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ABSTRACT

Small pelagic fish (SPF) play extremely important ecological roles in marine ecosystems, form some of the most economically valuable fisheries resources, and play a vital role in global food security. Due to their short generation times and tight coupling to lower trophic levels, populations of SPF display large boom-and-bust dynamics that are closely linked to climate variability. To reveal emerging global research trends on SPF as opposed to more recently published, ecosystem-specific reviews of SPF, we reviewed the literature published in two, 6-year periods in the new millennium (2001–2006, and 2011–2016) straddling the publication of a large, global review of the dynamics of SPF in 2009. We explored intrinsic and extrinsic (bottom-up) factors influencing the dynamics of SPF such as anchovies, sardines, herrings and sprats within the sub-order Clupeidae. Published research efforts within 16 different biogeographic ocean regions were compiled (more than 900 studies) and compared to identify i) new milestones and advances in our understanding, ii) emerging research trends and iii) remaining gaps in knowledge. Studies were separated into 5 categories (field, laboratory, mesocosms, long-term statistical analyses and spatially-explicit modelling) and discussed in relation to 10 bottom-up categories including 5 abiotic factors (temperature, salinity, pH, dissolved oxygen, density), 3 physical processes (advection, turbulence, turbidity) and 2 biotic factors (prey quantity and quality). The peer-reviewed literature reflects changes in the number of studies between the two time periods including increases (Mediterranean Sea, Humboldt Current) and decreases (Australia, Benguela Current). Our review highlights i) gaps in ecological knowledge on young juveniles and, in general, on the impacts of hypoxia and heatwaves on SPF, ii) the utility of paleo studies in exploring population drivers, iii) the continued need to develop spatially-explicit, full life-cycle models, iv) the importance of exploring how density-dependent processes impact vital rates (growth, survival, reproduction), and v) the benefits of international collaboration for knowledge transfer and building unifying hypotheses on the role of bottom-up factors and processes that regulate SPF populations.

1. Introduction

1.1. Importance of small pelagic fish

Catches of anchovies, sardines, herrings and other small pelagic clupeoid fishes are not only important for direct human consumption but also critical for fishmeal and fish oil used in agri- or aqua-feeds, making small pelagic fish (SPF) significant for global food security (FAO, 2016). In 2015, 4.3 million metric tonnes (MMT) of Peruvian anchoveta (*Engraulis ringens*) were landed by the largest single-species fishery in the world, while another six species of SPF were within the top 25 major global fisheries (FAO, 2017). Stocks of SPF such as Peruvian anchoveta are notorious for their rapid, large-scale changes in distribution and/or productivity in response to climate-mediated changes in bottom-up forcing (Lluch-Belda et al., 1992; Schwartzlose et al., 1999; Tourre et al., 2007; Salvatteci et al., 2018). For example, the large harvest of Peruvian anchoveta in 2015 was a 37% increase compared to 2014. These fishes are also emblematic of the relatively

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rapid (regime) shifts (dramatic and abrupt changes in the abundance and relative dominance of SPF that are persistent in time) documented in many marine ecosystems worldwide (e.g., Alheit and Niquen, 2004; Alheit et al., 2005; Watanabe, 2009). The high inter-annual variability of SPF biomass, their sensitivity to climate variability, and the occurrence of productivity regimes that are difficult to predict in terms of onset and duration all pose challenges to the sustainable management and efforts to prevent overfishing of SPF populations. These fish also play a pivotal role in marine food webs by acting as conduits of energy from lower to upper trophic levels (Pikitch et al., 2012). Thus, from both an ecological and a societal point of view, it is essential that we gain a full understanding of the factors and processes that drive changes in the productivity of populations and management units (stocks) of these fishes. This knowledge can buttress science-based advice to fisheries management (e.g., Kaplan et al., 2016) as well as the robustness of longer-term projections of future impacts of climate change (MacKenzie et al., 2012; Peck et al., 2013).

1.2. Scope of this review

The present study reviewed research conducted on SPF using a semi-structured review of literature published during 2001–2006 and 2011–2016. We compared the two time periods to reveal emerging research trends globally and to complement recently published, ecosystem-specific reviews of SPF (e.g., Takasuka, 2018). The first time period was chosen to capture research finalized at the start of the new millennium (e.g., published in 2001) that appeared in the peer-reviewed literature prior to a key, global review of the dynamics of SPF prepared in 2008 (Checkley et al., 2009) that arose from the GLOBEC Small Pelagics and Climate Change (SPACC) collaborative research programme, and two special issues on upwelling systems (Bertrand et al., 2008b; Fréon et al., 2009). The second period represented the same number of years after the SPACC book but just prior to a large, international symposium on SPF that was convened in March 2017 (Alheit and Peck, 2019; Alheit et al., 2019b).

The emphasis of this review was on how bottom-up processes and abiotic environmental factors regulate SPF populations or stocks. The review included peer-reviewed research on vital rates (e.g., feeding, growth, reproduction, survival) and ecophysiology, as well as studies exploring how key physical and biological features impact on habitat suitability. The following search was performed on ISI Web of Science:

"Sprattus" OR sprat OR "Engraulis encrasicolus" OR "European anchovy" OR "Cape anchovy" OR "Northern anchovy" OR "Sardina pilchardus" OR "European sardine" OR "European pilchard" OR "European sprat" OR "Engraulis japonicus" OR "Japanese anchovy" OR "Sardinops melanostictus" OR "Sardinops sagax" OR "Japanese sardine" OR "Pacific sardine" OR "South American pilchard" OR "Engraulis mordax" OR "Californian anchovy" OR "Engraulis mitchilli" OR "Anchoa mitchilli" OR "Bay anchovy" OR "Clupea harengus" OR "Atlantic herring" OR "Pacific herring" OR clupei* OR "small pelagic*") AND (temperature OR "climate change" OR climat* OR acidi* OR pH OR oxygen OR hypox* OR hypercapn* OR O2 OR salinity OR freshening OR stress* OR thermal OR tolera* OR limit* OR critic* OR lethal OR threshold* OR growth OR weight OR mass OR diameter OR develop* OR mortality OR surviv* OR metaboli* OR respir* OR oxygen consumption OR prefer* OR thermal window OR aerobic scope OR metabolic scope OR sensitivity OR matur* OR spawn* OR feed* OR prey OR predator OR produc* OR feed OR egg* OR "yolk sac*" OR larv* OR juvenil* OR light OR density OR recruitment) NOT (chem* OR enginee* OR technology).

This search string resulted in 1420 and 1700 studies from 2001 to 2006 and 2011 to 2016, respectively. Studies outside the scope of this review were excluded after reading the title, and additional studies were excluded after reading the abstract and/or complete paper. Studies were excluded because they either i) explored other topics (e.g., food science), ii) examined other small pelagic fish species (e.g., shads, mackerels), iii) reported on broad ecosystem overviews which included SPF in only an

ancillary manner, or iv) focused on predators of SPF (seabirds, marine mammals and fish). The majority of excluded studies was within the latter category. At this point, the list contained 374 papers published from 2001 to 2006 and 376 papers published from 2011 to 2016. Some papers were not found by our search string and, based on our collective knowledge and expertise in specific regions, a further 195 studies were added. The final list contained 945 studies (434 in 2001–2006 and 511 in 2011–2016). We recognize that there is insightful research that has or is being conducted that may not be included here, and we do not intend to be insular in our assessment. Rather the approach taken is an analysis of trends in the mass literature, not an analysis of the most important (or most all inclusive) research on planktivorous fishes. Although it is likely that some studies were missed during the two, 6-yr time periods, in our opinion, the 945 papers compiled here have captured trends during the new millennium in basic (fundamental) as well as emerging research themes on SPF among 16 regions (large marine ecosystems) around the world.

We also reviewed the types of studies including specific methods / themes (Section 2) and compared research conducted on SPF in different regions (see Section 3). For these and other sections, we integrated the findings of studies published before, between and after the two 6-yr time periods that were used to compare trends. For example, many studies were published from 2012 to 2015 and more than 150 references in this 4-yr period were used in this review. The 2017 symposium on SPF produced 38 publications in two special volumes (Alheit and Peck, 2019; Alheit et al., 2019b) and some of those and other recent studies are also included here.

1.3. Categories of studies

During the period between 2001 and 2006, field studies, statistical analyses/reviews, spatially-explicit modelling, laboratory experiments, and mesocosm research accounted for 70, 20, 10, 9 and 0.5%, respectively, of the studies published on SPF (some studies were in multiple categories) (Fig. 1A). Between 2011 and 2016, these same five categories accounted for 67, 20, 12, 10 and 1%, respectively, of the published studies (Fig. 1A). Studies were also categorized by life stage, separating work conducted on eggs (20%), larvae (35%), juveniles (32%) and adults (58%) (average for the two periods, papers often in more than one category (Fig. 1B)). Research specifically devoted to juveniles was scarce (7–8% of all studies). Moreoever, the five categories of methods were not equally applied across all life stages (Fig. 2). During the 1st and 2nd periods, 55 and 71% of all field studies, respectively, and 62 and 64% of all time series analyses, respectively, was conducted on both juveniles and adults (mostly adults). On the other hand, 55 (1st period) and 57% (2nd period) of all laboratory studies and 62 and 64% of all spatially-explicit modelling studies was conducted on early life stages (eggs and larve). Less than one-third of the laboratory studies included work on eggs and none of the studies that used mecososm was conducted on eggs or larvae. Out of the 945 studies reviewed across the two, 6-yr time peiods, only 19 (1st period) and 9 (2nd period) examined all four life stages and these tended to be statistical time series analysis (10 in 2001–2006) or full life-cycle modelling approaches (6 in 2011–2016).

Based on the search (and expert knowledge), the two time periods contained papers on 33 species (note, the search was limited to fish in the family Clupeidae and Engraulidae). The most research effort in the first period was on Atlantic herring (*Clupea harengus*), whereas in the second period most studies targeted European anchovy (*Engraulis encrasicolus*) (Fig. 3). Compared to the first period, the number of studies published on European anchovy almost doubled (78 to 145). Similarly, work published on Peruvian anchoveta (*Engraulis ringens*) tripled (10 to 30), and the first studies (based on our search terms) were published in the second period on Falkland sprat (*Sprattus fuegensis*) and Argentine anchovy (*Engraulis anchoita*) (Fig. 3). Some species seem to remain largely understudied (1 study in one of the two periods), such as scaled
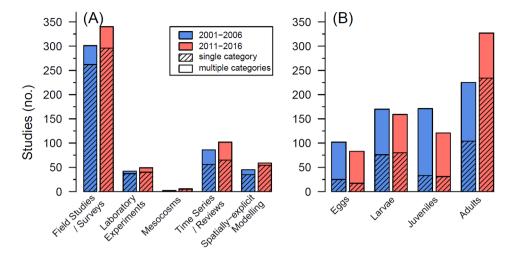
Fig. 1. Summary of 945 studies published on small pelagic fish in two time periods that examined bottom-up factors and/or processes impacting on small pelagic fish (Clupeids and Engraulids) Panel A: Type of study conducted. Panel B: Life stage examined.
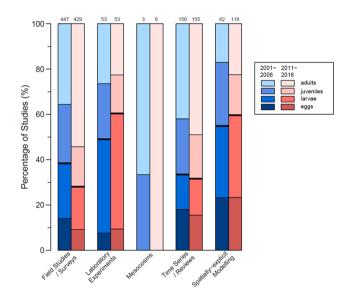

Fig. 2. Summary of the five types of studies published in each of two time periods on different life stages of small pelagic fish (Clupeids and Engraulids). The thick line separates studies conducted on early (eggs and larvae) versus later (juveniles and adult) life stages. Note, many studies were conducted on multiple life stages (e.g., juveniles and adults).

herring (*Harengula jaguana*) or sind sardinella (*Sardinella sindensis*).

2. Review of types of studies

2.1. Field studies

2.1.1. Productivity and distribution

The prominence of "field work" on SPF compared to other types of research was expected. Field surveys are routinely conducted to examine the status of these fisheries resources (changes in spawning stock biomass (SSB) or distribution), to identify nursery, feeding or spawning habitats and, to a lesser extent, to examine bottom-up processes that influence rates of mortality, growth and reproduction. In the majority of studies, multiple life stages were examined (e.g., juveniles with adults, eggs with larvae). Field research effort, therefore, appeared to be evenly distributed across these four life stages in the 1st period with a greater proportion targeting later life stages in the 2 ns period (as depicted in Fig. 2). Research focused solely on juveniles, however, formed only 8%

and 7% of the studies in the earlier and later 6-yr periods, respectively.

Species of SPF are known to shift their spatial distribution in response to changes in bottom-up forcing, and considerable research effort has been focused on reporting and understanding these changes. Examples of this research include studies documenting the (re-) appearance of European anchovy at its high latitudinal limit in the North Sea (Alheit et al., 2012; Petitgas et al., 2012), the basin-scale distribution of Japanese anchovy (*Engraulis japonicus)* in the Pacific (Murase et al., 2012) and projecting shifts in distribution in Pacific sardine (*Sardinops sagax*) in the California Current (Kaplan et al., 2016). These studies, covering relatively large spatial scales, were complimented by a myriad of field work at specific locations relating patterns of spatial distributions to habitat characteristics (e.g., Nevárez-Martínez et al., 2001; Islam et al., 2006; Song et al., 2012; Bonnano et al., 2014; Niu et al., 2014; Valencia-Gasti et al., 2015). That distribution shifts are a response to bottom-up forcing is supported by observations of consistent similarities and differences in the strategies of space occupation by *E. encrasicolus* and *S. sagax* at low and high biomass levels in the Southern Benguela (Barange et al., 2005) which suggested that spatial habiat utilization was density-independent.

Determining the *meta*-population structure is fundamental to understanding the ecologies (e.g., habitat utilization, life cycle strategies) of and distinguishing between, and adequately managing stocks. During the two time periods reviewed here, most of the research focused on identifying mixtures of stocks was performed on herring in either the Pacific (*Clupea pallasi*) or Atlantic (*C. harengus*). Atlantic and Pacific herring exhibit spawning site fidelity and, hence, more complex stock structure with management implications. A variety of techniques were employed to distinguish unique reproductive units of herring in the Pacific or Atlantic including genetic analyses (Siple and Francis, 2016), otolith shape or microchemistry differences (Geffen et al., 2011; Gröhsler et al., 2013; Vergara-Solana et al., 2013) or using parasites as natural tags (Unger et al., 2014). Otolith morphometrics and/or genetic analyses have also been employed to differentiate stocks of European anchovy (e.g., Magoulas et al., 2006; Viñas et al., 2014) and European sardine (Jemaa et al., 2015) across Mediterranean and Eastern Atlantic waters. Body and otolith shapes have been used to discriminate stocks of Pacific sardine in the California Current ecosystem (Vergara-Solana et al., 2013), and parasite biotags in particular but also some life history and meristic and morphometric characteristics have been used for sardine stock identification in the southern Benguela Current System (Reed et al., 2012; van der Lingen et al., 2015; Weston et al., 2015; Idris et al., 2016). The advancement of biochemical and genetic techniques allowing the identification of allozyme loci (in the 1980 s) or microsatellites (in the 1990 s), has revealed differences in the relatedness of
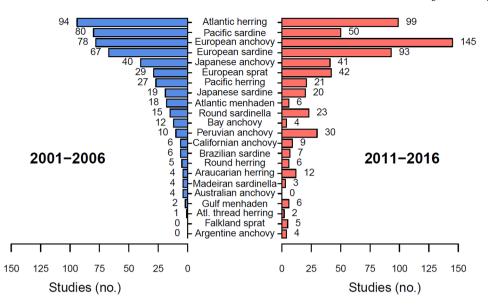
Fig. 3. The number of studies published on various species of small pelagic fish within two, 6-year time periods. Note, the 22 species shown are those investigated in at least 2 studies in either time period. In total, 33 species appeared in at least 1 study (see supplementary material).

conspecifics at small spatial scales. The application of these techniques to SPF such as Pacific sardine, northern anchovy and Atlantic herring has also identified 'chaotic patchiness' (Hedgecock, 1994), in which inter-annual genetic variation within spawning aggregates was often larger than the genetic variation among nearby populations (see Olsen et al., 2002 and references therein). A review by Eldon et al. (2016) identified four processes contributing to such patchiness in populations of marine fish and other taxa, including sweepstakes reproductive success and differences in phenology, larval dispersal and patterns of selection.

It is important to establish baseline patterns in abundance (e.g., size of specific populations) and compile evidence on changes in the historical spatial distributions of SPF to better understand ongoing changes or to better project what may happen in the future. The pioneering research in the late 1960s examining scales preserved in anoxic sediments (e.g., Soutar and Isaacs, 1969) led to important publications reporting on long-term fluctuations in small pelagic fish populations (e. g., Baumgartner et al., 1992) as reviewed by Field et al. (2009). Recent studies have continued to document these decadal to centennial patterns such as the 150-yr time series generated for Japanese anchovy (*Engraulis japonicus*) in the Yellow Sea (Huang et al., 2016) and the work by Kuwae et al. (2017) in Japanese waters. These long-term time series are crucial in providing an historical perspective on the current abundances and trends and for revisiting models and paradigms based on historic data sets. In the northern Humboldt Current System, for instance, centennial to multi-millennial reconstructions of the abundance of Peruvian anchoveta suggested that the commercial fishery developed during a period of relatively high abundance of this stock respective to the last millennia (Salvatteci et al., 2019). That study also refuted some important aspects such as anchovy-sardine alternation or the role of the Pacific Decadal Oscillation (PDO) as a direct driver of SPF dynamics (Gutiérrez et al., 2009; Salvatteci et al., 2019).

