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Worldwide Appraisal of Knowledge Gaps in the Space Usage of Small Pelagic Fish: Highlights Across Stock Uncertainties and Research Priorities

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ABSTRACT

Understanding the spatial structure of life cycle components of small pelagic fish (SPF) stocks is key for deciphering population dynamics and ensuring sustainable management. The spatial extent of different life stages and ecologically relevant processes (e.g., reproduction) is temporally dynamic and responds to environmental, genetic, and demographic constraints. Knowledge gaps on within-stock spatial variability of key life cycle processes for SPF worldwide were identified for clupeoid fish (Clupeidae/Engraulidae). From the 3229 Web of Science-indexed articles reviewed, data were systematically extracted from 299. This information was supplemented with another 105 documents and databases from official SPF surveys and stock assessments. Overall, this review compiled information from 111 datasets (77 stocks) involving 17 assessed or commercially relevant species across 19 Large Marine Ecosystems (LMEs) and 38 coastal ecoregions. Only approximately 40% of the stocks used in this study covered the known or presumed stock distribution for at least one life-cycle variable: Adults (feeding area, spawning migration, feeding migration, overwintering migration, spawning area, and presence/biomass), juveniles (presence/biomass, nursery area), and larvae (larval routes). Despite more extensive spatial information from some Eastern Boundary Upwelling Systems (EBUS) and long-managed stocks, some important gaps remain due to information quality, stock identity ambiguity, or spatial data biases. Key information on SPF spatial variability could be extracted from existing surveys, but there were various limitations due to data access and spatiotemporal coverage. The main consequences of the key identified gaps are reviewed, and a series of priority research/monitoring actions are recommended to mitigate these consequences and improve our ability to address spatial variability in SPF stocks.

KEYWORDS

Fisheries; forage fish; gap analysis; life history; small pelagics

Introduction

Small pelagic fish (SPF) are common forage fish that often form schools, typically including anchovies, sardines, and herrings. They serve as a vital food source for marine mammals, seabirds, and larger predatory fish (Cury et al. 2000; Palomera et al. 2007; Pikitch et al. 2012; Pikitch et al. 2014), and account for up to 25% of global landings, playing a crucial role in food security and the aquaculture feed industry (FAO

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2022a; Robinson et al. 2022). SPF exhibit high temporal variability and instability in abundance (Fréon et al. 2005), leading to characteristic “boom and boost” cycles (Lluch-Belda et al. 1989; Bakun 1996). Managing these resources is challenging due to their fluctuating population dynamics (Hilborn et al. 2022). Mortality and intrinsic population growth rates of SPF are high and, therefore, oscillations in many stocks are tightly linked to environmental fluctuations at different spatial and temporal scales (Cushing 1982; Bakun 1996; Brochier et al. 2018; Szuwalski et al. 2019). The importance of SPF for humans and the ecosystem has spurred comprehensive reviews on their ecology and fisheries, covering wide geographical areas, and numerous species (Fréon et al. 2005; Engelhard et al. 2014; Somarakis et al. 2019; Peck et al. 2021). These reviews delve into general and specific aspects, including the impact of multi-decadal scale oscillations (Tourre et al. 2007), potential climate change effects (Peck et al. 2013; Petitgas et al. 2013; Catalán et al. 2019; Huang et al. 2021), predictability over medium to short-term scales (Pinsky et al. 2011), or methodological advances in their study (Dickey-Collas et al. 2012). A critical gap analysis of the existing information on the spatial variability of the different life stages in a representative worldwide sample of existing stocks is still lacking and much needed.

The spatial extent and dynamics of SPF life history traits, such as reproduction and feeding, respond to environmental, genetic, and demographic factors. Understanding these mechanisms is essential for comprehending life cycle closure, population dynamics, and interactions with fisheries (Petitgas et al. 2010; Huse 2016; Siple et al. 2021). Within species, different populations and contingents (see below) exhibit varying spatial resource dependencies. Some rely on large-scale productive areas (e.g., Eastern Boundary Upwelling Systems [EBUS]) for feeding, reproduction, and larval development (Cushing 1969; Fréon et al. 2009) while others are bound to local productive and retention zones, including river plumes and deep chlorophyll maxima (Palomera et al. 2007). Understanding these spatial dynamics throughout the life cycle is essential for purposes such as defining stock boundaries (Harden-Jones 1968; Petitgas et al. 2010) and poses a contemporary challenge for sustainable management of SPF in various regions (Siple et al. 2021). Variability in spatial processes, as outlined below, exerts a fundamental effect on SPF population abundance by impacting recruitment. These processes encompass temporal changes in feeding and spawning areas, migration patterns, and the transport of eggs and larvae to suitable nursery grounds.

Spatial and temporal variations in recruitment result from density-dependent and independent processes which are, in turn, influenced by environmental factors (Rose et al. 2001). Habitat expansions, for example, can reveal density-dependent processes leading to fish schools being displaced to suboptimal areas (MacCall 1990), impacting recruitment. High temporal (annual) recruitment autocorrelation may be linked to food-dependent reproductive strategies (McBride et al. 2015; Somarakis et al. 2019). In this sense, spatial information on feeding areas holds varying importance for different species. Some income breeders (e.g., anchovies) adapt their reproductive dynamics to the spatial variability in feeding grounds, unlike strict capital breeders, such as Atlantic herring (*Clupea harengus*) that spawn during specific temporal windows at defined locations. Monitoring spatial effects across SPF life stages is essential. On short timescales (interannual or less), the predictability of recruitment relies partly on spatially resolved data (Payne et al. 2022). Long-term global warming projections impact upwelling dynamics in EBUS (Rykaczewski et al. 2015), leading to uncertain consequences for SPF due to modified primary productivity, oxygen, and species interactions (Bakun et al. 2015). Moreover, changes in upwelling intensity in EBUS modify SPF space use in spawning and connectivity (op. cit., Condie et al. 2011). Variability in spawning areas and larval transport can disrupt recruitment-related biological patterns (Cubillos et al. 2001). For species with segregated nursery and spawning areas, monitoring ocean circulation-induced shifts in larval routes is essential (Fréon et al. 2005) for understanding high-frequency recruitment oscillations (Petitgas et al. 2013; Somarakis et al. 2019).

Both adult and juvenile stages of some SPF undergo migration as an adaptation to environmental and physiological demands (Cury et al. 2000; Brochier et al. 2018). Migratory patterns, where they exist, remain poorly understood except for the largest stocks, where a migratory triangle (Harden-Jones 1968) has been identified: adult stock moves from feeding to spawning areas, to nursery areas, and back. Beyond documenting mere abundance and mortality, spatial patterns and migrations are challenging but valuable life history characteristics to study in fishery science. A notable implication of the former processes is hyperstability and the implementation of harvest control rules in shared stocks (Siple et al. 2021). The burgeoning field of movement ecology, focusing on the drivers, and tradeoffs of fish movement (Fiksen et al. 2007; Kristiansen et al. 2009), is increasingly relevant for understanding population dynamics

(Lowerre-Barbieri et al. 2019) and effectively managing SPF, particularly as the traditional maximum sustainable yield (MSY) approach is inadequate for these species (Patterson 1992; Hilborn et al. 2022). Large SPF populations often form metapopulations (McQuinn 1997), each with potentially distinct spatial patterns driven by behaviors, such as natal homing and learning. These subsets are referred to as "contingents" (Secor 1999) and disruptions of one or more contingents can lead to population collapses (Petitgas et al. 2010).

Analytical approaches used to examine spatial dynamics of SPF range from statistical to mechanistic, with data primarily sourced from snapshots of spatial occupancy derived from acoustic, eggs, and larval surveys or fishery operations. Sustaining these data sets, especially for the less economically relevant stocks, is challenging. Individual-based models (IBMs) with physiological-based (bioenergetics) subroutines, and a recent monitoring tool based on high-resolution satellite and *in situ* acoustic biomass SPF data (Spondylidis et al. 2023) have been created to simulate and study these dynamics, although their application has limitations for many stocks. Advanced end-to-end 3D full-life-cycle bioenergetic IBMs (Fietcher et al. 2015; Politikos, Somarakis, et al. 2015; Politikos, Huret, et al. 2015; Gkanasos et al. 2021) offer insights into the spatial factors influencing key output variables through life. Despite these advancements, gaps in information and difficulties in generalizing or validating assumptions remain a challenge for many species and life stages (Catalán et al. 2019; Peck et al. 2013; Politikos et al. 2021).

Recent advances in technology and information processing have ushered us into an era where spatial information is increasingly crucial in fisheries ecology and management (Lowerre-Barbieri et al. 2019). These data are revolutionizing ecosystem-based management, and it is vital to maintain comprehensive monitoring of key spatial components to understand the reproductive resilience of fish populations (Lowerre-Barbieri et al. 2017; Ospina-Alvarez et al. 2022). This concept aligns with earlier considerations of metapopulation contingents and the impact of individual biology, including behavior, on the fitness of larger groups (Krause and Ruxton 2002; Heino et al. 2015). Considering this background information, a fundamental question emerges: What is our current understanding of the spatial variability within the life cycle of the world's main SPF stocks? Achieving a global perspective on gaps in spatial information and strategizing approaches to address them – through alternative data sources, modeling exercises, or new data collection – is of paramount importance for fishery managers, research-focused policymakers, and scientists.

The International Council for the Exploration of the Sea/North Pacific Marine Science Organization (ICES/PICES) Working Group on SPF launched a collaborative, global initiative to identify knowledge gaps in the spatial variability of key life cycle processes in SPF. The goal was to critically evaluate the availability and gaps in spatial information in a broad number of commercially important SPF stocks and to pinpoint effective strategies to fill in the critical knowledge gaps. Contributors to this article systematically collected data on the spatial distribution of species from multiple SPF stocks through their life cycles. This included evaluating temporal variations in spatial processes within Large Marine Ecosystems (LMEs), as well as the analytical approaches, data types, and sources utilized. This comprehensive approach i) facilitated cross-regional discussions, ii) highlighted the strengths and limitations of existing data, and iii) enabled the formulation of a set of recommendations to efficiently bridge the most critical knowledge gaps.

Selection of processes, species, and stocks

This review evaluates the spatial knowledge of SPF across life stages, from spawners to juveniles, using species and stocks as primary units. The focus was on clupeoid fish (Clupeidae/Engraulidae), such as anchovies, sardines, and herrings, with selection prioritizing species representing both heavily and less-exploited populations, different types of productive habitats, and species with multiple stocks, based on the expertise of the authors. Experts in SPF from 19 LME conducted predefined systematic searches in the Web of Science up to 2022, enhanced by grey literature such as regional cruise and annual status marine fishery reports (see Supplemental material for more details). Nine "spatial components" were analyzed, encompassing all life stages and spatial uses, including spawning areas, larval connectivity, nursery areas, and various forms of migration (Table 1).

From 3229 Web of Science-indexed studies, 299 articles were analyzed providing comprehensive spatial and temporal information for at least one spatial component. Additionally, 105 assessment or cruise reports were analyzed (Tables S1 and S2 from the Online Supplemental Material). The final dataset comprised 111 datasets of spatial data, each covering nine potential spatial components for 17 species (Figure 1) across 77 stocks within 19 LME (aggregated into 17 LME for analytical purposes)

Table 1. Information collected from the systematic search, supplemented with additional details to elucidate the general patterns related to spatial variability in the use of habitat by small pelagic fish.

	Variable description	Type of variable	Variable levels/values	Explanation
Information extracted from systematic search and grey literature	Species	Nominal (fixed)	As needed (text)	Scientific name in the format *Genus_species*
	Large Marine Ecosystem (LME)	Nominal (fixed)	As needed (text)	Denotes the spatial distribution of populations within ecosystems that respond coherently across multiple scales.
	Management unit or spatial unit	Nominal (free)	As needed (text)	Defines the spatial scope for data collection, covering various ecological or administrative units (e.g., "Northern population").
	Demographic coherence of the stock/data set	Nominal (fixed)	From an automatic list: Y/N/NA	Assesses whether the defined stock/dataset aligns with biological or metapopulation concepts, essential for effective management.
	Suspected demographic stock area	Nominal (free)	As needed (text)	If known, specifies proposed regions for a coherent management unit.
	Spatial component	Nominal (fixed)	Automatic list: 9 main categories: adult feeding areas; spawning migration; adult feeding migration; spawning areas; larval routes; overwintering migration; nursery areas; adult presence/biomass; juvenile presence/biomass.	Defines nine spatial processes (components) relevant to life cycle closure. Some processes may overlap across species or ecosystems. Basic spatial data, such as presence/biomass are included as they provide a proxy for the realized spatial distribution of the stock at a given time. Genetics data are excluded except for stock delineation (Table S1).
	Time resolution of spatial component	Nominal (semi-fixed)	Automatic list: Fixed picture; interannual, seasonal, quarterly interannual; operational; decadal; NA, other (specify).	Describes the periodicity of data collection. "Fixed picture" integrates data from merged surveys to present an average pattern, usually after statistical processing (e.g., SDM). "Interannual" involves annual time series, typically, from stock assessments. "Seasonal" implies that spatial data are available for at least two seasons within one single year. "Quarterly-interannual" is as before, but several seasons are sampled for a number of years. "Operational" involves continuously collected data. "Decadal" data are available integrated at decadal scales. Additional options include daily, weekly, monthly (within one single year), monthly interannual (several years at monthly resolution), and triennial.
	Length of the time series	Continuous	Integer	Specifies the duration of data collection for a given time resolution. For example, if the time resolution is "quarterly interannual", a value of 3 indicates 3 years of seasonal data. Unknown values default to 1.
	Maximum length of time series interruption	Ordinal (fixed)	Automatic list: <=2; 3–5; 6–10; >10, NA	Indicates gaps in data collection, crucial for assessing continuity and reliability. Units align with time series length. For example, a "3-5" gap in a quarterly-interannual series signifies interruptions of 3–5 years in a row.
	Data sources for time series	Nominal (semi-fixed)	Automatic list: Otolith microchemistry, Isotopes, Artificial tagging, Parasites, Acoustic surveys, Egg & larval surveys, Surveys in general, Fishing operations, Historical, NA, other (specify).	Lists methods for spatial data collection. "Historical" applies if data lacks clear empirical sources.
	Mathematical model type for spatial component	Nominal (semi-fixed)	Automatic list: Mechanistic, statistical, and others (specify)	Identifies the type of model (e.g., statistical or mechanistic) used for spatial analysis, influencing insights on species movement.
	Explicit movement model	Nominal (semi-fixed)	Automatic list: Diel vertical migration, seasonal migration, NA, and other (specify)	Specifies if explicit movement patterns, such as seasonal migrations, are modeled.
Additional information	Model validation	Nominal (fixed)	Automatic list: Y/N/NA	Indicates whether the model was validated with external observations.
	Type of model validation	Nominal (free)	As needed (text)	Specifies methods of validation, such as using genetic data or recruitment indices.
	Coastal ecoregions	Nominal (fixed)	As needed (text)	Provides a finer spatial resolution following categories from Spalding et al. (2007).
	Statistical area	Nominal (fixed)	As needed (text)	Refers to FAO statistical areas, at varying resolution (e.g., FAO GSAs in the Mediterranean).
	Official name of managed stock(s)	Nominal (free)	As needed (text)	Designates the unit used to analyze spatial data for each species. For jointly managed stocks, the unified grouping is adopted.
	Single stock consideration for management	Nominal (fixed)	Automatic list: Y/N/NA	Reviews official reports to confirm whether a stock is managed as a single unit, regardless of underlying reasons.

Each entry must include this information. The complete data matrix is provided as Supplementary Material (Supplemental Tables S1 and S2).

and 38 ecoregions as defined in Spalding et al. (2007) (Figure 2, Tables S1 and S2 from the Online Supplemental Material). For each predefined "spatial component" or process, information was categorized by LME, species, stock (if known), data type and source, presence of models, temporal variability, and time series gaps (Table 1), with additional descriptors added retroactively. One species (*Sardinops melanostictus*) was included in the analyses with this name in aid of comparisons with other works, even though its accepted name is *Sardinops sagax*.

Gap analysis and summaries by LME

Following an initial evaluation of the available information for each species, stock, and geographic area, an analysis of data richness in terms of time series length, resolution, and fragmentation was conducted. The types of available data were examined, including fixed snapshots of spatial process, modeling outputs, or specific survey results, among others (Table 1). Additionally, the spatial descriptors used were assessed, if any. To facilitate plotting, when representing the length of the time series and its temporal gaps, units are only comparable within a given time-resolution (e.g., interannual time series are in years, but weekly time series are in weeks, see Table 1).

The retrieved information was filtered to prioritize spatially and temporally richer data for each species, area, and spatial component. For instance, when acoustic surveys covered a decade with multiple articles reporting subsets of these data, the longest time series, typically from routine surveys and stock assessments, were selected. For stocks with several short, non-coincident surveys, all were included in the analyses. When comparing mathematical models describing spatial components, mechanistic models were favored over statistical ones if time series length and coverage were similar.

The article outlines global patterns and summaries of selected stocks and populations in various LME. Each detailed summary applied a consistent format, emphasizing the key knowledge gaps in various spatial components for each stock concluding with remarks. The final section offers recommendations for further knowledge generation and the potential insights from integrating information across different areas and species.

A global picture on data of spatial components in SPF

Each LME studied contained 1–24 stocks and up to 4 species (Figure 2, Table S1 from the Online Supplemental Material). European anchovy (*Engraulis encrasicolus)* and European sardine (*Sardina pilchardus*) in the Mediterranean region dominated the datasets with over 20 life cycle datasets for each species (Figures 1 and 2). This data richness is likely due to the numerous countries conducting research and assessments on fisheries resources in the area (Peck et al. 2021). Species with high worldwide production, such as Peruvian anchovy (*Engraulis ringens*) and South American sardine (*S. sagax*), and Atlantic herring had fewer datasets, but generally more comprehensive data (detailed below). In contrast, SPF species with low fishery catches, such as Brazilian sardine (*Sardinella brasiliensis*) or round herring (*Etrumeus micropus*) tended to have limited data and were targeted by fisheries in only a few countries. The most ecologically meaningful stock assessments (approaching a biological stock concept) did not always occur in LME with long-exploited stocks or high economic importance, particularly if these metapopulations performed migrations and were shared by various countries (e.g., the Humboldt or California Current). Only approximately, 40% of the stocks aligned with their known or suspected demographic structure. Unlike other stocks, many commercially important ones tended to show ample and adequate areas of study for several life stages, including Atlantic herring in the Barents/Norwegian Sea, Baltic Sea, or North Sea, a few stocks in Mediterranean Sea regions and in areas around the Kuroshio–Oyashio system or the Sea of Japan (Figure 3, Table S1 from the Online Supplemental Material).

Of the 111 datasets covering various spatial processes, 70% corresponded to 77 managed stocks, of which 72 were officially assessed (Table S1 from the Online Supplemental Material). Some datasets did not align with any known assessed or unassessed stock, originating instead from scientific projects investigating spatial processes at different spatial scales, such as stage-specific habitat suitability areas in the entire Mediterranean (Giannoulaki et al. 2013) or long-term recruitment trends in coastal regions (Berg et al. 2022). Metadata on 18 unassessed stocks or datasets from zones too broad to be used for one stock were collected, predominantly located in the Mediterranean Sea, Yellow Sea, Celtic Biscay Shelf, and the Canary Current. For several assessed stocks, including up to nine in the Mediterranean Sea, there was a notable gap in understanding their demographic coherence (defined in Table 1). Essentially, demographic coherence refers to whether the dataset or stock aligns with the concept of a metapopulation. Specifically, if the dataset adequately represents the distribution of

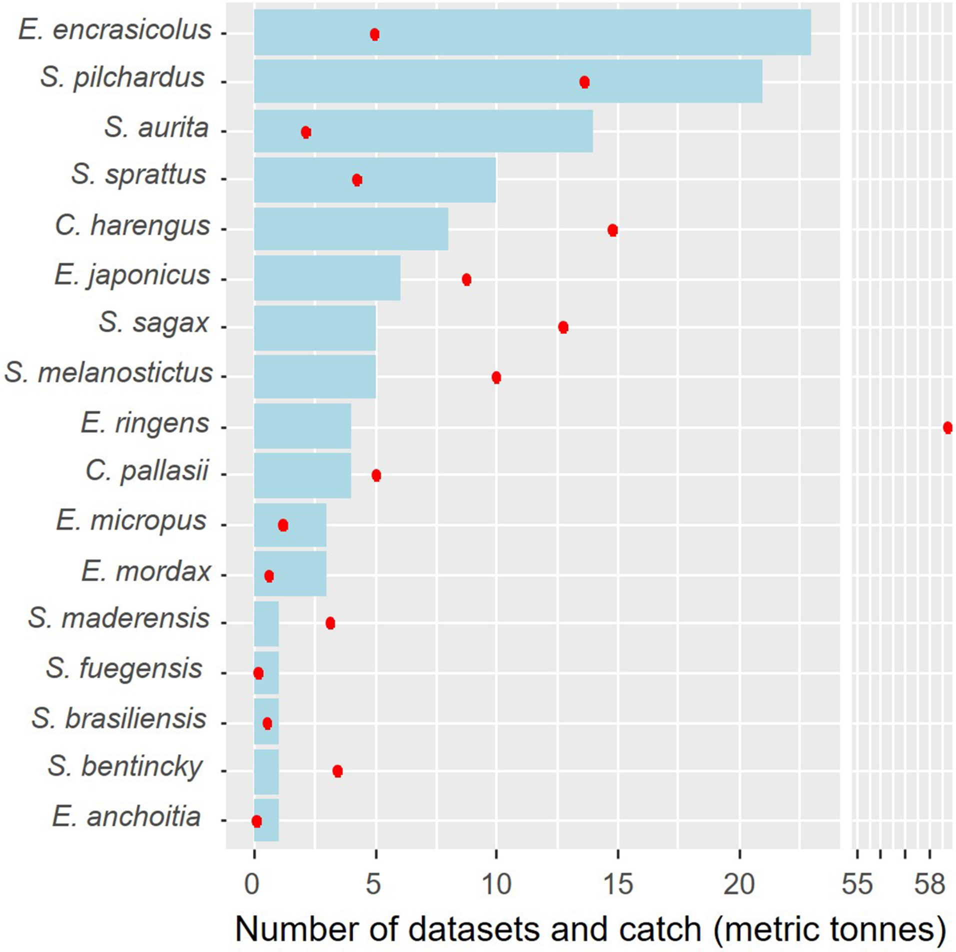

Figure 1. Number of datasets available per species of small pelagic fish (blue bars) and the corresponding worldwide catch (red points) according to FAO (2021) statistics. www.fao.org.

individuals that make up the biological stock under study, it is considered to be demographically coherent. In some major stocks, management practices have been undertaken on exploited fractions that cover only a portion of the metapopulation, as evident in areas such as the Humboldt current (notably the Peruvian-Chilean anchovy), Patagonian Shelf, Canary Current, Celtic Biscay Shelf, and the California Current (Figure 3, Table S1 from the Online Supplemental Material).

In several LME, including the Baltic Sea, the California Current, the Humboldt Current, South Benguela, and the Black Sea, information covering most spatial components was available for most of the stocks (Figure 4). Contrastingly, in other LME such as the Kuroshio and Oyashio, the Mediterranean Sea, the North Sea, Gulf of Alaska (GOA), Aleutian Islands (AI), Bering Sea (BS) and the Barents, and Norwegian Sea, rich information was limited to specific species. Predominantly, the spatial datasets fulfilled information on the presence and biomass of adult components in most stocks (Figures 5 and 6). Exceptions included some Mediterranean stocks and some stocks of the Kuroshio–Oyashio system, the East China Sea and Sea of Japan, and the Brazil shelf (Figures 5 and 6). These time series on adults' presence or biomass were generally interannual, featuring annual surveys, and in data-rich areas some surveys spanned over 50 years with minimal or no interruptions (<=2 years). Regions, such as the North Sea or the California Current, provided relatively long datasets with seasonal resolution.

Data on adult presence or biomass mainly originated from acoustic surveys for assessment, with a few instances using general surveys, fishing operations, or historical sources for "single shot" maps (Figures 7 and 8). Spatial models for these adult data were statistical and have been applied to a relatively small number of stocks. These models, often published in refereed journals, typically utilized only a fraction of the available information (Figure S1 from the Online Supplemental Material).

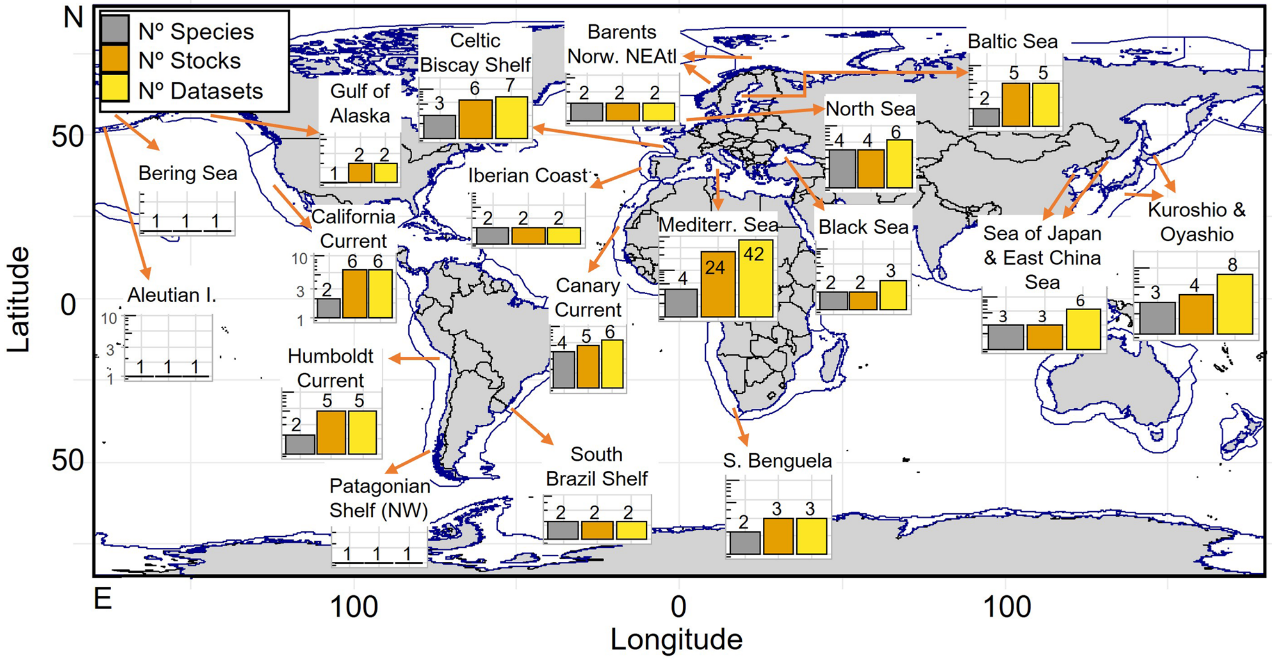

Figure 2. Distribution of datasets around the globe for several Large Marine Ecosystems (blue lines), including the number (N) of species, stocks, and datasets. Note, for few "stocks" in this figure, an aggregation was conducted to be consistent in all figures (see Supplemental Tables S1 and S2).

The data on spawning migration (Figures 5 and 6, Table S2 from the Online Supplemental Material), which aims at optimizing offspring survival, was notably thorough in regions characterized by strong seasonal cycles or production structures. Migration can be analyzed as temporally recurrent changes in spatial patterns before, during and after spawning, but mechanisms underlying these changes may differ. In relatively long-lived species, such as herring, social learning, a phenomenon that depends heavily on learning from previous cohorts (i.e., "wisdom of the crowd") is less influenced by environmental changes at the interannual scale (Corten 2002; Macdonald et al. 2018). In other cases, spatial variability in spawning is essentially caused by environmental cues or density-dependent processes (e.g., Brochier et al. 2018). Spawning migration was documented for 34% of the stocks reviewed here, including anchoveta in the Humboldt Current, Atlantic herring in the North Sea, Baltic Sea, Barents Sea, Norwegian Sea, and north Pacific, and stocks of SPF in Southern Benguela and the California current, as well as European sardine in the Gulf of Lions (Figures 5 and 6). Additionally, historical data from interannual acoustic surveys exists for other stocks. Notably, mathematical (mainly statistical) or conceptual models have been developed for the spawning migration in 12 of these stocks (Figure S1 from the Online Supplemental Material).

