008).

Most of our knowledge on feeding and food conversion rates comes from aquaculture experiments. Under the regulation of the neuro-endocrine system, feeding responds to fluctuating environmental factors and physiological requirements, depending on fish size/mass, stomach capacity, digestion time, and biorhythm (Killen et al. 2011; Stirling 1977). In size-graded groups, dominant fish may exert an influence on quantitative and qualitative aspects of feeding (e.g. social learning; Millot 2008), positively affecting FCE and growth (Stirling 1977). On the contrary, high density of individuals, especially in food-limited conditions, is detrimental to fish growth and survival (negative influence on food intake and FCE; Leal et al. 2011).

Energy and protein requirements, as well as metabolic costs and efficiency have been quantified in juveniles (Russell et al. 1996; Lupatsch et al. 2003, 2001). It has been suggested that food intake is regulated by protein (Peres and Oliva-Teles 1999a) rather than energy content (Boujard et al. 2004), optimal growth apparently correlating linearly with daily protein intake. Optimal dietary protein and lipid levels are 40–50% and 10–30% dry weight respectively (e.g. Peres and Oliva-Teles 1999; Zambonino Infante and Cahu 1999). The optimal level of digestible carbohydrates for marine fish is <20% (Lanari et al. 1999; see also temperature-dependent protein-sparing effect of carbohydrates: Pérez-Jiménez et al. 2007). When macronutrient levels are inadequate, juvenile sea bass seem able to adjust their ingestion rate accordingly (Aranda et al. 2001; Pérez-Jiménez et al. 2007).

Between 10 and 28 °C, food ingestion increases linearly with temperature, prolonged exposure to water temperatures out of this range negatively impacting juvenile feeding activity (Vinagre et al. 2012). Tolerance to low temperatures can however be increased through the accumulation of lipids and glycogen in autumn, a strategy to handle feeding inhibition below 7 °C (Russell et al. 1996). Optimum, maximum and maintenance feeding rations have been estimated for sea bass juve-

niles over the range 6–25 °C (e.g. Lupatsch et al. 2001; Peres and Oliva-Teles 2005; Russell et al. 1996). Metabolic requirements and feeding efficiency beyond maintenance increase with temperature up to 20 °C (Peres and Oliva-Teles 1999a; Russell et al. 1996), the latter becoming independent of fish mass, feeding level and temperature between 20–25 °C, the range of thermal preference for sea bass (Lupatsch et al. 2001). However, no consensus has been met concerning the impact of temperature on macronutrient requirements, assimilation efficiency and body composition (e.g. Peres and Oliva-Teles 1999b; Person-Le Ruyet et al. 2004). Assimilation efficiency estimates reflect how ingested food translates into available energy, and can be found in e.g. (Lupatsch et al. 2001; Peres and Oliva-Teles (1999a). Body composition of wild sea bass (Stirling 1972) can help in controlling the energy density of individuals in bioenergetic models (for aquaculture conditions, see Lupatsch et al. 2003, 2001).

In addition to food quality and quantity, feeding duration and frequency have a significant effect on fish growth and conversion efficiency (e.g. compensation growth in short-term starvation/multi-cycled feeding: Adaklı and Taşbozan 2015). Sea bass feeding activity follows a diel pattern controlled by a circadian clock (Sánchez-Vázquez et al. 1998). Under natural conditions, fish gradually invert their feeding activity from nocturnal during winter to preferentially diurnal in other seasons (e.g. Sánchez-Vázquez et al. 1998). The photoperiod effect could be modulated by the physiological state of the fish, inter/intra-specific interactions and cyclic variations in the environment such as tides (e.g. Cabral and Costa 2001; Laffaille et al. 2001).

Food consumption and condition status are also influenced by oxygenation (Pichavant et al. 2001; Thetmeyer et al. 1999) which also impacts fish maximum performance, distribution and habitat selection (Claireaux and Lagardère 1999). Sea bass tend to avoid waters whose oxygen saturation is below 40% to ensure sufficient metabolic scope (Claireaux and Lagardère 1999), and prolonged exposure to hypoxic waters ≤ 2 mg O₂/L can be lethal (Barnabé 1990). Moreover, temperature and oxygen concentration have synergistic effects on metabolic rate (Claireaux and Lagardère 1999), forcing fish to seek waters of increasing oxygenation with rising temperatures. Activity turns out to be the most critical factor influencing fish metabolism.