2.1.2. Reproduction

A considerable amount of information on the reproductive characteristics of SPF has been gained by using the daily egg production method (DEPM) to estimate spawning stock biomass (SSB) (Lasker, 1985; Alheit, 1993). This calculation requires ecologically relevant information on key reproductive characteristics such as the in situ concentration of eggs and the mean weight, batch fecundity, and spawning frequency of females during the peak period of reproduction whereby spawning frequency is determined by histological ageing of post-

ovulatory follicles based on the ground-breaking work of Hunter and Goldberg (1980). Thus, spawning times, spawning habitats and links between oceanographic conditions and SPF productivity have been revealed by collecting the data needed to apply the DEPM (Somarakis et al., 2002, 2006; Ettahiri et al., 2003; Twatwa et al., 2005; Amenzoui et al., 2006; van der Lingen et al., 2006a, Fissel et al., 2011; Bernal et al., 2012; Haslob et al., 2012a, 2013; Tsikliras and Koutrakis, 2013; Bouhali et al., 2015; Mhlongo et al., 2015; Rajasilta et al., 2015).

Beyond field studies describing the basic features of reproduction in SPF, recent research has explored resource partitioning including potential trade-offs between allocating energy to spawning or somatic growth. As opposed to some capital breeders such as gadoids that accumulate lipid reserved in the liver more than 6 months prior to spawning, SPF fuel reproduction based on relatively small lipid reserves in muscle tissue, and some SPF supplement energy requirements for spawning by feeding shortly before and during the spawning season. These fish depend less on the input of energy from feeding during their protracted spawning season (e.g., Hunter and Leong, 1981; Ganias et al., 2009; Nunes et al., 2011). Other SPF are more strictly income breeders, as shown for the Japanese anchovy, for which changes in the ratio of $\delta^{13}C$ to $\delta^{15}N$ in eggs closely follow the isotope ratios of the prey consumed by adult fish (Tanaka et al., 2016). The partitioning of resources by females to their eggs and offspring is not fixed, therefore, but is relatively dynamic, depending on recent feeding conditions. Garrido et al. (2007b, 2008b) demonstrated how the concentration and composition of essential fatty acids (FAs) in the muscle of female sardine (*Sardina pichardus*) corresponded to that in hydrated oocytes and how this maternal provisioning of FAs changed both spatially and during the spawning season with implications for changes in egg quality. Research on Atlantic herring populations identified energy trade-offs between somatic growth, fecundity and migratory behaviour: migrants had significantly higher somatic growth rate and lower relative fecundity compared to females in non-migratory populations (Silva et al., 2013).

Recent research in the NW Mediterranean investigated energetic consequences of environmental conditions unfavourable for growth (Brosset et al., 2015) and energetic trade-offs associated with lipid reserves, size-at-maturity, batch fecundity, spawning duration and egg quality (dry mass) of European anchovy and sardine (Brosset et al., 2016). Besides significant decreases in the length-at-maturity, both species displayed preferential allocation toward reproduction, even in fish that were in relatively poor condition (weight-at-length and length-at-age). This preferential allocation of energy to gonadal maturation and

spawning in females was also observed in Atlantic herring in the Baltic Sea (Rajasilta et al., 2015).

2.1.3. Feeding and diet

Due to the tight coupling of SPF populations to bottom-up processes impacting on lower trophic levels, it is important to understand which prey are preferred and how much are needed to cover energy requirements of SPF. Furthermore, as most SPF are income breeders, the richness of the feeding environment can have important and immediate consequences on reproductive output (Garrido et al., 2015). During the two periods reviewed here, a considerable amount of new information was published on the diets of various SPF species and the number of studies focusing on SPF diet almost tripled in the second period compared to the first (15 vs 42 studies). In the first period, a comprehensive comparison of the trophodynamics of sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) in the southern Benguela (van der Lingen et al., 2006b) underlined the trophic dissimilarity between the two species and indicated size-based resource partitioning of their zooplankton prey. That study led to the hypothesis that alternations in relative species dominance between the two species may be trophodynamically mediated. Between the periods assessed here, a comprehensive review that assembled available information on the feeding morphology, behaviour and diet of SPF from several regions (van der Lingen et al., 2009) supported the trophic dissimilarity hypothesis for sardine/anchovy species pairs in some (e.g., Ayón et al., 2011) but not all (e.g., Costalago et al., 2012) ecosystems where adequate data exist. During the second period, a review of the diet and feeding behaviour of sardine and anchovy species was published (Garrido and van der Lingen, 2014). That work also tested the trophodynamic hypothesis with more data including results from new techniques to study trophic ecology such as analyses of stable isotope ratios. These new data indicated support for the trophic dissimilarity hypothesis in most systems.

During the two time periods reviewed here, about three-fold more studies were published on the diet and feeding of juveniles and adults compared to larvae. Diet studies on larvae filled gaps in knowledge on rarely-studied species such as Falkland sprat (*Sprattus fuegensis*) and Araucarian herring (*Strangomera bentincki*) in fjords and channels in southern Chile (Contreras et al., 2014), and on well-studied species in specific habitats such as Atlantic herring in the Gulf of Riga in the Baltic Sea (Arula et al., 2012), European sardine in the Mediterranean Sea (Tudela et al., 2002; Fernandez and González-Quirós, 2006) and Japanese sardine and anchovy in the Kii Channel in Japan (Yasue et al., 2011). During the two periods, a similar (small) number of laboratory studies was conducted. During the first period most laboratory studies focused on the condition and growth of larvae (or post-larvae) in relation with feeding densities (e.g., Kono et al., 2003; Baumann et al., 2005). During the second period, most laboratory studies focused on the importance of protists for the diet of early larvae (Friedenberg et al., 2012; Illing et al., 2015). Field studies on larval feeding more than doubled in the second compared to the first period. In the first period, these studies mainly focused on gut content analysis to define changes in prey composition, size and preference with increasing larval length such as work by Llanos-Rivera et al. (2004) on Peruvian anchovy and Pacific sardine from Concepcion Bay, Chile. In the second period, a more holistic approach was often taken in which larval diet and feeding was studied in relation to environmental factors influencing prey availability or larval feeding success such as wind speed, temperature, turbulence and freshwater discharge (e.g., Arula et al., 2012; Landaeta et al., 2012). These holistic studies have been important to the development of subroutines for larval foraging in biophysical individual-based models (e. g., Hufnagl and Peck, 2011; Urtizberea and Fiksen, 2013).

In terms of diet studies performed on juveniles and adults, in the first period, most of these were single-species analyses, while studies comparing diets of two to several SPF in the same ecosystem were more common in the second period. For example, the diet of adult Pacific sardine (*Sardinops sagax*) was examined in coastal waters off California

and Oregon, USA (McFarlane and Beamish, 2001; Emmett et al., 2005) and the southern Benguela EBUS off South Africa (van der Lingen, 2002) in the first period. Examples of diet overlap studies comparing two or more species of SPF in the second period include analyses in the NE Atlantic (Bachiller et al., 2013; Langøy et al., 2012; Raab et al., 2012), Bay of Biscay (Chouvelon et al., 2015; Bachiller and Irigoien, 2015) and in the Mediterranean Sea (Costalago et al., 2012, 2014; Bourg et al., 2015).

Within many ecosystems, large schools of SPF have the capacity to locally deplete zooplankton (e.g., Ayón et al., 2008b; Koslow, 1981) and, in exceptional cases, exert top-down control of the zooplankton community (Arrhenius and Hansson, 1993). Juveniles likely exert particularly strong top-down pressure on standing stocks of zooplankton because they are relatively abundant and they have relatively high mass-specific feeding rates. Intensive predation may lead to density-dependent prey limitation during the juvenile period as was suggested by various studies conducted on European sprat (*Spattus sprattus*) (Cardinale et al., 2002; Baumann et al., 2007; Hawkins et al., 2012). In one study, Hawkins et al. (2012) obtained estimates of sprat abundance from hydroacoustic measurements and zooplankton abundance from pump samples and reported rapid rates of prey depletion by large schools in an embayment in Ireland. In a second study, Baumann et al. (2007) used trajectories of otolith growth of field-caught individuals and laboratory starvation-refeeding experiments to demonstrate that large schools of young juvenile sprat were in starving condition within warm, nearshore waters of the southwestern Baltic Sea. In both Atlantic herring and sprat in the Baltic Sea, more than 90% of the long-term variability in fish condition (weight-at-length) was explained by fish abundance, highlighting the importance of density-dependent competition for prey (Casini et al., 2006; Casini et al., 2014). van der Lingen et al. (2006a) analysed a 52-year time series of biological data on Pacific sardine (*Sardinops sagax*) in the southern Benguela and reported density-dependent effects on condition factor and length-at-maturity. Similarly, density-dependent growth and maturation of this species off California were suggested by Dorval et al. (2015) who compared the stock characteristics for fish born in three periods (1986–1993, 1996–2003 and 2004–2008). A plethora of studies has also documented the role of SPF as potential competitors with other groups of fish such as the overlap in zooplankton in the diets of Pacific herring and walleye pollock (*Theragra chalcogramma*) in Prince William Sound, Alaska (Sturdevant et al., 2001).

Long-held beliefs concerning the diet of some SPF are changing due to recent research, particularly studies estimating prey energy as opposed to prey number and those studying the trophic web by means of stable isotopic composition. For example, for decades, the Peruvian anchoveta (*Engraulis ringens*) was considered to feed directly on primary producers (Ryther, 1969; Rojas de Mendiola, 1989; Alamo and Espinoza, 1998) leading to the belief that the large populations of anchoveta were supported by an unusually short and efficient food chain (Ryther, 1969; Walsh, 1981; Pauly and Christensen, 1995). Recent work estimating prey carbon content refutes this assumption by demonstrating that Peruvian anchoveta forage mainly on macrozooplankton, in particular euphausiids and large copepods (Espinoza and Bertrand, 2008, 2014). The reliance of anchoveta on macrozooplankton was confirmed by analysis of stable isotopes indicating a trophic level between 3.4 and 3.7 (Espinoza et al., 2017). These results suggest an ecological role for forage fish that challenges most current trophic models for the Humboldt Current System (HCS), which are parameterized such that forage fish rely largely on diatoms.

Fish are continuous samplers of the ecosystem. Since many species of SPF display a high degree of opportunistic feeding, changes in diet can reveal fundamental shifts in marine ecosystems. In Peru, for example, no clear relationship was observed between the prey composition of Peruvian anchoveta and inter-annual variability in oceanographic features associated with El Niño and La Niña periods (Espinoza and Bertrand, 2008). However, at longer, decadal scales, Espinoza and Bertrand

(2014) reported a shift in the proportion of euphausiids in the diet of Peruvian anchoveta that tracked changes in the size of dominant zooplankton (Ayón et al., 2011). These diet studies are fundamental to understanding resource partitioning by co-occurring SPF in various ecosystems around the globe. Difference in the sizes of prey preferred by anchovy and sardine have been well-known for decades based on gill raker morphology (e.g., King and Macleod, 1976; van der Lingen et al., 2009; Rykaczewski (unpublished data)) and the "trophic-dissimilarity" hypothesis (van der Lingen et al., 2006b) forms one of the hypotheses attempting to explain the large-scale oscillations of populations of anchovy and sardine observed in the California, Peruvian and Benguela Eastern Boundary Upwelling Systems (EBUSs). In non-upwelling ecosystems, less research has been conducted on the potential diet differences between sardine and anchovy, although considerable work was done in the second, 6-yr period. In one example, stable isotope analyses of plankton and fish muscle in the Bay of Biscay revealed differences in the diets and a lack of competition between co-existing anchovy and sardine during spring, when prey resources were high, but greater diet overlap during autumn, a period of lower plankton productivity (Chouvelon et al., 2015). Importantly, seasonal changes in diets and trophic niche breadth have been documented in response to changes in hydrography (stratification and mixing periods) and prey availability. In a second example, Nikolioudakis et al. (2014) reported that relatively large copepods were the main prey for both anchovy and sardine in the eastern Mediterranean Sea, although adult sardine (but not anchovy) consumed phytoplankton. Finally, competition for prey has also been reported for other species of co-existing SPF such as European sprat and Atlantic herring in the Baltic Sea (Möllmann et al., 2004). In SPF, particularly in sardines and anchovies, the diets and potential intra-guild competition appears to depend on the ecosystem-specific processes regulating plankton community production and composition as discussed by Espinoza et al. (2009) who compared diets of sardines across three EBUS.

2.1.4. Intra-guild competition and predation

Although the present review is focused on the impacts of bottom-up processes, diet studies clearly indicate that intra-guild predation and cannibalism can be important controls of early life stage survival of SPF. For example, field work from the mid-1980s in the Benguela system indicated that 56% and 6% of the total mortality of anchovy eggs resulted from sardine predation and anchovy cannibalism, respectively, although mortality rates can be higher when SPF forage within dense patches of eggs (Valdés-Szeinfeld et al., 1987; Valdés-Szeinfeld, 1991). The proportions of egg cannibalism by anchovy were even higher in the Humboldt (21%) and the California (28%) Currents (Alheit, 1987). More recent work by Bachiller et al. (2015) reported that up to one-third of the total annual egg mortality of European anchovy was the result of predation by European sardine in the Bay of Biscay. Although population-level impacts were not quantified, Karaseva et al. (2013) documented substantial numbers of sprat eggs and larvae in the diets of Atlantic herring in the south-eastern Baltic Sea but little to no predation of sprat on herring early life stages. In the NW Pacific, Takasuka et al. (2004) reported that cannibalism of larvae by juveniles of Japanese anchovy was observed in 26% of fish analysed, which appeared to select slower-growing larvae. Finally, Garrido et al. (2015) estimated that cannibalism was responsible for 30% of the natural mortality of sardine eggs spawned off southern Portugal and laboratory experiments confirmed that eggs were one of the preferred prey items for the species (Garrido et al., 2007a).

2.1.5. Schooling and behaviour

In the field, the organisation/patchiness of SPF occur across a variety of scales (Gerlotto and Paramo, 2003; Fréon et al., 2005). At spatial scales from the individual (10s of mm), to the school (10s of m), self-organisation mechanisms are likely to be dominant and drive the formation and characteristics of schools. For gregarious fish, the school is

"an essential life unit in which fish feed, breed, rest, and flee" (Aoki, 1980). In SPF, larvae first start to display schooling behaviour directly after notochord flexion (e.g., Cotano et al., 2008; Somarakis and Nikolioudakis, 2010 and references cited therein). In *Engraulis* species, for example, schooling starts when larvae are between 11 and 17 mm in length (Hunter and Coyne, 1982; Masuda, 2011). This transition to schooling is correlated with the start of strong vertical migration and changes in diet. This shift is a 'game-changer' as it involves escaping the viscous flow regime (Müller and Videler, 1996), modifying the effects of bottom-up forcing (i.e., modifying the capacity to reach prey, interact with currents, etc.) as reviewed by Peck et al. (2012c). Since the development of multi-beam sonars (Gerlotto et al., 2000), knowledge on SPF school dynamics and behaviour has considerably increased (e.g., Misund et al., 2003; Handegard et al., 2017). School size, shape, and location depend on (i) local habitat characteristics, in particular the prey dynamics (e.g., Nøttestad et al., 1996; Mackinson et al., 1999; Bertrand et al., 2008a), hydrodynamic characteristics or the presence of predators (e.g., Axelsen et al., 2001; Nøttestad et al., 2004; Gerlotto et al., 2006; Bertrand et al., 2014), and (ii) intrinsic behaviour such as spawning (e.g., Axelsen et al., 2000). Once formed, these large school play a central role in how SPF respond to bottom-up (and top-down) processes and may contribute, through intra-guild competition, in the rapid shifts in dominance of SPF as described in "School Trap" hypothesis (Bakun and Cury, 1999).

Living organisms follow non-random yet non-uniform distributions and tend to aggregate in patches (Margalef, 1979; Legendre and Fortin, 1989). Both physical forcing (e.g., frontal zones (Munk et al., 1999)) and organismal behaviour initiate and maintain patchiness (Kotliar and Wiens, 1990). Bottom-up, physical processes structure pelagic habitats (Legendre and Fortin, 1989), introducing turbulence and/or creating convergence zones of nutrients and passive plankton. Trophodynamic coupling can transmit these spatial structures through the food web (Bertrand et al., 2008a, c). Over the last decade, advances in hydro-acoustics have increased our understanding of the schooling dynamics of SPF and how the environment structures the distribution of clusters of schools. Primary ecosystem interactions were believed to occur at the mesoscale but acoustic data on SPF in the Humboldt Current revealed that the dynamics of upper ocean waters at sub-mesoscales (less than10 km) played the foremost role in shaping the seascape from zooplankton to predators and that fish behaviour (foraging in schools) magnifies the physically induced spatial structuring (Bertrand et al., 2014). Work on Peruvian anchoveta, thus, suggests that patchiness at spatial scales greater than that of schools (e.g., clusters) is also driven by physical forcing such as ocean turbulence at meso- and sub-mesoscales and not only by the total abundance of SPF in a region (Bertrand et al., 2008a, 2014).