Spawning areas and their temporal variability were generally well-characterized, surpassing other spatial components, except presence/biomass, across numerous stocks within each LME (Figures 4–6). Typically identified *via* egg and larval surveys, and to a lesser extent through acoustics (Figures 7 and 8), these areas' time series often exceeded a decade of interannual and few seasonal surveys, albeit with occasional larger time gaps than those for biomass. This regularity was partly because many egg surveys are focused on the Daily Egg Production Method (DEPM) data provision. Acoustics also target the spawning period because fish aggregation is high during that period. While some stocks, such as those in the Southern Benguela and certain areas in the California Current or the Northeastern Pacific, possess high-resolution temporal data, many datasets are characterized by coarser time resolutions ranging from triennial to decadal (Figures 5 and 6). Statistical models linking spawning areas to environmental factors exist in certain areas. Some rely in over 15 years of data (e.g., Moraes, Gherardi, et al. 2012; Maynou et al. 2020), whereas most rely on limited data spanning a few years (e.g., Palomera 1991; Schismenou et al. 2008; Džoić et al. 2022). Mechanistic models for spawning areas were only available in a few stocks, including North Sea herring (e.g., Hufnagl et al. 2015; Kelly et al. 2022), Brazilian sardine in the southeastern Brazil (Dias et al. 2014) or European anchovy in the Mediterranean FAO Geographical

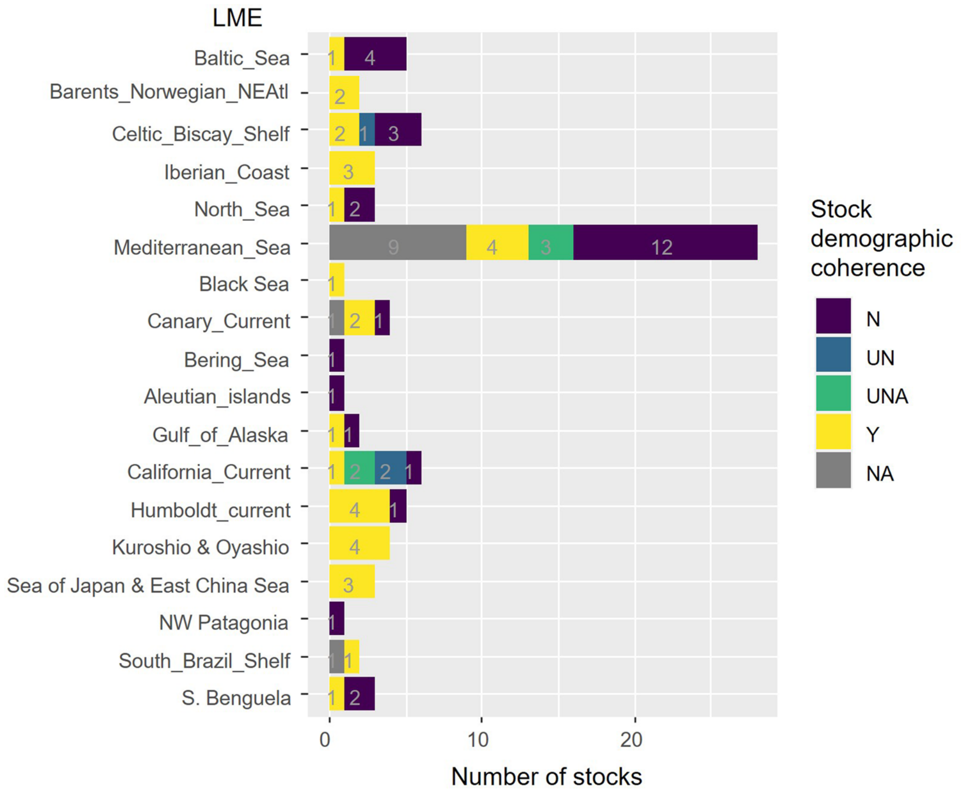

Figure 3. Number of fished stocks with respect to their demographic coherence (see text and Table 1 for explanation) according to the literature. For each stock, several datasets may exist for a given spatial component since datasets often correspond to only a part of one stock (Table S1). Codes for demographic coherence: Y: Yes, and almost always involves stock assessment; N: No/debated; U: unassessed; NA: not known.

Subareas 16 and 22 (e.g., Politikos, Somarakis, et al. 2015; Politikos, Huret, et al. 2015; Falcini et al. 2020).

The link between spawning and nursery areas, mediated through early-stage transport and survival, is a key factor in explaining recruitment variability and was modeled using several approaches. Information for larval routes was only available for 48% of the stocks, a figure that was similar for nursery areas (Figures 5–8, Table S2 from the Online Supplemental Material). For some stocks in northern Europe, California Current, southern Humboldt Current, and the East China Sea and Sea of Japan, time series of larval transport extended over 20 years, whereas shorter series exist for some other areas, such as the Mediterranean. Larval route data were usually derived from model outcomes, as seen in regions like the Humboldt current, Mediterranean, and Canary current, with minimal variability consideration. Lagrangian and IBM models, utilizing relatively modest datasets, have been developed for select stocks in the North Sea, Baltic Sea, and Mediterranean (Figure S1 from the Online Supplemental Material). High-resolution data, including weekly observations, were rare but available in a few cases, such as some stocks in the Baltic Sea.

Data on nursery areas were available across numerous stocks (Figures 4–6), although interannual time series were typically short with considerable gaps, except in the Barents and Norwegian Seas, the California Current, and North-Central Peru. For herring in the Baltic Sea, high-resolution data were accessible. Acoustic surveys contributed a substantial portion of time series data for nursery areas (Figures 7 and 8). Despite this, the spatial modeling of the nursery areas was uncommon, with exceptions in species and areas such as European sprat (*Sprattus sprattus*) in the Baltic Sea, European anchovy in the Black Sea, European sardine in the Mediterranean Sea including the Gulf of Lions and Greek areas, Brazilian sardine, and northern anchovy in the California Current (Figure S1 from the Online Supplemental Material).

Spatial time series on juvenile presence or biomass, usually derived from acoustic surveys with or without complementary sampling (Figures 7 and 8) were available in several areas (52% of the stocks). These kinds of data were notably lacking for several stocks in the Mediterranean Sea, the GOA, the Northeastern pacific stocks, and the South Brazil Shelf (Figure 4). Few datasets had higher than annual resolution (e.g., some

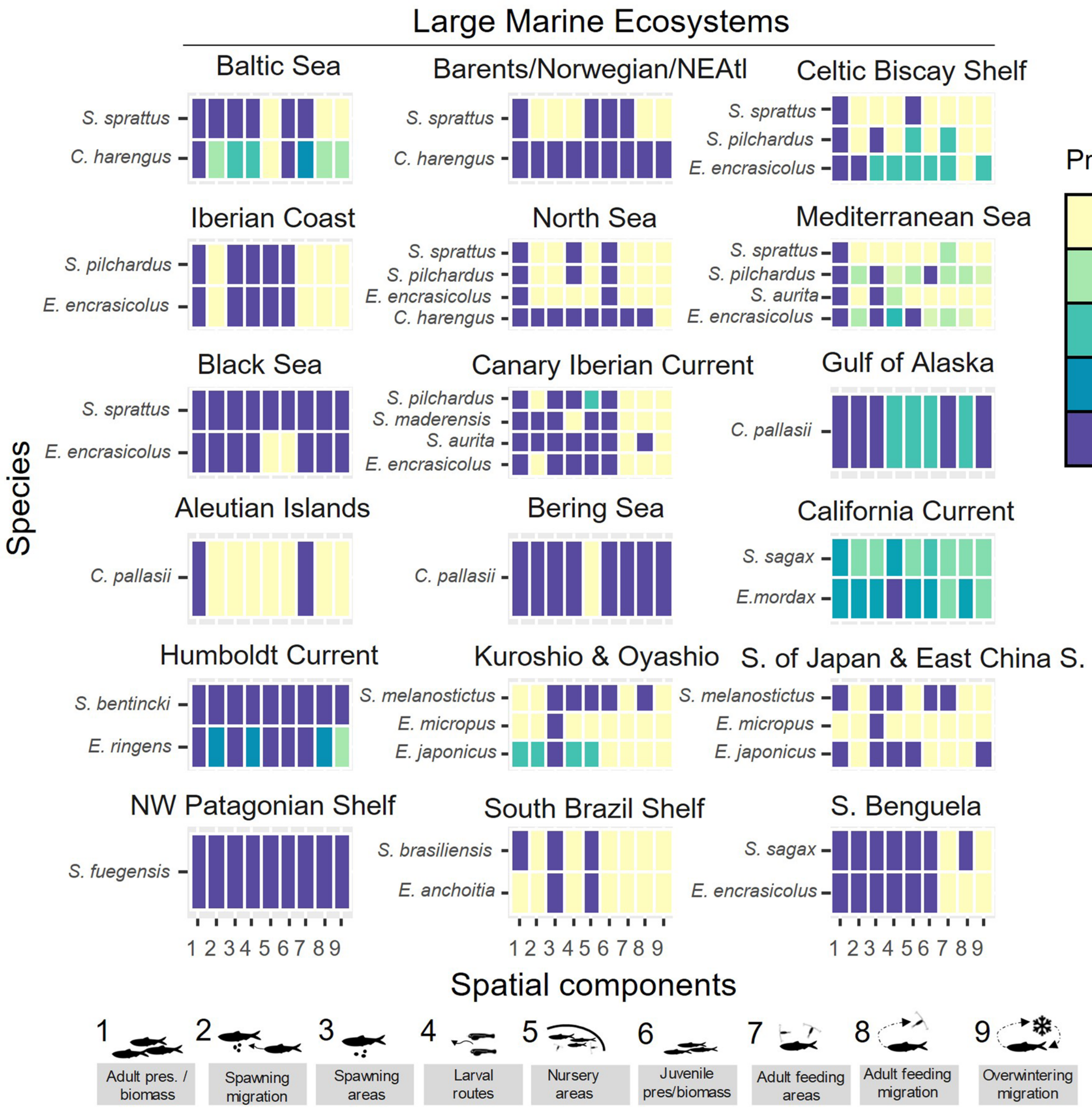

Figure 4. Proportion of stocks for each species and Large Marine Ecosystem (LME) that have data for each of the spatial components, from 1 to 9 (bottom legend). For the Mediterranean, one of the many stocks considered corresponds to data aggregated for the whole region (see Table S1). Further details on each stock per LME are given in Figures 5–8 and Supplemental Tables S1 and S2.

stocks in the California Current). Where data were available, they tended to cover longer durations compared to nursery areas, largely due to acoustic surveys and concurrent sampling (Figures 5–8).

Data on feeding areas and migration routes displayed comparable trends in both the stocks studied and the duration of the time-series available, except in few cases (Figures 4–8). Acoustic surveys also played a key role in gathering data on adult feeding areas (available for 35% of the stocks), explaining the similar patterns in time-series. In few cases, information on feeding and migration areas was also buttressed by the results of individual-based tracking methods (e.g., GOA, Figure 8). Spatial changes due to feeding were also studied using valuable sources of information including historical records (often static pictures), scientific surveys, or fishing operations. Interannual time series on migration spanned over 10 years for many stocks, including herring in the Northeastern Atlantic areas, North Sea, Baltic Sea, Norwegian Sea, and Barents Sea LME. Similarly, stocks in the California Current have been extensively researched. Statistical models for feeding areas have been developed for nine stocks, and their associated migrations have been modeled for four stocks statistically, two mechanistically, and one conceptually. Overwintering migration was only modeled

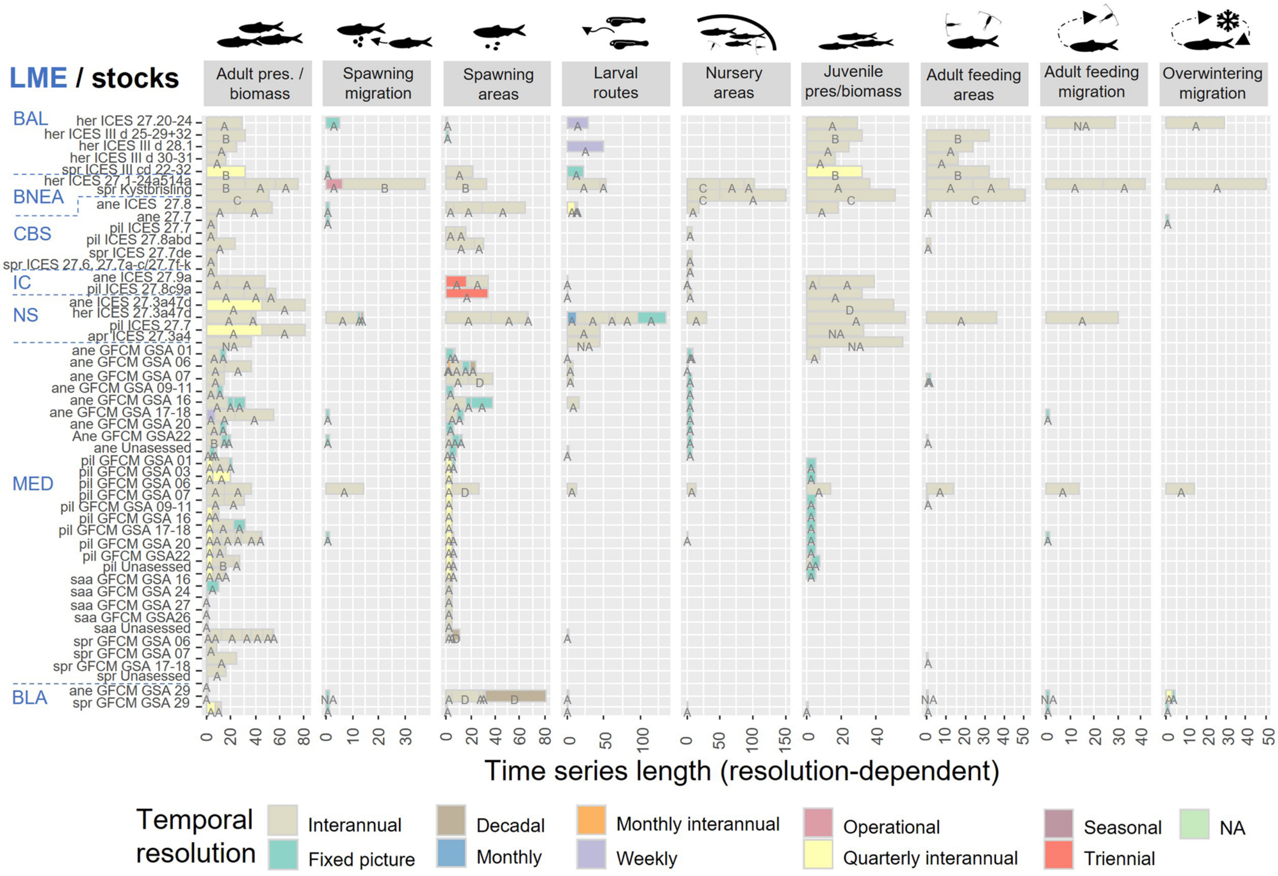

Figure 5. Quantity and quality of temporal information for nine spatial components (top icons) across stocks and Large Marine Ecosystems (LME) (see Figure 6 for additional LME). Bar colors represent temporal resolution, while bar length indicates time series duration. The x-axis label "resolution-dependent" signifies that time units correspond to the temporal resolution indicated by the color scale (e.g., "Monthly" means units are in months). Time gap labels (letters within bars) also follow the same temporal units as the time series resolution: A = <=2, *B*=3–5, *C*=6–10, D = >10, NA is unknown time gap. LME abbreviations are as follows: BAL: Baltic Sea; BLA: Black Sea; BNEA: Barents and Norwegian Sea; CBS: Celtic Biscay Shelf; IC: Iberian Coast; NS: North Sea; MED: Mediterranean Sea. For stocks, the first three letters are the species FAO codes, followed by the stock identifier (see Table S1): ane = E. encrasicolus, her = C. harengus, pil = S. pilchardus, saa = S. aurita, spr = S. sprattus. Note: Some datasets categorized as "unassessed" are included here but do not correspond to managed or officially assessed stocks (see relevant LME sections).

for four stocks (Figure S1 from the Online Supplemental Material).

Summaries by LME

Critical summaries for each LME are provided here. Some of them were combined for clarity, attending to geographical distance, shared species, and information richness. Nonetheless, each LME is specifically covered in its corresponding section. A summary of the history of each fishery is provided in the supplemental material.

Barents Sea and Norwegian Sea

Overview of spatial data and variability

Three SPF species are exploited in the Norwegian Sea and Barents Sea: Atlantic herring, capelin (*Mallotus villosus*, not dealt with in this work), and European sprat. This LME contained two primary stocks and datasets (Figure 2, Figure S2 and Table S1 from the Online Supplemental Material): one for sprat and one for herring. Notably, the herring stock is the largest in the world (FAO 2022a) (see supplemental information for management and trends). Both datasets exhibited robust spatial and temporal distribution coverage.

The Norwegian spring-spawning (NSS) herring stock has been extensively documented and researched for over a century (Hjort 1914; Toresen et al. 2019; Stenevik et al. 2022). Spawning occurs from February to April along the Norwegian coast, with specific spawning grounds shifting in response to stock size (Dragesund et al. 1997). Larvae drift mainly to the Barents Sea, serving as the main nursery area, although some enter fjords that also act as nursery

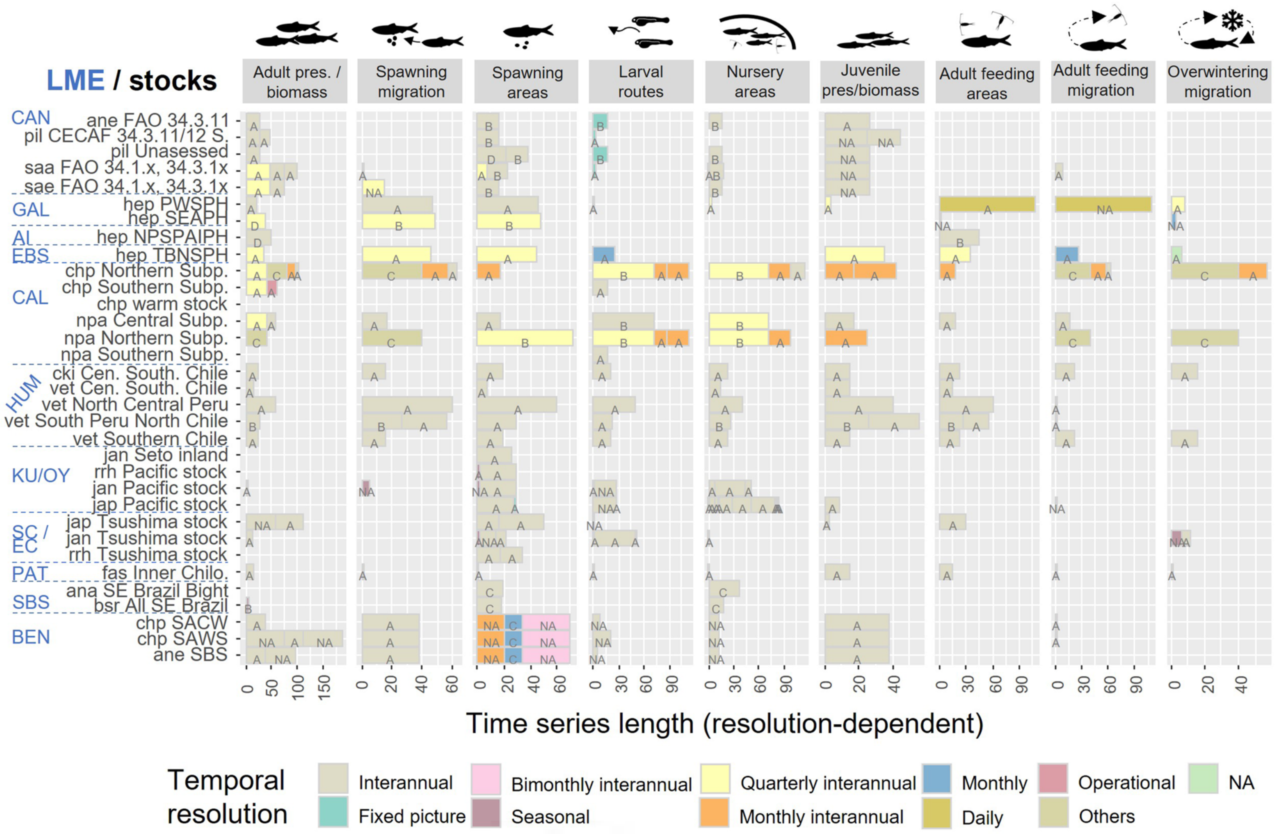

Figure 6. Continuation of Figure 5. Quantity and quality of temporal information for nine spatial components (top icons) across stocks and Large Marine Ecosystem (LME). See Figure 5 for explanations. LME abbreviations are as follows: AI: Aleutian Islands; BEN: South Benguela; CAL: California Current; CAN: Canary Current; EBS: Eastern Bering Sea; GAL: Gulf of Alaska; HUM: Humboldt Current; KU/OY: Kuroshio/Oyashio system; PAT: W. Patagonian Shelf; SBS: South Brazil Shelf; SJ/EC: Sea of Japan and East China Sea. For stocks, ana = E. anchoitia, ane = E. encrasicolus, bsr = S. brasiliensis, chp = S. sagax, cki = S. bentincky, fas = S. fuegensis, hep = C. pallasii, jan = E. japonicus, jap = S. melanostictus, npa = E. mordax, pil = S. pilchardus, rhh = E. micropus, saa = S. aurita, sae = S. maderensis, vet = E. ringens. Note: One dataset with category "unassessed" that does not correspond to managed or official stocks (see corresponding LME sections).

grounds (Skagseth et al. 2015). Several annual acoustic surveys are routinely conducted to estimate stock distribution and abundance (ICES 2023a; see more information below).

Annual monitoring of adult herring presence and biomass has relied on three distinct acoustic surveys (Figure 5, Table S2). Two are coordinated internationally: the "International Ecosystem survey in the Nordic Seas (IESNS)" in May and the "International Ecosystem summer survey in the Nordic Seas (IESSNS)" in June (ICES 2023a). Both have been conducted without any gap since 1996 and 2004, respectively, providing additional information on adult feeding migration and areas (Eliasen et al. 2021). The third, the national "Spawning survey of Norwegian spring spawning herring" has operated for over 30 years (Slotte 1999), with some missing years (Figure S2 and Table S2 from the Online Supplemental Material). This survey has also provided information on adult spawning migration and areas.

Information for coastal sprat was less extensive than for herring. Recent genetic analysis has revealed distinct populations (Quintela et al. 2020), demonstrating that sprat along the Norwegian Skagerrak coast belong to the same stock as sprat in the Norwegian Sea. Sprat spawn in batches from spring to summer, without clear spawning migration (Alheit 1988). Annual acoustic surveys have been conducted to monitor sprat populations the fjords (Stiti 2022). Interannual acoustic surveys, spanning 51 years (with 6–10 consecutive years of missing data) have monitored coastal sprat and estimated adult biomass in Norwegian fjords such as Trondheimsfjorden, Nordfjorden, Sognefjorden, or Hardangerfjorden (Figures 4–8; Stiti 2022). These annual surveys also provided insights into nursey areas, adult feeding areas, and juvenile presence/biomass of sprat, as well as information on herring nursery areas. Data have often been collected over a few weeks, so spatial variability in presence/biomass is only approximated for

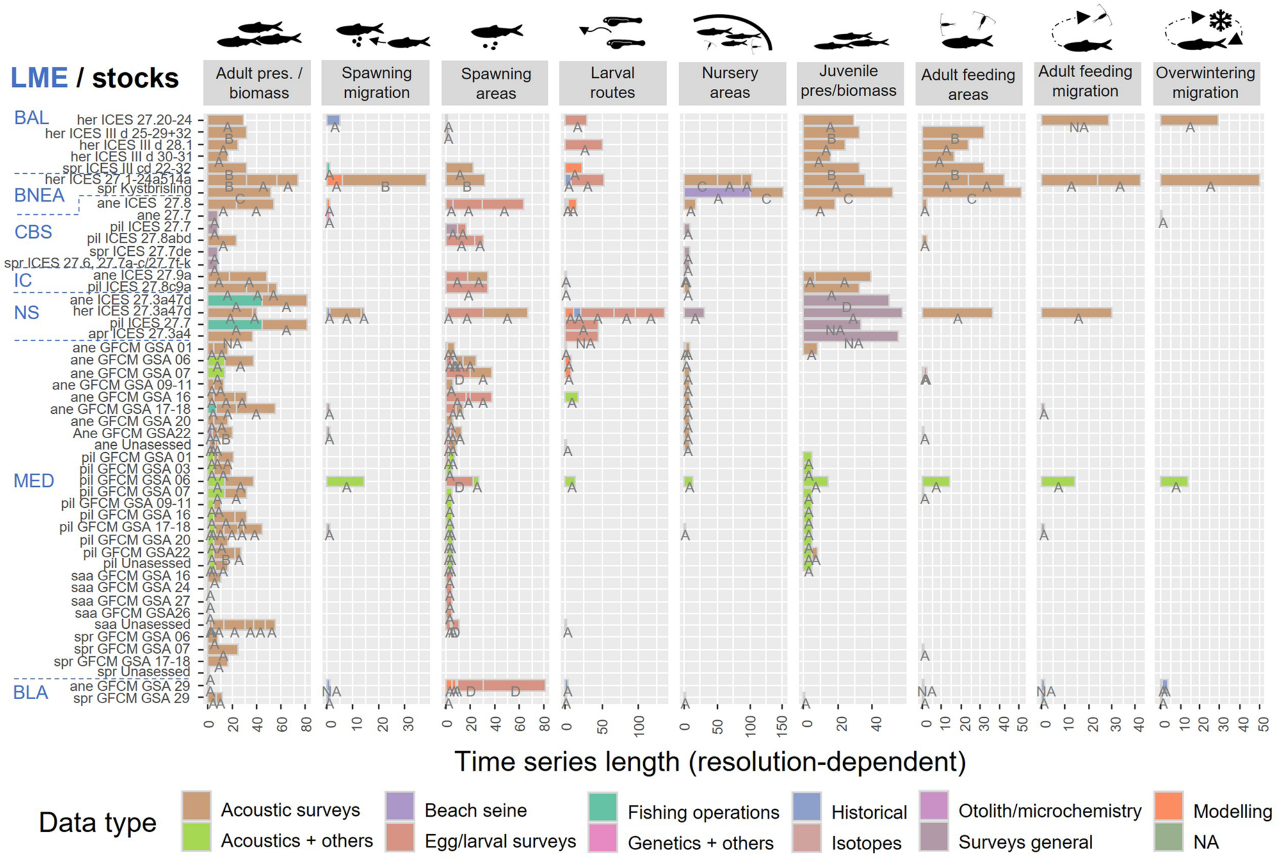

Figure 7. Types of data used in the spatially-resolved time series (see bottom color legend). Refer to Figure 5 for additional explanations. Bar lengths represent time series duration, with units consistent with those in Figure 5.

certain processes, such as feeding areas, while occupancy during other months of the year is less understood. Statistical models of spatial distribution are currently unavailable for coastal sprat (Figure S1 from the Online Supplemental Material).

Spawning spatial variability

Data on spawning migrations and spawning areas were available only for herring. The "Spawning survey of Norwegian spring spawning herring" provides information on spawning areas. Additionally, herring spawning migrations have been described through a mechanistic IBM over six years (Kelly et al. 2022).

Recruitment processes and spatial variability

Spatial data on larval routes and connectivity were only available for herring. For spring spawning herring, these processes have been monitored for 46 years through a dedicated herring larvae survey (Tiedemann et al. 2021), and connectivity and larval routes have been comprehensively described in combination with drift models (Skagseth et al. 2015). Currently, the aforementioned survey is no longer operating. Additionally, a historical sampling program, the Havforskningsinstituttets egg- og larveprogram (HELP), investigated larval and eggs dynamics along the Norwegian coast from 1987 to −1991, resulting in several reports (available at https://imr.brage.unit.no/imr-xmlui/handle/11250/115194, accessed 2024, April 28).

Information on sprat nursery areas has been gathered by the same acoustic survey employed for assessing adult presence. Additionally, a regular beach seine survey has been conducted along the Skagerrak coast since 1919 (missing less than 2 years), providing information on nursery areas and juvenile presence (mainly young-of-the-year, Berg et al. 2022). While the acoustic survey covered the western coast of Norway, the beach seine survey covers the eastern Norwegian coastline. Although young-of-the-year herring are also caught during the beach seine survey, they cannot be linked to the Norwegian Sea and Barents Sea LME.