Between 20 and 40% of routine energy consumption in teleosts could be invested into ionic homeostasis (Jobling 1994). In sea bass, salinity and stage-specific metabolic requirements are positively correlated over a 5–20 PSU range (Claireaux and Lagardère 1999). At high temperatures (>17 °C), salinity relates in a dome-shaped way to food intake (max at 15 PSU: Dendrinis and Thorpe 1985; Rubio et al. 2005) and FCE (max at 25–30 PSU; Dendrinis and Thorpe 1985). Hydrodynamics (Cerezo Valverde et al. 2005), wind-regime and rainfall (Bégout Anras 1995) have also been shown to impact sea bass feeding activity. Turbulence is thought to stimulate the feeding activity of sea bass juveniles (Pickett and Pawson 1994).

Food restriction experiments are a valuable source of information for modelling as they provide information on maintenance costs and the resilience of individuals to adverse

conditions. Under restricted feeding schemes, energy mobilization strategies in juveniles are closely related to environmental conditions and fish nutritional history (Pérez-Jiménez et al. 2007). Energy needs are first fulfilled through the mobilisation of reserves such as liver glycogen and lipids in all tissues, including gonads (Pérez-Jiménez et al. 2007). After about 50 days of starvation, when those reserves are almost depleted, structural reserves, proteins essentially from skeletal muscles, are used (Echevarria et al. 1997). Starvation leads to reduced fish activity and oxygen consumption for saving energy (Benhaïm et al. 2012). The energy and protein losses have been evaluated in starved sea bass ranging from 1 to 400 g (Lupatsch et al. 2001; Peres and Oliva-Teles 2005). In comparison to adults, lower protein and higher lipid losses (replaced by water) are observed in fasting juveniles (Stirling 1976).

Appetite recovery, compensatory growth and restoration of pre-fasting metabolic values are slower when fishes are exposed to water temperatures below 7 °C (Pastoureaud 1991). While moderate fasting only induces increased feeding rate, severe starvation triggers higher feeding rate and extended daily time allocation, especially in late spring (Rubio et al. 2005). Diet composition influences metabolic responses during starvation-refeeding trials (Pérez-Jiménez et al. 2007) while temperature and fasting duration have an impact on the choice of energy sources after a fasting period (Aranda et al. 2001). Capacity for fast growth (faster meal processing and energy mobilisation capacity, implying higher energy dissipation and requiring more frequent meals) may trade-off against tolerance to food deprivation (Dupont-Prinet et al. 2010). The physiological basis for this trade-off remains to be identified (McKenzie et al. 2014). The fish characterized by higher FCE lost less weight loss during food deprivation and exhibited lower weight gain during re-feeding (Grima et al. 2010; but Dupont-Prinet et al. 2010). These contrasting energetic strategies may represent valid alternatives to reach adult size-at-age in contrasted trophic environments. As small fish have a higher mass-specific metabolic demand and are more vulnerable to starvation, which may drive them towards more risk-taking behaviours to increase food intake (Killen et al. 2011). Following slower initial growth associated with a fasting period, dominant fish achieve, through higher feeding motivation, high and constant compensatory growth (Millot 2008). However, growth acceleration after food deprivation is associated with improved FCE rather than hyperphagia (Benhaïm et al. 2012). The relative contributions of behaviour and physiology to metabolic budget remain unclear.

5.4 Sexual physiology

During the early juvenile phase (up to 160 dpf), sea bass are still sexually undetermined. In addition to environmental mediation of sexual determination described above (see Sect. 4.4; Blázquez et al. 2001), it is worth noting that the osmotic stress caused by a transfer from low to high salinities has a masculinizing effect on juveniles (Saillant et al. 2003b). Histological gonadal differentiation initiates at ca. 8–9 cm SL and remains incomplete until the end of the first year of life (Mediterranean sea bass; ♀: 7–12 month old, 8–15 cm SL; ♂:

8–12 month old, 9–14 cm SL; Blázquez et al. 1998; Saillant et al. 2003a).