2.2. Statistical analyses and reviews

Given the importance of SPF to local economies, long-term records of catch often exist that can be exploited to understand historical fluctuations in the sizes of stocks and potential environmental drivers (e.g., Alheit and Hagen, 1997). In specific ecosystems, contemporary surveys of specific species of SPF have now amassed more than 25 years of field data that have been harnessed to explore the strength of association between changes in climate-driven, bottom-up processes (e.g., changes in temperatures and/or prey fields) and changes in the distribution or productivity of SPF. In some ecosystems, time series data are currently not available. For example, the absence of long-term, large-scale sampling programs in the Canary Current EBUS has hampered the analysis of historical trends in SPF dynamics, as well as management efforts (Braham et al., 2014). Efforts are underway to integrate national archived datasets and newly collected field data (Ba et al., 2016) together with the implementation of large international projects to increase the capacity to understand trends and drivers of SPF in that EBUS.

Within "data-rich" EBUS, recent studies have provided new insights

on the well-documented oscillations between anchovies and sardines in various marine ecosystems including the California Current (Deyle et al., 2013; Lindegren et al., 2013). Based on late 20th century fish landings, the paradigm was that anchovy and sardine alternate periodically and that fluctuations in the size of their populations were associated with large- (basin-) scale changes in climate variability as captured from indices such as the PDO (e.g., Schwartzlose et al., 1999; Chavez et al., 2003). As previously mentioned, this paradigm has been challenged by a variety of paleoceanographic studies conducted in the Humboldt and California Current systems (e.g., Valdés et al., 2008; Field et al., 2009; Gutiérrez et al., 2009; McClatchie et al., 2017; Salvatteci et al., 2018). Given prehistorical records of population sizes inferred from ocean sediments, alternations between sardine and anchovy appear circumstantial and do not follow a consistent pattern (MacCall, 2009; Field et al., 2009; Salvatteci et al., 2018, 2019). Indeed, periods when both species are either rare or abundant have occurred in the past. Furthermore, fluctuations occur across a variety of timescales (Salvatteci et al., 2018) apart from the 50- to 60-years periodicity derived from fishery landings (Schwartzlose et al. 1999; Chavez et al., 2003).

The availability of long-term data sets has allowed explorations of the impacts of climate variability on population fluctuations of SPF. In the 1990s, biologists focused on the impact of the North Atlantic Oscillation (NAO), the differences in the centers of low and high atmospheric pressure between Iceland and the Azores, on marine ecosystems and populations. Research in the late 1990s and early 2000s correlated changes in the NAO index and changes in the productivity of herring and sardines populations in NE Atlantic waters (Alheit and Hagen, 1997) and sprat in the Baltic Sea (Alheit et al., 2005). A decade later, the focus shifted to studying the impact of the Atlantic Multi-decadal Oscillation (AMO) on ecosystems (Alheit et al., 2014). The dynamics of populations of anchovy, sardine, sprat and sardinellas in the Baltic, North Sea, Bay of Biscay, the Mediterranean and the Canarian upwelling were shown to be associated with AMO variability (Alheit et al., 2012, 2014, 2019a; Edwards et al., 2013; Montero-Serra et al., 2015; Tsikliras et al., 2019). In the NW Pacific, the SST in the Kuroshio and the Tsushima Warm Current (Japan/East Sea) markedly declined between 1968/71 and the late 1980 s. This appears to be related to climatic shifts associated with decadal dynamics of the East Asian Winter Monsoon and the Arctic Oscillation. Indices of these atmospheric conditions exhibited obvious changes in the late 1960s and the late 1980 s, the timing of which corresponded well to changes in catches of sardine and anchovy in these regions (Tian et al., 2008, 2014; Alheit and Bakun, 2010).

Long-term data sets have also shed light on the potential (bottom-up) processes limiting year-class success (year-to-year variability) of specific species in specific regions such as Atlantic herring in the North Sea (e.g., Corten, 2013) and European sprat in the Baltic Sea (Voss et al., 2012). Broader analyses including the whole fish community have been conducted in some systems (Ralston et al., 2014; Norton and Mason, 2005). The availability of long-term data derived from ocean sediments has revealed population fluctuations occurring at long-term (multi-decadal to millennial) scales (e.g., Gutiérrez et al., 2009; Salvatteci et al., 2018, 2019). Adult biomass and year-class success (recruitment) often exhibit rapid changes and this so-called "boom-and-bust" phenomenon is emblematic of SPF. Time series data of sufficient length have allowed researchers to explore the potentially density-dependent changes in carrying capacity causing these rapid shifts (e.g., Tanaka, 2003). For example, Jacobson et al. (2001) calculated annual surplus production (ASP), the biological production required to maintain the previous year's biomass in the absence of fishing, and used this to identify regime shifts in eight anchovy and nine sardine stocks around the world. Those authors exploited survey time series collected until 1997 and suggested that $\geq$ 30 years of data may be needed, especially for sardine, to adequately capture the full range of density-dependent changes in ASP (Jacobson et al., 2001).

A first step towards understanding the bottom-up processes causing

large fluctuations in SPF stocks is to correlate changes in stock biomass to abiotic factors such as wind strength and/or water temperature. Sudden shifts in the size of SPF populations have been linked to changes in physical forcing. Examples include the changes in the biomass of European sardine and prevailing winds off the coast of Portugal (Borges et al., 2003) or annual variability in satellite-derived spatial gradients in sea surface temperature (an upwelling index) in the Canary Current (Santos et al., 2005a,b), and how intra-seasonal variability in upwelling strength (Roy et al., 2001) can impact recruitment strength of European (Cape) anchovy in the southern Benguela. The rapid increase in European anchovy in the North Sea in the late 1990s was related to physiologically favorable warming allowing over-winter survival of juveniles (Petitgas et al., 2012). Time series analysis of Pacific sardine and large-scale changes in temperature and winds in the northern Benguela Current system highlighted how intensive (over-) exploitation of fish stocks and reductions in population size may change life history strategies (e. g., changes in spawning area) that can alter the strength (or can even reverse the sign) of correlations between environmental factors and stock productivity (Daskalov et al., 2003). Similarly, Essington et al. (2015) reported on collapses in 15 SPF populations and indicated that only 4 populations would have collapsed from natural productivity declines alone.

2.3. Laboratory / mesocosm studies

Controlled laboratory experiments were a relatively small proportion (less than 10%, Fig. 1) of the studies published on SPF during the two periods reviewed here and the majority of that work was conducted on larvae (Fig. 3). This is not surprising given that, for most species examined in this review, it is very challenging to maintain and spawn adults and rear their eggs and larvae in the laboratory. These practical challenges have led to a paucity of research directly examining the effects of abiotic factors using appropriate experimental designs across most taxa of fish, particularly SPF (Catalán et al., 2019). The case is worse in clupeid fish which are relatively sensitive to handling and require large volumes of water to comfortably swim, school, feed and reproduce in captivity. Some species are more easily obtained and amenable to laboratory rearing such as Atlantic and Pacific herring which is the likely reason why these two species accounted for 61% and 42% of all laboratory work published in 2001–2006 and 2011–2016, respectively. Atlantic herring was also the only species to have been studied using mesocosms during the two time periods reviewed here. Laboratory studies on Atlantic herring have been performed on all life stages and have explored a variety of facets including the ecophysiology of development, growth, feeding and swimming as impacted by various factors such as temperature, oxygen and/or pH (pCO$_2$) (e.g., Domenici et al., 2002; Geffen, 2002; Fox et al., 2003; Utne-Palm, 2004; Frommel et al., 2014; Maneja et al., 2015). Similarly, recent studies on Pacific herring have examined natural mortality rates of eggs of different sub-populations (Shelton et al., 2014), the strength of the protozooplankton-ichthyoplankton link (Friedenberg et al., 2012) and the sensitivity of larvae to suspended sediments (Griffin et al., 2012). Work on larvae and juveniles has examined the acute and chronic effects of a viral disease (Lovy et al., 2012).

Historically, when captive broodstocks of SPF have been established, this had led to a plethora of seminal studies advancing our mechanistic understanding of how species of SPF develop, feed and grow. An example includes studies on adult sardine in the Benguela region in the 1990s (e.g., van der Lingen 1995, 1998). Recent success at maintaining spawning brood stocks of species never before reared in captivity in Europe such as the European anchovy and European sardine has provided new information on changes in prey selection during the larval ontogeny of sardine (e.g., Caldeira et al., 2014; Garrido et al., 2016) and aspects of the bioenergetics (e.g., rates of feeding, growth, swimming and metabolism) of sardine or anchovy larvae (e.g., Garrido et al., 2007a, 2012, 2016; Iglesias and Fuentes, 2014; Moyano et al., 2014;

Silva et al., 2014). In California, laboratory trials have been used to calibrate oxygen isotopic values of otoliths so that this measure can estimate water temperatures utilized by juveniles (Dorval et al., 2011). Using a variety of biochemical measures made on blood and tissue samples, Pribyl et al. (2016) defined physiological optimal and sub-optimal temperatures for 1- to 1.5-year old Pacific sardine. Recent laboratory work on Japanese anchovy included measurement of the escape response of adults at two temperatures and two pCO$_2$ levels (Nasuchon et al., 2016) as well as a series of studies exploring how temperature and feeding affect aspects of maturation and spawning (Yoneda et al., 2014, 2015). These and previous laboratory studies have advanced conceptual models of environmental impact and helped parameterize mechanistic, physiology-based models to explore how the environment regulates the early life stage survival and life cycle closure of SPF (discussed in the next section).

2.4. Spatially-explicit modelling studies

2.4.1. Physical processes impacting individuals

The development of biophysical models depicting the transport of passive particles (e.g., fish eggs and larvae) in the early 1990s was an important step forward in fisheries science as it allowed hypotheses on processes controlling in situ productivity to be generated and, in some cases, tested (Werner et al., 2001). Given the tight coupling between SPF populations and environmental (bottom-up) drivers such as changes in wind forcing (Cury and Roy, 1989) or aberrant drift (Iles and Sinclair, 1982), the number of studies utilizing 3-d particle tracking models to explore the transport dynamics (e.g., advection, dispersion, retention) of eggs and larvae of SPF continues to grow. Studies reporting on the results of biophysical model simulations of the transport of eggs and larvae of SPF comprised more than 40% of the studies classified as "biophysical modelling" during the two, 6-yr periods reviewed here. Some of the earliest applications of biophysical individual-based models (IBMs) to examine the transport dynamics of early life stages of SPF were developed during the first review period for European (Cape) anchovy (*Engraulis encrasicolus)* and Pacific sardine in the southern Benguela (see review by Lett et al., 2015). The growing availability of high-resolution hydrodynamic models in areas such as the Humboldt Current, Canary Current and Mediterranean Sea have allowed explorations of bottom-up factors influencing habitat connectivity and potential survival of SPF in these systems both in retrospective simulations and in future climate projections during the second review period (e.g., Brochier et al., 2011, 2013; Soto et al. 2012; Catalán et al., 2013; Ospina-Álvarez et al. 2015). This spatially-explicit modelling has been expanded to include elements of growth physiology such as foraging dynamics (Hufnagl and Peck, 2011) and food availability (Kone et al., 2013), as well as energy allocation between somatic and reproductive tissues in adults (Pethybridge et al., 2013).

2.4.2. End-to-end models

One of the most notable developments in the new millennium has been the demonstration and application of fully coupled, end-to-end spatially-explicit biophysical models. This type of modelling represented roughly 10% of all the biophysical modeling studies published on SPF during the two time periods. SPF are ideal candidates for this type of modelling because of their dependency on the dynamics and standing stocks of phytoplankton and zooplankton populations. Initial steps in creating these tools were to couple feeding requirements from bioenergetics-based growth models for Pacific herring as mortality terms on phytoplankton and zooplankton groups within lower-trophic-level, biogeochemical models (e.g., Rose et al., 2007, 2008). These tools now include movement sub-routines, dynamic predator–prey feedbacks and top-down forcing from predatory fish and fishing fleets (Fiechter et al., 2015; Politikos et al., 2015; Rose et al., 2015). These end-to-end models not only include life-stage-specific physiology and behaviour but also close the life cycle (from eggs to adults to eggs) and

can be projected forward for many generations. These models include the interaction between various bottom-up (temperature, mesoscale turbulence, prey field) and top-down (predators and fisheries) drivers of SPF stocks. They are complex, parameter-rich models designed for ecosystem-level, management strategy evaluation. The reason that these state-of-the-art tools have been advanced is because of the unique, tight coupling of the population dynamics of SPF to changes in lower trophic levels, the importance of SPF as prey in food webs and the commercial importance of SPF to human communities. An important step in the development of these end-to-end models for SPF was the transfer of knowledge derived from field data on the trophodynamic relationships of SPF into mass-balance trophic models such as Ecopath. Although not included in this review, these and other 0-D (time only) food-web models have been extensively applied to SPF as exemplified by work in the Benguela system in the early 2000s (Shannon and Cury, 2003; Shannon et al., 2003; Heymans et al., 2004; Shannon et al., 2004a,2004b).

2.5. Summary of bottom-up factors and processes

These 5 methods of study (field, laboratory, mesocom, spatially-explicit modelling, and statistical analyses/reviews) have been applied to investigate various aspects of bottom-up control of SPF. To compare across regions and identify gaps in knowledge, we organized studies by drivers and responses examined (Fig. 4). For drivers, we used 10 categories including six abiotic factors (i.e., temperature, salinity, dissolved oxygen, pH and water density), two biotic factors (prey quantity and quality) and/or important physical processes (advection, turbulence and turbidity) (Fig. 4). In terms of responses, we used nine categories, distinguishing between population- (e.g., changes in productivity and/or distribution) and individual-level responses such as vital rates (mortality, growth, feeding, reproduction) and energetic costs and losses (e.g., various aspects of internal physiology, swimming behaviour, impacts of disease / parasites). Papers often examined multiple drivers and responses. Some factors were examined a few times in specific regions that were not included in this overall scheme such as the impacts of pollution (e.g., sound, chemical). Nevertheless, these categories provided a useful graphical representation (Fig. 4) allowing one to visualize how the 5 categories of studies have been applied to factors, processes and responses across regions and/or species. Although it is compelling to make cross-hemisphere comparisons of the results of similar types of studies
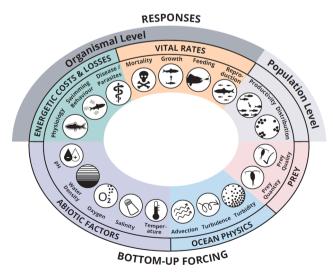
Fig. 4. The focus of peer-reviewed papers on SPF were categorized into 10 different bottom-up drivers (factors) and processes (forcing) and 9 different responses. Note, some research examined only responses (especially field surveys). This diagram serves as a template to map and compare research effort across regions and /or species.

on "anchovies" or "sardines", important physiological and/or morphological differences occur within these groups. For example, adult body size is smaller in the genus Sardina (Atlantic) compared to the Sardinops (Pacific) (e.g., 27.5 versus 39.5 cm).

3. Regional summaries

The research on SPF in various regions around the globe has focused on specific processes thought to be important in driving changes in the distribution and productivity of various populations. Global coverage in the research conducted on SPF is clear from a map showing the distribution of published studies (Fig. 5). There are differences between the two time periods in the number of studies published on species in certain habitats. Three regions had a considerable decline (NW Atlantic, Benguela Current System, Australia) and three had a considerable increase (Humboldt Current System, Mediterranean Sea, Baltic Sea). For example, some studies were published in the first 6-yr period in SW Australia but no studies were published in the second period. Similarly, far fewer studies were published on species in the Benguela EBUS in the second (19) compared to the first 6-yr period (43). A similar decrease was apparent in the NW Atlantic (36 vs. 15 published studies). Increases in publications were noted in the Humboldt EBUS and Mediterranean Sea. There are various reasons for these differences including changes in the strength of international collaboration, shifts in national funding schemes (e.g., as a response to understand large shifts in SPF resources, particularly collapses of populations).

The next sections briefly summarize research in 10 regions, where the majority of the SPF research reviewed here (899 of 945 studies) was conducted. During the two time periods, the most studies (18%) were published on SPF in the Mediterranean Sea followed by the NW Pacific, Baltic Sea, California Current and NE Atlantic (10 to 12% each). Studies on SPF in the Barents - Norwegian and Canary - Iberian systems accounted for 8 and 9%, respectively. Studies within the Northeast Atlantic, and Humboldt and Benguela Current systems were between 5 and 6% of those reviewed here. Research effort compared in this manner ignores the vast differences in the number of countries (EEZs) in these regions. For example, two countries are associated with the Humboldt Current System while more than 7 countries border regions such as the Mediterranean Sea, NE Atlantic and Baltic Sea. There are also large differences in the economic resources (e.g., GDP) potentially available for research and the economic (and cultural/societal) importance of SPF across all 17 regions. A relative view of research effort (normalized by the number of EEZs or GDP) would change this world-wide map, particularly with regard to the amount of research conducted in the Humboldt Current System relative to European and North American

regions. Moreover, more recent research programmes have been funded to advanced knowledge on the dynamics of SPF in developing regions such as sub-Saharan west Africa (e.g., Thiaw et al., 2017; Diankha et al., 2018) that were not included in this review.