Spatial data on nursey areas of herring were available from the Norwegian coast and the Barents Sea through three different acoustic surveys. Along the coast, an interannual acoustic survey has been conducted for 51 years (with 6–10 years of consecutive missing data; Figures 4–8; Stiti 2022). In the Barents Sea, the main

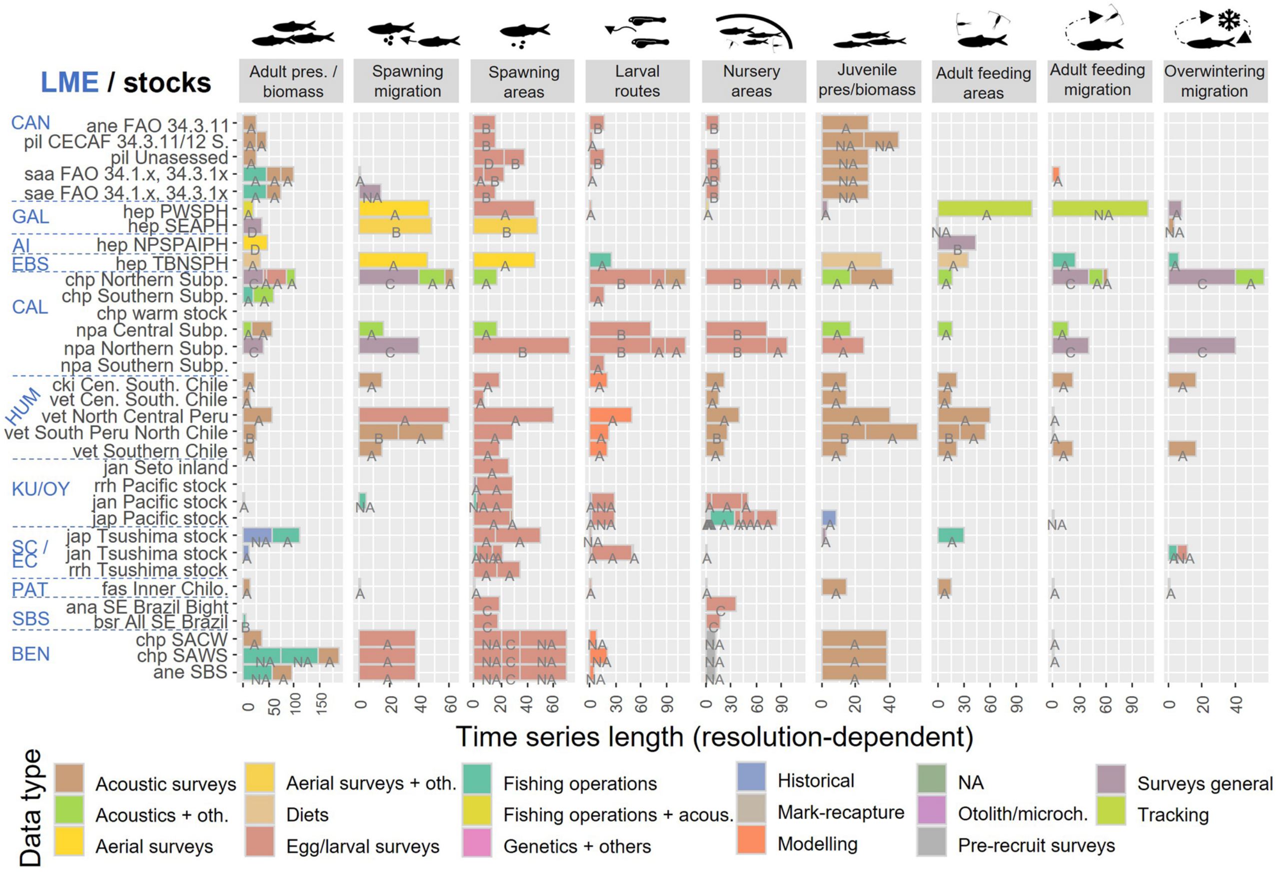

Figure 8. Continuation of Figure 7. Types of data used in the spatially-resolved time series (see bottom color legend). Refer to Figure 5 for additional explanations. Time series units (x axis) are consistent with those in Figure 5.

nursery area, two regular acoustic surveys are conduced: the "Winter Barents Sea Ecosystem survey" in January-February (since over 35 years ago) and the "Barents Sea Ecosystem survey" in August-September (since over than 16 years ago) (Eriksen et al. 2018). These two surveys provide information about the spatial distribution of juvenile herring in the Barents Sea.

Information on juvenile presence/biomass is routinely gathered for sprat by the same acoustic survey used to estimate sprat adult presence, and for herring by the same acoustic surveys used for nursery areas, the "Winter Barents Sea Ecosystem survey" and the "Barents Sea Ecosystem survey".

Feeding areas and migrations

Information on feeding areas has been gathered for sprat by the same acoustic survey used for adult presence, and for herring by the IESNS and the IESSNS surveys. Information on feeding migrations was only available for herring, provided by the IESNS and IESSNS. Data on overwintering migrations were only available for herring; the main herring fisheries have been taking place in the overwintering areas, as detailed in several articles (Huse et al. 2010, and references therein).

Key messages

- Improved knowledge on ecological connectivity, particularly for sprat along fjords and herring between fjords and the Barents Sea, is vital.
- Acoustics-based spatial information has typically relied on relatively short-duration surveys (weeks). Particularly for sprat, comprehensive spatial information on biomass and presence throughout most months is lacking.
- Despite the richness of spatial herring data (where and when do herring occur), the driving mechanism for shifts in migration patterns observed in the last half century are still unknown.

Baltic Sea

Overview of spatial data and variability

Two exploited SPF species inhabit the Baltic Sea: Atlantic herring and European sprat (Figure 2; Figure S3 and Table S1 in the Online Supplemental Material). Both species have been managed under the ICES multiannual management plan since 2016 (See Supplemental Material). Sprat is managed as a single stock, while herring is divided into four management units.

Across the Baltic Sea's salinity gradient, from fully marine in the west to almost freshwater in the north and east, multiple herring populations have evolved distinct morphometric characteristics as phenotypical responses to limited salinity (Bekkevold et al. 2005). These Baltic Sea herring populations exhibit considerable variation in their annual migration patterns and susceptibility to commercial fishing (Figures 2 and 3). Nearly every region harbors both spring-spawning and autumn-spawning populations, which are genetically distinguishable (Bekkevold et al. 2023). Their respective dominance has fluctuated over the history of Baltic Sea fisheries, influenced by over-exploitation and climate regimes changes (MacKenzie and Ojaveer 2018; Atmore et al. 2022). In the Central Baltic Sea, autumn spawners dominated until the 1950s (Aneer 1985), whereas in the Western Baltic Sea fishery, both ecotypes had equal proportions until the late 1960s, after which spring spawners became dominant (Weber 1974). Within the spring-spawning ecotype, modern stock separation techniques have identified up to 12 local populations (Martinez Barrio et al. 2016), currently managed as four stocks across the Baltic Sea and transition areas (ICES 2022a).

Sprat inhabits the entire Baltic Sea from the Belt Sea to the Gulf of Bothnia and the Gulf of Finland (Aro 2002). Despite the salinity gradient, sprat has been considered a single population and is managed accordingly (Shvetsov et al. 1995). Its highly migratory behavior and production of pelagic eggs result in high gene flow within the Baltic Sea, with minimal mixing between the Kattegat and Skagerrak (Aro 2002; Limborg et al. 2009).

All commercially exploited Baltic SPF stocks are subject to fisheries-independent acoustic surveys, yielding spatial data on adult presence and biomass (Figure 4). These surveys have combined hydroacoustic measurements with biological sampling using pelagic trawls and are organized, and results summarized, within ICES-coordinated survey working groups: the Baltic International Fish Survey Working Group (WGBIFS) and the Working Group on International Pelagic Surveys (WGIPS). The acoustic surveys have covered most Baltic Sea regions, capturing interannual variations in the distribution and biomass of sprat and herring during specific periods.

Adult sprat biomass has been estimated biannually in May (Baltic Acoustic Spring Survey, BASS) and October (Baltic International Acoustic Survey, BIAS). Adult Central Baltic herring and Gulf of Bothnia herring biomass has been estimated annually in October (BIAS), while adult Gulf of Riga herring biomass has been evaluated annually in July/August (Gulf of Riga Acoustic Herring Survey, GRAHS). Adult Western Baltic spring-spawning herring biomass has been assessed both within and outside the Baltic Sea through biannual acoustic surveys in July (Acoustic Survey in the Skagerrak and Kattegat, the North Sea, West of Scotland, and the Malin Shelf area, HERAS) and October (BIAS), as well as biannually with demersal trawl surveys in January/February and July/August (International Bottom trawl survey, IBTS).

Spawning spatial variability

Spatial data outside survey periods was limited, providing snapshots from individual years. Sprat, a batch-spawner, exhibits a spawning period spanning up to two months (Parmanne et al. 1994). Sprat spawning typically occurs in the deep basins of the central Baltic Sea between January and June, peaking between March and May (Haslob et al. 2013). Sprat eggs are pelagic, and recruitment displays significant year-to-year variability (ICES 2023b).

Spring-spawning herring populations undertake annual spawning migrations to shallow inshore systems, including bays, lagoons, and estuaries, occurring from March to early May in the Western Baltic to June–July in the northeastern distribution range. Pre-spawning aggregations often form in deeper areas near spawning grounds before the actual spawning event. Historically, these aggregations attracted a lucrative trawling fishery, currently suspended in the Western Baltic Sea.

Factors influencing the timing of herring spawning migration remain poorly understood, despite their critical role in recruitment success (Figure 4). Baltic Sea herring exhibits strong spawning site fidelity, but the exact spatial scale of this behavior is uncertain. Improved knowledge would have major implications for regional coastal zone management, which currently does not include important herring spawning grounds.

Time series data on herring spawning areas in the Baltic Sea were generally scarce (Figures 4 and 5). Previous tagging experiments suggested directed homing behavior in Baltic Sea herring (reviewed in Aro 2002). Recent studies have confirmed natal homing, where individuals return to their hatching sites. Approximately, 70% of school members exhibited natal homing, while around 30 % were strayers from different spawning sites, maintaining genetic diversity within metapopulations (McQuinn 1997; Moll 2018).

Herring spawn benthic eggs attached to bottom structures. In the Baltic, spring-spawning herring often utilize submerged aquatic vegetation (von Nordheim et al. 2018). Comprehensive records of specific spawning areas were lacking in the reviewed literature; most knowledge is based on historical and fishery-dependent observations of ripe and running fish area (Figure S3 from the Online Supplemental Material). For the Western Baltic stock, Greifswald Bay, an approximately 500 km^2 embayment in eastern Germany, serves as a major spawning and nursery area. This is based on a 30-year time series of larval abundance strongly correlating with the presence of one-year-old juveniles found in the outer Western Baltic Sea a year later. Given the presence of spawning adults and high abundance of all larval stages, this system has been recognized as an important spawning, larval retention, and nursery area (Polte et al. 2017). Spawning areas of Central Baltic herring have been monitored in case studies by scuba divers at the Lithuanian (Šaškov et al. 2014) and Finnish coast (Kääriä et al. 1997).

Sprat spawning occurs throughout the Baltic Sea, with key areas being the Bornholm Basin, the Gdansk Deep, and the Gotland Basin (Aro 1989; Parmanne et al. 1994). Although spawning has been observed in the Northern Baltic regions, salinities below 6 PSU result in egg mortality due to reduced buoyancy (Kändler 1949; Sjöblom and Parmanne 1980). The BASS survey, conducted for few weeks in May, cannot achieve complete coverage of the spawning area and timing.

Recruitment processes and spatial variability

Some Baltic Sea herring stocks, such as the Western Baltic and Gulf of Riga stocks, showed long-term larval abundance, growth, and survival surveys in major reproduction areas, spanning multiple decades (Figures 4 and 5). Some of these surveys have served as input variables for assessing the recruiting year class (ICES 2023c, 2023b).

Although standardized and regular sampling of sprat larvae is lacking, depth-stratified sampling suggests that feeding sprat larvae mostly occur in surface layers, making them prone to wind-induced drifting (Voss et al. 2003). Lagrangian particle simulations have shown that temperature and transport patterns significantly influence recruitment variability, which can be substantial between years (Baumann et al. 2006).

While herring larval nursery areas are well-documented, after metamorphosis, juvenile herring (0-group) disperse along outer beaches, often forming mixed schools with juvenile sprat, making quantification challenging. Consequently, data on the spatial and temporal variability were scarce (Figure 4). These fishes are not monitored until they migrate into adult habitats, where they are assessed as one-year-old individuals during the acoustic surveys. Spatial data on sprat nursery areas was limited, with coastal regions not routinely surveyed, hindering quantitative assessments of habitat importance.

Juvenile sprat has been regularly caught during the BASS and BIAS surveys in May and October, respectively. Juvenile Western Baltic spring-spawning herring have been representatively sampled in the BIAS survey and are included in the stock assessments. Further, the IBTS quarter 1 survey provides an abundance index used in assessments. Juvenile biomass of Central Baltic herring, Gulf of Bothnia herring, and Gulf of Riga herring is surveyed with acoustic methods, but coastal areas shallower than 20 m have not been adequately sampled due to survey depth limitations.

Despite a “blind spot” regarding the young-of-the-year herring abundance, advanced juveniles (1+ year) have been sufficiently surveyed (Figure 4) alongside adults in hydroacoustic surveys (ICES 2023c), resulting in a valuable time series of about 30 years (Figure 5). Environmental factors like temperature and wind regimes likely influence late larval and early juvenile stages (Voss et al. 2006; Baumann et al. 2006).

Feeding areas and migrations

Western Baltic herring’ feeding areas, located in the North Sea, adjacent to the Baltic Sea transition area (ICES SD 3a, Kattegat), have been surveyed annually in late June to July using the herring acoustic survey (HERAS) (Table S2 from the Online Supplemental Material). In this region, the stock coexists with North Sea stocks and is jointly targeted by fisheries. Surveys suggest that the stock’s feeding grounds have remained relatively constant between years. Following spawning, the spring-spawner component of Central Baltic herring migrates into the central Baltic Basins, where they have been surveyed by the BIAS in October.

Sprat’s feeding season extends from July to November in the southern and central Baltic and from August to December in the northern Baltic (Aro 2002). Sprat have been surveyed annually during their feeding season in October using the BIAS. The extent and distance traveled by Baltic Sea herring stocks differ widely among populations. Western Baltic herring, for example, undertake the largest migration, from inner coastal spawning areas through the

Skagerrak/Kattegat transition area to reach feeding grounds in the Northeastern North Sea (ICES SD 3a). This has been inferred from the presence of the parasite *Anisakis* sp., serving as a biotag since infestation can only occur in the North Sea where intermediate hosts like euphausiids are present (ICES 2001; Aro 2002). Other stocks, such as Central Baltic herring and Gulf of Riga herring are not considered to migrate as far, with feeding grounds located offshore adjacent to their inshore spawning grounds (ICES 2001).

Data on the feeding migration of Baltic sprat was unavailable; the October BIAS survey provides only a snapshot on the current species distribution. Due to their small size preventing tagging techniques, information on the extent of their feeding migration remains limited (Aro 2002).

Overwintering areas for BS herring stocks are generally well-explored (Figure 4). Nonetheless, limitations exist due to the static nature of surveys, which may not always align with herring behavioral dynamics. For most Western Baltic herring migrating from North Sea feeding grounds, overwintering occurs in the confined waters of the Øresund located between Denmark and Sweden (Rasmus Nielsen et al. 2001). These schools have been regularly assessed by the German Hydroacoustic survey GERAS (part of BIAS), covering the entire Western Baltic Sea and providing annual data on overwintering distribution over a 30-year time series (Figure 5). The survey's timeframe, spanning only three weeks, imposes limitations on analyzing spatiotemporal variability. Conversely, other local herring populations in the central and Northeastern Baltic Sea are considered to overwinter offshore near their spawning grounds, often resembling their summer feeding grounds (ICES 2001). Data concerning the overwintering migration of Baltic sprat were unavailable.

Key messages

- Acoustics-based surveys in the Baltic Sea usually span a few weeks, focusing on herring and sprat. Consequently, comprehensive spatial information of adults and juveniles for many species is lacking throughout most months. Current knowledge relies on individual studies covering only a few years, complicating year-to-year comparisons. Therefore, leveraging the increasing availability of harmonized acoustic data is recommended to better investigate and understand the spatial distributions of small pelagic species.
- Information on spawning areas comes from acoustic surveys for sprat and larvae surveys for Western Baltic Spring-spawning herring, with acoustic methods also used to estimate herring and sprat biomass during feeding seasons. Spatial time series for nursery areas and juvenile clupeids are sparse and should be promoted, although larger juveniles are partly monitored in these surveys.
- It is recommended to conduct comprehensive studies on annual spatial diet changes and to gather data on seasonal and interannual variations in feeding areas and movement patterns, including spawning migrations, to address the current lack of information.
- The small-scale distribution of herring spawning beds and nursery habitats of young-of-the-year juveniles is understudied. These knowledge gaps are relevant, as regional coastal zone management and marine spatial planning currently overlook key reproductive areas.
- Important knowledge gaps exist in migration patterns, feeding grounds variability, overwintering areas, and especially in the phenology of spawning migrations. Two acoustic surveys offer brief glimpses of distribution, but their static nature, due to seasonal timing and limited area coverage, restricts dynamic understanding. The baseline knowledge for these surveys and, consequently, fishery assessments come from tagging experiments about 40 years old. Potential shifts in migration phenology and changes in feeding and overwintering patterns remain poorly understood and should be further investigated (see Moyano et al. 2023 for details).

North Sea

Overview of spatial data and variability

SPF fisheries in this LME represent 45% of total landings (2020–2022; average) in the North Sea, primarily driven by Atlantic herring (*C. harengus*) and European sprat (*Sprattus sprattus*) with considerably lower landings of European sardine (*S. pilchardus*) and European anchovy (*E. encrasicolus*) (ICES 2022b, 2022c, 2022d). These species were grouped into four stocks and six datasets (Figure 2; Figure S4 and Table S1 in the Supplemental Material). The management and historical trend information is included in the Online Supplemental Material.

The biology of North Sea herring has been thoroughly reviewed (Nash and Dickey-Collas 2005; Payne et al. 2009) as has sprat (Daewel et al. 2011). Considerable knowledge on sardine (Voss et al. 2009) and anchovy (Petitgas et al. 2012) life histories has also been documented. There are four main spawning components of North Sea herring: Orkney/Shetland, Buchan, Banks, and Downs Downs (Schmidt et al. 2009). The first three components essentially spawn in the autumn (Dickey-Collas et al. 2010), whilst Downs herring spawn in the winter (Clausen et al. 2007). Furthermore, there are known occurrences of spring-spawning herring in the Thames estuary (Roel et al. 2004), the Wash (Dickey-Collas et al. 2010), Firth of Forth (Frost and Diele 2022), Shetland (Brigden et al. 2023), and Norwegian fjords (Berg et al. 2017). None of these are considered in the assessment of the North Sea herring stock and the herring in the Norwegian fjords is considered to be unrelated to the rest of the herring populations in the North Sea (Dragesund et al. 1997). Recent genetic studies on herring in the North Sea indicate that there are a number of populations from adjacent areas, that do not spawn on the main spawning grounds in the North Sea, that mixed with the North Sea herring stock (Bekkevold et al. 2023). North Sea sprat spawn mainly between March and August (Munk 1993) in the southern North Sea and German Bight (Baumann et al. 2009). Typically, European sardine spawn no further north than the English Channel (Munk et al. 2024) but spawning in the Southern North Sea had been documented at least since the early 1950s (Aurich 1953, von Westernhagen et al. 2002). In recent years sardine larvae are found in increasing numbers in the German Bight between June–July (Kanstinger and Peck 2009, Munk et al. 2024) and may also occur as far north as the Skagerrak in January (ICES 2021c, 2023c). Whilst anchovy historically spawned in the Zuider Sea (SE North Sea), the species was not present in substantial numbers until the mid-1990s (Beare et al. 2004). At present, anchovy spawn in May–June in the German Bight (Raab et al. 2012), Wadden Sea, and eastern Oosterschelde (Boddeke and Vingerhoed 1996). Statistical modeling approaches using various data sources were only available for herring and for components 1–4 and 7 (Table S2 and Figure S4 from the Online Supplemental Material, Figures 5 and 7).

All SPF stocks in the North Sea had spatially resolved data on adult presence or biomass at the stock level (Figure 4). These data were generally interannual (Figure 5) and namely from acoustic surveys, however, there are data from fishing operations and historical data sources (Figure 7; Table S2). Nonetheless, the new genetic data suggests that there are some uncertainties with respect to the designation to populations of herring in the North Sea (ICES 2024a). In addition, the data for anchovy and sardine were also resolved at quarterly interannual level (Figure 5; Table S2 from the Online Supplemental Material). Each time series were generally long with only one under 36 years in length (Table S2 from the Online Supplemental Material) with limited gaps (≤2 years); herring biomass/presence is particularly well studied with 160 years of available data, being the longest of any stock in this study (Figures 5 and 7; Table S2). Furthermore, over 75% of the herring biomass data sources have been spatially described by statistical models (Table S2 from the Online Supplemental Material and references therein).

Spawning spatial variability

Spatial data on spawning migrations were scarce and only available for herring through interpretation of surveys of adults through the year and larval surveys on the spawning grounds (Figures 4 and 5; Table S2 from the Online Supplemental Material). There were insufficient data available on the other three species to visualize the annual spawning migrations and their interannual variability.

Spatiotemporal data series of spawning areas were only available for herring in the North Sea (Figure 4). These data consisted of long time series of fisheries-independent surveys (Table S2 from the Online Supplemental Material), with an additional summary figure describing historical perceptions. Interannual acoustic survey data (6 years) from Beare et al. (2002) has been used to statistically model spawning areas, whilst Hufnagl et al. (2015) used mechanistic models to model these areas from larvae surveys (30 years) (Figure 5; Table S2 from the Online Supplemental Material). There were insufficient data available on the other three species to visualize the annual spawning locations and their interannual variability. This is primarily due to them being pelagic spawners and there were only periodic historical dedicated surveys which did not cover the whole potential spawning areas.

Recruitment processes and spatial variability

Data on the connectivity of eggs and larvae was available for 75% of the North Sea stocks (herring, sprat, and sardine), though not for anchovy (Figure 4). Herring data comprised *a* > 100-year time series consisting of interannual and summaries of larvae surveys and mechanistic transport modeling approaches (Table S2 from the Online Supplemental Material). Larval routes of sardine and sprat were also based on interannual egg and larval surveys (Figure 7; Table S2 from the Online Supplemental Material).

Spatial data on nursery areas were limited to herring (Figures 4 and 5). These data were available from general surveys (Figure S4; Table S2 from the Online Supplemental Material), which specifically target the early life history stages of herring and had a good spatial coverage of herring juveniles (e.g., Röckmann et al. 2011). There were insufficient data on the other species to adequately describe the nursery areas and their spatial and temporal variability.

Estimates of juvenile presence/biomass have been described for all North Sea SPF species (Figures 4 and 5; Table S2 from the Online Supplemental Material) by data collected from fishing operations during the interannual, ICES North Sea International Bottom Trawl Surveys in quarter 1 and 3 (NS-IBTS). Whilst the time series length varied between species, there remained a minimum of 33 years of available data with only the juvenile anchovy data set presenting considerable data gaps (12 years total) (Figure 7; Table S2 from the Online Supplemental Material).

Feeding areas and migrations

Corten (2001) detailed feeding areas for herring based on interannual acoustic surveys and the acoustic surveys represented the only available dataset (Figures 5 and 7) for all species in the North Sea (Figure 4).

Only one study (Corten 2001) provided data on feeding migrations of herring (Figures 5 and 7) in the North Sea consisting of 30 years of interannual acoustic surveys (Table S2 from the Online Supplemental Material). No data were present for sprat, sardine, or anchovy (Figures 4, 5, and 7).

Key messages

- Despite the North Sea being one of the better studied LME, only information on presence/biomass of both adults and juveniles are available for all SPF species. Similarly, all species except anchovy have information on larval routes. Herring is the only species with specific knowledge of spawning migrations and areas, nursey areas, adult feeding areas and feeding migrations. No information is available for any species on overwintering migrations for the North Sea. In the case of herring as autumn and winter spawners in the period post spawning and in the case of the other three species it is our understanding that these migrations occur in other LMEs.
- As a demersal spawner, data on herring spawning areas mostly came from fisheries-independent surveys that focused on recently hatched larvae (ICES 2024b). Nevertheless, as the other three species are pelagic spawners, spawning area information depended on the presence of adults in spawning condition or eggs within the water column, of which sufficient data were lacking, e.g., survey coverage (acoustic biomass and eggs) and sampling (eggs, larvae, and adults).
- Recent genetic studies suggested that the distribution, occurrence and mixing of populations of herring which spawn in adjacent waters is more complex than originally thought, e.g., North Sea herring west of Scotland, or various Baltic herring populations in the North Sea. To understand the ecology and also potentially input to management of herring in the North Sea, there is a need to quantify the presence and location of these populations.
- There is evidence of interactions between SPF species including shared schools (especially sprat and juvenile herring) and dietary overlap between all species, but the influence of sardine and anchovy is largely unknown.
- Though there is a wealth of information available describing spatiotemporal variability in herring spawning, there is a greater complexity beyond the assumed north-south gradient (the presumed northward shift of spawning grounds and later shifts is related to both autumn and winter spawning times). Spring spawning populations in the North Sea have received limited review and their influence on biomass, population mixing, spawning areas, and number of small-scale populations are not fully documented.

Celtic Biscay shelf

Overview of spatial data and variability

Primary SPF fisheries target European anchovy and European sardine in the Bay of Biscay, and sprat and European sardine in the Celtic Sea-English Channel region. These species are managed as six stocks (Figure 2, Figure S5 and Table S1 from the Online Supplemental Material). The management area for anchovy in the Bay of Biscay fits the population structure in the area; genetic studies confirmed that the Bay of Biscay population is separated from anchovy in the English Channel, which is a single population with North Sea anchovy (Zarraonaindia et al. 2012; Huret et al. 2020). Notably, Bay of Biscay anchovy extends southwards beyond the Celtic Sea – Biscay shelf LME, and its management unit consistently covers ICES subdivision 27.8.c which belongs to the Iberian Peninsula LME.

For sardine, the populations within the LME seem less structured (Caballero-Huertas et al. 2022), and the current management units distinguishing between the Bay of Biscay and the northern area may not be consistent with the genetic structure (McKeown et al. 2024). To the south, limited connectivity between ICES subdivisions 27.8.abd and 27.8.c supports the two existing management units (Bay of Biscay and Iberian Peninsula; (Silva et al. 2019). Two sprat stocks were considered: the English Channel (Walker et al. 2023) and the Celtic Seas, but a lack of genetic structure among samples from across the Northeastern Atlantic indicates connectivity across management boundaries (McKeown et al. 2020).

Spatial information for these stocks primarily relied on annual acoustic and DEPM surveys (Massé et al. 2018) In the first case, they have focused on adult and juvenile distributions and biomasses in the Bay of Biscay during spring and autumn and in the Celtic Sea-English Channel during autumn. DEPM egg surveys described spawning distribution and quantity, further detailed using Continuous Underway Fish Egg Sampler (CUFES) sampling onboard acoustic and demersal surveys. In the northern part of the study area, ichthyoplankton sampling provided insights into sardine spawning.

Spatial data on adult presence and biomass relied primarily on annual acoustic and DEPM surveys (Figure 7). Pelagic surveys occurred in a less consistent and coordinated manner before the 2000s (Massé et al. 2018). Since 2000, the Bay of Biscay has been sampled in spring using acoustic (PELGAS "monitoring of small pelagic fish in the Bay of Biscay" covering ICES subdivisions 27.8.abd and PELACUS "Pelagic ecosystem acoustic-trawl survey" covering ICES subdivision 27.8.c) and DEPM (BIOMAN, "Biomass of Anchovy") surveys. Since 2003, the JUVENA survey has focused on the acoustic estimation of anchovy juveniles in autumn. Anchovy biomass, after collapsing in 2005 and subsequent fishery closure until 2010, has significantly increased and remained consistent. Sardine biomass has remained relatively stable over the last two decades but has been assessed as overexploited and overfished in recent years. The growing annual survey time series has enabled statistical analysis of changes in adult distribution patterns (Petitgas et al. 2014) and species habitat description (Doray et al. 2018).

In the northern part of the area, the first survey was conducted in 2012 and takes place during autumn (PELTIC, "Pelagic ecosystem survey in the Western Channel and Celtic Sea"). The spatial distribution of the SPF community for the rest of the year remains poorly understood. Despite the short time series, ecological changes are evident, with sardine and anchovy increasing in abundance (van der Kooij et al. 2024), consistent with observations in the North Sea (Petitgas et al. 2012), while sprat and herring biomass have declined. Surveys within the LME have been coordinated annually to standardize methods (Massé et al. 2018).

Spawning spatial variability

The main spawning activity for anchovy is in the southeastern Bay of Biscay and extends from April to August (Motos 1996; Huret et al. 2018; Erauskin-Extramiana et al. 2019), progressively extending northwards as the season unfolds. Recently, earlier and northward spawning expansion has been observed (ICES 2021a), likely due to density-dependent effects from increased anchovy stock biomass. This has occasionally led to juvenile anchovy drifting northwards into the English Channel (van der Kooij et al. 2024). Anchovy spawning has not been observed north of the Bay of Biscay within the LME; instead, it occurs in the North Sea, originating from the northern population (Huret et al. 2020).

Sardine spawning in the Bay of Biscay overlaps with anchovy spawning but extends further north, with additional spawning components in the English Channel. The sardine spawning season spans from March to July (Coombs et al. 2006; Huret et al. 2018), shifting north later in the season (Stratoudakis et al. 2007), where a second spawning peak occurs in autumn (Coombs et al. 2010). Limited recent information is available on sprat spawning, but it is known to occur offshore in open waters within the English Channel and North Sea, running from January to July, peaking between February and March in the English Channel (Milligan 1986; Bréchon et al. 2013).

The absence of regular, dedicated seasonal sampling hinders understanding of SPF spawning migrations. Fixed representations (Figure 5) relied on historical information, genetics, and modeling (Figure 7). No anchovy spawning has been recorded in the Celtic Sea and Channel, where juvenile and adult fish have been increasingly observed in autumn. Genetic methods and anchovy catches from IBTS surveys suggest a late winter or early spring migration from the Channel to the southern North Sea (Huret et al. 2020).