6 Adult stage

Age and size at first maturity are life traits that depend on both sex and environment. In the Atlantic, first maturity of males occurs at 32–36 cm TL (4–5 year old) while females mature at 40–45 cm TL (5–8 year old) (Kennedy and Fitzmaurice 1972; Pawson et al. 2000; Pawson and Pickett 1996). For Mediterranean populations, first spawning occurs at 20–25 cm TL (2 year old) and 29–34.5 cm TL (3–4 year old) for male and female respectively (Ahmed 2011; Rodriguez et al. 2001; Saillant et al. 2001).

6.1 Distribution and behaviour

In the NEA, largest abundances are reported around the British Isles and in the Bay of Biscay (Pickett and Pawson 1994). Seasonal migration of adult sea bass has mainly been studied around the British Isles. Conventional tagging showed seasonal migrations between inshore summer feeding grounds and offshore overwintering and spawning areas (Pawson et al. 2007, 1987). Fidelity to summer habitats has been demonstrated while corresponding evidence for spawning areas is still pending. Sea bass perform more extensive movements as they approach the northern limit of their distribution range (Pawson et al. 2007; Quayle et al. 2009). Yet, more sedentary behaviour has been reported in Norwegian fjords (Ilestad et al. 2012), in Ireland and off the Channel Islands (Kennedy and Fitzmaurice 1972; Pickett and Pawson 1994). The English Channel would be made up of a mixture of residents and seasonal migrants (Pawson et al. 2007; see also Fritsch et al. 2007). Very little is known for other areas and notably for the Bay of Biscay and Iberian coasts.

In British waters, spawning migration is probably triggered by reduced growth and ovarian development in <9 °C waters (e.g. Pawson et al. 2000; Pawson and Pickett 1996). Over the NEA, spawning migrations initiate between October and December, corresponding return movements occurring from March to May (Pickett and Pawson 1994; Quayle et al. 2009). Knowledge on the precise location of spawning areas is incomplete over most of the NEA (Fig. 1). Whether offshore (50–100 m isobaths) or inshore (potentially including saltier deep estuarine waters), spawning occurs at depths not greater than 30–40 m (Pickett and Pawson 1994). Starting in winter off the Iberian Peninsula and in the Bay of Biscay, it progresses to the N-NE until late spring. With increasing temperatures in the North Sea, delayed winter migration could take place over shorter distances (Pawson et al. 2007). This could favour a northward expansion and a year-round residence of sea bass in the North Sea and Norwegian coastal waters (Colman et al. 2008; Pickett et al. 2004).

In adults, cruising speeds of ~0.8 TL/s have been measured by acoustic telemetry (Sureau and Lagardère 1991). Vertical behaviour of adult sea bass has been described in the wild through archival tagging (Quayle et al. 2009) and acoustic telemetry (Ilestad et al. 2012). Their range can span from

the surface to over a hundred meters, as suggested by trawl catches (Barnabé 1990; Boulineau-Coatanea 1969). In late winter/early spring, highest vertical movement amplitude is observed, adult fish staying at the surface at night while occupying deeper layers during the day (Ilestad et al. 2012; Quayle et al. 2009; Schurmann et al. 1998). Environmental factors are likely to impact juvenile and adult sea bass activity in the same way (see Sect. 5.1). Metabolism tuning strategies could match physiological needs to environmental conditions during migrations (Claireaux and Lagardère 1999). Fluctuating salinities do not negatively impact adult fish exercise, cardiac and metabolic performance (Chatelier et al. 2005).

6.2 Diet and nutritional physiology

As they grow larger, sea bass become dominant predators (Spitz et al. 2013), adapting their trophic ecology to the spatio-temporal availability of potential prey (e.g. Boulineau-Coatanea 1969; Laffaille et al. 2001). They increasingly consume crustacean (mostly moulting shore crabs, prawns and shrimps) and fish species (pelagic fish such as sand lance *Ammodytidae*, mackerel *Scomber scombrus*, horse mackerel *Trachurus trachurus*, sand smelt *Atherina presbyter* and several species of Clupeidae; demersal fish including several Gadiformes species; benthic species such as gobids, blennids and even small flatfish: Boulineau-Coatanea 1969; Spitz et al. 2013), bivalves and cephalopods being secondary diet items (Pickett and Pawson 1994).