3.1. The Humboldt Current System

Although the four EBUS have similar levels of primary productivity, the northern Humboldt Current System (HCS) has 5- to 10-times more productivity of SPF and this region has produced more fish per surface area than any other marine system in the most recent decades (Chavez et al., 2008). Alongshore winds are present year-round in northern Chile and along most of the Peruvian coast, but these upwelling-favourable winds are limited to spring, summer, and early autumn in central and southern-central Chile (30°–41°S). The HCS is subject to large fluctuations in climate, biological characteristics (e.g., community structure) and fisheries, from intra-seasonal to inter-annual (e.g., El Niño Southern Oscillation, ENSO) and secular to millennial time scales (Chavez et al., 2008; Gutiérrez et al., 2009; Salvatteci et al., 2014). El Niño, La Niña events, and climate variability in general, have had some of the largest documented impacts in this region (Keefer and Moseley, 2004; Chavez et al., 2008). A key feature of the HCS is the presence of a large, sub-surface oxygen minimum zone (OMZ) located a few tens of meters below surface waters which vertically compresses the ecosystem. The absence of oxygen in continental shelf sediments preserves organic matter and the remains of organisms, creating a record of ecosystem components and climatic variability over tens of thousands of years (Gutiérrez et al., 2009, 2011; Salvatteci et al., 2018, 2019). It is clear that periods of high and low SPF abundance have occurred long before the development of the commercial fishery in the HCS (Sandweiss et al., 2004; Gutiérrez et al., 2009).

Although work published on SPF in the HCS represented about 5% of studies reviewed here (Fig. 5), arguably, the HCS is one of the most intensively studied EBUS as monitoring has occurred here for more than 50 years including two to four field surveys per year since the early 1980 s. This effort has advanced understanding of i) the trophodynamics of sardine and anchovy (Espinoza et al., 2009; Espinoza and Bertrand, 2014), (ii) long-term changes in SPF prey field characteristics such as zooplankton size distributions (Ayón et al., 2011), (iii) the magnitudes of spawning activity of *E. ringens*; or (iv) the complex processes (from physics to seabirds and fisheries) impacting small pelagic fish (Bertrand et al., 2008a,c, 2014; Joo et al., 2014; Passuni et al., 2016; Barbraud et al., 2018).

The productivity of fish in the HCS is mostly controlled by climate-driven bottom-up processes impacting on the production of
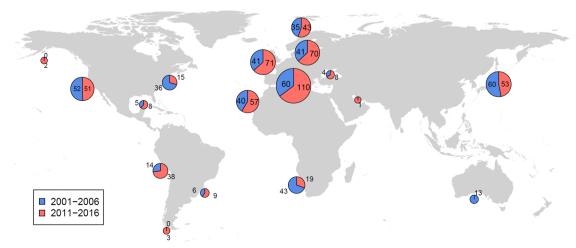

Fig. 5. The numbers of studies on small pelagic fish published during two, six-year time periods in 17 different biogeographic regions. The location of each circle often represents a much broader region (e.g., one or more large marine ecosystems). Some studies (statistical analyses / reviews) were counted in a multiple regions.

phytoplankton and higher trophic levels at a variety of scales (Gutiérrez et al., 2009; Ayón et al., 2011; Salvatteci et al., 2018). Although temperature was considered the main driver of the spatial dynamics of small pelagic fish in the HCS in the early 2000 s, the demonstration of plasticity in the response of pelagic fish towards temperature (e.g., McFarlane et al., 2002; Bertrand et al., 2004; Espinoza and Bertrand, 2008; Gutiérrez et al., 2008) suggested more complex relationships between SPF and vertical and horizontal water-mass characteristics, particularly in relation to the Oxygen Minimum Zones (OMZs) and prey distribution (Ayón et al., 2008a, 2011; Swartzman et al., 2008; Ballón et al., 2011; Bertrand et al., 2011; Salvatteti et al., 2019) at multiple, dynamic scales (Bertrand et al., 2014). These more complex ecosystem characteristics not only influenced bottom-up drivers but also the magnitude of top-down control from both predators and fisheries (Joo et al., 2015; Passuni et al., 2016; Barbraud et al., 2018). Between the two time periods compared in the present literature review, many long-held beliefs changed. This included diet studies suggesting that Peruvian anchoveta and Pacific sardine do not mainly feed on phytoplankton but on zooplankton (Espinoza and Bertrand 2008, 2014; Espinoza et al., 2009, 2017) in agreement with observations in the Benguela system, (van der Lingen et al., 2006b). Moreover, anchovy and sardine in the HCS forage on larger prey items such as euphausiids to a greater degree than in other systems (Espinoza et al., 2009). An important shift in knowledge was the realization that the sediment record indicates that anchovy and sardine do not consistently alternate in biomass at decadal scales (e.g., Chavez et al., 2003) but that these species display inconsistent patterns of alternation across a range of timescales which are not correlated with the PDO and other remote climate drivers (Valdés et al., 2008; Gutiérrez et al., 2009; Salvatteci et al., 2018).

During the two periods reviewed here, research effort on the main species (Peruvian anchovy) focused on field studies, statistical time series analyses on population-level responses (distribution and productivity) as well as reproduction (Fig. 6). Only a few papers reported results from laboratory studies but a notable amount of field and laboratory work reported on aspects of the early life-stage physiology. The coverage of abiotic drivers examined included not only temperature but also salinity with special emphasis on dissolved oxygen. Not only prey quantity but also prey quality was examined (Fig. 6).
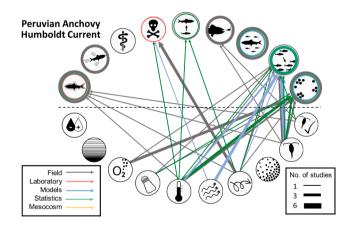

Fig. 6. Research emphasis in papers published during two time periods (2001–2006, and 2011–2016) on Peruvian anchovy in the Humboldt Current System. In total, 10 categories of bottom-up drivers (below dotted line) were used including 5 abiotic factors, 3 physical / mixing processes, and 2 aspects of prey. Responses (above dotted line) were separated into 9 categories including 7 at the individual level (from left, 3 energetic costs or losses and 4 vital rates) and 2 at the population-level (see Fig. 4 for legend). The thickness of lines represents the number of studies. The color represents the type of study (not all types may be present). The number and type of studies considering only responses are also shown (color and thickness of circles).

3.2. The Canary/Iberian Current System

The Canary/Iberian Current System (CanCS) is one of the four major EBUS, extending from the NW African coast (12°N) through the Iberian Peninsula (to 43°N). At the northern and southern limits, the strength and extent of upwelling varies seasonally (Arístegui et al., 2009; Kämpf and Chapman, 2016) while between 10 and 20°N upwelling becomes semi-continuous (Lathuilière et al., 2008). The system contains a broad diversity of marine habitats with three, distinct sub-regions: Iberian, Moroccan and West Saharan, and Mauritanian-Senegalese.

The Iberian subregion has two main components, related to the topography and orientation of the coastline. Productivity in the northwestern Iberian Peninsula is highly influenced by summer upwelling and by river runoff (Arístegui et al., 2009). In the southern Iberia, upwelling is weaker and more intermittent, mainly occurring during late spring/summer. The European sardine is the most landed fish in the Iberian subregion, representing approximately 40% of the total catch (DGRM, 2016). Mean annual catches of the Atlanto-Iberian sardine have declined three-fold in the last decade, with severe socio-economic consequences for Portuguese and Spanish fishing communities. The European anchovy has a stable population in the sheltered Gulf of Cadiz and intermittent bursts of recruitment off the NW coast likely linked to occasionally favorable environmental conditions. In this sub-region both SPF are often found in mixed shoals with other abundant coastal pelagic fish such as Atlantic chub mackerel (*Scomber colias*) and horse mackerel (*Trachurus trachurus*). In the Moroccan subregion (21 − 32° N), coastal upwelling (strongest in June-August) creates a complex array of meso-scale features (front, filaments and eddies) which interact with those generated in the nearby Canary archipelago to influence the life history dynamics of several species of SPF (see Arístegui et al., 2006; Rodríguez et al., 2009). Catches of SPF are dominated by European sardine (with peak abundance in Moroccan waters) followed by round sardinella (*Sardinella aurita*) (FAO, 2018a). European anchovy occurs in low abundance and, unlike other EBUS, inter-decadal shifts in dominance between sardine and anchovy (e.g., Alheit et al., 2009; Alheit and Bakun, 2010), have not been observed. Changes in the SPF community have been associated with episodic warming and hypoxia (Arístegui et al., 2009). For example, after a warming event in 1995/97, the abundance of round sardinella began to gradually increase while European sardine drastically decreased in the north of this subregion. The Mauritanian-Senegalese subregion (12 − 21 °N) is the most productive of the three sub-regions mainly due to the presence of nutrient-rich North Atlantic Central Waters and deposition of Saharan dust (Arístegui et al., 2009). Upwelling is highly seasonal and strongest in winter. In this subtropical region, the SPF assemblage is dominated by two sardinella species (round and flat sardinella (*Sardinella maderensis*)), stocks that are now considered to be over-exploited (FAO, 2018a).

Studies published on SPF in the CanCS represent about 9% of those included in this review (Fig. 5). Most studies focused on the European sardine (69%), followed by the anchovy (19%) and both *Sardinellas* (12%). The number of studies published in the two periods was similar but the majority of published research stems from the Iberian subregion. Relatively little research has been conducted on stocks of SPF in Mauritanian-Senegalese subregion with most historical research published in regional journals or within technical reports (e.g., Boely et al., 1982; Fréon, 1983; John, 1986). Interestingly, some of the seminal research on recruitment mechanisms of SPF stem from this subregion such as Cury and Roy's (1989) "optimal environmental window".

During the two periods reviewed here, a good balance of laboratory, field, statistical analyses and spatially-explicit modelling studies was published (Fig. 7). In the Iberian sub-region, long-term data from Spanish and Portuguese scientific surveys (since the 1980 s) and fisheries catch statistics (since the 1940 s) have provided insight on how environment factors and processes regulate the productivity of SPF. Examples include how prevailing wind conditions affect sardine recruitment (Borges et al., 2003; Guisande et al., 2004), how winter
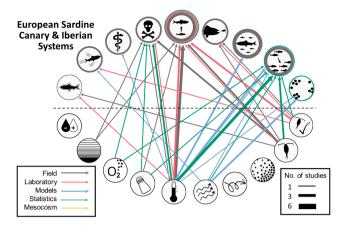
Fig. 7. Research emphasis in papers published during two time periods (2001–2006, and 2011–2016) on European sardine in the Canary Current and Iberian Systems. In total, 10 categories of drivers (below dotted line) were used including 5 abiotic factors, 3 physical / mixing processes, and 2 aspects of prey. Responses (above dotted line) were separated into 9 categories including 7 at the individual level (from left, 3 energetic costs or losses and 4 vital rates) and 2 at the population-level (see Fig. 4 for legend). The thickness of lines represents the number of studies. The color represents the type of study (not all types may be present). The number and type of studies considering only responses are also shown (color and thickness of circles).

upwelling events impact on the dispersal of sardine larvae (Santos et al., 2005a,b), and how sea surface temperature, intense easterly winds, and discharges from the Guadalquivir River are related to early life-stage mortality of anchovy in the Gulf of Cadiz (e.g., Ruiz et al., 2006). Work in the latter region has been used to help forecast the strength of anchovy recruitment, potentially increasing the reliability of process-based stock assessment models (Rincón et al., 2016).

Field work has also contributed fundamental knowledge on the reproduction and feeding of SPF. For example, to apply the Egg Production Method, new knowledge was generated on sardine egg mortality (Bernal et al., 2012), spawning seasonality and energy allocation (Nunes et al., 2011), and fine-scale spawning and larval distribution (Zwolinski et al., 2006). Field studies exploring the trophic ecology revealed the high efficiency of retention of microplankton prey by sardines (Garrido et al., 2007b) allowing adults of this species to consume phytoplankton, particularly during periods of low zooplankton abundance (Garrido et al., 2008a). Adult sardines were also shown to have high fish egg consumption (mainly from sardines and anchovies), similarly to Atlantic chub mackerel, which has high diet overlap with sardines (Garrido et al., 2015).

Laboratory experiments conducted on sardine larvae focused on the influence of temperature and prey quantity on larval feeding (Caldeira et al., 2014), growth and survival (Garrido et al., 2016), and swimming capacity (Silva et al., 2014). The strong influence of temperature on the vital rates of sardine larvae observed in the laboratory agree well with results of field studies (Coombs et al., 2006; Stratoudakis et al., 2007). Field studies have also described larval diel vertical migration (Santos et al., 2006; Zwolinski et al., 2007). These laboratory and field results have generated hypotheses on the bottom-up mechanisms controlling sardine recruitment strength (e.g., Garrido, 2017).

In the Canary and African sub-regions, more than 70% of research studies were field studies with half of those performed on early life stages (eggs and larvae) of European sardine and anchovy (e.g., Ettahiri et al., 2003; Bécognée et al., 2006; Moyano et al., 2014; Abdelouahab et al., 2016). In the most recent period, hydrodynamic modelling examined the transport dynamics of early life stages (Brochier et al., 2011). Twice as many research articles were published on SPF in the Mauritanian-Senegalese region in the most recent period (see Fig. 5) including attempts to compile unpublished, archived datasets (e.g.,

logbooks) on catches and field ecology of *Sardinella* spp (Braham et al., 2014; Ba et al., 2016). The increase in scientific contributions from this sub-region is expected to continue as the results of large international projects continue to be released (see Ba et al., 2017; Tiedemann et al., 2017; Balde et al., 2019). The number of relatively large-scale studies investigating stock structure or spawning dynamics of sardine or anchovy also doubled in the 2011–2016 time period (from 2 to 5 studies), especially those using genetic tools (e.g., Baibai et al., 2012; Silva et al., 2014).

3.3. The Benguela Current System

Studies on SPF in the Benguela Current System (BCS) represented about 6% of the total number of papers included in this review with about 70% of the studies published in the first (2001–2006) period (Fig. 5). The BCS off southwestern Africa is bounded by the warm Angola Current in the north and the warm Agulhas Current in the south, and is divided into northern (NB) and southern (SB) sub-systems by the Lüderitz upwelling cell in Namibia (ca. 27°S; Hutchings et al., 2009; Kirkman et al., 2016). The NB and the coast of South Africa west of 20°E are wind-driven, coastal upwelling systems whereas the south coast of South Africa, also considered part of the SB, shows characteristics of both an upwelling and a temperate, shallow shelf system with seasonal coastal, shelf-edge and dynamic upwelling. Upwelling is perennial and strongest in the NB, seasonal and moderate off the South African west coast, and seasonal and weakest off the south coast (Lamont et al., 2018). Due to these differences in upwelling intensity, productivity is highest in the NB and lowest off the South African south coast.

Economically and ecologically important SPF found in the BCS include European (Cape) anchovy, west coast (redeye) round herring (*Etrumeus whiteheadi*), Pacific sardine and the sardinellas *Sardinella aurita* and *S. maderensis*, all of which are primarily caught using purse-seines. Small catches of sardinellas are only taken in the NB and small catches of west coast round herring are only taken in the SB, and these species are not considered further here. The Lüderitz upwelling cell limits the exchange of epipelagic ichthyoplankton between the NB and SB due to the combination of a surface hydrodynamic and a subsurface thermal barrier (Lett et al., 2007), hence anchovy and sardine are considered to comprise separate sub-populations in the two sub-systems. Sardine was the initial target of purse-seiners in both sub-systems, and annual catches peaked during the 1960s before declining rapidly (van der Lingen et al., 2006c). Whilst sardine catches in the NB have not recovered to historical levels, those in the SB peaked again in the early 2000s but have again declined (de Moor et al., 2017). Anchovy were targeted in both sub-systems following the 1960s decline in sardine, but initial moderate catches in the NB declined to insignificant levels and there is almost no anchovy currently caught off Namibia (Roux et al., 2013). In contrast, anchovy (primarily juveniles) sustained the South African small pelagic fishery in years of low sardine catches and remains an important target species in the SB. Whereas both the NB and the SB were historically characterized by large populations and high catches of SPF, these species have virtually been removed from the NB, primarily by overexploitation (Boyer et al., 2001; Roux et al., 2013) but likely also by adverse environmental conditions during the mid-1990s (Jarre et al., 2015). Their removal, particularly of sardine, has had substantial and possibly irreversible impacts on the structure and functioning of the NB, and appears to have promoted the proliferation of jellyfish there (Roux et al., 2013).

Several studies exploring environmental links to recruitment and abundance of anchovy and sardine in both the NB and the SB were published during 2001–2006. In the NB, studies on sardine included a synopsis of population fluctuations and possible environmental causes during the 1990s (Boyer et al., 2001), and relating recruitment to SST in the tropical Atlantic and coastal wind stress (Daskalov et al., 2003) and to sea surface height (Hardman-Mountford et al., 2003). Studies in the SB focused on anchovy recruitment, considered at the turn of this

century to be negatively correlated with southeasterly wind anomalies during the October-March spawning period because of advective loss of early life history stages (van der Lingen and Huggett, 2003). Those studies included an assessment of how within-season variation in wind-driven upwelling impacted anchovy recruitment strength (Roy et al., 2001), attempts to predict anchovy recruitment using a deterministic expert system using classification trees (Miller and Field, 2002), and how anchovy recruitment was related to SST patterns (Richardson et al., 2003; Wilhelm et al., 2005). No such studies were published in the second 6-yr period reviewed here.