In the Bay of Biscay, main anchovy spawning is in the southeast from April to August (Motos 1996; Huret et al. 2018; Erauskin-Extramiana et al. 2019). Uriarte et al. (1996) described a winter migration to the southeastern Bay of Biscay following a more dispersed autumn distribution. Using an IBM with a bioenergetic module, Politikos, Huret, et al. (2015) provided insights into the energy budget benefits of this spawning migration. Sardine is more widespread throughout the year, with no known spawning migration.

Egg data from annual surveys (Figure 7) offer insights into spawning locations and their interannual variability. CUFES and DEPM regular surveys in spring cover anchovy and sardine spawning in the Bay of Biscay (Huret et al. 2018; Erauskin-Extramiana et al. 2019). Recurrent annual sampling covering over 30 years for some stocks has allowed statistical analysis of the spatiotemporal changes and their drivers. Bellier et al. (2007) described changes in the general spawning distribution and main locations for both species between the late 1960s and current surveys. Anchovy distribution is age dependent (Ibaibarriaga et al. 2013) and the range expansion or contraction has been related to population biomass (Erauskin-Extramiana et al. 2019). Offshore sardine spawning observed in the 2000s has disappeared over the last decade (Petitgas et al. 2020).

In the Celtic Sea and English Channel, ichthyoplankton data from acoustic surveys provide a snapshot of sardine autumn spawning (Figures 5 and 7). Since 2014, this has been supplemented by egg data collected with the CUFES onboard IBTS surveys (EVHOE survey in the Bay of Biscay and CGFS survey in the Channel (Mahe and Laffargue 1987; Le Roy et al. 1988)). Ongoing fixed station sampling in the western Channel has provided a multi-decade time series of sardine spawning activity, showing an increase in the autumn component (Coombs et al. 2010). Historical data are the sole source of information on sprat spawning activity in the northern LME (Wallace and Pleasants 1972; Milligan 1986).

Recruitment processes and spatial variability

Larval dispersal pathways in the Bay of Biscay have been delineated for anchovy through dedicated larval surveys (Figure 7), based on size distribution (Urtizberea et al. 2008), otolith microchemistry (Aldanondo et al. 2010), and modeling studies based on larval dispersal (Huret et al. 2010) or IBM models (Figure 5). The longest available time-series spanned 12 years and pertained exclusively to anchovy.

Spatial data on nursery areas were scarce for most stocks (Figures 7 and S4 from the Online Supplemental Material). Young-of-the-year sardine, anchovy, and sprat are captured by annual acoustic surveys in the Celtic Sea and western English Channel, providing emerging information on nursery areas (Campanella and van der Kooij 2021). The most consistent nursery dataset originates from the dedicated juvenile anchovy survey in the Bay of Biscay, encompassing nearly two decades and providing insights into size distribution of late larvae and juveniles (Boyra et al. 2013). Over several years, stomach content analysis conducted on samples from this survey has yielded valuable information on juvenile feeding patterns and diet (Bachiller et al. 2013).

Within this LME, this survey was also the primary source for the recruitment index for Bay of Biscay anchovy (Boyra et al. 2013). An additional acoustic survey in the Celtic Sea – English Channel region, spanning < 10 years, has provided information on the distribution and abundance of the SPF community, including juveniles of sardine, anchovy, and sprat (Figure 7, Figure S5 from the Online Supplemental Material).

Feeding areas and migrations

Trophic investigations in the region predominantly rely on ad hoc stomach analyses during surveys (two years of data, Figure 5). Comprehensive stomach analysis studies encompassing the entire SPF community were available for the Bay of Biscay (Bachiller et al. 2015) and the Celtic Sea – English Channel area (Plirú et al. 2012; Lamb et al. 2019), complemented by trophic modeling exercises (Patel et al. 2023).

Due to the absence of routine dedicated seasonal sampling, knowledge on overwintering or feeding migrations of SPF in the area remains limited. Available information is largely confined to fixed historical depictions (Figure 5) or genetic insights (Figure 7). For anchovy, overwintering migrations follow a route opposite to their spawning migrations, both in the Bay of Biscay (Uriarte et al. 1996; Huret et al. 2020) and in the northern region, migrating from the southern North Sea to the English Channel (Huret et al. 2020).

Key messages

- Recurrent annual surveys using acoustics and eggs sampling in the area have been crucial for detecting distribution and biomass changes across egg, juvenile, and adult stages. Statistical techniques have been employed to identify spatiotemporal patterns of these changes and map essential habitats. Occasionally, historical surveys enabled comparisons between present and historic distributions, spanning several decades. However, there has been a lack of data on larval distribution and the evolution of overwintering habitats for most SPF species over time.

- Information regarding adult migration patterns and early life stage connectivity primarily stemmed from process studies, comprising dedicated, often short, surveys, genetic investigations, or modeling exercises, without much dedicated information to validate.
- Descriptions of feeding areas and migrations are infrequent in the literature, largely due to the protracted spawning seasons of SPF, which often blur the distinction between spawning and feeding periods.

Iberian coast

Overview of spatial data and variability

SPF fisheries in the Atlanto-Iberian waters constitute 30% of total landings (average 2018–2021) and rely primarily on European sardine and European anchovy (ICES 2023d), grouped into three official stocks (Figure 2, Figure S6 and Table S1 from the Online Supplemental Material). These resources are crucial for Spain and Portugal, both culturally and socio-economically, representing an important part of fish production and a relevant supply for the canning sector (see the Online Supplemental Material for management and trends).

The core distribution areas of adult anchovy registered in spring acoustic surveys are the coastal areas of the Southern Bay of Biscay (Gironde and Landes coast, ~46°N), the Gulf of Cadiz (~37°N), and the northwestern Portuguese coast, north of Cape Mondego (~40°N). A knowledge gap exists in the distribution of anchovy between the western and southern Iberian populations for several life stages (eggs, juveniles, and adults) and seasons. Landings reflect this discontinuity, with most Portuguese landings (>90%) occurring off the northwestern coast. Morphometric and genetic studies indicate differentiation between western/Cantabrian populations and those from the Gulf of Cadiz (ICES 2021b), although additional analyses are needed due to the presence of two ecotypes (marine and coastal) (Le Moan et al. 2016; Montes et al. 2016). Anchovies from the western Iberia are similar to those from the Bay of Biscay and may have originated from a colonization due to anomalous currents during 2014 and 2015 (Teles-Machado et al. 2024). Spawning mostly occurs during April to July, peaking in June, concentrated in the areas defined above.

In the Atlantic area of the Iberian Peninsula, the sardine stock comprises ICES subdivisions 27.8.c and 27.9.a, between the Gulf of Cadiz and the French border in the Bay of Biscay. Within the Iberian sardine stock, connectivity between Cantabrian/North Galicia and western Portugal has been observed, with complex larval transport patterns (García-García et al. 2016; Santos et al. 2018). Otolith microchemistry data confirm sardine cohorts' movement from western Iberia to North Galicia and Cantabrian Sea during early life (Correia et al. 2014). While regional substructure is evident, especially in areas like the Gulf of Cadiz, multidisciplinary studies have revealed independence in population dynamics between Iberian and Bay of Biscay sardine stocks. Cohort data analysis indicates limited straying of cohorts from the Bay of Biscay stock to the Cantabrian Sea, implying minimal impact on the Southern stock's dynamics (Silva et al. 2019). Heterogeneity exists in growth patterns among regions, notably in Biscay and Cantabrian areas. Conversely, spawning area continuity, overlapping seasons, and genetic similarities support stock mixing, with potential migrations from Biscay to Cantabria, warranting further research (ICES 2021b).

Sardine and anchovy stocks in the Atlantic Iberian Ecosystem have available spatial information on adult abundance and biomass (Figures 4 and 5), spanning over three decades in some cases. These interannual data have been collected from spring acoustic surveys (PELACUS in the Cantabrian Sea and Galicia and PELAGO in the Portuguese waters and Gulf of Cadiz) since 1986, with few gaps, especially at the beginning of the time series (Figure 7). Additionally, DEPM surveys for sardine were first applied in 1988 and have provided adult biomass data for the whole stock on a triennial basis since 1997 (SAREVA and PT-DEPM-PIL surveys) (Figure 5).

In the Gulf of Cadiz during summer, estimates of anchovy and sardine biomass have been obtained annually since 2004 through the acoustic survey series ECOCADIZ, occurring every three years since 2005 (with interruptions). Anchovy biomass in this area has also been estimated during a DEPM survey (BOCADEVA).

Collaborative efforts between Portugal and Spain have resulted in enhanced coordination and standardized methodologies for acoustic and egg surveys within ICES groups SGSBSA (Study Group on the Estimation of Spawning Stock Biomass of Sardine and Anchovy) and WGACEGG (Working Group on Acoustic and Egg Surveys for Sardine and Anchovy in areas 7–9) (Massé et al. 2018).

Spawning spatial variability

There is no evidence of breeding migrations for these species; eggs tend to be distributed in the same core areas as the adults. European anchovy mainly spawns near the estuaries of major rivers in Southern Iberia and the northwestern Portuguese coast whereas sardine spawning is spread throughout the stock's distribution area covered by the DEPM survey, with core areas varying from annually. In some years, eggs are also observed offshore, likely due to advection (Massé et al. 2018).

Spatial data have been obtained from the RADIALES project, a multidisciplinary program on the northern and northwestern coasts of Spain, with 20 stations sampled monthly since 1988 (with some interruptions, Figure 5). This initiative collects physical, chemical, and plankton observations (including ichthyoplankton samples of sardine and anchovy) across five transects representing upwelling and stratified dynamics (Valdés et al. 2021).

DEPM surveys targeting sardine (since 1997) or anchovy (since 2004) have been conducted every three years, for sardine in the whole distribution area and for anchovy only in southern Iberia, providing snapshots of spawning area extent and egg production (Figure 7). Triennial mackerel and horse mackerel surveys (coordinated in the framework of the ICES WGMEGS, ICES 2023d) have also covered the distribution area of sardine and anchovy, providing information mostly on sardine egg abundance in the year preceding triennial sardine and anchovy surveys.

Starting from 2002, CUFES data derived from acoustic surveys (PELACUS, PELAGO, and ECOCADIZ) have provided annual information on spawning area extent and egg abundance estimates using a vertical distribution model (Petitgas et al. 2006).

Recruitment processes and spatial variability

Information on connectivity of sardine and anchovy eggs was available from the DEPM and acoustic survey data using CUFES for the entire distribution area. Several Lagrangian and IBM models have been developed to describe sardine and anchovy connectivity, analyzing, and modeling larval routes (García-García et al. 2016; Santos et al. 2018; Casaucao et al. 2021). Estimates from the larval sardine IBM support the existence of a metapopulation in the area. In contrast, the anchovy IBM estimated a potential influx of eggs of this species from western Iberia to the Bay of Biscay and low connectivity between western larvae and those from the Gulf of Cadiz, although infrequent strong and persistent countercurrents could increase connectivity between southern and western areas. These exercises, however offer a static picture based on few years of data (Figure 7).

Spatial data on post-larval SPF were scarce for both species. Data on early juveniles have been collected for sardines in the recruitment surveys in the fall (surveys IBERAS and ECOCADIZ-reclutas).

For sardine, the three core areas of juvenile distribution are the northern Portuguese shelf, the coastal region near the Tagus estuary, and the eastern Gulf of Cadiz (Silva et al. 2009; Rodríguez-Climent et al. 2017). The west coast (9a Central-North subdivision) is considered the main recruitment area, with a secondary area of importance in the Gulf of Cadiz. Although the Cantabrian Sea is also a spawning area, 27.8.c ICES subdivision is not considered important for recruitment.

Anchovy juvenile distribution in the western component of the Iberian stock is mostly concentrated in the northwestern coast and the eastern Gulf of Cadiz and is associated with the main estuaries.

The abundance of juvenile sardine and anchovy in the Iberian ecosystem has been monitored since 1984 through more than 30 surveys with varying spatial coverage and some interruptions (surveys SAR-PT-AUT, ECOCADIZ-R, JUVESAR, and IBERAS, Supplemental Table S2, Figure 7), providing valuable insights into recruitment changes over time.

Feeding areas and migrations

Sardine and anchovy feed throughout their distribution area off the Iberia. Several single-time studies using stomach content analysis and stable isotopes have described the spatial and temporal variability of sardine and anchovy feeding, mostly for juveniles and adults (Bode et al. 2007; Garrido et al. 2008; Fonseca et al. 2022), while trophic studies of SPF larvae are rare. Biological sampling of sardine and anchovy is conducted regularly from annual surveys and monthly or fortnightly at major fisheries ports in Portugal and Galicia. This sampling includes classifying stomach fullness following Cunha et al. (2005), allowing study of diel, interannual, seasonal, and spatial variability of feeding intensity over the years. No feeding or overwintering migration has been described for sardine and anchovy in this area, and the spatial distribution of these species is fairly similar throughout the year.

Key messages

- It is recommended to prioritize studying anchovy spawning areas in western Iberian waters, where data is currently lacking. While comprehensive spatial biomass information for both European anchovy and sardine has been gathered from acoustic surveys, and spawning area data is available for sardine throughout the area and for anchovy in the Gulf of Cadiz through DEPM surveys, there is a need to fill the gap for anchovy in western Iberian waters. Coupled hydrodynamic and IBMs are available to study the connectivity of early life stages in that area.
- It is recommended to obtain information on the fraction of juveniles closer to the coast. While spatial time-series data for juvenile populations are available for sardine and anchovy in most of the Atlantic Iberian waters, recruitment surveys may miss a portion of anchovy recruits that frequently aggregate near the shelf edge, as also observed for Bay of Biscay juveniles.

Mediterranean and Black Sea

Overview of spatial data and variability

SPF fisheries in the Mediterranean represent 43.6% of total landings (average 2018–2020), primarily relying on European anchovy, European sardine, and round sardinella (*Sardinella aurita*) (FAO 2022b). In the Black Sea, SPF fisheries account for 76.5% of total landings for the same period, historically dominated by anchovy and sprat in the twentieth century (Prodanov et al. 1997) (see the Online Supplemental Material for detailed fisheries information). In this review, the Mediterranean was the LME harboring the largest number of stocks (24 and up to 42 datasets) (Figure 2, Figures S6 and S7 and Table S1 from the Online Supplemental Material). Only five datasets included stocks with demonstrated demographic coherence, specifically anchovy and sardine in the central Mediterranean and the Adriatic Sea (Figure 3) (Simmonds et al. 2017). In the Black Sea, only the sprat stock showed demographic coherence, with debates existing on anchovy contingents. These two LME have separated into 30 FAO Geographical Sub-Areas (GSA) (GFCM 2009) for statistical purposes, with historical implications for ecological studies, stock assessments, and management.

The ecology of these SPF has been extensively reviewed (Chashchin 1996; Palomera et al. 2007; Morello and Arneri 2009; Saraux et al. 2019). In the Mediterranean, spawning occurs during protracted seasons: European anchovy and round sardinella spawn from April to October and April to July, respectively, while European sardine and sprat spawn from October to April and December to April, respectively (D'ancona 1931; Tsikliras et al. 2010). In the Black Sea, particularly for the sub-species Azov anchovy (*E. encrasicolus neoticus*), a distinct pattern emerges. Anchovy actively spawns and forages across the Sea of Azov from May to August. As the colder months set in, around September and October, the Azov anchovy migrates through the Kerch Strait into the Black Sea, adapting to the seasonal temperature shifts (Chashchin 1996). In the black sea, anchovy spawning period extends from May to September (Chashchin 1996), before initiating migration to the southern Black Sea (Prodanov et al. 1997). European sprat spawn from late autumn to early spring, peaking from December to February (Prodanov et al. 1997).

In the Mediterranean, spawning primarily occurs in coastal areas, with late larval stages schooling in areas favored by environmental conditions (Agostini and Bakun 2002; Costalago 2015; Malavolti et al. 2018). In the Black Sea, anchovy distribution during summer spawning covers almost the entire sea. Statistical models characterizing spawning and nursery areas exist for some species in both LME (Figure S1 from the Online Supplemental Material) (Giannoulaki et al. 2008; Giannoulaki et al. 2011; Tugores et al. 2011; Giannoulaki et al. 2013).

Most SPF stocks in the Mediterranean and Black Sea have spatial data on adult presence or biomass (Figure 4). The data inspection showed that data are typically interannual, primarily from acoustic surveys (Figure 7) although some stocks have limited data (e.g., five years for European sardine and anchovy in GSA 9–11), and others have longer time series, such as over 30 years in the Adriatic Sea (GSA 17–18) for anchovy, with minimal data gaps (Figure 5, Table S2 from the Online Supplemental Material). Although these surveys were historically irregular and occasionally lacked spatial coherence, recent years have witnessed a harmonized pan-Mediterranean acoustic multinational program (MEDIAS) focusing on generating biomass data (Leonori et al. 2021). Some quarterly interannual time series were available for sardine in GSA03 (Southern Alboran Sea) and decadal data exist for anchovy and sardine in GSA16 (Southern Sicily). The longest time series for European anchovy and sardine were found in the Adriatic Sea, Gulf of Lions (GSA 07), the northeastern Spanish coast (GSA 06), and the Aegean Sea (GSAs 20 and 22), spanning nearly 20 years (Table S2 from the Online Supplemental Material). Round sardinella is gaining commercial importance, but spatial time series on adult biomass/presence were available for only about 50% of the stocks, primarily unassessed and with short time series (Figures 5 and 7). The longest time series for this species was observed in the Central Mediterranean in GSA 16. For three assessed stocks of Round sardinella, no spatial data were found (Eastern Mediterranean, GSAs 24, 26, and 27). Spatial data for sprat mainly came from the northernmost areas, particularly the relict population in the Adriatic Sea and the Northwestern Mediterranean, where acoustic data spanned 16 and 24 years in the northeastern Spanish coast and the Gulf of Lions, respectively. In the Black Sea, in GSA29, some time series data for sprat were identified, including interannual and seasonal datasets, but detailed time series data for anchovy were lacking.

Spawning spatial variability

Spatial data on spawning migrations in the Mediterranean were notably limited (Figures 4 and 5, Table S2 from the Online Supplemental Material), likely due to the absence of comprehensive seasonal surveys. Historical (fixed picture) data were available for anchovy and sardine in the Adriatic Sea (GSA 17–18, Morello and Arneri 2009) and for anchovy in part of the Aegean Sea (GSA 22) (Mantzouni et al. 2007). Interannual data covering over 14 years for anchovy were available in GSA6 (Pennino et al. 2020). Seasonal migrations variability has been modeled, both mechanistically (in Greece for anchovy) and statistically (NW Mediterranean, see cited references), using data from acoustic and demersal surveys, as well as landings (Figure S1 and Table S2 from the Online Supplemental Material). In the Black Sea, historical and fixed-picture information exists regarding reproductive migrations of anchovy and sprat (Chashchin 1996; STECF 2013).

Spatial time series for spawning areas was found for approximately 75% of Mediterranean anchovy stocks and about 50% of sardine stocks (Figure 4), but were scarce for Round sardinella and sprat. Anchovy exhibited relatively long interannual datasets in the Central Mediterranean (e.g., Patti et al. 2020; Quinci et al. 2022) and the Northwestern Mediterranean (GSA07, Maynou et al. 2020), spanning up to 20 years (Figure 5, Figure S7 and Table S2 from the Online Supplemental Material). In the Black Sea, spatial time series data were available for anchovy spawning but were lacking for sprat. Much of the data for the two LME has been derived from egg and larval surveys (Figure 7, Table S2 from the Online Supplemental Material). Statistical methods have been utilized to create fixed snapshots for comprehensive datasets covering both the Mediterranean and Black Seas (Schismenou et al. (2008), Figure S1). For sardine, spatial data were limited to fixed pictures from a few years' data. These include statistical habitat models for the entire Mediterranean using acoustic data (Tugores et al. 2011), including the Adriatic (GSAs 17–18, Morello and Arneri 2009), Tunisia (GSA 14, Zarrad et al. 2020), and Greek areas (Somarakis et al. 2006; Ganias 2008), although there are likely raw acoustic data available to extract further information (Leonori et al. 2021). While longer interannual maps exist for the Northwestern Mediterranean, large time gaps were present (Olivar et al. 2001; Olivar et al. 2003; Maynou et al. 2008). In the Alboran Sea, approximately 10 years of acoustic-based data were available (FAO 2022c). The few spatial data with higher resolution than a single survey per year (Northwestern Mediterranean) were monthly and concentrated in one year (Sabatés 1990). Only three datasets were found for Round sardinella, predominantly short-interannual and based on eggs and larval surveys (Figures 5 and 7), one of them for the entire Mediterranean, associated to a statistical predictive model (Schismenou et al. 2008), and another for the Northwestern Mediterranean (Maynou et al. 2020).

Recruitment processes and spatial variability

Information on egg and larval connectivity was primarily available for anchovy, covering approximately 50% of its stocks (Figure 4). The longest interannual time series, nearly 20 years without gaps, pertain to anchovy in the Central Mediterranean (GSAs 17–18), including eggs surveys, catch data, acoustic surveys, and mechanistic (Lagrangian) transport models (Patti et al. 2020, Figures 5 and 7, Figure S1 and Table S2 from the Online Supplemental Material). Shorter series, utilizing a range of data types and IBM models, have elucidated anchovy larval connectivity in the Northwestern Mediterranean (GSA 6 and 7) (Ospina-Alvarez et al. 2015) and southwestern Mediterranean (Catalán et al. 2013). In the Black Sea (GSA29), anchovy larval routes have been studied using short-term (<3 years) hydrodynamic data coupled to an IBM (Fach 2014).

Spatial data for round sardinella were available in the central Mediterranean, including IBM modeling studies (Torri et al. 2018), likely because their summer spawning coincides with anchovy, facilitating research efforts. Statistical modeling has been employed to analyze and model larval connectivity for sardine in the Northwestern Mediterranean (Pennino et al. 2020). In many stocks, surveys using DEPM (e.g., Somarakis et al. 2006) can potentially provide initial positions for eggs to initialize connectivity analyses (e.g., *sensu* Ospina-Álvarez et al. 2013). Nevertheless, these data typically represent only a fraction of the spawning season.

Spatial data on nursery areas were scarce and only accessible for sardine and anchovy in the Mediterranean Sea and for sprat in the Black Sea (Figures 4 and 5, Figure S8 from the Online Supplemental Material). Active nurseries often exhibit temporal mismatches with general acoustic surveys, necessitating specific, often more coastal surveys. Some works utilized early juveniles to characterize nursery grounds. Most available data comprise modeled static images from a few years of surveys (Figure S1). Figure 7 and Table S2 (Online Supplemental Material) show that data were generated from "general surveys" (e.g., Morello and Arneri (2009) for both species in the Adriatic) or from acoustic surveys (e.g., Catalán et al. 2013; Giannoulaki et al. 2013; Ventero et al. 2021). The longest spatial time series for nursery area sampling was observed for sardine in the Northwestern Mediterranean, spanning 14 years and utilizing various survey methods, underpinning a statistical model to predict nursery habitat (Pennino et al. 2020).

Estimates of juvenile and immature biomass estimates were often derived from acoustic surveys, yet there was dearth of spatial distribution time series (Figures 4 and 5). In the entire Mediterranean, a spatial statistical model served as a "fixed picture" for sardine juveniles, based on five years of environmental and acoustic survey data (Giannoulaki et al. 2011). Such models were not available for other species (Figure 7, Figure S1 and Table S2 from the Online Supplemental Material). In the Black Sea, historical and fixed-picture information exists regarding the juvenile presence of sprat (STECF 2013).

Regarding nursery areas, the longest interannual spatial time series spanned 14 years for sardine in the Northwestern Mediterranean (Figure 5, GSAs 6 and 7) and was based on a statistical model incorporating several data sources (Pennino et al. 2020). Another interannual spatial time series for sardine, coupled to a statistical spatial model based on acoustic surveys, covered three years in the Eastern Mediterranean (GSA 22, Tsagarakis et al. 2008). This stock is shared with Turkey, although the available data only covered the Greek part. For anchovy, there exists an eight-year interannual spatial time series in the Alboran Sea (GSA 1), based on collaborative work from Spain, Morocco, and Algeria (FAO 2022c).

Feeding areas and migrations

Feeding areas are typically identified through trophic analyses across different life stages in different areas and temporal periods, but such data were scarce. Fixed depictions of adult feeding areas based on isotopic analyses and stomach content analyses were found for sprat, anchovy, and sardine in the Gulf of Lions (Figure 7, GSA 7 and parts of GSA 6; Le Bourg et al. 2015; Bachiller et al. 2020). A representation of feeding areas for the Greek segment of the Greek-Turkish anchovy stock was established through mechanistic modeling (Figure 7, Mantzouni et al. 2007). The only interannual spatial time series for feeding areas was again for sardine in the Northwestern Mediterranean (Pennino et al. 2020). Notably, there was a lack of comprehensive data for round sardinella feeding areas in the Mediterranean and for anchovy in the Black Sea. For sprat in the Black Sea, historical data offered a fixed-picture view of feeding areas (STECF 2013).

Out of over 40 Mediterranean datasets examined, only three furnished data on feeding migrations (Figures 5 and 7). Two studies offered fixed snapshots for anchovy and sardine in the Adriatic Sea (GSA 17–18, Tičina et al. 2000; Morello and Arneri 2009) and one consisted of a statistical model output for sardine in the Northwestern Mediterranean (Pennino et al. 2020). In the Black Sea (GSA 29), there was a fixed picture of feeding migration for sprat. Location and timing of the feeding migration of anchovy in the Black Sea was more speculative, relying primarily on observations from fisheries rather than focused research studies (STECF 2013).

The only dataset on overwintering migration pertained to sardine in GSA 6 (Catalan coast), consisting of a model-based interannual analysis spanning 14 years. In the Black Sea, research on the migration and overwintering of anchovy and sprat (STECF 2013) included short-term studies under three years (Chashchin 1995; Prodanov et al. 1997; Guraslan et al. 2017) (Table S2 from the Online Supplemental Material). Two migration patterns have been identified: i) Azov anchovies spawn and forage in the Sea of Azov (GSA30) from May to August and migrate through the Kerch Strait into the Black Sea (GSA29) in autumn (Chashchin 1996); ii) In the Black Sea, anchovy migration from the northern to the southern part as water temperatures decline (Prodanov et al. 1997).

Key messages

- Short-duration acoustic surveys in the Mediterranean, focusing on the two key species, have provided limited year-round spatial information on biomass and presence for several species at both regional and smaller scales. Leveraging the growing availability of harmonized acoustic data is recommended to expand spatial knowledge and address these limitations.
- Data on spawning areas has been primarily obtained from surveys of eggs and larvae, covering only about 50% of the stocks. Although statistical models offer some predictive insights, their general applicability and validation for many areas and stocks remain limited.
- The scarcity of mechanistic models hinders predictions of future impacts; however, existing bioenergetic models for certain species could be used to study several stocks. It is recommended to utilize surveys of spawning female distributions to develop spatial models of larval connectivity, coupled with IBM, to address the lack of studies on this critical spatial component of the life cycle.
- Enhancing research efforts to improve spatial time-series data for juvenile populations is advised. Currently, only one species has comprehensive coverage throughout the Mediterranean, and interannual time series for the main two species are restricted to specific areas. Additionally, there is a lack of information on annual spatial changes in diet and limited data on seasonal or interannual variations in feeding areas, which could illuminate environmental drivers behind observed trends in body condition. Similar gaps exist regarding seasonal movement patterns, such as spawning migration.

Canary Current

Overview of spatial data and variability

Four exploited SPF species are present in the Canary Current system between the northern Atlantic border of Morocco and the southern border of Guinea- Bissau (Figure 2, Figure S9 and Table S1 from the Online Supplemental Material): European sardine, European anchovy, round sardinella and flat sardinella (*Sardinella maderensis*). Sardine accounts for around 50% of the annual catches (FAO 2021). Each species is assigned to one stock in the area, except for sardines, which are divided into northern and central stock, and southern stock. Due to the absence of stock identity data for sardinellas, despite being a research priority for over a decade (FAO 2020), each sardinella species is considered a single stock.

Seminal studies on the spatial distribution, spawning grounds, and seasonal migrations of sardine and sardinellas rely on data from 1930s (e.g., Boely 1982; Boely et al. 1982; Garcia 1982) accessible through COPACE/CECAF reports (e.g., Boely and Freon 1979) and other publications (Freon 1988). Due to challenges in accessing metadata for these surveys, including sampling years, seasons, and methods, they were not included in the data analysis, although relevant publications are cited.

European sardine dominates in colder northern communities, while round sardinella dominates at lower latitudes (Brochier et al. 2018). Each species exhibits year-round spawning with distinct thermal preference-related peaks: sardines peak during winter, while anchovy and sardinellas peak in summer (Berraho et al. 2005; Berraho 2007; Diankha et al. 2018; Abdelouahab et al. 2021). Spawning occurs in coastal areas (Roy et al. 1989) with anchovy spawning closer to the shelf break than the other species. Eggs and larvae disperse offshore, with greater retention than previously assumed due to mesoscale features like eddies and filaments (Brochier et al. 2011; Moyano et al. 2014). Lagrangian models have been used to study dispersal (Brochier et al. 2011). Round sardinella's spawning peaks across Mauritania and Senegal are thought to balance local retention and food availability (Mbaye et al. 2015). A mechanistic full life cycle model has been created for round sardinella, revealing insights into seasonal migrations and homing (Brochier et al. 2018), highlighting the importance of the coastal area off Mauritania, which has been subject to intense fishing since 2014 (Corten et al. 2017). Acoustic surveys have been conducted regionally every 2-5 years by Morocco, Senegal, and Mauritania, as well as international expeditions (EAF-Nansen program, Russian cruises onboard R/V Atlantida, or RV AtlantNiro). These datasets have rarely been collectively analyzed to explore system-wide patterns (Braham et al. 2024).