Optimum, maximum and maintenance feeding rations should be examined for adults. As in juveniles, metabolic requirements increase with temperature up to 20 °C and stabilise afterwards for temperatures between 20 and 25 °C, the thermal preference for sea bass (Claireaux and Lagardère 1999). Thermal environment rather than gonad development largely account for most active feeding being reported in spring and late fall in the wild (Boulineau-Coatanea 1969; Pickett and Pawson 1994). For modelling purposes, we will consider that the nutritional physiology of juvenile and adult sea bass is similar.

6.3 Sexual physiology

Genetic factors, metabolic signals and environmental cues (notably photoperiod after the summer solstice: e.g. Rodríguez et al. 2012) act as triggers of the pubertal phase, by stimulating a hormonal cascade along the hypothalamic pituitary gonadal axis (Carrillo et al. 2015, 2009; Rodríguez et al. 2005). Gonad maturation in females would require waters to be at least 10 °C (no inhibition for males at lower temperatures: Pawson et al. 2000).

As in many species, first maturity in sea bass is more related to individual size/mass than age (min. reserve energy threshold; Escobar et al. 2014; Espigares et al. 2015; Pawson and Pickett 1996). Males attain sexual maturity at inferior size and age than females (see Sect. 3.3).

The annual pattern of gonad development has been assessed in Asturiano et al. (2000) and Rodríguez et al. (2005) for males and in Mayer et al. (1990, 1988) and Asturiano et al. (2000) for females. In the wild, ripe gonads in males and fe-

males represent resp. 1.75–7% and 5–12% of fish total mass, while resting gonads represent ~0.3 and ~0.7% of fish total mass for each sex (Barnabé 1976; Kennedy and Fitzmaurice 1972; Pawson and Pickett 1996). Gonad maturation begins in June, followed by an accelerating phase in October by which time fecundity for the next spawning season is determined (ca. 60% of pre-vitellogenic oocytes present at that time; Mayer et al. 1990). During the vitellogenic phase, somatic growth ceases (e.g. November-May; Rodríguez et al. 2001).

Gonad maturation occurs earlier in older/bigger individuals (Pickett and Pawson 1994), which hence spawn up to one month before their conspecifics (Mayer et al. 1990). Mean investment in gametogenesis is homogeneous in males while in females it is positively related to size/mass and growth (Saillant et al. 2001).

Oocyte development being group-synchronous, sea bass spawning is fractionated in 2–4 discrete batches recruited in quick succession (7–14 days span) from a large heterogeneous oocyte population (Asturiano et al. 2002). Increasing with fish age and size/mass until senescence, absolute fecundity varies from 2×10^5 to 10^6 eggs in first-time and >8 year old spawners respectively ($146\text{--}538.10^3$ eggs/kg wet weight: Mayer et al. 1990; Prat et al. 1990). During the first two reproductive seasons, relative fecundity is 20–50% lower than in subsequent spawning years (Mayer et al. 1990). Negatively correlated to temperature and photoperiod, egg diameter is greater early in the reproductive season (Mayer et al. 1990; Mylonas et al. 2003) and in the Atlantic (1.21–1.39 vs. 1.02–1.30 mm in the Mediterranean). While viability does not change over consecutive batches (Mylonas et al. 2003), egg quality and hatching rate improve as females grow (Navas et al. 1997). In males, spermiation rate and fish mass/size are positively correlated (Rodríguez et al. 2012). At the end of the spawning season, gonads are completely empty (Mayer et al. 1988).

Gametogenesis duration, and hence the timing of spawning season, as well as clutch number and fecundity, depend on the interplay between environmental and endogenous signals, notably steroidogenesis (e.g. Asturiano et al. 2002; Prat et al. 1999; Rodríguez et al. 2012). Chiefly controlled by photoperiod, gametogenesis usually occurs under a decreasing phase (ca. October; Pickett and Pawson 1994). On the contrary, the late stages of gonad maturation and spawning, which take place under an increasing photoperiod, would be mainly influenced by temperature, especially at higher latitudes, accounting for latitudinal variability in spawning (Fig. 5; Pickett and Pawson 1994; Zanuy et al. 1986). Both wild and experimental studies suggest that the thermal spawning window for females is in the range of 9 to 16 °C (e.g. Thompson and Harrop 1987; Zanuy et al. 1986). Contrary to females, no inhibition of testes maturation has been observed at low temperatures (Pawson et al. 2000), while 25 °C is incompatible with gametogenesis in both sexes (Bruslé and Roblin 1984). Bruslé and Roblin (1984) determined that vitellogenesis is stopped when salinity is 2 PSU while Zanuy and Carrillo (1985) found only spawning impairment (normal vitellogenesis) at 3.5 PSU. In adults, low salinities are responsible for enhanced lipid retention or modification/inhibition of fat mobilisation for gametogenesis (Roche et al. 1989). On a daily scale, spawning occurs during the early morning or just after sunset (Villamizar et al. 2012),