Because the spawning and nursery areas of anchovy (and to a lesser extent sardine) in the SB are spatially separated, with most spawning occurring on the western Agulhas Bank and south coast and the major nursery ground located on the west coast, substantial research effort focused on the transport of eggs and early larvae from spawning to nursery grounds, and several biophysical IBMs were developed during the first review period. These were principally for Cape (European) anchovy in the SB (Mullon et al., 2002; Huggett et al., 2003; Mullon et al., 2003; Parada et al., 2003; Skogen et al., 2003) (see Fig. 8), but also for sardine (Miller et al., 2006) in the SB and the NB (Stenevik et al., 2003). The IBMs developed for anchovy suggested a low probability of successful transport to the west coast nursery ground for eggs spawned east of Cape Agulhas, and that transport success of eggs spawned to the west of this cape was markedly seasonal and increased with increasing spawning depth. The latter is counter-intuitive given that most anchovy eggs occur in the upper 20 m (Dopolo et al., 2005). The IBM developed for SB sardine suggested the same results and identified Cape Agulhas as a break point between transport-based (west coast) and a retention-based (south coast) recruitment systems. Lett et al. (2006) reinforced these differences using a Lagrangian approach to simulate enrichment and retention, two processes fundamental to SPF recruitment (Bakun, 1996). Similar to anchovy, the successful recruitment of sardine to nursery areas increased in both the SB and NB with increasing depth of spawning which, again, was inconsistent with observations of near-surface sardine egg vertical distributions in both sub-systems (Stenevik et al., 2001; Dopolo et al., 2005). Only one biophysical IBM (Kone et al., 2013) and a review of previous IBMs (Lett et al., 2015) were published from the Benguela during the second 6-year period reviewed here. The decrease is attributed to a decrease in international (particularly French) collaborative programs (CvdL personal communication).
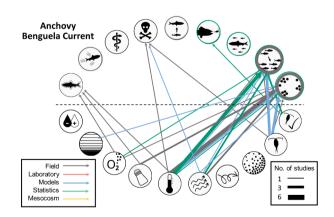

Fig. 8. Research emphasis in papers published during two time periods (2001–2006, and 2011–2016) on anchovy in the Benguela System. The species was reported as either European or Cape anchovy. In total, 10 categories of bottom-up drivers (below dotted line) were included: from left, 5 abiotic factors, 3 physical / mixing processes, and 2 aspects of prey. Responses (above dotted line) were separated into 9 categories including 7 at the individual level (from left, 3 energetic costs or losses and 4 vital rates) and 2 at the population-level (see Fig. 4 for legend). The thickness of lines represents the number of studies. The color represents the type of study (not all types may be present). The number and type of studies considering only responses are also shown (color and thickness of circles).

Anchovy and sardine in the SB have both shown recent, eastward expansions of their distributions (van der Lingen et al., 2011) that appear to be linked to a cooling of inshore waters along the South African southwest and south coasts since the 1980s (Blamey et al., 2015) and may be a result of climate change. Similarly, sardine in the NB has shifted its preferred spawning location southwards which has been attributed to a general warming of that system (Kreiner et al., 2011), also possibly driven by climate change. Another bottom-up impact, possibly arising from climate change, is the deleterious effect on SB sardine of spatially and temporally extensive harmful algal blooms (HABs) that have occurred off the South African south coast in recent years. van der Lingen et al. (2016) reported that sardine in HAB areas had particularly low condition factors compared to conspecifics outside of bloom areas, and that low condition was attributed to a cessation of feeding likely due to chemical irritation by the small (50 μm) dinoflagellates being entrapped on the sardine's gill rakers. Because of their coarser branchial baskets, neither anchovy nor round herring are able to entrap these small particles and hence were unaffected.

Important publications examining bottom-up controls on SPF in the SB have been published outside of the two periods reviewed here. Roy et al. (2007) investigated potential environmental drivers of the abrupt change during the mid-1990s in the relative (i.e., proportion of total) distribution of European (Cape) anchovy spawners from being predominately located off the South African west coast to being predominantly located off the south coast. Those authors reported a significant positive correlation between the cross-shelf SST gradient on the south coast and the proportion of the anchovy spawner biomass there for the period 1984–2005, and suggested that coastal cooling in that region resulting from increased wind-induced upwelling off the south coast may have enhanced anchovy feeding conditions relative to those on the west coast. Subsequent inclusion of data up to 2011 corroborated this positive relationship and supported the hypothesis that the distribution change was environmentally mediated (Augustyn et al., 2018). Recent results from simulations using a regional oceanographic model of the south coast (Agulhas Bank) run with long-term (1948–2008) environmental forcing corroborated the mid-1990s shift from warmer to colder temperatures and suggested that this was caused by a north–south migration in the large-scale wind belts rather than by changes in the Agulhas Current itself (Malan et al., 2019). van der Sleen et al. (2018) investigated the relationship between Cape anchovy recruitment and upwelling over the period 1985–2014 and found that recruitment was significantly and positively correlated with cumulative December-March (austral summer) upwelling. Those authors also reported that the slope of that positive, linear relationship increased when anchovy spawner biomass off the west coast in November/December of the preceding year was above a threshold of 0.74 MMT. By combining the two regressions for spawner biomass levels above and below that threshold, van der Sleen et al. (2018) accounted for 82% of the observed variability in anchovy recruitment. Sakamoto et al. (2020) examined otolith oxygen isotope ratios and microstructure of sardine from the SB and showed that nursery temperature affected early growth rates, with fish from cooler (by around 3 °C) waters in the west reaching 37–46 mm FL at 60 dph compared to those in warmer waters to the east that reached 43–52 mm. Those studies have provided strong evidence that bottom-up processes can have marked impacts on the distribution, abundance and vital rates of SPF in the SB.

3.4. The California Current System

The California Current System (CalCS) was among the regions with the most studies published on SPF in the two periods reviewed here (Fig. 5). The CaICS is broadly defined as the eastern limb of the North Pacific subtropical gyre and includes an equatorward flowing core that is generally offshore of the shelf break and more coastal, poleward flowing currents with seasonal variability in their depths and intensities. The CalCS extends from the eastern edge of the North Pacific Current

near Vancouver Island, Canada at about 50°N to Baja California Sur, Mexico near 25°N where the surface flow turns westward to eventually merge with the North Equatorial Current. Wind-driven upwelling (both coastal upwelling and positive wind-stress curl) is a crucial element of the physical climate processes influencing biological productivity in the CalCS. Similar to other wind-driven EBUS, biological productivity in the CalCS is rich, but temporally variable across multiple time scales.

A number of noteworthy review articles describe the physical oceanography of the CalCS. Perhaps the most recent of these reviews includes description of the current understanding of the biological responses to physical variability (Checkley and Barth, 2009). The body of literature on processes in the CalCS describes relationships between physical processes and fisheries in the region, but also recognizes that these descriptions remain incomplete; observational and modelling constraints often limit understanding of processes that occur at the mesoscale and submesoscale, while the durations of observational time series limit abilities to describe processes occurring at multidecadal time scales. The seasonal cycles of upwelling favourable winds and biological productivity vary along a meridional gradient in the CalCS. Upwelling favourable winds are relatively weak but persistent year-round in the southern portion (south of Pt. Conception near 35°N) of the system. The meridional direction and intensity of the winds exhibit increasing seasonality from Pt. Conception northward, typically with intense winds from the north (upwelling favourable) in summer and winds from the south (downwelling favourable) in winter. Variability in ecosystem conditions has been attributed to changes in the intensity, persistence, spatial pattern, and seasonal timing of these upwelling winds (Barth et al., 2007; Bograd et al., 2009; Rykaczewski and Checkley, 2008). Additional sources of ecosystem variability stem from regional scale changes in characteristics of the subtropical gyre circulation and coastally trapped Kelvin waves (stimulated by El Niño events in the tropics) that can modulate the depth of the nutricline (Jacox et al., 2018). Low-frequency variability (e.g., at decadal and multidecadal time scales) in the climate conditions in the region have been associated with changes in fish and invertebrate assemblages with implications for commercial fisheries (Chelton et al., 1982).

Historically, commercial fisheries focused on massive populations of northern anchovy (*Engraulis mordax*) and Pacific sardine which made significant contributions to the regional economies in California and Baja California. The fishery for Pacific sardine grew to be the largest fishery in North America in the 1930s and 1940s and inspired pioneering research on SPF dynamics and the sustainability of their fisheries (Sette, 1943). The alarming collapse of the sardine population in the mid-1940s, however, had severe consequences for communities of central California (John Steinbeck: *Cannery Row*). Observation of this astonishing rearrangement of pelagic species in the mid-20th century was the initial motivation for 1949 commencement of the California Cooperative Oceanic Fisheries Investigations (CalCOFI), an oceanographic survey program with a mission of understanding the human impacts and the influence of climate variability and climate change on living marine resources in the CalCS (McClatchie, 2013). Despite substantial investment in the collection of physical, chemical and biological data associated with the initial decades of the CalCOFI program, debate concerning the relative influence of commercial fishing and natural climate and population variability persisted (Clarke and Marr, 1955) and inspired alternative approaches to explore SPF variability. Investigation of ocean sediments provided a perspective on population variability that precedes records of commercial landings (Soutar, 1967). This paleoceanographic approach stimulated a new field of SPF research and has been repeated in other ecosystems around the globe.

Although the magnitudes of the commercial SPF catches have declined substantially since the mid-20th century, the research methodology developed in the region formed the foundation for many modern SPF surveys (e.g., the examination of batch fecundity by Hunter and Leong (1981) and the development of DEPM by Lasker (1985)). The CalCOFI Program has now continued for more than 70 years and

expanded its focus beyond its original goal of investigating reasons for variability in the sardine population to include sampling that is relevant to ocean responses to climate variability and change. The observations off California are now complimented by the Investigaciones Mexicanas de la Corriente de California (IMECOCAL) Program off Baja California which was initiated in 1997.

Recent research on SPF in the CalCS has been shaped by a long history of studies in the region that began in the first two decades of the 20th century with the rapidly expanding industrial fishery. The species of focus for these research efforts has varied through time as the populations of commercial interest have alternated; northern anchovy became the focus of most research in the 1960s, 1970s, and 1980s during periods of anomalously low biomass of Pacific sardine. Research originating from the region has contributed to about 10% of the total work assessed during the two periods considered in this manuscript (2001–2006 and 2011–2016) with a consistent number of studies published during the two periods (n = 52 and 51, respectively). Roughly 75% of the publications during these periods focused on Pacific sardine, though several studies also considered species interactions. As noted above, much of the fundamental physiological and life-history work on SPF in the CalCS was conducted in the 20th century. Work published in recent decades has emphasized the consequences of changes in ocean conditions (e.g., physical conditions and planktonic prey fields) on the distribution and population productivity of SPF (Fig. 9).

In the first period considered here (2001–2006), a notable amount of research was dedicated to investigating some of the physical processes that influence the distribution, composition, and survival of larval SPF and other members of the ichthyoplankton. These works were facilitated by the 5 decades of ichthyoplankton data collected by CalCOFI (e.g., Logerwell et al., 2001; Smith et al., 2001; Smith and Moser, 2003; Lynn, 2003). Additionally, changes in distribution associated with the 1997–1998 El Niño event and the initiation of the IMECOCAL Program inspired investigation of the stock structure and distribution that spanned political boundaries (e.g., Funes-Rodríguez et al., 2001; Nevárez-Martínez et al., 2001; Morales- Bojórquez et al., 2003; Avendano-Ibarra et al., 2004; Felix-Uraga et al., 2004; Sánchez-Velasco et al., 2004; Morales-Bojórquez and Nevárez-Martínez, 2005).

Research during the second period (2011–2016) also included significant contributions from scientists at Mexican institutions aimed at resolving patterns of ichthyoplankton distribution and the sensitivity of
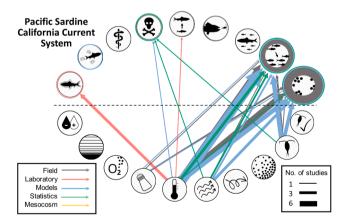

Fig. 9. Research emphasis in papers published during two time periods (2001–2006, and 2011–2016) on Pacific sardine in the California Current System. In total, 10 categories of bottom-up drivers (below dotted line) were used including 5 abiotic factors, 3 physical / mixing processes, and 2 aspects of prey. Responses (above dotted line) were separated into 9 categories including 7 at the individual level (from left, 3 energetic costs or losses and 4 vital rates) and 2 at the population-level (see Fig. 4 for legend). The thickness of lines represents the number of studies. The color represents the type of study (not all types may be present). The number and type of studies considering only responses are also shown (color and thickness of circles).

those patterns to climate conditions in the IMECOCAL region and the Gulf of California (e.g., Funes-Rodríguez et al., 2012; Vergara-Solana et al., 2013; Valencia-Gasti et al., 2015). Contributions that were focused on the Pacific sardine stock found along the US west coast included several efforts aimed at exploring the implications of climate variability for resource management, including end-to-end models (Fiechter et al., 2015; Rose et al., 2015) and stock forecasts (Kaplan et al., 2016); population dynamics (Lindegren et al., 2013; Asch et al., 2013; Song et al., 2012; Weber et al., 2015); and migration patterns (Demer et al., 2012; McDaniel et al., 2016; Zwolinski et al., 2011). During both time periods, this region produced a large amount of papers reporting the results of modelling studies exploring changes in the productivity and distribution (exampled for Pacific sardine shown in Fig. 9). A resurgence in investigation of vital rates was also evident during this more recent period (e.g., Zwolinski and Demer, 2013, 2014), perhaps motivated by early evidence that the northern stock of Pacific sardine was exhibiting successive recruitment failures. Although the population of northern anchovy was studied during both periods, a greater amount of anchovy-specific research was evident in the latter period (e.g., Takahashi et al., 2012; Fissel et al., 2011). Additionally, the decades of regular observations to quantify physical and biological conditions in the CalCS has facilitated one of the more unique aspects of research the region: application of theoretical numerical approaches to explore causal relationships in long time series of observational data (Sugihara et al., 2012; Deyle et al., 2013) (green arrows, Fig. 9). As data continue to accumulate over time, the value of oceanographic and fisheries observations to exploratory numerical analyses is certain to increase.

3.5. The northwest Pacific

The oceanographic setting of the Northwest Pacific (NW Pacific) is characterized by dynamic fronts, meanders, and eddies formed during the interaction between cold- and warm-water currents (Nakata et al., 2000; Yasuda, 2003). The western boundary current system in the North Pacific is formed from the interaction between the warm Kuroshio and cold Oyashio Currents which converge off the coast of Japan and flow eastward forming the Kuroshio Extension and Kuroshio-Oyashio transition regions. In shelf areas to the north and east of the Kuroshio, a number of smaller currents interact in the vicinity of the Korean Peninsula including the warm Tsushima and East Korean Water Currents which intersect the cold Liman Current in the Sea of Japan. The dynamic mixing of these relatively nutrient-poor warm-water currents and nutrient-rich cold currents creates a highly productive environment supporting a variety of SPF such as Japanese sardine (*Sardinops melanostictus*), Japanese anchovy (*Engraulis japonicus*), round herring (*Etrumeus teres*), and Pacific herring. Studies published during the two time periods on these 3 species were the second most numerous of any region reviewed here (Fig. 5).

The SPF in the NW Pacific utilize water current systems for passive drift and as migration pathways to create spatially complex life cycle strategies. For example, Japanese sardine and anchovy utilize coastal spawning grounds in the Pacific and a major portion of their eggs and larvae are transported offshore by the Kuroshio Current. Juveniles migrate north in the Kuroshio Extension to nursery and feeding grounds in the Kuroshio–Oyashio transition region. As these fish grow and recruit to adult stocks, they return inshore and move south for spawning. The distribution and spawning areas of sardine and anchovy contract coastward or expand offshore during period of low and high SSB, respectively (Watanabe et al., 1996; Takasuka et al., 2008a). In contrast, round herring is a subtropical species mainly distributed and spawning in coastal waters whereas Pacific herring is a sub-Arctic species mainly distributed and spawning in the cold waters of the Oyashio and Liman Currents (Watanabe, 2007). The spawning patterns of SPF have been well documented from monthly ichthyoplankton and zooplankton surveys conducted off the Pacific coast of Japan since 1978 (Oozeki, 2018)

along with fishery-dependent stock surveys (Ichinokawa et al., 2017) and complimentary acoustic surveys (Miyashita, 2018). In waters off South Korea, the distribution and abundance of SPF has been examined using trawls along with some acoustic data (Park et al., 2016).

The population dynamics of SPF in the Kuroshio Current system are characterized by alternating cycles of abundance linked to basin- and multidecadal-scale climate variability. A prominent example is the shifts in dominance between anchovy and sardine which coincides with different phases of the Pacific Decadal Oscillation (PDO) index (Mantua and Hare 2002). When the PDO index was positive(negative), SST was lower(higher) in the NW Pacific and sardine(anchovy) was relatively abundant (Takasuka et al., 2007). In the early 1980 s, sardine was abundant while anchovy was relatively scarce and, by the end of that decade, the situation was reversed. Since 2010, sardine has started to increase in abundance while the SSB of anchovy has declined. This type of cycle has occurred twice during the last 100 years. The pattern of the species alternation in the NW Pacific was synchronous with that observed in eastern regions of the Pacific (California and Humboldt Current systems) despite the reversed temperature regimes between the opposite sides of the Pacific in the past, although the pattern observed in the California Current system has already been out of synchrony (Kawasaki, 1983; Chavez et al., 2003; Takasuka et al., 2008b).