All SPF stocks in the Canary Current system had spatial data on adult presence or biomass (Figure 4).

These interannual data spanned 27 years with minimal interruptions (<= 2 years) (Figure 6, Figure S9 and Table S2 from the Online Supplemental Material), primarily originating from acoustic surveys (Figure 8, Figure S9 from the Online Supplemental Material). Each nation conducts surveys within its national waters, supplemented by international surveys (EAF-Nansen program, Russian cruises onboard R/V Atlantida, or RV AtlantNiro). Data was often limited to national waters in any given year, generally seasonal surveys extending several weeks and spanning different seasons.

Regular seasonal acoustic surveys have contributed to describing seasonal migrations for sardine, anchovy, and round sardinella (Belveze and Erzini 1983; Arístegui et al. 2009; Brochier et al. 2018). Fishery operations have also provided relevant information on adult presence and biomass for sardine and round sardinella (Thiaw et al. 2017; Brochier et al. 2018; Braham et al. 2024). Before regular acoustic cruises, an intense research period with dedicated cruises (not included in the dataset) occurred in the 1970s and 1980s. These included catch (e.g., Freon 1988) and acoustic data (Demarcq et al. 1991).

A comprehensive IBM focusing on round sardinella's spatial distribution was developed (Brochier et al. 2018), utilizing environmental factors like currents, temperature, and plankton, considering reproductive success related to coastal ichthyoplankton retention and temperature preferences. As a result, it offered insights independent of fishery data.

Spawning spatial variability

Spawning migrations have been described for sardine and sardinellas but not for anchovy (Figures 4 and 6, Table S2 from the Online Supplemental Material). Most studies were published decades ago (Garcia 1982; Belveze and Erzini 1983), and current surveys lack comprehensive seasonal coverage, leaving a large knowledge gap on the spawning migrations of European sardine (spatial component 2, Figure 4). Seasonal migration variability has been mechanistically modeled for round sardinella along the Mauritanian-Senegalese coast (Brochier et al. 2018).

Spatial time series for spawning areas exist for all four SPF species (Figure 4), based on ichthyoplankton surveys by Morocco and international expeditions (e.g., Nansen program and Russian cruises). These time series were limited to a few years (Ettahiri et al. 2003; Berraho et al. 2005; Abdelouahab et al. 2021). More extensive datasets were available for the northern and central sardine stock and the Senegalese round sardinella (Conand and Fagetti 1971; Conand 1977). These datasets have also been used to study environmental windows for spawning for sardine and anchovy (Cury and Roy 1989; Brochier et al. 2009) and round sardinella (Diankha et al. 2018).

Recruitment processes and spatial variability

Information on eggs and larvae was collected for sardine, anchovy, and round sardinella, but not flat sardinella (Figure 4). Time series from ichthyoplankton surveys were relatively short (10–16 years) with gaps (3–5 years) (Figure 6). Moreover, several fixed cruises have been conducted in the Canaries Coastal Transition Zone, which have provided valuable data on connectivity across the Northwestern African coast and to the Canary Islands (Rodriguez et al. 2009; Moyano et al. 2014). All these datasets were used to validate a Lagrangian model studying larval connectivity (Brochier et al. 2011).

Information on nursery areas was available for all four species from international ichthyoplankton surveys (Figure 4). Additional information is available for the sardinellas in Mauritania and Senegal from older studies based on acoustic or fisheries data (Boely et al. 1982; Garcia 1982), but source datasets were not specified.

Biomass of juvenile or immature individuals is often derived from acoustic surveys, matching trends for presence/biomass of adults for all 4 SPF (Figures 4 and 6) (spatial component 1). These surveys did not target juveniles, who are generally closer to shore than adults, at least for sardine and sardinellas (Boely and Freon 1979). As with adults, datasets covering the entire Northwestern African coast have been rarely analyzed collectively.

Feeding areas and migrations

Feeding areas are typically identified through trophic analyses across different life stages in different areas and times, although such type of data is limited for the four SPF in this region. Only a fixed picture was found for the two sardinella species (Figure 6) (Roy et al. 1989).

General seasonal migrations related to feeding have been described in punctual studies for sardine and sardinellas (e.g., Belveze and Erzini 1983; Boely 1982; Boely and Freon 1979; Garcia 1982), but specific data sources are unclear. For example, Boely and Freon (1979) mention that migration maps were based on i) industrial fisheries from non-riparian countries (large-scale fishing), which generally follow the movements of adult concentrations (particularly purse seiners); ii) semi-industrial and artisanal fisheries in Senegal, mainly capturing juveniles and young spawners (beach seining, encircling net fishing, line fishing); and iii) experimental fishing by oceanographic research vessels.

Key messages

- Providing access to metadata from surveys in the Canary Current region, following the FAIR principles, will be a crucial first step to properly evaluate the existing knowledge and data for SPF in the region. While some metadata are summarized in CECAF reports and the metadata for the Nansen cruises have recently been made publicly available on the FAO website (https://figisapps.fao.org/fishery/eafnansen/en/eafnansen/survey/search), accessing information from other cruises remains difficult.
- There is a lack of comprehensive spatial information on biomass and presence for many species and throughout most months. Expanding the analysis of spatial time series data for juvenile SPF can enhance our understanding of juvenile populations and contribute to more effective management strategies in the region. While some of these data may be available through regular acoustic surveys, they have rarely been analyzed outside of the stock assessment process.
- Round sardinella has been the focus of recent research in the region. For this species, applying otolith-based methods to further validate the existing full life cycle IBM as suggested by Sakamoto et al. (2022), is recommended. Recent intensive research has already achieved a relatively good understanding of their seasonal migrations and connectivity, and the available IBM has been validated using seasonal variability of Catch Per Unit Effort (CPUE) in Mauritania and Senegal, as well as fisher ecological knowledge in Senegal.
- For sardine, anchovy, and round sardinella, collecting annual-based spatial data on the distribution of adults and their seasonal and feeding migrations is desirable, as current information is limited to punctual studies without annual spatial changes. Additionally, conducting regular studies to document annual spatial changes in diet is recommended, since existing insights are derived from occasional studies.

South Benguela system

Overview of spatial data and variability

The main two species of SPF in one well-studied part of the Benguela ecosystem were reviewed: the European anchovy (*E. encrasicolus*), and South African sardine (*S. sagax*), in the south and south-west of Africa. Part of the southestern area, the Agulhas bank, was also included as one of the stocks inhabits both areas. The West Coast redeye round herring (*Etrumeus whiteheadi*) is increasingly important but was excluded from this review. Together, these three species comprise over 95% of the pelagic purse seine harvest (DFFE 2023). Anchovy and sardine are critical to South Africa's SPFs, encompassing 3 stocks (Ramírez et al. 2022, Figure 2).

Sardine populations along South Africa's west and south coastlines (continental shelf waters between Hondeklip Bay (~30°S) off the west coast and Durban off the east coast), were long considered a single, well-mixed population for evaluation and management. Recent genetic markers and other analyses indicate adaptation to water temperature, supporting the existence of two stocks (Figure 2, Table S1 from the Online Supplemental Material): one linked to South Africa's warm-temperate west coast and the other to its cool-temperate south (DFFE 2023). The anchovy stock in the southern Benguela upwelling ecosystem, situated off the west coast of southern Africa, is characterized by spawning and nursery grounds located in separated regions.

Data on these three stocks were available from semiannual hydroacoustic surveys and numerous ichthyoplankton surveys (see van der Lingen and Huggett 2003), which have improved the understanding of adult and juvenile biomass, spawning migration, and spawning and nursery areas (Figure 4, Figure S10 from the Online Supplemental Material). The first hydroacoustic survey typically occurs in November, targeting adult biomass, whereas the second, known as the "recruit survey", takes place in May/June and surveys 0-year-old fish (Coetzee et al. 2008, Figure 6).

Since the early 1940s, South Africa has supported a substantial sardine purse-seine fishery in St Helena Bay, initially driven by food requirements during World War II (Crawford 1981). Sardine dominated catches until overfishing led to a substantial decline, prompting a shift in 1964 to target juvenile anchovy (van der Lingen and Huggett 2003). Time series of sardine landings have been available from 1949 onward, with anchovy records starting in 1964 (Figure 8). Commercial catch samples provide data on species composition, catch position, date, and length frequency distributions, critical inputs for species-specific population dynamics models (DFFE 2023).

The annual November pelagic spawner biomass hydro-acoustic survey (Figure 8, Figure S10 from the Online Supplemental Material) (Coetzee et al. 2022), has been conducted since 1984, with one interruption in 2021 (38 years; Figure 6). It covers the shelf between Hondeklip Bay and Port Alfred to coincide with peak anchovy spawning. The survey helps estimating the biomass and length composition of anchovy and sardine (Barange et al. 1999), essential for stock assessments and setting annual Total Allowable Catches. Acoustic surveys provide reliable estimates compared to modeling from commercial catch data, allowing optimal resource utilization during periods of high biomass and protection during periods of low biomass (DFFE 2023).

Over 50 years of ichthyoplankton surveys provided insights into spawning areas and larval distributions (Van der Lingen and Huggett 2003; Figure 6 and Table S2 from the Online Supplemental Material). CalVET net samples taken during the spawner biomass survey offered a long time series on the distribution and abundance of anchovy and sardine eggs (composite maps over 38 years), allowing regional comparisons of spawning habitats. Early surveys between 1950 and 1969 covered regions from Lamberts Bay to Saldanha Bay, extending to Quoin Point in 1959 and to Cape Infanta in 1961, covering around 80 sampling stations (Figure 8 and Table S2 from the Online Supplemental Material). South African SARP ichthyoplankton surveys performed monthly between August 1993 and March 1994 and between September 1994 and March 1995 encompassed 17–189 stations on west and southwest coasts (Figure 8, Figure S10 and Table S2 from the Online Supplemental Material). In addition, SARP monitoring line targeted ichthyoplankton samples bimonthly from 1995 to 2003 off Cape Peninsula encompassing 12–20 stations (Figure 8, Figure S10 and Table S2 from the Online Supplemental Material).

Spawning spatial variability

Anchovy mainly spawn over the Agulhas Bank during austral spring/summer (September to March), peaking in November (Huggett et al. 1998; van der Lingen et al. 2001). Since the 1990s, the main spawning areas shifted from the western Agulhas Bank (Shelton et al. 1993; Roel et al. 1994) to offshore regions of the central and eastern Banks (van der Lingen et al. 2002). Recently, Coetzee et al. (2022) have updated the information of spatial and temporal spawning variability of sardine in South African coasts. Sardine can spawn year-round and is more widespread than anchovy. The peak spawning season off the west coast occurs between September and February, while the peak occurs between June and November for the spawning season off the south coast (Coetzee et al. 2022). During winter, sardines spawn off the east coast, representing a genetically separate population, with common spawning dates from June through November (Coetzee et al. 2022). Environmental characteristics of the spawning habitat vary among the west (17 °C), south (19.5 °C), and east coast (22 °C) (Mhlongo et al. 2015).

Biophysical models and observations (Figure 8) indicate that eggs spawned off the west coast are carried northward to nursery grounds north of Cape Columbine by a jet current linked to a strong thermal front between warmer oceanic water and colder upwelled water (Miller et al. 2006; McGrath et al. 2020). Most south coast-spawned eggs were retained in local nursery grounds, with a small portion transported to the west coast, contributing to recruitment there (Lett et al. 2006). Anchovy eggs from the Agulhas Bank are carried to the west coast nursery area by a shelf-edge jet current passing through the upwelling center near Cape Pont and Cape Columbine (Hutchings et al. 1998). Simulations based on biophysical models (Figure 8) including several mechanisms, such as advection, growth, buoyancy, and diel vertical migration for anchovy eggs and larvae (Parada 1999; Parada et al. 2003, 2008) confirm that these transport mechanisms align with juvenile distributions (Parada et al. 2008).

Recruitment processes and spatial variability

A May hydro-acoustic survey covering the west coast from the Orange River to Cape Infanta on the east coast has estimated anchovy and sardine recruits (Figure 8). These surveys have been undertaken annually since 1984, with one gap in 2022 (38 years, DFFE 2023, Figure 6, Figure S10 from the Online Supplemental Material). The survey area was expanded eastward in the late 1990s to verify the assumption made in modeling and management that recruitment was negligible east of Cape Infanta (Barange et al. 1999). Pre-recruit surveys have been carried out annually since March 1991 – onwards on the west coast using a Methot frame trawl (O'Toole and Crous 1989; van der Lingen and Huggett 2003).

Anchovy recruitment success is influenced by the transport of eggs and larvae from spawning to nursery grounds (Hutchings et al. 1998). Eggs spawned in this area may be carried shoreward by the Agulhas Current onto the western Agulhas Bank and into the jet stream to the west coast, retained on the central and eastern Agulhas Banks, and recruit on the south coast. Another possibility is that eggs are entrained into the southern Indian or Atlantic Oceans, where they are unlikely to contribute to recruitment (van der Lingen et al. 2002).

Feeding areas and migrations

Available information came from conceptual models or single-point studies (Table S2 from Online Supplemental Material). Sardine and anchovy in southern Benguela have a migratory life cycle, involving a migration to the more productive west coast for recruitment and feeding after adult spawning on the Agulhas bank (Teske et al. 2021; Ortega-Cisneros et al. 2024). Sardine spawns off the west and south coasts (van der Lingen et al. 2001), while anchovy migrates from west coast nursery grounds to the Agulhas Bank in spring for spawning (Hutchings et al. 1998). Early life stages of both species, including some south coast spawned sardines, are transported to nursery regions to the north of the west coast (van der Lingen and Huggett 2003). Return migration to spawning areas starts at juvenile stages, arriving at Agulhas Bank during fall and winter. Recent modeling has linked the migration of anchovy and sardine to environmental variables. With a stronger relationship for anchovy (Ortega-Cisneros et al. 2024).

Sardines migrate to the subtropical east coast of South Africa during the “sardine run”, which occurs from the eastern part of their temperate core habitat (van der Lingen et al. 2010). Teske et al. (2021) found that sardines participating in the sardine migration were mainly from the Atlantic, preferring cooler waters. During brief times of cold-water upwelling, they move into temporarily advantageous habitat in the Indian Ocean. When the upwelling stops, they are left in a subtropical habitat that is physiologically challenging and become highly vulnerable to predators.

Key messages

- Long-term time series from ichthyoplankton, pre-recruits, and acoustic surveys have considerably advanced our knowledge of the life history of sardine and anchovy in south Benguela. Further, research is recommended on the horizontal and vertical distribution of pre-recruit stages off the west coast, their interactions with meso- and submesoscale oceanographic features, and implications for survival. Further, examining aspects like the importance of parental condition, and its spatial dependencies could be key to understanding the potential impacts of climate change on spawner biomass and physiological resilience to environmental shifts.
- Spawning and nursery regions are geographically separated, underscoring the significance of transport processes in influencing recruitment strength. The potential of these processes to predict recruitment, particularly for anchovy, has been emphasized. Although spatial and temporal changes in spawning habitats have been monitored and characterized, we recommend a larger effort in the study of the potential effects of climate-associated variables, such as deoxygenation, warming, and acidification, on these habitats.
- Data on species composition, capture position, dates, and length frequency distributions from commercial catches are routinely collected and are crucial for species-specific population dynamic models. Isotope analysis, microstructure studies, and genomic data have confirmed the existence of two mixed sardine stocks off the coast of South Africa, each adapted to different water temperatures. Fitness and survival diminish outside these temperature ranges. These findings have important ramifications for sardine fisheries management, suggesting that spatial-temporal differentiation in a multiple-stock sardine management strategy could be the way forward to avoid overexploitation.

Bering Sea, Aleutian Islands, and Gulf of Alaska

Overview of spatial data and variability

Despite hosting some of the largest groundfish and salmon fisheries in the world, SPF fisheries in Northeastern Pacific systems are limited and essentially focused on one species, Pacific herring (*Clupea pallasii*), an abundant and important commercial species in this region (Figure 2, Table S1 from the Online Supplemental Material). Pacific herring live up to 15 years and mature (first spawn) at age 3–5 (Barton and Wespestad 1980). Herring inhabit continental shelf regions and spend much of their lives nearshore (Hay 1985) and overwinter in dense schools nearshore as juveniles and offshore as adults (Stokesbury et al. 2002). In March, adults migrate to spawning beaches (Norcross et al. 2001); spawning begins mid-April and lasts 5–21 d. Embryonic herring incubate in intertidal and shallow subtidal areas for 22–24 d prior to hatching in May (Brown et al. 1996). Pelagic larvae are retained in nearshore nursery areas by local currents (McGurk et al. 1993).

There are several management areas designated for discrete Pacific herring stocks in the Chukchi Sea, BS, AI, and GOA. These include the Norton Sound and Arctic Management areas in the Beaufort, Chukchi, and northern BSs (Tiernan et al. 2021), the Alaska Peninsula-AI Management Area in the Alaska Peninsula and AI (Keyse and Lawson 2023), and Prince William Sound (Shepherd and Haught 2019) and southeast Alaska stocks in the GOA (Hebert 2020). Pacific herring are managed to maintain threshold spawning biomass and monitored *via* catch data (all areas), aerial surveys (GOA), hydroacoustic surveys (GOA), spawn deposition and dive surveys (GOA), and test fisheries (GOA, BS; Figures 6 and 8).

Adult presence or biomass has been estimated primarily through fishing operations and aerial or acoustic surveys, but also as sampled in diets and non-target surveys (Gunther et al. 2024). Data spanned 20–48-year timeframes, depending on the dataset and region (Figures S11–S13 and Table S2 from the Online Supplemental Material). Stock assessments have been conducted for management (Hebert 2020; Keyse and Lawson 2023), including Bayesian analyses (Muradian et al. 2017) and in some cases extensive research and monitoring programs are supported (Pegau and Aderhold 2021; Lindeberg et al. 2022). Forecasts for herring biomass use either age-structured analysis or biomass accounting methods where estimates of growth and mortality are applied to observed spawning biomass and age composition.

Spawning spatial variability

Spatial data on spawning migrations were relatively well documented, predominantly *via* aerial surveys of spawn deposition along coastlines (Tiernan et al. 2021; McGowan et al. 2021). Data supported both mechanistic and statistical models of explicit movement and timing (Figures S11–S13, Table S2 from the Online Supplemental Material). In March and April adult herring migrate toward spawning beaches. Spawning begins mid-April and lasts from 5 to 21 d, although spawning phenology is influenced by environmental and population-level factors (Dias et al. 2022). Spawning, feeding and overwintering areas may be separated by 1000s of kilometers (Tojo et al. 2007; Beacham et al. 2008) and migration patterns may vary according to local populations within a spawning aggregation. In the GOA and AI, movements after spring spawning are largely unknown. Previous studies of movement in the GOA used mark-recapture techniques (Hay and McKinnell 2002) or catch-per-unit effort (Tojo et al. 2007). Herring spawning in the BS have geographically distinct northern and southern feeding and overwintering grounds (Tojo et al. 2007); fish spawning in exposed coastal areas migrate offshore, while fish spawning in mainland inlets remain resident.

Due to targeted fisheries on spawning herring, large amounts of data were available on spawning aggregation or biomass, timing, and location (Menard et al. 2022). Spatial patterns in spawning have been determined by population size and processes that affect site fidelity and dispersal (Ware and Schweigert 2001). Interannual variations in herring spawn timing have been primarily attributed to population demographics and temperature (Hay 1985; Ware and Tanasichuk 1989). In populations comprising multiple age cohorts, spawning may be staggered in waves with older fish spawning earlier than younger fish (Hay 1985; Ware and Tanasichuk 1989). During spawning, females deposit eggs on kelp in the inter-tidal zone, and these egg-encrusted kelp fronds are harvested by spawn-on-kelp fisheries. This phenomenon facilitates egg and larval surveys and aerial surveys (45-year time series), which inform statistical and mechanistic models of movement. The location and timing of spawning can affect subsequent recruitment (McGowan et al. 2021).

Recruitment processes and spatial variability

Dynamics related to larval stages and transport are well-documented and monitored in certain regions (GOA; Doyle et al. 2019) and support both mechanistic and conceptual models (Gibson et al. 2022). Pelagic larvae are thought to be retained in nearshore nursery areas by local currents (McGurk et al. 1993; Ormseth et al. 2019) but may be widely distributed in areas with strong currents and tidal dynamics (e.g., Shelikov Strait, Doyle et al. 2019; Bering Strait, Baker et al. 2022).

Research on nearshore areas used by SPF in the Northeastern Pacific is limited, although aerial and beach seine surveys are extensive in certain regions (e.g., Prince William Sound; Dias et al. 2022) and nearshore embayments in the GOA (Ormseth et al. 2019). The complex topography and bathymetric relief prominent in these nearshore areas (Baker et al. 2019) appear to provide important habitat for juvenile herring (Hay and McCarter 1997). Data on juvenile or pre-recruit presence and abundance were extremely limited. Juvenile fish have been recorded in beach seine surveys in the nearshore in the GOA and AI

(Ormseth et al. 2019) and in predator diets in the BS (Gunther et al. 2024), but are poorly sampled in typical surveys, including trawl and acoustic surveys. Data were available on juvenile growth and condition (Sewall et al. 2019).

Feeding areas and migrations

Although limited in both space and time, data were available on adult foraging patterns through trawl surveys, directed net surveys, acoustics, and diet analyses. Data on feeding migration are limited but non-target surveys, tag data (Hay and McKinnell 2002; Bishop and Eiler 2018), and fisheries observations of bycatch (Funk 1990; Tojo et al. 2007) provide some insight. Data on overwintering and winter movement patterns were not available in most areas, though there is evidence that juvenile herring overwinter in dense schools nearshore while adults remain offshore (Stokesbury et al. 2002) and recent analyses provide insight to dynamics in southeast Alaska (Boswell et al. 2016) and Prince William Sound (Sewall et al. 2019).

Key messages

- Although information on adult foraging patterns exist, comprehensive data on feeding areas and migrations of Pacific herring in these LMEs were limited. More extensive research using diverse methods including targeted trawl surveys, net surveys, acoustics, and diet analyses would enhance understanding of adult foraging and movement. These approaches would also enhance monitoring and interpretation of recent shifts in distributions in response to climate.
- Data on overwintering and winter movement patterns of Pacific herring were scarce. Further age-specific studies on seasonal distributions might provide insights with relevance to understanding how these shifts might inform stock differentiation and inform assumptions related to assessments of recruitment, abundance, and ecosystem interactions (e.g., availability to predators). Comparisons of genetic composition in overwintering and spawning grounds might also provide greater insight to population structure.
- The presence and abundance of juvenile Pacific herring are poorly sampled in typical surveys. Enhanced data collection efforts, including beach seine surveys, mid-water offshore assessments, and predator diet analysis, are necessary to better understand juvenile stages, early-stage survival, and pre-recruit dynamics.
- Nearshore areas for SPF in the Northeastern Pacific are poorly understood. Given the complex topography and bathymetric relief in these areas, particularly throughout the GOA, focused research on these habitats is crucial to understand early life stages and recruitment processes of Pacific herring.

California Current

Overview of spatial data and variability

The California Current Large Marine Ecosystem (CCLME), comprising the United States and Mexico, hosts two exploited clupeoids: Pacific sardine, *S. sagax* and Northern anchovy, *Engraulis mordax*. Comprehensive ecological studies for these species have been conducted over the last 75 years (e.g., Talbot 1973; Finney et al. 2002; Litz et al. 2008; Demer et al. 2012; Lindegren et al. 2013; Koslow et al. 2014; Kaplan et al. 2017; Sydeman et al. 2020; Swalethorp et al. 2023). Three subpopulations for each of these species (Figure 2) have been defined based on serological studies (Vrooman 1964; Vrooman et al. 1981) without significant evidence to support genetic differentiation (Hedgecock et al. 1989; Lecomte et al. 2004).

The northern subpopulation of Pacific sardine (cold stock) ranges from northern Baja California, Mexico to southeastern Alaska, U.S.; the southern subpopulation (temperate stock) ranges from the tip of the Baja California peninsula, Mexico to southern California, U.S.; the third subpopulation (warm stock) occurs in the Gulf of California, Mexico (Smith 2005). The northern and southern subpopulation adults synchronously migrate northward in late spring and summer, and southward in the fall and winter. Although their ranges overlap, they have separate spawning aggregations; the northern subpopulation spawns in southern California and adjacent northern Baja California, and the southern population does so off central Baja California (Ahlstrom 1954; Ahlstrom 1967). The subpopulation in the Gulf of California spawns in the central Gulf in late winter and early spring (Hammann et al. 1988).

Northern anchovy is separated into northern (British Columbia, Canada to central California, U.S.), central (San Francisco, California to central Baja California peninsula, Mexico), and southern (mid Baja California peninsula, Mexico and into the Gulf of California) subpopulations (Schwartzkopf et al. 2022). The northern subpopulation of Northern anchovy primarily spawns in the summer, in coastal areas from southern Washington to central Oregon. The central subpopulation spawns monthly from late winter to early spring, peaking in February, across multiple coastal areas in southern and central California. The southern subpopulation spawns year-round, with a peak in winter, in coastal areas off the Baja California peninsula.

A variety of trawl surveys in the northern CCLME have been conducted over different time periods, collectively providing adult presence/biomass data on northern subpopulations of Pacific sardine and northern anchovy (Litz et al. 2008). Monthly trawl surveys were conducted for 16 years in central and southern California providing adult presence/biomass information on Pacific Sardine, Northern Anchovy, and other taxa (Figures 6 and 8). Subsequently, acoustic capabilities were added to these pelagic fish surveys with a reduction in sampling frequency to quarterly surveys. An extended break (6–10 years) ended with the development of the interannual Acoustic–Trawl–Method survey, which extended the sampling region to the northern extent of the CCLME and in recent years (2022–2023) southward to central Baja California, Mexico (Renfree et al. 2023). A third trawl survey focused primarily on juvenile rockfishes (*Sebastes* spp.) has been conducted with minimal interruptions off California providing valuable information on juvenile sardine and anchovy (Sakuma et al. 2016). All three trawl surveys provide adult presence/biomass data as well as data on adult spawning migration and feeding areas, nursery areas, and juvenile presence/biomass for sardine and anchovy subpopulations in U.S. waters and partially for subpopulations of both species off northern Baja California, Mexico (Table S2 from the Online Supplemental Material). For Mexico, adult presence/biomass, spawning migration, and nursery areas for both species are based on conceptual models from catch and landings data (Hammann et al. 1988; Félix-Uraga et al. 2004).

Spawning spatial variability

Extensive research based on egg and larval surveys conducted continuously from 1949 to present (Figure S14 and Table S2 from the Online Supplemental Material) has been instrumental in developing the DEPM for Northern Anchovy and Pacific Sardine in the CCLME, which includes critical information on spawning area, and space/time variability (Lasker 1985; Lo et al. 1996). Similar surveys in the Gulf of California have estimated spawning areas for these species (Table S2) (Hammann et al. 1988; Félix-Uraga et al. 2004).

Recruitment processes and spatial variability

Egg and larval studies in the CCLME provide the longest time series data in the region from which studies on larval routes and connectivity have been conducted (Figure S14 and Table S2 from the Online Supplemental Material) (e.g., Thompson et al. 2014; Weber et al. 2015; Valencia-Gasti et al. 2018; Aceves-Medina et al. 2019). These data, along with juvenile surveys, have been used to infer suitable nursery areas for both anchovy and sardine in the northern and central CCLME (Brodeur et al. 2003; Sakuma et al. 2016) and catch and derived environmental data in the southern CCLME (Hammann et al. 1988; Félix-Uraga et al. 2004). Annual abundance trends for juvenile sardines and anchovies in the central and northern CCLME were similar to those of adults for most years based on trawl surveys (Figure 8, Table S2 from the Online Supplemental Material) (Emmett et al. 2005; Sakuma et al. 2016). Research in the Gulf of California has detailed local sardine migration patterns, including juvenile distribution (Hammann et al. 1988).

Feeding areas and migrations

Trawl and acoustic-trawl surveys throughout the CCLME provide data on feeding areas and migrations for both anchovy and sardine species in the region (Table S2 from the Online Supplemental Material; e.g., Emmett et al. 2005; Demer et al. 2012; Zwolinski et al. 2017 and references therein). Habitat models on Pacific Sardine based on acoustic-trawl and egg and larval surveys suggest sardines migrating from the south in spring do not overwinter in the north (Zwolinski et al. 2011). Spawning migrations have been modeled for the central subpopulation of Northern Anchovy, and all three subpopulations of the Pacific sardine utilizing a variety of methods (e.g., statistical habitat and spatial distribution models) based on trawl, acoustic-trawl, and egg and larval surveys (Figure 8, Figure S1 and Table S2 from the Online Supplemental Material) (e.g., Hammann et al. 1988; Sydeman et al. 2020). Results from an early (1936–1942) Pacific sardine tagging study provided one of the first descriptions of sardine migration patterns along much of the Pacific coast of North America (Clark and Janssen 1945).