Area	Spawning Period						
	DEC	JAN	FEB	MARCH	APRIL	MAY	JUNE
Iberian Peninsula							
Bay of Biscay							
Brittany & W. English Channel							
E. English Channel							
Bristol Channel							
Ireland							
South. North Sea							
North Wales							

Fig. 5. Progression of spawning activity in the Northeast Atlantic.

locomotor activity and egg viability being correlated with light intensity.

Timing, ration and quality of diet influence in both sexes gonad development, fecundity, spawning date, rhythmicity and performance (Cerdá et al. 1994a, 1994b; Navas et al. 1997), though the biochemical composition of gametes remains unchanged (Cerdá et al. 1994a; Escobar et al. 2014). As might be expected, seasonal patterns of fish condition, reproductive activity (gonado-somatic index) and fat content are strongly interrelated (max. and min. just prior to and after the spawning period: e.g. Pawson and Pickett 1996).

7 Discussion

Despite the huge amount of work conducted on sea bass since Pickett and Pawson (1994), this knowledge remains very scattered and critical issues concerning sea bass population dynamics and fishing management remain unanswered: How does spawning behaviour and environmental variability shape nursery settlement? How does the latter relate in turn to stock recruitment? How do migration and reproduction investment variability impact population dynamics? How sensitive is the population to spatial and seasonal distribution of fishing pressure? Anticipating managers' calls for developing a spatially-explicit end-to-end model approach for this species, the objective of this review has been to bring together dispersed sources of information to produce a synthesis on sea bass ecology and physiology. As we have shown, the development of this species, its behaviour, its feeding and nutritional physiology, as well as its physiological optima have been investigated in numerous studies.

Sea bass life traits are characterized by a relatively slow growth and late maturity, increasing its vulnerability to over-exploitation. Another relevant aspect is a pronounced sexual dimorphism in growth which suggests that males and females should be separated in population dynamics models. Classified as a dominant predator, sea bass feeds opportunistically, adapting its feeding behaviour to its environment. Able to survive over a wide range of salinities and temperatures (provided op-

timal food conditions), juveniles occupy coastal habitats over an extended period. Showing increasing mobility as they approach maturity, several studies have shown adults' ability to perform long-range migrations and site fidelity to feeding areas.

Shortcomings regarding sea bass spatial distribution at different life stages still remain, particularly in the northern and southern parts of the species distribution area. Similarly, it is still unknown whether NEA is made up of a mosaic of self-sustaining stock components or a panmictic population. Sexual maturity timing, maximum length and life expectancy seem to vary between Atlantic and Mediterranean populations. It remains hence to be determined whether observed discrepancies are determined genetically or can be explained solely by different environmental conditions. Phenotypic variation within species, characterised by different morphs, developmental pathways, life-history strategies or behaviours, can also drive patterns in the distribution and abundance of organisms. In many experiments exploring the integrative influence of environmental and endogenous factors, the origin of fish is not always clearly indicated, hence potentially implying unspecified use of selected strains of Mediterranean origin. Aside from the effects of different genetic backgrounds, patterns are unlikely to be the same in the wild, where substantial energetic expenditure is linked to migrating and chasing a prey in a variable medium with significant predation pressure. For these reasons, it is necessary to take into account the heterogeneity of information sources and quantify the accuracy and representativeness of the derived population dynamics when defining the parameter values of a model. In addition, contradictory interpretations (e.g. metamorphosis criteria, stage-specific temperature influence on food conversion and metabolic requirements) and missing scientific evidence concerning sea bass ecology exist (i.e. egg density variability, larval vertical behaviour, sex determination under natural "low" temperatures, metabolic cost of standard reproductive investment in males). However, there are several ways to deal with knowledge gaps and uncertainty.