Although "regimes" in productivity and abundance of different SPF have been recognized since Kawasaki (1983) compared sardine among various current systems, the physical-biological mechanisms linking climate variability to the population dynamics of SPF are still debated. Some hypotheses are based on changes in the winter mixed layer depth and spring phytoplankton bloom in the nursery grounds of sardine (Noto and Yasuda, 1999; Nishikawa and Yasuda, 2008; Nishikawa et al., 2011, 2013). For example, Noto and Yasuda (1999) found a close relationship between the mortality during the early life stages and winter SST in the nursery ground of sardine. Other hypotheses are based on changes in water temperature and species-specific differences in the optimal thermal regimes for the early growth and spawning (Takasuka et al., 2007, 2008b). It is likely that an amalgam of factors are responsible for fluctuations in the productivity of different SPF such as the interaction between temperature and food availability reported to control the growth rate of larval anchovy (Takahashi and Watanabe, 2005) or prey availability, temperature and intra-guild competition (Kawasaki and Omori, 1995; Kim et al., 2006) and/or fishing pressure (Suda et al., 2005; Katsukawa, 2007; Wan and Bian, 2012).

Research effort (in terms of the number of publications) was similar in the earlier (n = 60) and later (n = 53) periods reviewed here with most of the studies being field research. Unlike EBUS such as the HCS where anchovy often obtains the highest SSB, sardine obtained the highest biomass within the Kuroshio western boundary current system. Such a difference seems to be reflected in the study effort during the 1980s and 90s when most studies were focused on Japanese sardine. In the two more recent periods reviewed here, however, the majority of studies focused on anchovy (~70%) with fewer on sardine (~30%). Also, the number of studies examining both species has increased in the most recent period. Since the late 2000s, studies have attempted to advance a mechanistic understanding of the differences between Japanese sardine and Japanese anchovy. These include inter-specific comparisons of the response of growth (Takasuka et al., 2007, 2009; Itoh et al., 2011), spawning (Oozeki et al., 2007; Takasuka et al., 2008a, 2008b), and transport (Itoh et al., 2009, 2011) to environmental factors. Laboratory studies have also examined energy allocation strategies for reproduction (Yoneda et al., 2014; Tanaka et al., 2016). The biological parameters obtained through those field and laboratory studies have been incorporated into bioenergetics sub-routines for Japanese sardine and saury (*Cololabis saira*) within end-to-end ecosystem models designed to test different hypotheses of biological mechanisms and to make projections of future population dynamics of these species (Ito et al., 2004; Kishi et al., 2007; Ito et al., 2010; Okunishi et al., 2012a, b). The number of modelling studies and review articles were higher in the more recent

period (2011–2016). The research map for Japanese anchovy in the NW Pacific (Fig. 10) highlights the emphasis placed on field work exploring aspects of the vital rates at the individual level (growth, feeding, reproduction and survival) and the spatial distribution and productivity of the population.

3.6. The Baltic Sea

The Baltic Sea is the largest semi-enclosed, brackish water area in the world with an opening in its southwest corner through the straights of Denmark to the North Sea. The Baltic has a large catchment area and river runoff creates a permanent halocline between surface waters with low salinity and deeper, more saline waters (Fonselius, 1970). The Baltic Sea has a series of submarine sills and deep basins whose deep waters are hypoxic or anoxic (Fonselius, 1970). Atmospheric conditions cause episodic inflow events of dense marine water from the North Sea which renew and ventilate deep waters. In the most recent decades, these inflow events are often followed by long stagnation periods (Lehmann et al., 2002) and a decrease in the frequency of inflow events since the 1990s has been correlated to changes in zooplankton and fish populations within deep basins including the two main SPF, European sprat and Atlantic herring (Alheit et al., 2005). Studies on SPF in the Baltic Sea formed a relatively high proportion of those reviewed here (within the top 4 of the 17 regions) (Fig. 5).

During the two periods reviewed here, a considerable amount of research was conducted on various life stages of both Atlantic herring and sprat including reviews of how bottom-up processes may impact on the recruitment dynamics of sprat (Köster et al., 2003; Voss et al., 2012), herring (von Dorrien et al., 2013) or both species (Möllmann et al., 2005; Casini et al., 2006). These and other studies have exploited rich (long-term, often spatially-explicit) historical field data on the dominant zooplankton and fish species (e.g., Casini et al., 2014), such as reconstructions of sprat spawning stock biomass back to the early 1930s (e.g., Eero, 2012). These time series continue to grow in length and be exploited to understand environmental drivers of recruitment success of SPF. An example is examining seasonal / thermal windows of larval survival using the Rügen Herring Larvae Survey, a survey started in the mid-1970s and continued consistently since the mid 1990s, which includes weekly monitoring of larvae at one of the most important,
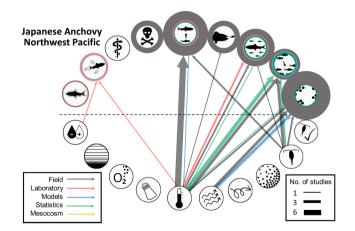
nearshore spawning grounds for herring in the SW Baltic (e.g., Dodson et al., 2019).

Reviewing the research conducted on sprat in the SW Baltic Sea, Voss et al. (2012) indicated that bottom-up processes (temperature, transport, prey abundance) had a greater influence on year-class survival compared to top-down processes (predation mortality). For example, at high spawning stock biomass, warm water temperatures and wind-driven transport of sprat larvae from offshore spawning grounds to coastal areas was correlated with poor year-class success (Baumann et al., 2006). This was postulated to be due to density-dependent, top-down control of zooplankton resources in coastal areas leading to poor condition and starvation (Baumann et al., 2005). Post-larval sprat have high rates of growth and feeding and considerable laboratory work has been conducted to calibrate in situ proxies for these rates (Peck et al., 2012a, 2015; Günther et al., 2015). A second, critical period was considered to be the long over-winter period when relatively small, young-of-the-year (age-0 juvenile) sprat may not survive (Peck et al., 2012a; Voss et al., 2012). The work on Baltic sprat demonstrates how environmental controls (such as temperature thresholds) can affect various life stages to affect life cycle closure and population dynamics (Haslob et al., 2012b). Research in the Baltic Sea has also revealed how changes in the abundance of SPF can lead to density-dependent impacts on their growth and/or condition (Casini et al., 2006) highlighting how population dynamics of SPF are tightly coupled to the interaction between extrinsic (environmental) drivers and intrinsic factors.

There are a number of unique features of the Baltic Sea (from its topography and hydrography to its populations of SPF) driving specific research efforts. First, the Baltic Sea contains different sub-populations and genetically distinct populations of Atlantic herring which display different migration patterns and spawning seasons and locations. Considerable work was conducted in the time periods reviewed here to resolve the spatial stock dynamics across the N. Atlantic basin (McPherson et al., 2004) and among co-existing herring stocks in the Baltic Sea (e.g., Jorgensen et al., 2005; Gröhsler et al., 2013; Teacher et al., 2013). A second feature is the strong vertical and depth gradients in temperature, salinity and oxygen (water mass characteristics) structuring and controlling the survival and development (Peck et al., 2012b, Moyano et al., 2016), feeding dynamics (Rajasilta et al., 2014), growth (Baumann et al., 2006), spatial distribution (Nielsen et al., 2001; Nissling et al., 2003), and recruitment dynamics (Arula et al., 2016) of herring and sprat. Finally, given potential changes in prey availability and type driven by abiotic forcing, both laboratory and field studies have examined how changes in the quantity and quality (such as the contents of lipid including fatty acids or trophic upgrading) of zooplankton can influence larval survival and somatic growth of Atlantic herring (Illing et al., 2015; Paulsen et al., 2014, 2016) and sprat (Peck et al., 2015; Peters et al., 2015) (see Fig. 11).

3.7. The Mediterranean Sea

The semi-enclosed, temperate Mediterranean Sea is rich in mesoscale activity resulting from its complex topography and strong and varied local winds (reviewed in Millot and Taupier-Letage, 2005). There are several unique features of the Mediterranean Sea which offer opportunities to advance our understanding of bottom-up controls of SPF. First, both temperate and tropical (e.g., round sardinella) SPF co-occur in the region which offers a good test bed to examine historical (and projected) changes in climate will impact SPF (e.g., Sabatés et al., 2006; Maynou et al., 2014, 2020; Stergiou et al., 2016). Second, although the whole region is classified as a Large Marine Ecosystem (McLeod et al., 2005), considerable east-to-west and north-to-south gradients exist in abiotic factors, biological productivity and patterns of biodiversity. The mean annual temperature and salinity, degree of oligotrophy and number of introduced invasive species all increase from the NW to the SE (Coll et al., 2010). Third, differences in topography, river discharge and amounts of upwelling and mesoscale activity have created several

Fig. 10. Research emphasis in papers published during two time periods (2001–2006, and 2011–2016) on Pacific sardine in the California Current System. In total, 10 categories of bottom-up drivers (below dotted line) were used including 5 abiotic factors, 3 physical / mixing processes, and 2 aspects of prey. Responses (above dotted line) were separated into 9 categories including 7 at the individual level (from left, 3 energetic costs or losses and 4 vital rates) and 2 at the population-level (see Fig. 4 for legend). The thickness of lines represents the number of studies. The color represents the type of study (not all types may be present). The number and type of studies considering only responses are also shown (color and thickness of circles).
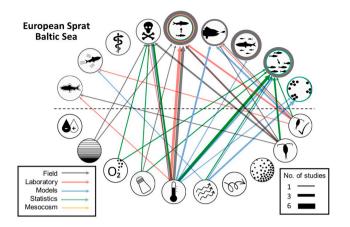
Fig. 11. Research emphasis in papers published during two time periods (2001–2006, and 2011–2016) on European sprat in the Baltic Sea. In total, 10 categories of bottom-up drivers (below dotted line) were used including 5 abiotic factors, 3 physical / mixing processes, and 2 aspects of prey. Responses (above dotted line) were separated into 9 categories including 7 at the individual level (from left, 3 energetic costs or losses and 4 vital rates) and 2 at the population-level (see Fig. 4 for legend). The thickness of lines represents the number of studies. The color represents the type of study (not all types may be present). The number and type of studies considering only responses are also shown (color and thickness of circles).

important, sub-regions supporting productive SPF populations (e.g., the Aegean Sea, the Gulf of Lions and nearby Catalan Coast, the Alboran Sea, the Straits of Sicily/Tunisian Coast, and the Adriatic Sea: Agostini and Bakun, 2002; Basilone et al., 2006; Zarrad and Missaoui, 2006; Tugores et al., 2011; Giannoulaki et al., 2013; Bonanno et al., 2014). From 2000 to 2013, four species contributed roughly 50% of the SPF landings including, in order of economic value, European anchovy, European sardine, round sardinella and European sprat (FAO, 2018b). The large economic and cultural importance of European anchovy (see Fig. 12 for research conducted on this species) and other SPF in Mediterranean countries has generated a wealth of research on bottom-up controls and this is reflected by this region having the most published research on SPF during the two time periods reviewed here (Fig. 5).
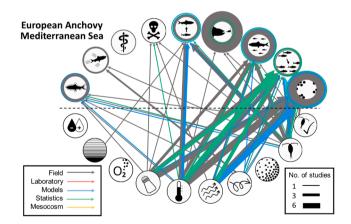

Fig. 12. Research emphasis in papers published during two time periods (2001–2006, and 2011–2016) on European anchovy in the Mediterranean Sea. In total, 10 categories of bottom-up drivers (below dotted line) were used including 5 abiotic factors, 3 physical / mixing processes, and 2 aspects of prey. Responses (above dotted line) were separated into 9 categories including 7 at the individual level (from left, 3 energetic costs or losses and 4 vital rates) and 2 at the population-level (see Fig. 4 for legend). The thickness of lines represents the number of studies. The color represents the type of study (not all types may be present). The number and type of studies considering only responses are also shown (color and thickness of circles).

Short-term, bottom-up processes impacting the dynamics of SPF populations in the Mediterranean Sea include changes in riverine inputs (Lloret et al., 2004; Santojanni et al., 2006; Macías et al., 2014), advection and eddies (Sabatés et al., 2007a, Catalán et al., 2013; Ruiz et al., 2013, Álvarez et al., 2015; Ospina-Alvarez et al., 2015) and temperature (Maynou et al., 2014). Changes in the strength of bottom-up control are clearly associated with climate variability and climate change (e.g., Martín et al., 2011). For example, the mean temperature-at-catch has steadily increased during the last two decades (Tsikliras and Stergiou, 2014; Tzanatos et al., 2014) and Stergiou et al. (2016) reported strong relationships between warming and shifts in abundance of SPF, particularly after the 1990s. A northward expansion of round sardinella in the Mediterranean Sea tracks warming in the northern (Sabatés et al., 2006; Maynou et al., 2014), central (Sinovcic et al., 2004) and eastern regions (Tsikliras, 2008) and has been linked to a marked decline in the abundance of European sardine. In the Gulf of Lions, decreases in somatic growth rate, size-at-age and somatic condition, and an increased age truncation of European anchovy and sardine have co-occurred with an order of magnitude increase in the abundance of European sprat (Van Beveren et al., 2014; Brosset et al., 2016). Bottom-up processes impacting the community composition of zooplankton, together with reduced trophic niche partitioning are thought to be the drivers of these intra-guild changes (Van Beveren et al., 2014; Brosset et al., 2016). Shifts in seasonal spawning triggers have also occurred (Tsikliras et al., 2010; Palomera et al., 2007). Similar to other regions, low frequency teleconnections and periodic oscillations in local climate conditions have been linked to fluctuations in SPF stocks (Grbec et al., 2002; Lloret, 2000; Martín et al., 2011; Katara et al., 2011).

This region had the highest number of publications in both of the two periods reviewed here including a considerable number of review articles. A thorough review of the research conducted on European anchovy across the Mediterranean was published in 1996 (Palomera and Rubíes, 1996) and the latest period has seen an upsurge in reviews that are both regional (Palomera et al., 2007; Sabatés et al., 2007b, Van Beveren et al., 2016) and thematic-oriented (Peck et al., 2013; Stergiou et al., 2016). Despite this wealth of research, it is challenging to disentangle the effect of bottom-up processes controlling SPF when stocks experience heavy fishing pressure and this is the case in the Mediterranean Sea. Efforts to curtail the over-exploitation of SPF in this region are challenged due to the plethora of countries, shared stocks, abundant shelters/ports and high number of small fishing boats (e.g., Tsikliras et al., 2015). Moreover, the region is experiencing rapid warming and accelerated species invasion (Libralato et al., 2015) disrupting the provision of natural ecosystem services such as healthy, historically dominant catches of SPF (Liquete et al., 2016; Stergiou et al., 2016). The intense exploitation and warming combined with accelerated ecosystem changes due to species invasions and other species changes (Stergiou et al., 2016; Brosset et al., 2016) offers many examples of potential situations that SPF may suffer elsewhere. Gaps exist, however, due to a scarcity of work employing laboratory experiments to study the ecophysiology of different life stages (reviewed in Peck et al., 2013). Also, similar to most systems, habitats and potential life-cycle bottlenecks related to the juvenile stage are poorly investigated. Increased research in southern Mediterranean areas fostered within programs of the United Nations Food and Agricultural Organization (FAO) may partly ameliorate this situation.

During the two periods reviewed here, research has been imbalanced with respect to species, stages, bottom-up drivers and geographic locations. For example, in both periods, ≥ 90% of the published studies stemmed from European as opposed to African countries. The majority of research has been conducted by Spain, Greece and Italy (on their local, SPF sub-components). There was, however, a five-fold increase in the number of studies published that stemmed from African countries (Algeria, Tunisia, Morocco) between 2001 and 06 and 2011–16. The increase in the number of publications in the second period was Mediterranean-wide with almost twice the number of papers published in the second compared to the first period. Most publications examined

European anchovy (58% and 73% in consecutive periods) followed by European sardine (33% and 21%) and Round sardinella (8% and 1%). A second notable trend is the increase in basin-wide research from the first to second periods on essential habitats of European sardine and anchovy, including juveniles (Tugores et al., 2011; Giannoulaki et al., 2013). A remarkable upsurge in the amount of research on sprat and round sardinella track the increase in abundance of these SPF species.

Similar to other areas, most of the research conducted in the Mediterranean Sea was field research (79% in 2001–2006 and 63% in 2011–2016). In both periods, field research focused on relationships between environmental variables and distribution/abundance/structure, followed by studies on maturation or spawning and somatic growth. Our review found no published studies employing laboratory studies (e.g., Fig. 12 for Europen anchovy). During the second period, there was a marked increase in the number of studies examining diets across life stages (e.g., Nikolioudakis et al., 2012; Costalago et al., 2012; Costalago and Palomera, 2014; Rumolo et al., 2016) and exploring SPF using physical-biogeochemcal models and Lagrangian, particle tracking simulations conducted on anchovy (Catalán et al., 2013; Ospina-Álvarez et al., 2013; Schismenou et al., 2013; Palatella et al., 2014) or end-to-end models (Politikos et al., 2014; Coll et al., 2016).