Key messages

- Many studies based on the rich datasets on Pacific sardine and Northern anchovy in the CCLME conclude that both species inhabit waters within specific temperature ranges throughout ontogeny.

- Independent fishery datasets, often supplemented with catch and landings data, are vital for understanding population dynamics in the CCLME. In Mexico, multiple species are grouped into "Pacific Sardine" when landings are reported, which can obfuscate results and interpretation. It is recommended to incentivize a better classification of this commercial category to improve data accuracy and interpretation.
- Despite extensive ecological research in the CCLME, gaps persist, particularly in studies on juvenile's presence/biomass and nursery areas. Basic biological studies have not been conducted in over a decade in large areas. Refining existing sampling programs could yield more precise data on these aspects for both species.

Humboldt Current

Overview of spatial data and variability

Four SPF species inhabit the Humboldt Large Marine Ecosystem (HLME), encompassing the coast of Peru, Chile, and the Patagonian shelf: Peruvian anchoveta (*E. ringens*), common sardine or Araucanian herring (*Strangomera bentincki*), South American sardine (*S. sagax*), and Chilean sprat (*Sprattus fuegensis*) (Figure 2, Figures S15 and S16 and Table S1 from the Online Supplemental Material). These species play vital roles in trophic interactions and possess relevant economic value, constituting well over half of the catches and including the largest SPF fishery in the world, centered on anchoveta (see the Online Supplemental Material). Even though the Chilean sprat inhabits parts of another LME, the Patagonian Shelf, it is included here for geographic proximity and because the Patagonian shelf LME from the Atlantic side is not dealt with in this work.

Extensive literature covers the ecology of anchoveta in both Chile and Peru. Anchoveta exhibits year-round spawning with two peaks, a primary one in winter and a secondary one in late summer (Perea et al. 2011; Claramunt et al. 2014). In Peru, key management measures include fishing bans during peak spawning periods, which can span at least six months per year.

Over the past decade, northern stocks in both countries have shown an increase in juvenile fish proportions within the population, while total biomass remains stable (Gutierrez et al. 2022, in review). Various hypotheses have been proposed to explain this variation, including shifts in the distribution of adults and juveniles and the detection of large nursey areas (Gutierrez op cit.), with no clear pattern in the distribution of early life stages (Flores-Valiente et al. 2023).

In northern Chile, anchoveta distribution extends from near the coast out to 60 nautical miles in winter (Castillo et al. 1993). Spawning grounds, located on the coastal edge, exhibit important spatiotemporal variability in their zonal, and southern extent (Moreno and Claramunt 2022). Juveniles typically recruit to the fisheries around five months after hatching (Castillo and Plaza 2016).

In central Chile (third stock), the spawning season occurs between winter and early spring (Böhm et al. 2017), with spawning grounds located in coastal bays where coastal retention increases (Bucarey et al. 2021) between 20°S and 31°S. In central-southern Chile, within a seasonal upwelling system influenced by rivers, anchoveta, and common sardine share the same reproductive and feeding habitat (33°–41°S). Here, the continental shelf widens, and the distribution of SPF extends up to 20 nm offshore, with spawning grounds located in gulfs and bays. The common sardine spawns during the southern winter, while anchoveta has a longer spawning season from late winter to spring (Cubillos et al. 2001). Recruitment of anchoveta and common sardine occurs during the summer/autumn, with spatial distribution linked to ENSO-scale circulation dynamics (Vásquez et al. 2016; Aedo et al. 2020).

The Chilean sprat is distributed between northern Patagonia in Chile and southern Argentina through the ecosystem of channels and fjords. In northern Patagonia, it inhabits an estuarine system where the spawning grounds are located. There is little evidence of the recruitment of this species, although acoustic surveys have detected it in the same spawning locations (Galleguillos et al. 2012). In this region, sprat cohabits with anchoveta and common sardine, supporting a mixed fishery where 65% of the catches consists of sprat (Aranis et al. 2006).

The anchoveta fishery has been intensively monitored since the 1960s, not only at landing points but also aboard the fleet during synoptic surveys called Eureka (Gutiérrez et al. 2000). The two stocks in Peru have been assessed annually during multidisciplinary surveys since 1983 (Figure 8), including acoustic assessments of both adult and juvenile segments (Gutiérrez et al. 2012).

In Chile and Peru, all the SPF stocks now benefit from spatial data on adult and juvenile presence or biomass from scientific surveys (Figure 4). These data are typically collected annually, with some stocks undergoing assessments twice a year, such as anchoveta in Chile and Peru, and common sardine in central-southern Chile. The primary source of these data has been regular acoustic surveys (Figure 8). For the northern Chilean anchoveta stock (second stock, shared with Peru), scientists have applied the DEPM since the early 1990s to estimate spawning biomass, furnishing spatial insights into the spawning structure. This method has been similarly applied to anchoveta (fourth stock) and common sardine since the early 2000s in central-southern Chile and, more recently, from 2015, in the central Chile anchoveta stock (third stock).

On the Patagonian shelf, regular acoustic surveys have been conducted since the mid-2000s to estimate the biomass of adults and recruits for Patagonian sprat, anchoveta, and the common sardine inhabiting the inland sea of northern Patagonia. Most data originate from surveys extending over a few weeks, rendering spatial variability in presence/biomass for certain processes, such as spawning aggregations, while understanding of space occupancy during other months remains limited.

Spawning spatial variability

During the first decades of the fishery, experiments in Peru and northern Chile studied possible seasonal migration of anchoveta. Tagging and analysis of recaptured individuals failed to reveal discernible patterns. Eggs, larvae, post-larvae, juveniles, and adults are observed throughout the region without timed latitudinal or longitudinal gradients. In central-southern Chile, no mark-and-recapture experiments have been carried out to study reproductive migrations of SPF. Nevertheless, from seasonal multidisciplinary surveys including acoustic detection of recruits and adults (Figures 4 and 8), general patterns of reproductive migrations for anchoveta and common sardine have been established. On the Patagonian shelf, spatial information is notably limited, and migratory patterns remain largely uncharted.

Monitoring of spawning areas and their variability dates to the establishment of the Sea Research Institute (IMARPE) in Peru and the Institute of Promotion of Fisheries (IFOP) in Chile in 1963, and long time series of up to 60 years were available (Figures 6 and 8, Table S2 from the Supplemental Online Material). In both countries, anchoveta has been observed as a partial spawner throughout the year, with two distinct peaks in winter and summer (Perea et al. 2011).

In northern Chile, since 1992, the DEPM has been conducted once a year during peak reproductive activity. Planktonic cruises with high spatial resolution have delineated and quantified the spawning area and its interannual variability. During periods of high population abundance, anchoveta expands its spawning area southward and offshore, coinciding with periods of larger female predominance (Moreno and Claramunt 2022). Spatial variations in spawning stock distribution have also been linked to ENSO dynamics influencing the habitat of northern Chile (Hernández-Santoroet al. 2019). In central-southern Chile, similar scientific surveys have been ongoing since 2002 to evaluate anchoveta and common sardine spawning (Figures 6 and 8, Table S2 from the Supplemental Online Material). Both species show overlapping distributions, with egg densities mainly associated to shallow and coastal zones, emphasizing the significance of coastal topography and bottom depth for their spawning (Castillo-Jordán et al. 2007). On the Patagonian shelf, where anchoveta, common sardine, and Patagonian sprat coexist, specific projects using short-term series have identified their spawning areas (e.g., Castro et al. 2015). These SPF species have low spatial segregation of spawning grounds, associated with coastal margins of inland seas near river mouths characterizing this estuarine region.

Recruitment processes and spatial variability

Brochier et al. (2008) used a coupled physical-biological spatially explicit IBM to investigate factors influencing egg and larval survival rates of anchoveta in the northern Humboldt upwelling region off Peru (Figure S15 from the Online Supplemental Material). The study examined spatial and temporal variability in release locations of retained virtual particles, comparing findings to observed egg concentration patterns reconstructed from a 40-year monitoring period. Results indicated maximal coastal retention near the surface in winter and in deeper layers in summer. Egg buoyancy and larval vertical behavior significantly impacted coastal retention. The model suggested an optimal temporal spawning pattern with two peaks, in austral winter and summer, with higher retention observed from 10° S to 20° S.

Similar approaches have been applied to anchoveta in central-southern Chile Parada et al. 2012; Soto-Mendoza et al. 2012). These studies coupled a climatological ROMS with an IBM, showing that northward circulation forced by seasonal winds promotes transport of anchoveta eggs and larvae, facilitating recurrent nursery grounds between 35° and 37°S. Vásquez et al. (2016) expanded this approach by incorporating interannual variability in atmospheric forcing and freshwater input from rivers, in addition to time- and space-varying biological parameters, highlighting considerable interannual variability in coastal circulation influenced by ENSO dynamics, resulting in higher levels of coastal retention during positive ENSO phases. On the Patagonian shelf, climatological modeling suggested high levels of retention of SPF eggs and larvae associated with estuarine dynamics of the inland sea of northern Patagonia (Castro et al. 2015). Coupled modeling with interannual variability was developed for anchoveta from northern Chile (Vásquez et al. 2016), demonstrating that the transport routes of eggs and larvae primarily follow a northwest direction with high interaction with the stock distributed in southern Peru, varying interannually in response to ENSO dynamics.

Since 1983, nursery areas for anchoveta have been observed along the Peruvian coast, showing a consistent trend where pre-recruits are increasingly found closer to the coast. The primary nursery area is located from 6 to 8° S, a pattern stable from 1983 to 2009. From 2010 onward, there was an increase in the proportion of juvenile fish (smaller than 12 cm) in the population. Despite interannual variations, since 2016, the juvenile proportion has risen to 80% of the population in terms of number of fish and 60% in terms of biomass (Gutierrez et al. 2022, in review). Consequently, nursery areas are now observed along the coast, primarily south of Callao (12°S).

In northern Chile, monitoring of anchoveta nursery grounds has been ongoing since the early 1990s through multidisciplinary scientific surveys (Figusre 8). Anchoveta pre-recruits are found near the coast, with highest concentrations between 22° and 26°S. This pattern remained stable during the 1990s. Nevertheless, since 2016, there has been an increase in the proportion of juveniles, distributed in a more restricted latitudinal band, possibly due to phenotypic variation in response to habitat conditions, mirroring the trend in the shared stock of southern Peru and northern Chile (2023, Dec 10 email from M Gutierrez).

In central southern Chile, nursery grounds of anchoveta and common sardine have been documented since the early 2000s through multidisciplinary surveys. These nursery grounds are located further north than the spawning areas, centered between 35° and 37°S. In general, the location of nursery grounds has remained stable over time, although recent studies have shown that El Niño/La Niña events modify the distribution of early juveniles of both species (Aedo et al. 2020). On the Patagonian shelf, records of Patagonian sprat nursery grounds are more recent, with pre-recruits distributed near spawning areas in response to higher retention in inland seas.

Continuous monitoring is in place along the coast of Peru and central and northern Chile through multidisciplinary surveys. In central-northern Peru, acoustic surveys are conducted twice a year. A dedicated survey to assess anchoveta spawning is conducted annually, while in southern Peru/northern Chile, annual acoustic surveys are performed. In central-southern Chile, where anchoveta and Araucanian herring are jointly evaluated, surveys are conducted twice a year. In addition, permanent size control of fish at landing points allows detection of the presence and biomass of juvenile SPF.

Feeding areas and migrations

Espinoza and Bertrand (2008, 2014) analyzed historical data dating back to 1954 to gain insights into the ontogenetic and spatiotemporal variability in the diet of anchoveta. They found that, whatever the period, anchoveta foraged mainly on macrozooplankton, with the significance of euphausiids in its diet directly related to their abundance. This bottom-up effect was also observed at smaller scales, as the proportion of euphausiids in the diet increased with anchoveta total length and euphausiids accessibility. By selecting larger prey like euphausiids, anchoveta gains an energetic advantage in an ecosystem where oxygen depletion imposes strong metabolic constraints on pelagic fishes. The authors concluded that the plasticity of anchoveta allows it to cope with the highly variable environment it encounters.

No clear pattern of feeding migrations is evident in anchoveta. Extensive process cruises conducted from 1967 to 1970, and from 2002 to 2010 as part of surveys on behavioral ecology, failed to detect seasonal migrations (Figure 4). Tagging and recapturing fish were equally unsuccessful in identifying migration among the three anchoveta stocks along the Chilean and Peruvian coasts.

Rather than dedicated seasonal migrations, anchoveta exhibits changes in coastal distribution, expanding further offshore during cold conditions and contracting during warmer conditions such as El Niño events. Forced migrations may occur during strong El Niño events, resulting in decreased biomass, as demonstrated by Gutierrez et al. (2012). Bertrand et al. (2004) hypothesized that during the strong El Niño event of 1997–1998, anchoveta sought refuge in coastal areas out of reach of fishing and research vessels. Anchoveta biomass decreased from 9 MT in April 1997 to 1.2 MT in September 1998, later rebuilding to 2.8 MT in December 1998 and 5.2 MT in March 1999. Subsequent acoustics surveys (four per year since 1998–2002) monitored latitudinal variations to explain the biomass decrease, but no gradient was observed, supporting the loophole hypothesis proposed by Bertrand et al. (2004).

As previously discussed, anchoveta in the Humboldt Current lack defined migration patterns, with migration events primarily associated with warm El Niño conditions. Anchoveta, a partial spawner, releases 12–14 egg batches annually, peaking in summer and winter, with each female producing 12,000–15,000 eggs per batch (Perea et al. 2011). In the southern Humboldt region, no SPF mark-and-recapture studies have examined active migrations. Nevertheless, drawing from multidisciplinary surveys and biological-fishery data, Cubillos et al. (2007) proposed a conceptual model for anchoveta's spatial dynamics, applicable to common sardine.

During summer-autumn (January-March), recruitment occurs with an average size of 6–7 cm, primarily north of the Gulf of Arauco. Adults (>11 cm, over one-year old) tend to concentrate south of 38°20′S (from Isla Mocha to Corral) and secondarily in the north (Carranza, Itata river mouth). In autumn-winter (April–August), juveniles from the previous year's spawning develop into pre-adults, and adults over one-year old actively migrate to form pre-reproductive aggregations. Surviving juveniles in protected coastal areas achieve sexual maturity at one year, completing their life cycle by spawning for the first time near their nursery grounds, particularly between Constitución and the Gulf of Arauco. Subsequently, individuals that have spawned for the first time disperse north and south. In the southern sector, the largest individuals may eventually migrate northward toward the coast to reproduce in spawning areas during the spawning season, exhibiting natal homing behavior.

Key messages

- While evidence indicates that ENSO dynamics affect the spatial distribution of SPF (e.g., Gutierrez et al. 2012; Moron et al. 2019; Aedo et al. 2020; Armas et al. 2024), the mechanisms, particularly during early, hard-to-monitor stages, are not well understood. Uncertainties are heightened by the diversity of El Niño events (coastal *vs.* canonical), their triggers, and their impacts on SPF spatial dynamics. Comprehensive regional surveys are recommended to investigate SPF population responses to ENSO variability, focusing on transboundary and widely distributed species like anchoveta and sardine in this LME.
- In the northern Humboldt region, anchoveta size decreases with scarce zooplankton (e.g., euphausiids and copepods), yet the specific effects of prey fluctuations on anchoveta size and health remain unclear, necessitating detailed research. Despite stable abundance over 25 years, an increase in juveniles suggests possible phenotypic responses to habitat changes, such as earlier spawning due to limited food availability and reduced fat content, that require further study. Anchoveta biomass appears to depend on successful recruitment conditions rather than spawning alone, possibly influenced by unmonitored migration of larger adults (e.g., Gulf of Guayaquil, IPIAP 2023). This monitoring gap underscores the need of implementing migration tracking programs and studying recruitment factors to enhance species management and conservation.
- Although surveys and monitoring have provided insights into SPF spatial dynamics in the Humboldt system, the underlying mechanisms remain inadequately understood. Environmental changes, including climate change, pose significant concerns due to the species' diverse habitats: equatorial upwelling systems, river-influenced seasonal upwelling, and Patagonian estuaries. In regions, such as central-southern Chile and the Patagonian shelf, coexisting SPF populations share habitats and support mixed fisheries but exhibit varying responses to environmental fluctuations, necessitating further research into species-specific responses.
- The hypothesized spatial life cycles patterns for anchoveta and common sardine in southern Humboldt stocks, based on spawning areas, adult distribution, and larval transport, require further study. Research should focus on variations in spawning, nursery, and feeding areas relative to population size and environmental conditions, considering the diverse coastal ecosystems they inhabit, such as seasonal upwelling systems, freshwater-influenced regions, and upwelling bays.
- In the southern Humboldt region, data on annual spatial diet variation and spatial information on seasonal or interannual changes in feeding areas are lacking for most stocks. Similarly, there is insufficient information on seasonal movement patterns, such as spawning migrations.

South Brazil Shelf

Overview of spatial data and variability

Two main exploited SPF species are found in the South Brazil Shelf LME: the Brazilian sardine (*S. brasiliensis*) and the Argentine anchovy (*Engraulis anchoita*). These species are managed independently as two stocks (Figure 2, Figure S17 and Table S1 from the Online Supplemental Material). The Brazilian sardine is a strategic resource locally, accounting for up to 13% of Brazil's total fish catches. It is the main target for the Brazilian purse seine fisheries and is promptly processed as canned fish by local industries, although its total production may not equate to the same level of importance as other small pelagic species (online supplemental material). The Argentine anchovy is economically important only to the Argentine and Uruguayan fishery fleets and is considered to be in "healthy" state (Carvalho and Castello 2013; CTMFM 2022).

Adults of the Brazilian sardine are found between 10 m and 50 m depth, often associated with thermal fronts created by subsurface intrusions of the South Atlantic Central Water (SACW), mostly during the austral summer. Reproduction occurs between October and March, with multiple spawning events during the reproductive season. Juveniles remain close to the coast and inside bays and estuaries.

Due to its restricted distribution within the Southeastern Brazilian Bight (SBB), the Brazilian sardine population is considered as a single stock unit, even though different aggregation areas can be inferred from acoustic surveys (Johanneson 1975; Rijavec and Amaral 1977) and fisheries data (Moraes, Gherardi, et al. 2012). Geographic differences in biochemistry, growth patterns, size-class distribution, and spawning behavior for the Brazilian sardine led some authors to hypothesize the existence of northern and southern population sub-units (Vazzoler and Ngan, 1976; Vazzoler et al. 1987; Saccardo et al. 1988). Nonetheless, Matsuura (1998) highlighted that truncated size structures could result from space-time shifts in spawning events during extended spawning seasons, rather than distinct population units with independent life histories.

The Argentine anchovy is broadly distributed from the Gulf of San Jorge (Argentina, 48°S) to Cape São Tomé (Brazil, 20°S) (Bakun and Parrish 1991) and spawns year-round with a peak in the SBB during late spring and early summer (Matsuura et al. 1992). Within this wide geographic distribution, three stocks with biological differences have been identified, of which only one belongs to this LME: the Patagonic (48°–41°S; Argentina), the Bonaerense (41°–28°S; northern Argentina, Uruguay, and southern Brazil) and the SBB stock (Carvalho and Castello 2013; Favero, Katsuragawa, Oliveira, et al. 2017; Favero, Katsuragawa, Oliveira, et al. 2017). While the Bonaerense stock exhibits older individuals up to age 4, the SBB stock predominantly consists of 1-year-old individuals (Carvalho and Castello 2013).

Data on the acoustic spatial distribution of adult *S. brasiliensis* were found to be scarce and irregular over time, limited to two survey reports from the 1970s (Johanneson 1975; Rijavec and Amaral 1977) and later surveys conducted after the 1990s (ECOSAR cruises), with data available mostly as grey literature (Castello et al. 1991; IBAMA 1995; IBAMA 2011) (Figures 6 and 8, Table S1 from the Online Supplemental Material). A more consistent spatiotemporal dataset was provided by compiling logbook data acquired between 2000 and 2006, covering more than 80% of the SBB (Moraes 2012) (Figures 4 and 6, Figure S17 from the Online Supplemental Material). This allowed the identification of recurrent spatial patterns and interannual variability in fisheries aggregations, even though the underlying oceanographic (e.g., local enrichment and feeding areas) and biological (social interactions and schooling behavior) drivers remain subjects for further investigation.

Scientific survey data were scarce for *S. brasiliensis* and have been often acquired as ancillary data on recent acoustic surveys (Figures 6 and 8; ECOSAR cruises) (Castello et al. 1991; IBAMA 1995; IBAMA 2011). Adult biomass estimates using Virtual Population Analysis (VPA) was provided by Cergole et al. (2002), spanning from 1977 to 1997, but no explicit information on spatial distribution is provided. Knowledge about the spatial variability of Argentine anchovy is limited to the SBB stock, and a comprehensive assessment of the whole South Brazil Shelf LME is still lacking (see Figures 4 and 6, Table S2 from the Online Supplemental Material).

Spawning spatial variability

It is not yet known whether Brazilian sardines perform spawning migrations within the South Brazil Shelf LME. Results from spawning probability maps based on ichthyoplankton surveys (Figure 8 and Figure S17) suggest that the reproductive strategy is based on the selection of the nearest suitable spawning areas (Gigliotti et al. 2010; Dias et al. 2014). This is reinforced by a lower probability of occurrence of spawning events at the northernmost sector of the SBB (Figure S1 from the Online Supplemental

Material), influenced by seasonal coastal upwelling where optimal conditions for larval development (i.e., vertical stability; warmer temperatures) are less frequent.

There were no available spatial data on spawning migrations of Argentine anchovy in the South Brazil Shelf (Figures 4 and 6, Table S2 from the Online Supplemental Material). Acoustic surveys supplemented by midwater trawling from five cruises (August 1980, October/November 1982, October 1987, September 1988, and January 1990) showed that during the austral winter, adults of Argentine anchovy migrate from Uruguayan and Argentinean waters off the Plata River (35 – 34°S) to Brazilian waters (34–29°S) where favorable spawning and feeding conditions seem to prevail, returning southward in late spring (Lima and Castello 1995, data not available). Eggs sampled during the winter in the northern sector of the SBB are larger than those sampled in summer, possibly because larger adults coming from the south are spawning (Favero, Favero, Katsuragawa, Oliveira, et al. 2017; Favero, Katsuragawa, Oliveira, et al. 2017).

Information on the spatiotemporal variability of spawning and nursery grounds for Brazilian sardine was first presented by Gigliotti et al. (2010), based on geostatistical modeling of egg and larvae data acquired in ichthyoplankton surveys between 1976 and 1993 (Figure S18, Table S2 from the Online Supplemental Material). The spatial arrangement of spawning habitats determined from geostatistical and individual-based modeling (Gigliotti et al. 2010; Dias et al. 2014) (Figure 8, Figure S17 and Table S2 from the Online Supplemental Material) indicated the presence of six spawning areas. Eggs released from these spawning habitats induced the concentration of larvae along the mid to southwestern portion of the South Brazil Shelf, being mostly coastal (<50 m depth) and patchy. Spawning areas with high egg and larvae concentrations were connected by areas with lower concentrations and tend to experience periods of expansion and contraction (Gigliotti et al. 2010).

There was only one dataset on spawning variability of the *E. anchoita* in this LME, based on eggs and larval surveys (Figures 6 and 8) spanning 19 years but with many missing years (Figure S17 and Table S2 from the Online Supplemental Material). Eggs and larvae were sampled throughout the SBB, but no consistent or recurrent spawning areas were identified. A large patch around 27°S with high probability of egg presence (>0.6) was classified as occasional spawning area in the southern portion of the SBB. Other occasional spawning areas were identified in the central portion of the SBB, off Santos Bay and north of São Sebastião Island (Favero, Favero, Katsuragawa, Oliveira, et al. 2017; Favero, Katsuragawa, Oliveira, et al. 2017). Egg abundance sharply decreased toward deeper sites and farther from the coast. Spawning sites exhibited local depths between 12 and 115 m, with a preference range from 26 to 70 m. Areas with depths greater than 115 m and more than 55 km from the coast were mostly avoided (Favero, Favero, Katsuragawa, Oliveira, et al. 2017; Favero, Katsuragawa, Oliveira, et al. 2017).

Recruitment processes and spatial variability

Using the same ichthyoplankton surveys carried out between 1976 and 1993 (Figure S17 from the Online Supplemental Material), Moraes, Paes, et al. (2012) showed that Brazilian sardine nursery grounds were spatially structured at scales ranging from 50 km to 400 km. Shorter spatial scales are also likely but could not be assessed due to the coarse (> 37 km) sampling resolution of the cruises. Results highlighted a spatial persistence of the main spawning grounds, even though expansions and contractions may occur interannually (Gigliotti et al. 2010). Argentine anchovy eggs were more aggregated than larvae, and the frequency of occurrence of larvae was higher (e.g., from 1974 to 2010), even in sites distant from where eggs were sampled (Favero et al. 2018). Nonetheless, spatial data on nursery areas for Argentine anchovy were scarce, as the long time series presented large gaps between 6 and 10 years (Figures 4 and 6, Figure S17 from the online Supplemental Material). No data were available for juveniles (Figures 4 and 6, Table S2 from the Online Supplemental Material).

Feeding areas and migrations

There were no data on the spatial structure of feeding habits and diet for Brazilian sardine, and available studies were limited and local, covering both larval and adult stages and seasonal differences in diet (Goitein 1978; Kurtz 1999; Schneider and Schwingel 1999). For Argentine anchovy, there were no feeding data in this LME (Figures 4 and 6, Table S2 from the Online Supplemental Material).

Argentine anchovy may show some cross-shelf movement during winter, but knowledge on overwintering migrations in the area is still lacking. Feeding and overwintering migrations of the Brazilian sardine can be hypothesized from recurrent temporal shifts in fishing aggregations. For example, probability maps for sardine catches generated from logbook data acquired between 2000 and 2006, covering more than 80% of the SBB, showed five consecutive periods: post-spawning (March–April), pre-wintering

(May–June), wintering (July–August), post-wintering (September–October) and pre-spawning (November) (Moraes 2012). Spatiotemporal patterns of the Brazilian sardine fishing operations seem to be well adjusted to the onset of the spawning activity and the main enrichment mechanisms of the SBB. Increased activity in northern fishing areas during austral spring and summer coincides with the intensification of the SACW intrusions from the outer shelf. Wintering concentration of fisheries in the southernmost areas coincides with a northward influx of cold surface waters from the Brazilian Coastal Current. Both processes generate thermocline fronts, vertical stability, and potential feeding grounds (Castro and Miranda 1998; Muelbert et al. 2008).

Key messages

- The Brazilian sardine is a geographically confined stock that demands high spatial resolution (< 30 km) and continuous shallow-water (< 70 m) surveys of larvae and adult abundances to allow a more accurate determination of its spatial structure.
- Coastal currents and upwelling dynamics can affect the spatial structuring of the Brazilian sardine stock, influencing all developmental stages, their dietary components, and potential predators. Their role needs to be assessed to support stock management strategies.
- Modeling the effects of fisheries on the pelagic ecosystem with end-to-end or mass-balance systems would help to test alternative management policies in the absence of data.
- The Argentine anchovy is not a commercially important resource in the South Brazil Shelf LME and is not a priority for investment in stock assessment.

Kuroshio and Oyashio LME and their transition region

Overview of spatial data and variability

The main target SPF species in the Kuroshio–Oyashio area are the Japanese anchovy *Engraulis japonicus*, Japanese sardine *S. melanostictus*, and Pacific round herring *Etrumeus micropus*. The first two species are the most abundant and commercially important pelagic fish in the western North Pacific. Both Japanese anchovy and sardine are distributed from the subtropical Kuroshio to the subarctic Oyashio areas along the Pacific coastal waters off Japan, leading to the management of these two species as the Pacific stock in Japan (Figure 2, Figure S18 and Table S1 from the Online Supplemental Material). For anchovy, there is another subpopulation in the Kuroshio area, known as the Seto Inland Sea stock. The fisheries catch in the Seto Inland Sea stock is comparable with that in the Pacific stock and the third, Tsushima Warm Current (TWC) stock. The distribution range of round herring is limited to the Kuroshio area, resulting in the SPF in the Kuroshio area comprising three species with four stocks, whereas in the Kuroshio–Oyashio and the Oyashio area there are two species (Japanese anchovy and sardine) and two stocks.

All mentioned stocks undergo assessment based on fishery-dependent data, including catch, effort and age-specific catches. Catch variability for Japanese sardine is larger in the Pacific coastal waters off northern Japan than in central and southern regions. Fishing areas for Japanese anchovy and round herring predominantly lie in the central and southern Pacific coastal waters and southern waters, respectively. Fishery-independent surveys include a coastal-wide monthly survey of eggs and larvae using plankton nets, conducted by prefectural fishery stations and Japan's fisheries research institute (Takasuka et al. 2008; Niino et al. 2021). To gauge recruitment abundance, particularly for Japanese sardine, midwater trawls, and acoustic surveys are performed in the Kuroshio–Oyashio transition area in late spring and the subarctic Oyashio region in late summer.