One option is to further develop data collection from the wild over the whole distribution range of the species. Sampling

surveys in coastal and estuarine areas should provide invaluable information regarding the 3D distribution of early-life stages which remains largely unknown in the wild. Large-scale tagging surveys, taking advantage of the ongoing advances in biologging, should undoubtedly provide valuable information on essential habitats, movements and migrations of juvenile and adult sea bass. Population connectivity could also be addressed through new genetic studies based on genome-wide SNP markers and micro-chemistry analyses, for instance otolith or scale elemental and isotopic analysis. In addition to survey data, crossed data analysis of vessel and commercial information (e.g. vessel monitoring positions and electronic log-book) could be used to better understand the spatio-temporal distribution of the individuals at marketable size, notably by identifying fishing hot spots that often correspond to reproduction aggregations. We also call for additional studies in controlled experiments using NEA fish strain(s) subjected to realistic environmental rearing conditions. Environmental acclimatization affects fish growth, reproduction, spontaneous activity, feeding behavior and metabolism. Specific efforts should hence be directed to the assessment of strain/stage/size-specific tolerance ranges and the plasticity of growth, behaviour and sexual physiology. Similarly, characterizing the relative contribution of behaviour and physiology to metabolic budget and sexual dimorphism deserves more attention. A fish can invest up to 60% of its energy into searching for food and its ingestion, digestion and assimilation (Brett and Groves 1979). Therefore, collecting more information concerning the nutritional value of organisms (variability of the energy content of sea bass and its prey) and the trophic structure of NEA ecosystems (spatio-temporal distribution of prey species, but also of potential competitors and predators) would be particularly beneficial.

When dealing with fragmentary information, it is also possible to develop mechanistic models to investigate and validate, through simulations, the consistency of some hypotheses regarding processes and parameter values (e.g. different spatio-temporal distributions of spawning effort, passive vs. active displacement during the larval phase, different metamorphosis criteria, altered hydroclimatic conditions, size-dependent predation mortality). As a formalization of reality, models are relevant tools for comprehending spatio-temporal population dynamics (Lehuta et al. 2013a, 2013b). Provided adequate knowledge integration and formulation of equations and hypothesis, we could explore the variability of environmental, behavioural and physiological processes and loop on the life cycle of the population. Model outputs would then be confronted to observations or expert opinion (Lehuta et al. 2013a, 2013b). Whenever the alternatives are too numerous (often the case for data-poor settings), sensitivity analysis can be used to screen the most pertinent ones by identifying and ordering key parameters and dynamic processes (Mahévas and Iooss 2013). This analytic approach is also relevant for making recommendations for specific data collection to increase the accuracy with which dynamics are described.

This review provides most of the information required as a starting point for the parameterisation of two types of models: bioenergetics (fish physiology) and bio-physical (fish environment and behaviour) models. The first kind of model re-

quires knowledge of the way a given level of ingested energy would, under specified initial (amount of energy reserves) and environmental conditions, translate into growth and maturation (e.g. Kooijman 2010). Experiments where the growth and the reproductive investment of sexed individuals is monitored under different rearing conditions (e.g. in terms of temperature and food levels) are the most appreciated source of information to build this kind of model (e.g. Cerdá et al. 1994a; Saillant et al. 2001). Biophysical models depend in turn on information about spatio-temporal environmental data (e.g. hydrodynamics, hydroclimate, potential prey and predators) and fish behaviour (e.g. ontogenic change of diet, swimming capacity, environment mediation of feeding activity, spawning phenology, migration) (Grimm and Railsback 2013; Miller 2007). The selected models provide flexibility for life-cycle approaches, by dealing with both data uncertainty and inter-individual variability (e.g. different behavioural traits and physiological capacities: Huret et al. 2010; Pecquerie et al. 2009). The coupling of bioenergetic and biophysical models is expected to result in an improved understanding of recruitment drivers, habitat connectivity and profitability, and an enhanced predictive capacity of population(s) response to environmental change. Emerging properties from individual-based simulation outputs (e.g. spatio-temporal variability of growth and survival) would help developing sea bass population dynamics models. The knowledge gained through these modelling exercises should feed stock assessment models for which adequate description of the functional structure and dynamics of (recreational and professional) fishing components would be a prerequisite. Collectively, this end-to-end model scheme would allow the evaluation, in a dynamic environment, of the cost-to-benefit ratio of spatialised management strategies (Pelletier et al. 2009; Punt and Hilborn 1997).

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