3.8. The northeast Atlantic

This region includes the European continental shelf area from the Bay of Biscay in the south, the North Sea and waters surrounding the British Isles, a spatial extent that includes a transition zone between warmer-water (anchovy, sardine) and colder-water (sprat, herring) SPF. The hydrography of these shelf systems is dynamic with an array of tidal-mixing, river plume and shelf break fronts fuelling an extremely productive and complex food web. That many of these mesoscale features are strongly influenced by changes in physical forcing and many SPF occur near their (high or low) latitudinal limit, are reasons why strong changes in the distribution and/or abundance of SPF populations have been correlated to climate variability in this region (Beare et al., 2004; Petitgas et al., 2012; Alheit et al., 2012).

A variety of field studies published during the second 6-year period (2011–2016) sought to understand habitat and resource partitioning by a "novel" co-occurrence of SPF in the southern North Sea (Raab et al., 2012; Bils et al., 2012). In, 2006, the productivity of a relict (coastal) population of European anchovy in the southern North Sea dramatically increased due to more favourable temperature and feeding conditions and adult anchovy started to be identified in offshore trawl surveys (Petitgas et al., 2012; Raab et al., 2013). During the same time period, ichthyoplankton surveys found mixtures of European sardine and sprat in the southern North Sea (Kanstinger et al., 2009). In late spring (May/June), early life stages of European sardine, sprat and anchovy in offshore frontal areas (Kanstinger et al., 2009) indicated the close proximity and timing of spawning by the three species although European anchovy were more abundant at shallower stations closer to the coast.

A number of research groups have consistently used laboratory studies to explore aspects of the ecophysiology of North Sea Atlantic herring such as how intrinsic and/or extrinsic factors influence fundamental aspects of growth physiology. Examples include parental effects on traits of early life stages (Bang et al., 2006) and how environmental factors affect otolith ring formation (Fox et al., 2003), embryonic growth (Geffen, 2002), muscle development (Temple et al., 2001; Temple et al., 2001) or schooling behaviour (Domenici et al., 2002). This laboratory work is complimented with large field datasets such as the dedicated autumn and winter surveys for herring larvae that have been conducted in the North and Irish Seas since 1959. Indices of abundance of larvae from different spawning sites are available since 1972. Exploration of these long-term survey data have helped researchers understand environmental drivers of recruitment such as winter water temperature and /or zooplankton (Payne et al., 2009; Lusseau et al., 2014; Alvarez-

Fernandez et al., 2015) and to thoroughly document long-term changes in the intensity of site-specific spawning (Harma et al., 2012) and productivity (Corten, 2013). A primary impetus for exploring these herring data was to understand the collapse (in the early 1970 s) and recovery (by the mid 1980 s) of the autumn-spawning North Sea herring stock.

In the Bay of Biscay, considerable research has been conducted on many life history facets of European anchovy, particularly because this stock collapsed and has now been rebuilt after a 5-yr closure of the fishery (2005 to 2010). The fishery closure provided opportunities to study natural mortality rates which appear very high for two-year olds, suggesting senescence is an important, intrinsic limitation impacting on population dynamics (Uriate et al., 2016). Retrospective analyses of the seasonal dynamics of growth and/or distribution (Ibaibarriaga et al., 2013; Petitgas et al., 2014; Boyra et al., 2016) have made use of annual, broad-scale surveys conducted since the early 1990s during the anchovy spawning season in spring. Separate in-shore and offshore spawning populations have been identified (Montes et al., 2016). The potential diet overlap between anchovy and sardine has also been extensively studied (e.g., Chouvelon et al., 2015).

In both the North Sea and Bay of Biscay, spatially-explicit models have been extensively employed to advance understanding of various aspects of the ecology of SPF (Fig. 13a,b). Some of the earliest biophysical models for fish early life stages were championed in the NE Atlantic such as the drift modelling of herring early life stages by Bartsch et al. (1989) in the North Sea. When IBMs started to be used more frequently to examine SPF in the early 2000 s, an important advance was coupling a Lagrangian tracking model to otolith-based back-calculated growth trajectories of anchovy in the Bay of Biscay (Allain et al., 2003). Daewel et al. (2011) illustrated how an IBM for European sprat could be linked to a lower trophic level model to explore both direct (temperature, water currents) and indirect (prey field) impacts of climate variability on potential survival to the end of the larval stage. The rich spatiotemporal data series and laboratory work on herring larvae in the North Sea were employed to create physiological-based (foraging and growth) biophysical model to formulate and/or test hypotheses on bottom-up drivers of recruitment (Hufnagl and Peck, 2011; Huebert and Peck, 2014; Hufnagl et al., 2015). In the Bay of Biscay, juvenile and adult life stages were included in spatially-explicit, bioenergetics models of growth and movement in anchovy (Politikos et al., 2015). This IBM approach was linked to a Dynamic Energy Budget (DEB) model including energy allocation rules (Gatti et al., 2013) giving rise to one of only a handful of end-to-end models linking physics, lower trophic levels (zooplankton), and life cycle ecophysiology of SPF.

3.9. The northwest Atlantic

The NW Atlantic includes regions supporting warmer and cooler water species of clupeoid fish such as bay anchovy (*Anchoa mitchilli*) in the Chesapeake Bay and other coastal areas at lower latitudes, Atlantic herring using spawning grounds on Georges Bank and in the Gulf of Maine., as well as Atlantic menhaden (*Brevoortia tyrannus*) overlapping in some habitats with both of the former species. Atlantic menhaden supports one of the oldest and largest fisheries (by volume) in the NW Atlantic (for fishing communities in Chesapeake Bay and other areas of the mid-Atlantic bight of the east coast of the United States). That stock declined dramatically in the 1990s and remained low for nearly a decade but has subsequently increased under lower levels of fishing pressure despite low recruitment indices.

In this region in the 1970s and 1980s, seminal laboratory studies were conducted on Atlantic menhaden that provided a rare, mechanistic understanding of the relationship between swimming, feeding (and diet) and somatic growth (e.g., Durbin and Durbin, 1975; Durbin et al., 1980). During the first of the two periods reviewed here, studies on menhaden utilized those ecophysiological results to create various types of growth models such as one providing 3-D estimates of the carrying capacity of
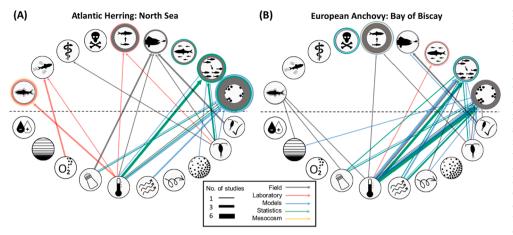
Fig. 13. Research emphasis in papers published during two time periods (2001–2006, and 2011–2016) in the northeast Atlantic including Atlantic herring in the North Sea (Panel A) and European anchovy in the Bay of Biscay (Panel B). In total, 10 categories of bottom-up drivers (below dotted line) were used including 5 abiotic factors, 3 physical / mixing processes, and 2 aspects of prey. Responses (above dotted line) were separated into 9 categories including 7 at the individual level (from left, 3 energetic costs or losses and 4 vital rates) and 2 at the population-level (see Fig. 4 for legend). The thickness of lines represents the number of studies. The color represents the type of study (not all types may be present). The number and type of studies considering only responses are also shown (color and thickness of circles).

Chesapeake Bay for menhaden populations (Luo et al., 2001) and another linking primary production to growth (Annis et al., 2011). A specific life history trait of menhaden includes offshore spawning with transport and ingress of larvae to coastal estuarine nursery areas and several studies examined the sources and characteristics of cohorts entering nursery grounds (Warlen et al., 2002; Light and Able, 2003; Lozano et al., 2012). Although fundamental studies on topics such as ontogenetic changes in diets (Friedland et al., 2006) continued in both periods, long-term data from menhaden sampling programs was mined in the second period to explore temperature-growth characteristics (Humphrey et al., 2014), mortality rates of larvae (Simpson et al., 2016) and links between recruitment climate indices such as the Atlantic Multi-decadal Oscillation (Buchheister et al., 2016). The impetus for most of these studies has been to understand the decreased recruitment strength of menhaden in this region since the 1990 s.

Bay anchovy represents another species that was studied intensively in the laboratory and mesocosms in the 1980s to gain fundamental data on bioenergetics rates leading to seminal modelling studies of its role (as predator and prey) within Chesapeake Bay (Lou and Brandt, 1993). Within both periods reviewed here, our search string found 11 papers that explored a variety of processes from larval transport (North and Houde, 2004), recruitment dynamics (Jung and Houde, 2004) and the growth dynamics of a population close to the high latitudinal limit of the species (Lapolla et al., 2001a,b). An emphasis of several of these studies was to test hypotheses by applying spatial or ecosystem (size-based) models to field data. This was continued in the only study published on Bay anchovy in the second period by Adamack et al. (2014) who explored how hypoxia (driven by scenarios of nutrient loading and rainfall) would impact on the mortality of larvae (see research map, Fig. 14). That work followed on from field measurements indicating that Bay anchovy recruitment was inversely related to dissolved oxygen concentrations in different regions of the estuary (Jung and Houde, 2004). The marked decline in studies published from the first to the second period suggests a waning interest in conducting studies on bottom-up processes and factors affecting Bay anchovy.

Long-term bottom trawl survey data allowed an exploration of how habitat occupancy contracted under stock collapse and expanded again after the recover of Atlantic herring across three key sub-regions of the NW Atlantic as well as within a specific sub-region (Overholtz, 2002; Overholtz and Friedland, 2002). Another study explored small-scale swimming movements of adult spawners using ultrasonic tags revealing, in some cases, selective tidal stream transport (Lacoste et al., 2001). Work on movement patterns of adult spawners was continued in earnest in the second period with studies using spatial and temporal data derived from hydroacoustic survey revealing seasonal movements including spawning aggregations (Jech and Stroman, 2012; Wurtzell et al., 2016). The locations of adult spawner aggregations and
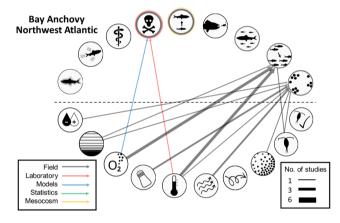

Fig. 14. Research emphasis in papers published during two time periods (2001–2006, and 2011–2016) in the northwest Atlantic on bay anchovy. In total, 10 categories of bottom-up drivers (below dotted line) were used including 5 abiotic factors, 3 physical / mixing processes, and 2 aspects of prey. Responses (above dotted line) were separated into 9 categories including 7 at the individual level (from left, 3 energetic costs or losses and 4 vital rates) and 2 at the population-level (see Fig. 4 for legend). The thickness of lines represents the number of studies. The color represents the type of study (not all types may be present). The number and type of studies considering only responses are also shown (color and thickness of circles).

subsequent larval rentential areas a few months were examined by Stephenson et al. (2015) showing the complex behavioural and bio-physical (advective) processes influencing the metapopulation structure of herring in the Bay of Fundy.

3.10. Sub-polar regions (Gulf of Alaska and Bering, Barents and Norwegian Seas)

Two sister species of herring dominate the SPF assemblage in sub-polar waters in the northern hemisphere (e.g., between 50 and 70°N). Atlantic herring dominates in the Nordic, and Irminger and Labrador Seas while Pacific herring dominates in the Gulf of Alaska and Berring Sea. Both Pacific and Atlantic herring are extremely valuable fisheries resources not only to commercial fisheries but also to indigenous peoples in sub-polar regions. Atlantic and Pacific herring are, arguably, among the most thoroughly studied fish species in the world for which seminal research has established fundamental paradigms of factors controlling fish productivity and year-class success (e.g., Hjört, 1914). This review, mostly focusing on a 12-year period in the new millenium, ignores a long history of examination fuelled then and now by the unique life history attributes and traits of herring. These traits include a

complex stock structure, recurrent migration patterns (feeding and reproductive migrations including homing to specific spawning sites, e. g., Holst et al., 2002), relative ease of laboratory culture, and intense long-term changes including stock collapses and recoveries. In the sub-polar NE Atlantic, large stocks of plantivorous fish co-occur and may compete for resources, which has been a catalyst for studying diets (e.g., Godiksen et al., 2006; Óskarsson et al., 2015) and distributions (Utne et al., 2012b) and for the development of individual-based models of movements and habitat utilization (Utne and Huse, 2012).

Long-term field data exist for herring in sub-polar waters and, not unexpectedly, a number of retrospective studies have been published. In the NE Atlantic, the Norwegian Spring Spawning (NSS) herring stock collapsed to very low biomass levels in the 1960s and was rebuilt in the 1980s. Reproductive characteristics differed between high and low (collapsed) stock biomass levels with fish maturing at larger body sizes and at decreased ages during the collapse period (Engelhard and Heino, 2004) which could suggest a release from density-dependent growth regulation. For NSS herring in the Barents Sea, the relationship between recruitment and temperature was relatively weak (e.g., Fiksen and Slotte, 2002) which agrees with the results of a longer (1913 to 2007) time series analysis in which only a weak (albeit significant) positive relationship was observed, where recruitment variability was not correlated with temperature, and recruitment variability was lower prior to the stock collapse (Bogstad et al., 2013). In Pacific herring, density dependence was suggested in a time series of stock size and temperature during certain regimes identified using fuzzy logic (Chen, 2001). In the analysis of a shorter (10-year) but highly seasonally resolved (e.g., weekly to monthly sampling) time series, Reum et al. (2013) found no evidence for density-dependent growth of larvae (but growth was related to temperature) but significant density-dependent growth during the early juvenile phase highlighting how the dominant mechanisms controlling growth can be stage-specific.

There were a considerable number of studies published on the spatial dynamics of populations of both sister species of herring (Fig. 15). In sub-polar waters of both the Atlantic and Pacific, complex herring stock structures exist and a variety of studies have employed genetics to explore the relatedness between and within herring species (Jørstad, 2004). For instance, comparisons of allozyme loci and vertebral numbers suggested large differences between NSS herring captured simultaneously with individuals more closely related to Pacific herring

sampled in the Japan Sea and the Gulf of Alaska ((Jørstad et al., 2004). Work in the early 2000s developed more powerful techniques to distinguish both intra- and inter-stock genetic variation (e.g., kinship analysis) using microsatellites (Olsen et al., 2002). Inter-breeding between NSS and a coastal (fjord) stock explained the loss of differences in larval growth rate and vertebral numbers over several decades suggesting that metapopulation structure in herring is dynamic (Johannesen et al., 2014). Studies of introgression between these Pacific and Atlantic sister species have generated hypotheses regarding post-glacial population separation and (re-)mixing (e.g., Laakkonen et al., 2015).

Studies have examined behavioural-mediated movements of herring at a variety of spatial scales from the sub-micro (thin layers and diurnal vertical migration (DVM) of larvae) to meso (feeding migrations of adult). For example, field sampling by Ferreira et al. (2012) found that Atlantic herring larvae perform type I DVM (shallow during day, deep at night) likely resulting mainly from foraging tactics. Laboratory work on Pacific herring demonstrated how the presence of thin layers but not necessarily prey patches can attract larvae and impact their vertical distribution (Clay et al., 2004). In adult Atlantic herring in the Barents Sea, foraging tactics were also used to explain the large-scale feeding migrations. In that case, the seasonal movements of schools appeared to be linked to regional differences in the timing of the ascent into shallow waters of a key prey species, the copepod *Calanus finmarchicus* (Broms et al., 2012). Earlier work by Kvamme et al. (2003) documented changes in the movement of herring schools towards locations with higher concentrations of prey. Changes in depth distribution of adult Atlantic herring across 12 years were suggested to be due to inter-annual differences in the strength of intra- and inter-specific competition for prey, indicating density-dependent changes in habitat utilization (Huse et al., 2012). In another example, Langård et al. (2014) documented consistent, pre-spawning schooling dynamics of herring in a coastal Norwegian fjord and reported on the influence of variation in fish size and spawning phase on school tightness. Finally, work on first-time migrants and changes in wintering grounds demonstrated the importance of social learning in shaping the large-scale migration patterns of NSS herring (Huse et al., 2010).

The ability to artificially spawn and rear herring in the laboratory has promoted laboratory research on various aspects of early life stages such as the effects of environmental stressors on survival (Lefebvre et al., 2005; Froehlich et al., 2015), feeding (Utne-Palm, 2004; Ingvarsdóttir
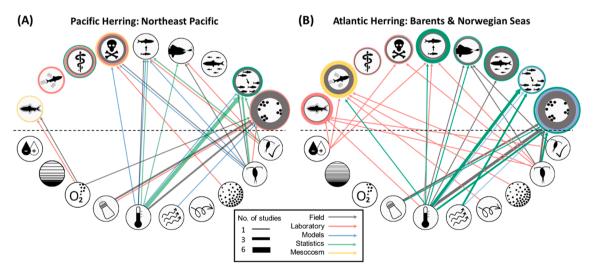

Fig. 15. Research emphasis in papers published during two time periods (2001–2006, and 2011–2016) in sub-polar systems in the northern hemisphere including Pacific herring in the northeast Pacific (Panel A) and Atlantic herring in the Barents and North Sea (Panel B). In total, 10 categories of bottom-up drivers (below dotted line) were used including 5 abiotic factors, 3 physical / mixing processes, and 2 aspects of prey. Responses (above dotted line) were separated into 9 categories including 7 at the individual level (from left, 3 energetic costs or losses and 4 vital rates) and 2 at the population-level (see Fig. 4 for legend). The thickness of lines represents the number of studies. The color represents the type of study (not all types may be present). The number and type of studies considering only responses are also shown (color and thickness of circles).

et al., 2012) and behaviour (Maneja et al., 2015) of embryos and larvae (Fig. 15). Research on herring larvae includes seminal studies documenting ontogenetic changes in digestive capacity (e.g., Rojas-Garcia et al., 2016) and nutritional requirements (e.g., Conceiçãoa et al., 2002). Similarly, the ability to capture and maintain large juvenile and adult herring in small-scale in situ enclosures has led to studies examining adaptive schooling behaviour such as changes in schooling in reponse to sounds made by predators or ships (Wilson et al., 2002; Handegard et al., 2015) or simulated attacks by predators (Rieucau et al., 2016). It should be noted that, across the 10 years of published research reviewed here, herring was the only SPF studied using mesocosms / in situ enclosures.