Spawning spatial variability

Information on spawning areas and seasons has been mainly based on egg and larval surveys and spatiotemporal changes in maturation index of fisheries catch of SPF fish off the Pacific coast of Japan, providing long time from the late 1970s (Figures 4, 6, and 8, Table S2 from the Online Supplemental Material). Spawning of Japanese sardine occurs mainly in the Pacific coastal waters off southern Japan along the Kuroshio Current from January to May. The spawning grounds expand toward offshore waters south of the Kuroshio Current as the population increases (Watanabe et al. 1995; Watanabe et al. 1996; Takasuka et al. 2008). Japanese anchovy spawns year-round, except in winter, in areas overlapping with those of Japanese sardine (Takasuka et al. 2008). In the Kuroshio–Oyashio transition and Oyashio regions, the spawning season for Japanese anchovy is shorter than that in the Kuroshio region and the Seto Inland Sea region (Suhara et al. 2013). The spawning occurrence of Japanese anchovy in the Pacific coastal waters off northern Japan is regulated by water temperature and day length, as observed in egg and larval surveys during the 1980s–2010s (Hayashi et al. 2019). Round herring spawns in the Pacific coastal waters off southwestern Japan throughout the year excluding in summer, and the egg abundance has increased with the rise in stock biomass (Nyuji et al. 2022).

Recruitment processes and spatial variability

Larval transport information for Japanese anchovy and sardine has been investigated using particle tracking models based on datasets of egg distribution and horizontal water velocity and direction (Figures 4, 6, and 8, Table S2 from the Online Supplemental Material). Studies were conducted during 1978–1988 (Kasai et al. 1997), in 1993 and 1994 (Heath et al. 1998), and during 1978–2004 (Itoh et al. 2009). The results indicated that more than half of the particles released in the anchovy spawning area were transported eastward by the Kuroshio Current, moving from the Kuroshio region to the Kuroshio–Oyashio transition region (Itoh et al. 2009).

Two different nursery areas have been postulated for Japanese anchovy and sardine in the Pacific stocks based on spawning area and larval transport data (Figures 4, 6, and 8, Table S2 from the Online Supplemental Material). One is the shore region corresponding with the *shirasu* ("larva" in Japanese) fishing area, in the Pacific coastal waters off southern Japan. The other is the offshore waters along the Kuroshio, the Kuroshio Extension, and the Kuroshio–Oyashio transition regions. The nursery area varies with the population size of Japanese anchovy and sardine in both the coastal waters (Nakata et al. 2000) and the offshore Kuroshio–Oyashio transition region (Takahashi et al. 2009).

Recruitment abundance of SPF in the Kuroshio–Oyashio transition region has been assessed since the mid-1990s using midwater trawl surveys (Figures 6 and 8). Data sets were accessible for Japanese anchovy and sardine (Takahashi et al. 2001; Takahashi et al. 2008; Takahashi et al. 2009; Furuichi et al. 2020; Niino et al. 2021). Sardine juvenile abundance in these surveys has been used as an indicator of the recruitment abundance in the Pacific stock.

Feeding areas and migrations

While comprehensive information on feeding areas was limited for all SPF, the feeding migration of young-of-the-year sardine has been researched using a Two-Dimensional individual-based fish movement model coupled with fish bioenergetics (Figure 8; Okunishi et al. 2009; Okunishi et al. 2012). Recently, combining thermal trajectories indicated by otolith oxygen isotope ratios with numerical simulations has revealed migration routes for young-of-the-year sardine feeding through the Kuroshio Extension, the Kuroshio–Oyashio transition, and the Oyashio regions (Sakamoto et al. 2019).

Historically, spawning migration has been studied based on seasonal changes in size-specific distribution in fishery catches for Japanese anchovy (Kondo 1969) and sardine (Kondo 1988). These studies identified a large-scale southward migration along the Pacific coastal waters off northern Japan from winter to spring in the mid-1960s for anchovy and in the late 1980s for sardine. Additionally, a small-scale migration for sardine spawning has been observed through acoustic surveys around the major spawning grounds off southern Japan in winter (Aoki and Inagaki 1993).

Key messages

- While there was some information on the feeding migration of young-of-the-year sardine, comprehensive data on feeding areas and migration patterns for all SPF in these regions was limited. Enhanced research using modern techniques like individual-based movement models and otolith oxygen isotope ratio analysis (e.g., Sakamoto et al. 2019) is needed to better understand these aspects.
- The spawning season and area of Japanese sardine and anchovy in these regions is known, but details on the variability of these events in relation to environmental factors like water temperature and day length, need further exploration.
- Despite some studies on larval transport and recruitment abundance, there is a need for more robust and continuous data collection in the offshore nursery and feeding grounds, especially in the Kuroshio–Oyashio transition region.

East China Sea and Sea of Japan

Overview of spatial data and variability

As on the Pacific side, the main targeted SPF in the East China Sea, Yellow Sea, and Sea of Japan area are Japanese anchovy *E. japonicus*, Japanese sardine *S. melanostictus* and round herring *E. micropus*. Both anchovy and sardine are distributed along the TWC, encompassing the region from the East China Sea to the Sea of Japan, leading to their management as the TWC stocks in Japan (Figures 2 and 3, Figure S19 and Table S1 from the Online Supplemental Material). Round herring is limited to the East China Sea and the southwestern Sea of Japan and is also managed as the TWC stock. Thus, there are three SPF species and three stocks along the TWC in this region.

All stocks are regularly assessed using both fishery-dependent and independent data. Catch variability of Japanese sardine is higher in central Japan's coastal waters compared to western Japan, while Japanese anchovy and round herring show greater variability in western than in central Japan in the Sea of Japan. Fishery-independent surveys, including egg and larvae studies, also extend to the East China Sea and Sea of Japan. However, midwater trawl and acoustic surveys in these areas face spatial limitations and have a shorter history than those on the Pacific side (Figures 6 and 8), leading to knowledge gaps in recruitment and spawning migration processes, especially for the TWC stocks of Japanese sardine.

Spawning spatial variability

Knowledge on spatial variability in spawning in the East China Sea and Sea of Japan has background studies based on eggs and larval surveys and spatiotemporal changes in maturation indices of fisheries catches in the Pacific side (Figures 4, 6, and 8, Table S2 from the Online Supplemental Material). Japanese sardine spawning occurs mainly in the Japanese coastal waters of the Sea of Japan along the TWC from February to May. The main spawning ground shifted to the southwestern Sea of Japan, corresponding with the upstream waters of the TWC, during the population increase in the late 1970s and early 1980s (Goto 1998; Kim et al. 2006; Furuichi et al. 2020). The distribution range of Japanese sardine expands into an entire area of the Sea of Japan with population increase (Muko et al. 2018). Spawning of Japanese anchovy was reported in the southern waters off the Korean Peninsula during 1993–1994 based on ichthyoplankton surveys (Kim and Lo 2001). Mature females of Japanese anchovy appear from spring to fall in the Japanese coastal waters of the East China Sea and Sea of Japan (Shimura et al. 2008; Suhara et al. 2013). Round herring spawns along the TWC in the East China Sea and the Sea of Japan from winter to spring, with the spawning area positively correlated with spawning stock biomass during 1997–2013 (Suzuki et al. 2018).

Recruitment processes and spatial variability

The spatial scale for estimating larval transport in the East China Sea and the Sea of Japan was smaller than that in the Pacific side (Figures 6 and 8). Takeshige et al. (2015) demonstrated that the larval transport of Japanese anchovy in the northern East China Sea is associated with long-term changes in intensity of the onshore-offshore current toward the western Kyushu during the 1960s–2000s, based on a particle tracking model. Recent developments in analyzing otolith oxygen and carbon isotope ratios have allowed addressing the transportation routes for larvae of Japanese anchovy and sardine in the Toyama Bay in the central Sea of Japan (Nishida et al. 2020).

Four retention areas for larval anchovy were identified using a particle tracking model, with variable instantaneous retention rates from spring to summer in Chinese coastal waters in the Yellow Sea (Xing et al. 2020). Considering wintering areas as nursery areas, the location of wintering areas for Japanese anchovy shows a meridional shift based on the expansion of a cold-water mass indicated by the 10 °C isotherm seasonally from November to March in the Yellow Sea and East China Sea (Iversen et al. 1993) and interannual variations in the latitude of the center of biomass during 2000–2015 in the Yellow Sea (Niu and Wang 2017). There are no reports of distinct nursery areas between coastal and offshore waters in the Sea of Japan, as opposed to the Pacific area, mainly due to limited survey areas in each of the surrounding countries.

The distribution of young-of-the-year Japanese sardine has been reported in the western waters off Kyushu, Japan, in 1992 and 1993 during a population collapse (Ohshimo et al. 1997). Trawl and acoustic surveys for estimating juvenile abundance are currently in progress in the East China Sea and the Sea of Japan. Consequently, there are fewer published reports on indices of recruitment abundance compared to the Pacific side.

Feeding areas and migrations

Information on adult feeding areas from fishing operations is vast for the TWC Japanese sardine, but scarce for other stocks and life stages (Table S2 from the Online Supplemental Material). Young-of-the-year Japanese sardine are distributed in summer in the central Sea of Japan, where the quality and quantity of prey organisms were higher than in the coastal spawning grounds in the southwestern Sea of Japan (Yasuda et al. 2021). Among larval Japanese sardine hatched in the coastal spawning ground in the southwestern Sea of Japan in spring, individuals with faster growth rates are considered to migrate to the offshore nursery grounds in the central Sea of Japan in summer (Aono et al. 2024).

Spawning migration has been assessed based on seasonal changes in size-specific distribution in fishery catches for Japanese sardine (Ito 1961). Although spawning area varied depending on population size (Goto 1998; Furuichi et al. 2020), there was no information on variability in the spawning migration.

Key messages

- There is information on the distribution and migration of Japanese anchovy and sardine, although its amount is limited compared to that of the Pacific side.
- There are few reports on the variability in the feeding and nursery areas and their causes for these LME. Further studies are needed to identify and understand the causes of changes in feeding habits and migration patterns of these species.
- Cooperative research among countries surrounding the Sea of Japan is needed to reveal recruitment processes and spawning migrations, especially for Japanese anchovy and sardine. This will help in developing effective management strategies for the sustainable exploitation and conservation of SPF species in these regions.

Evaluation and synthesis

This study compiled and critically compared the available time series of spatial data for nine key components in the life cycle of SPF, for 77 stocks and 17 species worldwide. The existence of information gaps was evident before start: a process-oriented multiple hypotheses approach may be the only way to tackle this persisting problem (Hare 2014), and information at several spatial scales and life stages may be needed for successful assessments and Management Strategy Evaluations (Punt et al. 2016; Siple et al. 2021). The gap analysis revealed important disparities in the availability and comprehensiveness of data across different regions and species of SPF. Figures 4, 6, and 8 delineate these knowledge deficiencies at the level of stocks and provide a good snapshot of where more effort should be made. Nevertheless, knowledge on all spatial components is not needed for all stocks. For example, knowledge on the location and timing of overwintering migration or some other mid-scale (hundreds of km) adult movement are only valuable for metapopulations from EBUS and for relatively long-lived species, whereas more confined stocks may not display important migrations throughout the year.

Most of the information retrieved in this review has been presented and discussed within specific sections for each of the LME. Therefore, this section briefly summarizes the limitations of the study, distills the most important information gaps, and provides recommendations for better understanding stage-specific variability in spatial habitat use, important to life cycle closure and population dynamics.

Limitations of the study

The collection of spatial datasets was challenging. Despite the large effort in metadata compilation, only a sample of potential LME are included, and some of them are only partly represented (e.g., the south of Benguela). Furthermore, it is acknowledged that the information compiled is restricted to what can be retrieved from WoS and what is available to the experts involved, including assessment and cruise reports. Some information in different languages from grey literature may have been missed. Despite this potential misrepresentation of some spatial components, it is believed that the general, comparative picture across LME is robust. Some information sources were deliberately excluded. For example, genetic information was included to describe the potential cohesion of a given stock (Table S1 from the Online Supplemental Material), but otherwise it was not included in the analysis, as these analyses seldom offer information on variability at ecological scales. Furthermore, data that potentially offer important information on connectivity, such as otoliths, may have been unintentionally omitted for some spatial components, as "otoliths", was not made explicit in our search string. Nevertheless, data provided by microchemistry have been incorporated in the definition of ecological coherence of the stocks when the assessment of that stock incorporated such data. Further, mention to this and other techniques is made throughout the LME summaries.

Some research has been conducted on present-day and projected (future) spatial patterns of stage-specific (potential) habitat residency at scales larger than LME, based on multiple regional surveys (e.g., Lima, Garrido, et al. 2022; Lima, Baltazar-Soares, et al. 2022). These have not been included in the graphs, as their information was captured by regional data compilations.

Some data from models applied to short-time series may have been overlooked in this review if richer (longer-term) model data were available for a specific stock in an LME, and these short-term data may be important to better calibrating and validating models.

The broad classification of spatial processes aggregated subpopulation processes that involve "contingents". These processes typically involve transient environmental constraints separating these contingents, or behavioral processes (schooling, learning) that can strengthen or weaken the spatial coherence of stocks. It is assumed that the components covered in our review, in most cases, capture this sub-structure. Furthermore, this global review focused on the available information on the spatial structure of officially defined stocks (both targeted and untargeted) and not contingents. In this sense, it would be interesting to collect data on variability in growth and abundance, as spatial processes can be partly explained by density-dependent processes. These explanatory mechanisms potentially causing spatial changes were beyond the scope of this work.

Conclusions and recommendations

The analysis of each LME section and recommendations shows that there are common knowledge gaps in the spatial variability that are necessary to better understand life cycle closure of SPF. Some LME, however, show knowledge deficiencies that should be specifically addressed. Most of the gaps already stand out from Figures 3 to 8.

The following bullet points synthesize the main identified gaps and recommendations to improve them.

- Addressing the limitations of acoustic-based spatial information is recommended by extending survey durations for some stocks and improving accessibility to survey data. This has been mentioned in multiple LME, including Barents and Norwegian Seas, Baltic Sea, Mediterranean and Black Sea, and the Canary Current. The vast potential of acoustic data for developing phenomenological or mechanistic models of changes in spatial distribution at different ages remains largely underutilized. The scientific community is urged to move beyond using acoustic data solely for basic assessments and to focus also on describing spatial variation with this data. In some regions of the globe, useful initiatives exist compiling acoustic and trawl surveys (e.g., the ICES Northeastern Atlantic and Baltic Sea Acoustic trawl surveys https://acoustic.ices.dk/). The authors advocate for the construction of similar public databases in other areas, enabling scientists and governing agencies to fully exploit such information. It is also recommended to upload more disaggregated data for re-processing.
- Knowledge on some spatial components of stocks, including migration patterns, feeding grounds, or nursery areas was lacking for some stocks in almost all LME, partly due to the lack of temporal coverage of the surveys. When it exists, it was often based on historical information or short-term surveys and was frequently represented in the form of conceptual static diagrams. While extensive and frequent surveys may not always be feasible due to reasons like the low value of these fisheries or decarbonization policies, exploring the consequences of this lack of information on the reliability of assessments is suggested. Furthermore, work is needed to understand the minimum frequency, spatiotemporal coverage, and resolution at which surveys need to be conducted to capture how SPF stocks may be responding to environmental drivers during these times of rapid, climate-driven changes within LME.
- Managing SPF stocks coherently with their ecological distribution, as revealed by population markers including molecular or biochemical tools, is advocated. In only five out of 19 LME examined here were all SPF stocks managed coherently in this way. In many cases, management units and data collected for stock assessment and management may be inappropriate for understanding spatial variability in habitats utilized by many SPF metapopulations. Efforts to harmonize of data from countries sharing stocks should continue, as well as proper identification of the seascape used by the stocks through a combination of approaches and new technologies, such as life history and habitat reconstruction from otoliths, spatially explicit full life cycle models, SDMs, and novel molecular tools.
- Leveraging data-rich stocks occur in archetypical systems (e.g., EBUS, boreal seas, and river plumes) to inform survey designs in similar data-poor regions is recommended, especially where investment to conduct surveys is limited. Compiling a database on time series length of several spatial processes, like the one in this work, can help choosing a reasonable dataset

for a given species to capture the expected variability. Such knowledge can then be incorporated into ecological or Management Strategy Evaluation models in data-poor areas (e.g., Punt et al. 2016).

- Previous overarching projects, such as Global Ocean Ecosystem Dynamics (GLOBEC) established national or multi-national regional programs (e.g., Peck et al. 2012) that offer opportunities to make consistent cross-ecosystem comparisons of data needed to identify commonalities across different SPF stocks. We encourage such programs, as they can identify spatial and temporal data gaps and align survey designs to fill these gaps. Currently, the application of new methods to extract patterns from vast amounts of data could bolster the identification of these data needs, and how knowledge could be directly used across similar ecosystems. Within large areas in Europe (e.g., through ICES Working Groups like WGACEGG, WGALES), national survey datasets (acoustic and eggs) are now set in common to build maps (https://www.ices.dk/data/data-portals/Pages/Eggs-and-larvae.aspx) of adult and egg distribution of some SPF species, together with their environmental covariates. These maps reveal the main spots of spawning aggregation in a consistent manner at the scale of the species distribution range within Europe. Additional progress can still be made based on large-scale multinational projects using genetic studies and process-oriented studies (e.g., larval drift modeling experiments and movement ecology studies), especially when combined, to study the connectivity within and between LME, at different temporal scales.
- Analyzing spatial patterns with regard to age or size structure to distinguish the effects of environmental factors and fishing is recommended, as both drivers usually have distinct impacts. Spatial distribution and abundance patterns can be altered by both by the environment and by fishing. Analyzing these spatial patterns can indicate differential pressures. While spatially explicit management at high resolution is increasingly advocated for, typically only a few life history components are typically used (Siple et al. 2021), which limits opportunities to improve short-term forecasts. To address this, stock-specific research needs have been identified and will need to be covered in the coming years.

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The authors report there are no competing interests to declare.

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References

Abdelouahab H, Berraho A, Baibai T, Larissi J, Charib S, Agouzouk A, Makaoui A, Ettahiri O, Errhif A. 2021. Long term variation of sardine Sardina pilchardus spawning along the Atlantic coast of northwest Africa (21–26°N): characterization and spatiotemporal variability in spawning habitat. Oceanologia. 63(1):1–11. doi: 10.1016/j.oceano.2020.08.006.

Aceves-Medina G, Jiménez-Rosenberg SPA, Durazo R. 2019. Fish larvae as indicator species of interannual environmental variability in a subtropical transition area off the Baja California peninsula. Deep Sea Res Part II. 169–170:104631. doi: 10.1016/J.DSR2.2019.07.019.

Aedo G, Garcés C, Niklitschek E, Musleh S, Cubillos LA, Quiñones RA. 2020. Spatial distribution of small pelagic fishes: implications for fishing quota allocations. Mar Policy. 120:104147. doi: 10.1016/j.marpol.2020.104147.

Agostini VN, Bakun A. 2002. Ocean triads" in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). Fish Oceanogr. 11(3):129–142. doi: 10.1046/j.1365-2419.2002.00201.x.

Ahlstrom EH. 1954. Distribution and abundance of egg and larval populations of the Pacific sardine. Fishery Bull. 93(56):83–140. https://fisherybulletin.nmfs.noaa.gov/sites/default/files/pdf-content/fish-bull/fb56.4.pdf

Ahlstrom EH. 1967. Co-occurrences of sardine and anchovy larvae in the California Current region off California and Baja California. Cal Coop Oc Fish Inv Rep. 11:117–135. https://www.calcofi.com/publications/calcofireports/v11/Vol_11_Ahlstrom.pdf

Aldanondo N, Cotano U, Tiepolo M, Boyra G, Irigoien X. 2010. Growth and movement patterns of early juvenile European anchovy (*Engraulis encrasicolus* L.) in the Bay of Biscay based on otolith microstructure and chemistry. Fish Oceanogr. 19(3):196–208. doi: 10.1111/j.1365-2419.2010.00537.x.

Alheit J. 1988. Reproductive biology of sprat (*Sprattus sprattus*): factors determining annual egg production. ICES J Mar Sci. 44(2):162–168. doi: 10.1093/icesjms/44.2.162.

Aneer G. 1985. Some speculations about the Baltic herring (Clupea harengus *membras*) in connection with the Eutrophication of the Baltic Sea. Can J Fish Aq Sci. 42(S1):83–90.

Aoki I, Inagaki T. 1993. Acoustic surveys of abundance and distribution of the Japanese sardine *Sardinops melanostictus* in the spawning grounds off southern Kyushu, Japan. Nipp Suis Gakk.59(10):1727–1735. doi: 10.2331/suisan.59.1727.

Aono T, Sakamoto T, Ishimura T, Takahashi M, Yasuda T, Kitajima S, Nishida K, Matsuura T, Ikari A, Ito S. 2024. Migration patterns of the Japanese sardine in the Sea of Japan by combining the microscale stable isotope analysis of otoliths and an ocean data assimilation model. Front Mar Sci..11:1394801. doi: 10.3389/fmars.2024.1394801.

Aranis AL, Caballero L, Cerna F, Gómez A, López A, Bernal C. 2006. Monitoreo de la pesquería de pequeños pelágicos en aguas interiores de la X Región, Año 2004. Valparaíso, Chile: Instituto de Fomento Pesquero. Report No.: Informe Final, Proyecto FIP 2004-39: 96 pp. [accessed 2024 Apr 22]. https://www.subpesca.cl/fipa/613/w3-article-89072.html.

Arístegui J, Barton ED, Álvarez-Salgado XA, Santos AMP, Figueiras FG, Kifani S, Hernández-León S, Mason E, Machú E, Demarcq H. 2009. Sub-regional ecosystem variability in the Canary Current upwelling. Prog Oceanogr. 83(1–4):33–48. doi: 10.1016/J.POCEAN.2009.07.031.

Armas E, Arancibia H, Neira S, Marín MC. 2024. Neural network approach for detecting spatial changes in catch probability of *Engraulis ringens* during El Niño-southern oscillation events in northern Chile. Fish Oceanogr. 33:e12672. doi: 10.1111/fog.12672.

Aro E. 2002. Fish migration studies in the Baltic Sea. ICES Marine Science Symposia 215. Copnehnaguen (Denmark): ICES; p. 361–370. doi: 10.17895/ices.pub.8875.

Aro E. 1989. A review of migration patterns in the Baltic Rapp P-V Reun Cons int Explor Mer. 190:72–96.

Atmore LM, Martínez-García L, Makowiecki D, André C, Lõugas L, Barrett JH, Star B. 2022. Population dynamics of Baltic herring since the Viking Age revealed by ancient DNA and genomics. Proc Natl Acad Sci U S A. 119(45):e2208703119. doi: 10.1073/pnas.2208703119.

Aurich HJ. 1953. Verbreitung und Laichverhältnisse von Sardelle und Sardine in der südöstlichen Nordsee und ihre Veränderungen als Folge der Klimaänderung. Helgolander Wiss Meeresunters. 4(3):175–204. doi: 10.1007/BF01609112.

Bachiller E, Albo-Puigserver M, Giménez J, Pennino MG, Marí-Mena N, Esteban A, Lloret-Lloret E, Jadaud A, Carro B, Bellido JM, et al. 2020. A trophic latitudinal gradient revealed in anchovy and sardine from the Western Mediterranean Sea using a multi-proxy approach. Sci Rep. 10(1):17598. doi: 10.1038/s41598-020-74602-y.

Bachiller E, Cotano U, Boyra G, Irigoien X. 2013. Spatial distribution of the stomach weights of juvenile anchovy (*Engraulis encrasicolus* L.) in the Bay of Biscay. ICES J Mar Sci. 70(2):362–378. doi: 10.1093/icesjms/fss176.

Bachiller E, Cotano U, Ibaibarriaga L, Santos M, Irigoien X. 2015. Intraguild predation between small pelagic fish in the Bay of Biscay: impact on anchovy (*Engraulis encrasicolus* L.) egg mortality. Mar Biol. 162(6):1351–1369. doi: 10.1007/s00227-015-2674-0.

Baker MR, De Robertis A, Levine RM, Cooper DW, Farley EV. 2022. Spatial distribution of arctic sand lance in the Chukchi Sea related to the physical environment. Deep Sea Res II. 206(1):105213. doi: 10.1016/j.dsr2.2022.105213.

Baker MR, Palsson W, Zimmerman M, Rooper CN. 2019. Model of trawlable area using benthic terrain and oceanographic variables—Informing survey design and habitat maps in the Gulf of Alaska. Deep-Sea Res II. 28(6):629–657. doi: 10.1111/fog.12442.

Bakun A, Black BA, Bograd SJ, García-Reyes M, Miller AJ, Rykaczewski RR, Sydeman WJ. 2015. Anticipated effects of climate change on coastal upwelling ecosystems. Curr Clim Change Rep. 1(2):85–93. doi: 10.1007/s40641-015-0008-4.

Bakun A, Parrish RH. 1991. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the southwestern Atlantic. J Cons Int Explor Mer. 48:342–361. doi: 10.1093/icesjms/48.3.343.

Bakun A. 1996. Patterns in the oceans: ocean procesess and marine population dynamics. La Jolla: California Sea Grant.

Barange M, Hampton I, Roel BA. 1999. Trends in the abundance and distribution of anchovy and sardine on the South African continental shelf in the 1990s, deduced from acoustic surveys. S Afr J Mar Sci. 21(1):367–391. doi: 10.2989/025776199784126088.

Barton LH, Wespestad VG. 1980. Distribution, biology, and stock assessment of western Alaska's herring stocks Proceedings of the Alaska Herring Symposium. Anchorage (AL): University of Alaska. Report No.: Alaska Sea Grant Report.:80–84.

Baumann H, Hinrichsen HH, Möllmann C, Köster FW, Malzahn AM, Temming A. 2006. Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. Can J Fish Aquat Sci. 63(10):2191–2201. doi: 10.1139/f06-112.

Baumann H, Malzahn AM, Voss R, Temming A. 2009. The German Bight (North Sea) is a nursery area for both locally and externally produced sprat juveniles. J Sea Res. 61(4):234–243. doi: 10.1016/j.seares.2009.01.004.

Beacham TD, Schweigert JF, Macconnachie C, Le KD, Flostrand L. 2008. Use of microsatellites to determine population structure and migration of pacific herring in British Columbia and adjacent regions. Trans Am Fish Soc. 137(6):1795–1811. doi: 10.1577/T08-033.1.

Beare DJ, Burns F, Greig A, Jones EG, Peach K, Kienzle M, McKenzie E, Reid DG. 2004. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. Mar Ecol Prog Ser. 284:269–278. doi: 10.3354/meps284269.

Beare DJ, Reid DG, Petitgas P. 2002. Spatio-temporal patterns in herring (*Clupea harengus* L.) school abundance and size in the northwest North Sea: modelling space-time dependencies to allow examination of the impact of local school abundance on school size. ICES J Mar Sci. 59(3):469–479. doi: 10.1006/jmsc.2002.1201.

Bekkevold D, André C, Dahlgren TG, Clausen LAW, Torstensen E, Mosegaard H, Carvalho GR, Christensen TB, Norlinder E, Ruzzante DE. 2005. Environmental correlates of population differentiation in Atlantic herring. Evolution. 59(12):2656–2668.

Bekkevold D, Berg F, Polte P, Bartolino V, Ojaveer H, Mosegaard H, Farrell ED, Fedotova J, Hemmer-Hansen J, Huwer B, et al. 2023. Mixed-stock analysis of Atlantic herring (*Clupea harengus*): a tool for identifying management units and complex migration dynamics. ICES J Mar Sci. 80(1):173–184. doi: 10.1093/icesjms/fsac223.

Bellier E, Planque B, Petitgas P. 2007. Historical fluctuations in spawning location of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the Bay of Biscay during 1967–73 and 2000-2004. Fish Oceanogr. 16(1):1–15. doi: 10.1111/j.1365-2419.2006.00410.x.

Belveze H, Erzini K. 1983. The influence of hydroclimatic factors on the availability of the sardine (*Sardina pilchardus*, Walbaum) in the Moroccan Atlantic fishery. FAO Fish Rep. 292(2):285–328.

Berg F, Kvamme C, Nash RDM. 2022. The dynamics of 0-group herring *Clupea harengus* and sprat *Sprattus sprattus* populations along the Norwegian Skagerrak coast. Front Mar Sci. 9:831500. doi: 10.3389/fmars.2022.831500.

Berg F, Slotte A, Johannessen A, Kvamme C, Clausen LAW, Nash RDM. 2017. Comparative biology and population mixing among local, coastal and offshore Atlantic herring (*Clupea harengus*) in the North Sea, Skagerrak, Kattegat and western Baltic. PLoS One. 12(10):e0187374. doi: 10.1371/journal.pone.0187374.

Berraho A, Ettahiri O, Letourneur Y, Orbi A, Yahyaoui A. 2005. Importance des paramètres hydrologiques dans la distribution des œufs et des larves des petits pélagiques du sud de l'Atlantique marocain. Cybium. 29(1):21–31. https://sfi-cybium.fr/sites/default/files/pdfs-cybium/04-Berraho211.pdf

Berraho A. 2007. Relations spatialisées entre milieu et ichtyoplancton des petits pélagiques de la côte Atlantique Marocaine (Zones central et sud) [Ph.D]. Rabat, Morocco: Mohammed V University.