In sub-polar waters, there is a rich history of using spatially-explicit models to develop and test hypotheses on mechanisms behind observed patterns in the growth and/or distribution of herring in both the Pacific (Snauffer et al., 2014; Ito et al., 2015) and Atlantic (Huse et al., 2002; Sætre et al., 2002; Vikebø et al., 2010) as well as the potential top-down control of *Calanus finmarchicus* (Utne et al., 2012a). As previously mentioned, these efforts stem from development of high-resolution physical and/or biogeochemical models in the 1990s in both regions. Since 2008 in the Barents and Norwegian Seas, operational oceanographic tools have been forecasting the drift and distribution of larvae and young juveniles of Atlantic herring to, among other things, aid in survey design and implementation (Vikebø et al., 2011).

3.11. Regional summaries and time periods

Although we have attempted to highlight key research exploring bottom-up controls of SPF which was published prior to (≤2000), between (2007–2010) and after (≥2017) the two, 6-year time periods exhaustively reviewed here. It should be noted that our global maps and figures would look considerably different if these other time periods were also included in a rigorous, systematic literature review. For example, considerable field research on SPF was conducted in the 1980s and 1990s in California as part of the long-running CalCOFI program. The types (and amounts) of studies performed in various regions are also influenced by the types of large-scale (global) initiatives such as GLOBEC (regional and national programs from 1990 to 2009) or specific regional programs such as BENEFIT (1998–2007) in the Benguela (Hampton and Sweijd, 2008), or the Humboldt Conference in 2006 (Bertrand et al., 2008b) and the DISCOH (Dynamics of the Humboldt Current System, 2010–2019) International Joint Laboratory in the Humboldt. These programs are often conducted in response to large-scale changes (collapses or increases) of stocks. For example, the Cal-COFI program was promoted because of serious concerns over the decline of sardine (https://calcofi.org/about-calcofi/history.html). The type (and amount) of publications on SPF in specific regions can also be influenced by the research interest (and productivity) of principle investigators who have 'championed' SPF research. For example, the late 1970s through the 1990s was a very productive period at the Chesapeake Biological Laboratory for research conducted on bay anchovy). Finally, the history of research conducted in specific regions likely influenced the types of studies that were published in this millennium. For example, studies including robust conceptual and process models are, arguably, only possible in areas where long-term field data were available.

Differences among the types of studies across regions can be visualized by comparing the 'research maps' (Fig. 16). In regions at relatively high latitudes, herrings and sprat are amenable to laboratory and /or mesocosm research, allowing a wider array of responses (including physiology and behaviour) to be examined. These research maps also indicate that a considerable amount of field work has been published documenting the spatial distribution of SPF but that many of those studies did not explicitly examine any potential bottom-up driver(s) influencing those patterns (e.g., thick outline around spatial distribution symbols in 7 of the 12 regions) (Fig. 16). The availability of field data is likely a reason for the greater emphasis placed on spatially-explicit

biophysical modelling in some (e.g., California Current, NE Atlantic, Mediterranean Sea) but not all (e.g., NW Pacific, Humboldt System) of those regions. In terms of vital rates, relatively few studies were published on reproduction compared to growth and feeding. Disease and parasites were rarely studied nor were aspects of the physiology of SPF. In terms of physical factors, turbidity was least examined followed by water density, pH and dissolved oxygen (albiet regional differences exist). Turbulence was the physical process least often studied. We speculate that at least two reasons might explain this lack of research effort on turbulence. First, seminal work in the 1980s and 1990s (e.g., see review by Dower et al., 1997) produced results on the effects of turbulence (microscale, on early life stages) that researchers may perceive are applicable across species and regions. Second, from a methodological point of view, turbulence is not straightforward to study under controlled laboratory conditions. Another clear gap in knowledge is that relatively few studies were published that examined the effect of prey quality (e.g., changes in lipid or fatty acid content of phyto- and zooplankton) on SPF populations. Although only selected species are shown for each region, these species were dominant in terms of the amount of research conducted during the two 6-yr periods reviewed here.

4. Over-arching research needs in the new millennium

4.1. Projecting future productivity of SPF

Although it is beyond the scope of the present study to exhaustively review projections of climate change impacts on SPF populations, understanding how bottom-up factors such as temperature and prey availability regulate SPF populations is critical to making these projections. Moreover, making robust projections of changes in bottom-up forcing and SPF are critical because of the economic (and ecological and cultural) importance of SPF, particularly for providing fish meal and fish oil required by the growing aquaculture industry. For example, based on future changes in water temperature projected by climate climate models, the center of the distribution of Peruvian anchoveta was expected to shift to higher latitudes at rates between 13 and 33 km / decade depending on the severity of global warming (Jones and Cheung, 2015; Jones et al., 2015). These shifts in distribution will impact accessibility of stocks and landings with downstream, global impacts on fish meal and fish oil prices. Finally, a mechanistic understanding of how physical and biogeochemical processes impact SPF populations is required for advancing short-term forecasts (months to years) that could be valuable for management of SPF stocks.

Within the four EBUS (Humboldt, California, Benguela and Canary), understanding how upwelling strength is linked to phytoplankton and zooplankton production and how upwelling may change will be key to making robust projections of how climate change impacts. In the northern Humboldt, recent trends in SST are in accordance with the hypothesis that increasing greenhouse gas concentrations will force intensification of upwelling-favourable winds in EBUS (Bakun, 1990). Although this hypothesis was challenged by projections from global climate models (Vecchi and Soden, 2007; Lu et al., 2007), these models poorly represent the regional wind forcing and upwelling (Gent et al., 2010). Overall, a consensus is emerging that the intensity and duration of upwelling-favourable winds will increase in the southern Humboldt Current system, off Chile and will (moderately) decrease off Peru (Garreaud and Falvey, 2009; Falvey and Garreaud, 2009; Goubanova et al., 2011; Echevin et al., 2012; Belmadani et al., 2014; Garcia-Reyes, 2015; Wang, 2015). Decreased upwelling would decrease the productivity of lower trophic levels and warming-induced increases in stratification would ultimately increase the area of the OMZ. Such changes are in agreement with those constructed from the paleo record in sediments (Salvatteci et al., 2019). In central Chile, upwelling is predicted to occur earlier, end later and be of greater intensity, especially in summer (Garreaud and Falvey, 2009; Belmadani et al., 2014; Rykaczewski et al.,
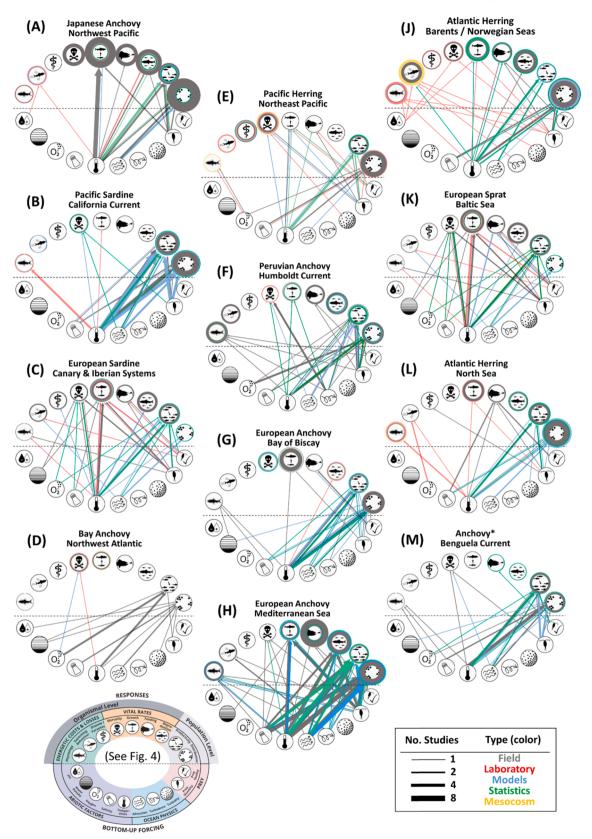
Fig. 16. Research maps of studies exploring fundamental aspects of small pelagic fishes focusing on bottom-up factors and processes. The number of field studies (grey lines), laboratory experiments (red lines), spatially-explicit modelling (blue lines), statistical time series analyses (green lines) and mesocosm studies (yellow lines) conducted on key small pelagic fish species in 12 different regions is shown. This is based on the pooled studies published across 12 years (2001–2006, 2011–2016). Line thickness denotes the number of studies (also for symbol outlines indicating the number of studies that examined only a response and not any bottom-up forcing factor or process). The legend for the symbols (see insert) are more easily seen in Fig. 4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2015; Wang et al., 2015). Furthermore, climate change may significantly reduce the spawning success of small pelagic fish in the Humboldt Current (Brochier et al., 2013). In this EBUS, therefore, changes in bottom-up factors (temperature, prey and dissolved oxygen) are expected to cause relatively dramatic shifts in the productivity and distribution of SPF with implications for the world's largest, single-species fishery.

Climate-induced shifts in bottom-up factors are more complicated and less distinct in other EBUS. For example, recent trends in upwelling intensity in the Canary EBUS remain unclear (Sousa et al., 2017), especially when compared to other EBUS (Sydeman et al., 2014; Wang et al., 2015). During the recent period of global warming (1967–2007), no increase in upwelling intensity in the Iberian and NW African sectors was observed and sea surface temperature only marginally increased at a rate greater than 0.01 °C yr^{-1} (Barton et al., 2013). Zonal (sub-region specific) and seasonal shifts in bottom-up processes, however are expected in the future. Recent projections suggest an overall increase in upwelling intensity in the W Iberian Peninsula and decrease in NW Africa (Wang et al., 2015; Sousa et al., 2017), and total cumulative upwelling has increased off the South African south coast in the southern Benguela but not in the northern Benguela (Lamont et al., 2018). Similarly, the magnitude and impact of ongoing ocean acidification is expected to be region-specific and highly dependent on changes in upwelling intensity (González-Dávila et al., 2009). It is important to note that predation pressure on SPF has shifted and may also markedly shift in the future due novel mixtures of species resulting from climate-driven warming and latitudinal shifts of populations (e.g., Garrido et al., 2015) or physical changes within ecosystems such as the shoaling of OMZ waters and habitat compression tending to increase overlap with predators. These top-down processes are not included in this review. As discussed in the Benguela section, other indirect (bottom-up) effects related to climate change appear highly relevant such as the increase in HABs associated with decreased somatic condition of sardine (van der Lingen et al., 2016).

Outside of the four, major EBUS regions, projecting how climate change may alter bottom-up processes impacting the productivity of SPF is also challenging for a few reasons. First, in oligotrophic areas such as the Mediterranean Sea, the results of different biogeochemical models (e.g., depictions of the dynamics of the deep chlorophyll maximum) agree poorly in some regions (e.g., Ramírez-Romero et al., 2020) and making robust projections of the impacts of climate change on SPF will require a better representation of i) mesoscale ocean physics in topographically complex areas, ii) nutrient loading by rivers fueling local production, iii) conditions causing local upwelling events. Projecting the effects of climate change will not only require better representations of these physical processes but also continuing to collect time-series data as well as new physiological data from laboratory experiments testing climate change-related drivers across life stages.

Climate change may cause no-analog combinations of abiotic and biotic conditions, at least in terms of modern-day field observations in various ecosystems. Reconstructing paleorecords, such as time periods when productivity was lower and OMZs were larger than at present in the HUC (Salvatteci et al., 2019) or changes in winter sea surface temperature in the NW Pacific (Kuwae et al., 2017) may provide valuable analogs to situations that could be faced in the future (in the absence of fishing).

5. Recommendations

Based on our global review of the studies published on SPF, we are able to make a number of recommendations for future research needed to advance our understanding of how bottom-up factors and processes control the dynamics of these ecologically and economically important fishes. These recommendations are not independent from one another.

- Understanding bottom-up drivers requires a close marriage between laboratory experiments, field surveys and biophysical modelling. This tripartite approach has been fully realized in studies conducted on Atlantic herring, a species relatively easy to grow in the laboratory, but not for most other SPF (clupeid) species. Establishment of broodstocks, captive rearing and programs studying the ecophysiology of various life stages will allow species-specific parameterizations of mechanistic (physiological-based) models.
- Quantitative field sampling of young-of-the-year (YOY) juveniles needs to be developed. The body size of young juveniles reduces their catchability in gears often used in surveys. Young-of-the-year (YOY) juveniles can avoid plankton nets used to catch eggs and larvae and can be too small to be reliably retained by purse seines and trawl nets used to capture adults in stock assessment surveys. Due to their large numbers and high mass-specific rates of feeding, YOY juveniles can have very large trophodynamic impacts on prey and suffer food limitation, reducing rates of growth and survival. Where young juveniles have been studied (e.g., Voss et al., 2012), it is clear that the dynamics of this life stage can have large impacts on the strength of recruitment.
- More emphasis is needed on understanding the role of density-dependence in population dynamics of SPF (e.g., Takasuka et al., 2019) to examine the magnitude of top-down regulation of prey resources as well as intra-guild dynamics such as competition and predation. More emphasis on intra-guild processes may help unravel mechanisms controlling fluctuations in SPF stocks.
- Continued study of the influence of climate variability on SPF and their ecosystems is needed including investigations of the impacts of ocean–atmosphere interactions and climate modes and current systems (Alheit et al., 2019a). These explorations should not only be correlative (detecting patterns in field time series data) but also advance knowledge on the mechanisms and processes in ocean ecosystems represented by changes in these atmospheric / oceanic indices of climate variability that affect the growth and survival of SPF.
- Oxygen minimum zones and seasonal extents of hypoxia are expanding. More research is needed on the acute (survival) and chronic (reductions in growth, reproduction) impacts of hypoxia on SPF. At the same time, explorations of how low dissolved oxygen and other drivers of SPF populations (either via laboratory experiments or statistical analyses of field data) need to recognize the complexity and context-specific effects of multiple direct and indirect factors (e.g., Bertrand et al., 2011). Taking this holistic view will help better build and parameterize end-to-end models that attempt to depict how expanding OMZs and other processes affect complex ecosystem dynamics.
- The use of otoliths to infer exact ages and somatic growth rates of early life stages is challenging in some species of SPF. Continued work is needed to verify and corroborate daily increment formation in the otoliths of SPF, particularly when environmental conditions cause relatively low rates of somatic growth (cold temperatures, low prey abundance). Quantifying and reducing the error associated larval growth trajectories (first weeks of life) from the otoliths of much older juveniles is needed to apply a "characteristics of survivors" approach (Plaza et al., 2019). The application of advanced chemical analyses such as δ^{18}O (Javor 2013; Darnaude et al., 2014; Sakamoto et al., 2020) could yield important information on population structure, spatial dynamics and movement patterns.
- Mesocosm studies contributed less than 1% of the research published on SPF in the time periods (2001–2006 and 2011 to 2016) reviewed here. In the 1980s and 1990s, mesocosm studies provided useful data on the growth, feeding and survival of SPF in semi-natural settings (Fuiman and Gamble, 1988; Cowan and Houde, 1990). The use of large mesocosms is, arguably, the best way to advance understanding on how both direct (e.g., temperature, pH) and indirect (prey field) factors influence the growth and survival of SPF (Sswat et al., 2018).

Research programs utilizing mesocosms may, thus, provide much-needed information on how environmental factors interact to affect SPF.

- Due to their global distribution, their economic and ecological importance and the similarity in their biology, research on SPF has been traditionally characterized by large international cooperation. Some of the shifts in the amount of peer-reviewed publications (and their research emphasis) between the two, 6-year periods reviewed here, can be attributed to changes in the magnitude of international collaboration. There is a successful history of multinational projects and meetings on SPF (Sharp and Csirke, 1983; Csirke and Sharp, 1984; Alheit and Bakun, 2010). For example, the regional GLOBEC program SPACC (Small Pelagic Fish and Climate Change), started in 1994, lasted 15 years and culminated in the publication of the SPACC book in 2009 (Checkley et al., 2009). Although recent symposia have provided important platforms for knowledge exchange (Peck et al., 2014; Alheit et. al., 2019b, Alheit and Peck, 2019), a coordinated, global platform with sufficient funding for participation of scientists from developing countries is needed to foster not only knowledge exchange but also comparative studies. A first, new step towards formal, global collaboration was recently taken by establishing a working group on small pelagic fish supported by two international marine science organizations (ICES – International Council for the Exploration of the Seas - WGSPF; and PICES – North Pacific Science Organization - WG43). The present review represents the first product stemming from this international collaborative effort.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2020.102494.

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