Bertrand A, Segura M, Gutiérrez M, Vásquez L. 2004. From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. Fish Fish. 5(4):296–316. doi: 10.1111/j.1467-2679.2004.00165.x.

Bishop MA, Eiler JH. 2018. Migration patterns of post-spawning Pacific herring in a subarctic sound. Deep Sea Res 2 Top Stud Oceanogr. 147:108–115. doi: 10.1016/j.dsr2.2017.04.016.

Boddeke R, Vingerhoed B. 1996. The anchovy returns to the Wadden Sea. ICES J Mar Sci. 53(6):1003–1007. doi: 10.1006/jmsc.1996.0125.

Bode A, Alvarez-Ossorio MT, Cunha ME, Garrido S, Peleteiro JB, Porteiro C, Valdés L, Varela M. 2007. Stable nitrogen isotope studies of the pelagic food web on the Atlantic shelf of the Iberian Peninsula. Progr Oceanogr. 74(2–3):115–131. doi: 10.1016/j.pocean.2007.04.005.

Boely T, Chabanne J, Fréon P, Stéquert B. 1982. Cycle sexuel et migrations de *Sardinella aurita* sur le plateau continental ouest-africain, des Illes Bissagos à la Mauritanie. Rapp Proc Verb Réun Cons Int Exp Mer. 180:350–355. https://www.documentation.ird.fr/hor/fdi:17549

Boely T, Freon P. 1979. Les ressources pélagiques cotières. In Troadec JP, Garcia S editors. Les ressources halieutiques de L'Atlantique centre-Est. 1. Les ressources du Golfe de guinée, de l' Angola à la Mauritanie. Rome, Italy: FAO. FAO Document Technique Sur Les Pêches.1:186.

Boely T. 1982. Les resources en poissons pélagiques des côtes ouest- africaines entre la Mauritanie et le fleuve Congo. Rapp Proc Verb Réun Cons Int Exp Mer. 180:423–431. https://horizon.documentation.ird.fr/exl-doc/pleins_textes/pleins_textes_6/b_fdi_45-46/010006312.pdf

Böhm G, Hernández C, Díaz E, Pérez G, Ojeda R. 2017. Programa de seguimiento de las principales pesquerías pelágicas de la zona norte de Chile XV-IV Regiones, año 2016. Valparaíso, Chile: Instituto de Fomento Pesquero. Report No.: Informe final. Convenio de desempeño 2016, Subsecretaría de Economía y EMT.

Boswell KM, Rieucau G, Vollenweider JJ, Moran JR, Heintz RA, Blackburn JK, Csepp DJ. 2016. Are spatial and temporal patterns in Lynn Canal overwintering Pacific herring related to top predator activity? Can J Fish Aquat Sci. 73(9):1307–1318. doi: 10.1139/cjfas-2015-0192.

Boyra G, Martínez U, Cotano U, Santos M, Irigoien X, Uriarte A. 2013. Acoustic surveys for juvenile anchovy in the Bay of Biscay: abundance estimate as an indicator of the next year's recruitment and spatial distribution patterns. ICES J Mar Sci. 70(7):1354–1368. doi: 10.1093/icesjms/fst096.

Braham CB, Ahmed-Jeyid M, Bensbai J, Ngoum F, Corten A, Gascoigne J. 2024. Overexploitation of round sardinella may lead to the collapse of flat sardinella: what lessons can be drawn for shared stocks. Fish Res. 269:106873. doi: 10.1016/J.FISHRES.2023.106873.

Bréchon AL, Coombs SH, Sims DW, Griffiths AM, HCS, WSD, MGA. 2013. Development of a rapid genetic technique for the identification of clupeid larvae in the Western English Channel and investigation of mislabelling in processed fish products. ICES J Mar Sci. 70(2):399–407. doi: 10.1093/icesjms/fss178.

Brigden KE, Farrell ED, Fraser S, Ayres S, Laurenson K, Powell A, Riley D, Wood C, Angus C. 2023. Identification of herring in Shetland waters -Full report Lerwick: UHI Shetland. Report No: p42. European Maritime and Fisheries Fund (Ref. SCO2721).

Brochier T, Auger P, Pecquerie L, Machu E, Capet X, Thiaw M, Cheikh B, Braham C, Ettahiri O, Charouki N, et al. 2018. Complex small pelagic fish population patterns arising from individual behavioral responses to their environment. Prog Oceanogr. 164:12–27. doi: 10.1016/j.pocean.2018.03.011.

Brochier T, Colas F, Lett C, Echevin V, Cubillos LA, Tam J, Chlaida M, Mullon C, Fréon P. 2009. Small pelagic fish reproductive strategies in upwelling systems: a natal homing evolutionary model to study environmental constraints. Prog Oceanogr. 83(1–4):261–269. doi: 10.1016/j.pocean.2009.07.044.

Brochier T, Lett C, Tam J, Fréon P, Colas F, Ayón P. 2008. An individual-based model study of anchovy early life history in the northern Humboldt Current system. Prog Oceanogr. 79(2–4):313–325. doi: 10.1016/j.pocean.2008.10.004.

Brochier T, Mason E, Moyano M, Berraho A, Colas F, Sangrà P, Hernández-León S, Ettahiri O, Lett C. 2011. Ichthyoplankton transport from the African coast to the Canary Islands. J Mar Sys. 87(2):109–122. doi: 10.1016/j.jmarsys.2011.02.025.

Brodeur RD, Pearcy WG, Ralston S. 2003. Abundance and distribution patterns of nekton and micronekton in the Northern California current transition zone. J Oceanogr. 59:515–535. doi: 10.1023/A:1025548801541.

Brown ED, Norcross BL, Short JW. 1996. Introduction to studies on the effects of the Exxon Valdez oil spill on early life history stages of Pacific herring (*Clupea pallasi*), in Prince William Sound, Alaska. Can J Fish Aq Sci. 10:2337–2342. doi: 10.1139/f96-211.

Bucarey D, Zuñiga MJ, Quiroz MJ. 2021. Estatus y posibilidades de explotación biológicamente sustentables de los principales recursos pesqueros nacionales, año 2021. Anchoveta y Sardina española Región de Atacama a Región de Coquimbo. Valparaíso, Chile: Instituto de Fomento Pesquero. Report No.: Segundo Informe. Convenio de Desempeño 2020 Subsecretaría de Economía y EMT.

Caballero-Huertas M, Frigola-Tepe X, Coll M, Muñoz M, Viñas J. 2022. The current knowledge status of the genetic population structure of the European sardine (*Sardina pilchardus*): uncertainties to be solved for an appropriate fishery management. Rev Fish Biol Fisheries. 32(3):745–763. doi: 10.1007/s11160-022-09704-z.

Campanella F, van der Kooij J. 2021. Spawning and nursery grounds of forage fish in Welsh and surroundings waters. Lowestoft (UK). Cefas. Project Report for RSPB. p. 65.

Carvalho FM, Castello JP. 2013. Argentine anchovy (*Engraulis anchoita*) stock identification and incipient exploitation in southern Brazil. LAJAR. 41(5):820–827. doi: 10.3856/vol41-issue5-fulltext-2.

Casaucao A, González-Ortegón E, Jiménez MP, Teles-Machado A, Plecha S, Peliz AJ, Laiz I. 2021. Assessment of the spawning habitat, spatial distribution, and Lagrangian dispersion of the European anchovy (*Engraulis encrasicolus*) early stages in the Gulf of Cadiz during an apparent anomalous episode in 2016. Sci Total Environ. 781:146530. doi: 10.1016/j.scitotenv.2021.146530.

Castello JP, Habiaga RP, Amaral JC, LimaJrID. 1991. Prospecção hidroacústica e avaliação da biomassa de sardinha e anchoita, na região sudeste do Brasil (outubro/novembro de 1988). Publ Esp Inst Oceanogr São Paulo. 8:15–30.

Castillo F, Plaza G. 2016. Daily growth patterns of juveniles and adults of the Peruvian anchovy (*Engraulis ringens)* in northern Chile. Mar Freshwater Res. 67:899–912. doi: 10.1071/MF15032.

Castillo J, Braun M, Blanco JL. 1993. Cuantificación estacional de la biomasa de los recursos pelágicos y vigilancia bio-oceanográfica, Zona Norte. Septiembre 1992. Santiago, Chile: Instituto de Fomento Pesquero. Report No: Programa Investigaciones pesqueras de recursos pelágicos zona norte 58.

Castillo-Jordán C, Cubillos LA, Paramo J. 2007. The spawning spatial structure of two co-occurring small pelagic fish off central southern Chile in 2005. Aquat Living Resour. 20(1):77–84. doi: 10.1051/alr:2007018.

Castro BM, Miranda LB. 1998. Physical oceanography of western Atlantic continental shelf located between 4° N and 34° S. In: Robinson AR, Brink KH, editors. The sea. 11: The Global Coastal Ocean: Regional Studies and Syntheses (The Sea: Ideas and Observations on Progress in the Study of the Seas). New York (Wiley); p. 209–251.

Castro L, Soto S, Llanos A, Pérez-Santos I, Cubillos L, Alarcón R, Claramunt G, Herrera G, Parada C, Eduardo E, et al. 2015. Identificación de zonas de desove y estadios tempranos de pelágicos pequeños en aguas interiores de la X y XI regiones. Concepción, Chile. Fondo de Investigación Pesquera y de Acuicultura, Report No.: Proyecto FIP 2013-17.

Catalán IA, Auch D, Kamermans P, Morales-Nin B, Angelopoulos NV, Reglero P, Sandersfeld T, Peck MA. 2019. Critically examining the knowledge base required to mechanistically project climate impacts: a case study of Europe's fish and shellfish. Fish Fish. 20(3):501–517. doi: 10.1111/faf.12359.

Catalán IA, Macías D, Solé J, Ospina-Álvarez A, Ruiz J. 2013. Stay off the motorway: resolving the pre-recruitment life history dynamics of the European anchovy in the SW Mediterranean through a spatially-explicit individual-based model (SEIBM). Prog Oceanogr. 111:140–153. doi: 10.1016/j.pocean.2013.02.001.

Cergole MC, Dias-Neto J. 2011. Plano de gestão para o uso sustentável da sardinha-verdadeira *Sardinella brasiliensis* no Brasil. Brasilia (Brazil), Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, IBAMA. p. 1–180. http://www.ibama.gov.br/sophia/cnia/livros/planogestaosardinhaverdadeiradigital.pdf [accessed December 2024]

Cergole MC, Saccardo SA, Rossi-Wongtschowski CLDB. 2002. Fluctuations in the spawning stock biomass and recruitment of the Brazilian sardine (*Sardinella brasiliensis):* 1977–57 1997. Rev Bras Oceanogr. 50:13–26. doi: 10.1590/S1413-77392002000100002.

Chashchin A. 1996. The Black Sea populations of anchovy. Sci Mar. 60(2):219–225.

Chashchin AK. 1995. Abundance, distribution and migration of the Black Sea anchovy stocks. Turk J Zool. 19(2):173–180.

Claramunt G, Cubillos LA, Castro L, Hernández C, Arteaga M. 2014. Variation in the spawning periods of *Engraulis ringens* and *Strangomera bentincki* off the coasts of Chile: a quantitative analysis. Fish Res. 160:96–102. doi: 10.1016/j.fishres.2013.09.010.

Clark FN, Janssen JFJ. 1945. Movements and abundance of the sardine as measured by tag returns. Cal Fish Game Fish Bull. 61:1–42.

Clausen LAW, Bekkevold D, Hatfield EMC, Mosegaard H. 2007. Application and validation of otolith microstructure as a stock identification method in mixed Atlantic herring (*Clupea harengus*) stocks in the North Sea and western Baltic. ICES J Mar Sci. 64(2):377–385. doi: 10.1093/icesjms/fsl036.

Coetzee JC, De Moor CL, van der Longen CD, Butterworth DS. 2022. A summary of the South African sardine (and anchovy) fishery. Cape Town (S Afr). MARAM/IWS. Report No.: MARAM/IWS/2022/Sardine/BG1. p. 1–19.

Coetzee JC, Merkle D, De Moor CL, Twatwa NM, Barange M, Butterworth DS. 2008. Refined estimates of South African pelagic fish biomass from hydro-acoustic surveys: quantifying the effects of target strength, signal attenuation and receiver saturation. Afr J Mar Sci. 30(2):205–217. doi: 10.2989/AJMS.2008.30.2.1.551.

Conand F, Fagetti E. 1971. Description et distribution saisonnière des larves de sardinelles des côtes du Sénégal et de la Gambie en 1968 et 1969. Cch ORSTOM,Sér Océanogr. IX(3):293–318. [accessed 2023 Dec 21] https://horizon.documentation.ird.fr/exl-doc/pleins_textes/cahiers/oceanographie/19608.pdf

Conand F. 1977. Oeufs et larves de la sardinelle ronde (*Sardinella aurita*) au Sénégal: distribution, croissance, mortalité, variations d'abondance de 1971 à 1976. Cahiers ORSTOM. Sér Océanograph. 15:201–214. https://horizon.documentation.ird.fr/exl-doc/pleins_textes/cahiers/oceanographie/19745.pdf

Condie SA, Mansbridge JV, Cahill ML. 2011. Contrasting local retention and cross-shore transports of the East Australian Current and the Leeuwin Current and their relative influences on the life histories of small pelagic fishes. Deep Sea Res 2 Top Stud Oceanogr. 58(5):606–615. doi: 10.1016/j.dsr2.2010.06.003.

Coombs S, Smyth TJ, Conway DVP, Halliday NC, Bernal M, Stratoudakis Y, Alvarez P. 2006. Spawning season and temperature relationships for sardine (*Sardina pilchardus*) in the eastern North Atlantic. J Mar Biol Ass. 86(5):1245–1252. doi: 10.1017/S0025315406014251.

Coombs SH, Halliday NC, Conway DVP, Smyth TJ. 2010. Sardine (*Sardina pilchardus*) egg abundance at station L4, Western English Channel. J Plankton Res. 32(5):693–697. doi: 10.1093/plankt/fbp052.

Correia AT, Hamer P, Carocinho B, Silva A. 2014. Evidence for meta-population structure of *Sardina pilchardus* in the Atlantic Iberian waters from otolith elemental signatures of a strong cohort. Fish Res. 149:76–85. doi: 10.1016/j.fishres.2013.09.016.

Corten A, Braham CB, Sadegh AS. 2017. The development of a fishmeal industry in Mauritania and its impact on the regional stocks of sardinella and other small pelagics in Northwest Africa. Fish Res. 186:328–336. doi: 10.1016/j.fishres.2016.10.009.

Corten A. 2001. Northern distribution of North Sea herring as a response to high water temperatures and/or low food abundance. Fish Res. 50(1–2):189–204. doi: 10.1016/S0165-7836(00)00251-4.

Corten A. 2002. The role of "conservatism" in herring migrations. Rev Fish Biol Fish. 11:339–361. doi: 10.1023/A:1021347630813.

Costalago D. 2015. Review on the links between the distribution of larvae and juveniles of anchovy and sardine with their ecological dynamics in the northwestern Mediterranean. Vie et. Milieu. 65(2):101–113. https://wwwphp.obs-banyuls.fr/Viemilieu/index.php/volume-65-2015/65-issue-2.html

Crawford RJM. 1981. Distribution, availability and movements of pilchard *Sardinops ocellata* off South Africa, 1964. Fish Bull South Afr. 14(1976):1–46.

CTMFM. 2022. Comisión técnica Mixta del Frente marítimo (in Spanish). 2022. [accessed 2024 Aug]. https://ctmfm.org/wp-content/uploads/2022/07/FICHA-ANCHOITA.pdf.

Cubillos LA, Arcos DF, Bucarey DA, Canales MT. 2001. Seasonal growth of small pelagic fish off Talcahuano, Chile (37° S, 73° W): a consequence of their reproductive strategy to seasonal upwelling? Aquat Living Resour. 14(2):115–124. doi: 10.1016/S0990-7440(01)01112-3.

Cubillos LA, Ruiz P, Claramunt G, Gacitúa S, Núñez S, Castro LR, Riquelme K, Alarcón C, Oyarzún C, Sepúlveda A. 2007. Spawning, daily egg production, and spawning stock biomass estimation for common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens)* off central southern Chile in 2002. Fish Res. 86(2–3):228–240. doi: 10.1016/j.fishres.2007.06.007.

Cunha ME, Garrido S, Pissarra J. 2005. The use of stomach fullness and colour indices to assess *Sardina pilchardus* feeding. J Mar Biol Ass.. 85(2):425–431. doi: 10.1017/S0025315405011367h.

Cury P, Bakun A, M Crawford RJ, Jarre A, Quiñones RA, Shannon LJV, Cury HM, Ones Q. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in ""wasp-waist"" ecosystems. ICES J Mar Sci.57(3):603–618. doi: 10.1006/jmsc.2000.0712.

Cury P, Roy C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can J Fish Aquat Sci. 46(4):670–680. doi: 10.1139/f89-086.

Cushing D. 1969. Upwelling and fish production. FAO Fish Tech Pap. 84:40. https://www.fao.org/4/89204e/89204e00.htm

Cushing D. 1982. Climate and fisheries. London: Academic Press.

D'ancona U. 1931. Famiglia Engraulidae. In: Bardi G, Friedlander R, editors. Uova, larve e stadi giovanili di teleostei. Fauna e flora del Golfo di Napoli. Vol. 38. Rome: FAO.

Daewel U, Peck MA, Schrum C. 2011. Life history strategy and impacts of environmental variability on early life stages of two marine fishes in the North Sea: an individual-based modelling approach. Can J Fish Aquat Sci. 68(3):426–443. doi: 10.1139/F10-164.

Demarcq H, Samb B, Cury P, Roy C. 1991. Influence des variations de l'upwelling sur la répartition des poissons pélagiques au Sénégal. In: Cury P, Roy, editors. Pêcheries ouest-africaines – variabilité, instabilité et changement. Rome: Orstom; p. 290–306.

Demer DA, Zwolinski JP, Byers KA, Cutter GR, Renfree JS, Sessions TS, Macewicz BJ. 2012. Prediction and confirmation of seasonal migration of Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem. Fish Bull. 110(1):52–70. https://spo.nmfs.noaa.gov/sites/default/files/demer.pdf

DFFE. 2023. Status of the South African marine fishery resources 2023. Department of forestry, fisheries and the environment. Cape Town, South Africa: DFFE.

Diankha O, Ba A, Brehmer P, Brochier T, Sow BA, Thiaw M, Gaye AT, Ngom F, Demarcq H. 2018. Contrasted optimal environmental windows for both *ardinella* species in Senegalese waters. Fish Oceanogr. 27(4):351–365. doi: 10.1111/fog.12257.

Dias BS, McGowan DW, Campbell R, Branch TA. 2022. Influence of environmental and population factors on Prince William Sound herring spawning phenology. Mar Ecol Prog Ser. 696:103–117. doi: 10.3354/meps14133.

Dias DF, Pezzi LP, Gherardi DFM, Camargo R. 2014. Modeling the spawning strategies and larval survival of the Brazilian sardine (*Sardinella brasiliensis*). Prog Oceanogr. 123:38–53. doi: 10.1016/j.pocean.2014.03.009.

Dickey-Collas M, Nash RD, Brunel T, Van Damme CJ, Marshall CT, Payne MR, Corten A, Geffen AJ, Peck MA, Hatfield EM, et al. 2010. Application and validation of otolith microstructure as a stock identification method in mixed Atlantic herring (*Clupea harengus*) stocks in the North Sea and western Baltic. ICES J Mar Sci. 67(9):1875–1886.

Dickey-Collas M, Somarakis S, Witthames PR, van Damme CJG, Uriarte A, Lo NCH, Bernal M. 2012. Where do egg production methods for estimating fish biomass go from here? Fish Res. 118:6–11. 117–doi: 10.1111/j.1365-2419.2011.00600.x.

Doray M, Hervy C, Huret M, Petitgas P. 2018. Spring habitats of small pelagic fish communities in the Bay of Biscay. Prog Oceanogr. 166:88–108. doi: 10.1016/j.pocean.2017.11.003.

Doyle MJ, Strom SL, Coyle KO, Hermann AJ, Ladd C, Matarese AC, Shotwell SK, Hopcroft RR. 2019. Early life history phenology among Gulf of Alaska fish species: strategies, synchronies, and sensitivities. Deep Sea Res II Top Stud Oceanogr. 165:41–73. doi: 10.1016/j.dsr2.2019.06.005.

Dragesund O, Johannessen A, Ulltang Ø. 1997. Variation in migration and abundance of norwegian spring spawning herring (Clupea harengus L.). Sarsia 82(2):97–105. doi: 10.1080/00364827.1997.10413643.

Džoić T, Zorica B, Matić F, Šestanović M, Čikeš KV. 2022. Cataloguing environmental influences on the spatiotemporal variability of Adriatic anchovy early life stages in the eastern Adriatic Sea using an artificial neural network Front Mar Sci 9:997937. doi: 10.3389/fmars.2022.997937.

Eliasen SK, Homrum EÍ, Jacobsen JA, Kristiansen I, Óskarsson GJ, Salthaug A, Stenevik EK. 2021. Spatial distribution of different age groups of herring in Norwegian Sea, May 1996–2020. Front Mar Sci. 8:778725. doi: 10.3389/fmars.2021.778725.

Emmett RL, Brodeur RD, Miller TW, Pool SS, Bentley PJ, Krutzikowsky GK, McCrae J. 2005. Pacific sardine (*Sardinops sagax*) abundance, distribution, and ecological relationships in the Pacific Northwest. Cal Coop Oc Fish Inv Rep. 46:1–122. https://calcofi.com/publications/calcofireports/v46/Vol_46_Emmett_et_al_Pacific_Sardine.pdf

Engelhard GH, Peck MA, Rindorf A, Smout C, Van Deurs S, Raab M, Andersen K, Garthe KH, Lauerburg S, Scott RAM, et al. 2014. Forage fish, their fisheries, and their predators: who drives whom? ICES J Mar Sci. 71(1):90–104. doi: 10.1093/icesjms/fst087.

Erauskin-Extramiana M, Alvarez P, Arrizabalaga H, Ibaibarriaga L, Uriarte A, Cotano U, Santos M, Ferrer L, Cabré A, Irigoien X, et al. 2019. Historical trends and future distribution of anchovy spawning in the Bay of Biscay. Deep Sea Res 2 Top Stud Oceanogr. 159:169–182. doi: 10.1016/j.dsr2.2018.07.007.

Eriksen E, Gjøsæter H, Prozorkevich D, Shamray E, Dolgov A, Skern-Mauritzen M, Stiansen JE, Kovalev Y, Sunnanå K. 2018. From single species surveys towards monitoring of the Barents Sea ecosystem. Prog Oceanogr. 166:4–14. doi: 10.1016/j.pocean.2017.09.007.

Espinoza P, Bertrand A. 2008. Revisiting Peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the Humboldt Current system. Prog Oceanogr. 79(2–4):215–227. doi: 10.1016/j.pocean.2008.10.022.

Espinoza P, Bertrand A. 2014. Ontogenetic and spatiotemporal variability in anchoveta *Engraulis ringens* diet off Peru. J Fish Biol. 84(2):422–435. doi: 10.1111/jfb.12293.

Ettahiri O, Berraho A, Vidy G, Ramdani MD, Chi T. 2003. Observation on the spawning of Sardina and Sardinella off the south Moroccan Atlantic coast (21–26°N). Fish Res. 60(2–3):207–222. doi: 10.1016/S0165-7836(02)00172-8.

Fach BA. 2014. Modeling the influence of hydrodynamic processes on anchovy distribution and connectivity in the black sea. Turk J Fish Aquat Sci. 14(2):353–365. doi: 10.4194/1303-2712-v14_2_06.

Falcini F, Corrado R, Torri M, Mangano MC, Zarrad R, Cintio A, Di Palatella L, Jarboui O, Missaoui H, Cuttitta A, et al. 2020. Seascape connectivity of European anchovy in the Central Mediterranean Sea revealed by weighted Lagrangian backtracking and bio-energetic modelling. Sci Rep. 10(1):18630. doi: 10.1038/s41598-020-75680-8.

FAO. 2020. Report of the working group on the assessment of small pelagic fish off Northwest Africa 2019. Casablanca, Morocco: FAO. [accessed 2024 Apr 18]. https://openknowledge.fao.org/items/efb19ba7-7ec5-4c7c-966d-41bb1f917ea0.

FAO. 2021. FAO working group on the assessment of small pelagic fish off Northwest Africa 2021. virtual meeting. [accessed 2024 Apr 18]. https://www.ldac.eu/images/2021_WGSPN_summary_EN.pdf.

FAO. 2022b. The state of Mediterranean and black sea fisheries 2022. Rome, Italy: FAO. doi: 10.4060/cc3370en.

FAO. 2022c. Scientific advisory committee on fisheries (SAC). Working group on stock assessment of small pelagic species (WGSASP). Rome, Italy: FAO. GFCM website; [accessed Apr 2024] https://www.fao.org/gfcm/technical-meetings/detail/en/c/1506154/.

FAO. 2022a. The state of world fisheries and aquaculture 2022. Towards blue transformation. Rome, Italy: FAO. doi: 10.4060/cc0461en.

Favero JM, Katsuragawa M, Oliveira FSC, Tannure NC, Zani-Teixeir AML, Turner JT. 2017. Seasonal and regional variation in egg size of the Argentine anchoita

(*Engraulis anchoita*) in the southeastern Brazilian Bight. FB. 115(4):517–531. doi: 10.7755/FB.115.4.8.

Favero JM, Katsuragawa M, Zani-Teixeira M de L, Turner JT. 2017. Spawning areas of Engraulis anchoita in the Southeastern Brazilian Bight during late-spring and early summer. Prog Oceanogr. 153:37–49. doi: 10.1016/j.pocean.2017.03.004.

Favero JM, Katsuragawa M, Zani-Teixeira ML, Turner JT. 2018. Modeling long-term fluctuations in the distribution and abundance of *Engraulis anchoita* eggs and larvae in the southeastern Brazilian bight. Mar Ecol Prog Ser. 587:159–173. doi: 10.3354/meps12375.

Félix-Uraga R, Gómez-Muñoz VM, Quiñónez-Velázquez C, Melo-Barrera FN, García-Franco W. 2004. On the existence of Pacific sardine groups off the west coast of Baja California and southern California. Cal Coop Oc Inv Rep. 45:146–151. https://www.semanticscholar.org/paper/ON-THE-EXISTENCE-OF-PACIFIC-SARDINE-GROUPS-OFF-THE-F%C3%A9lix-Uraga-G%C3%B3mez-Mu%C3%B1oz/394cbc14668d95b0ed56a063ad390d72d388e5c1

Fietcher J, Rose K, Curchister E, Hedstrom KS. 2015. The role of environmental controls in determining sardine and anchovy population cycles in the California Current: analysis of an end-to-end model. Prog Oceanogr. 138:381–398. doi: 10.1016/j.pocean.2014.11.013.

Fiksen Ø, Jørgensen C, Kristiansen T, Vikebø F, Huse G. 2007. Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. Mar Ecol Prog Ser. 347:195–205. doi: 10.3354/meps06978.

Finney BP, Gregory-Eaves I, Douglas MSV, Smol JP. 2002. Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. Nature. 416(6882):729–733. doi: 10.1038/416729a.

Flores-Valiente J, Lett C, Colas F, Pecquerie L, Aguirre-Velarde A, Rioual F, Tam J, Bertrand A, Ayón P, Sall S, et al. 2023. Influence of combined temperature and food availability on Peruvian anchovy (*Engraulis ringens*) early life stages in the northern Humboldt Current system: a modelling approach. Prog Oceanogr. 215:103034. doi: 10.1016/j.pocean.2023.103034.

Fonseca P, Silva AD, Angélico MM, Garrido S. 2022. Seasonal and spatial variability of Atlanto-Iberian pelagic fish diet with estimates of intraguild predation. Mar Ecol Prog Ser. 687:95–111. doi: 10.3354/meps14011.

Fréon P, Barange M, Arístegui J. 2009. Eastern boundary upwelling ecosystems: integrative and comparative approaches. Prog Oceanogr. 83(1–4):1–14. doi: 10.1016/j.pocean.2009.08.001.

Fréon P, Cury P, Shannon L, Roy C. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. Bull Mar Sci. 77(2):385–462.

Freon P. 1988. Réponses et adaptations des stocks de clupéidés d'Afrique de l'ouest à la variabilité du milieu et de l'exploitation: analyse et réflexion à partir de l'exemple du Sénégal [PhD]. Paris, France: Orstom.

Frost M, Diele K. 2022. Essential spawning grounds of Scottish herring: current knowledge and future challenges. Rev Fish Biol Fisheries. 32(3):721–744. doi: 10.1007/s11160-022-09703-0.

Funk FC. 1990. Migration of eastern Bering Sea herring, as inferred from 1983 to 1988 joint venture and foreign trawl bycatch rates. Alaska: Alaska Department of Fish & Game, Division of Commercial Fisheries, Regional Information Report. Report No. 5J90-04

Furuichi S, Niino Y, Kamimura Y, Yukami R. 2020. Time-varying relationships between early growth rate and recruitment in Japanese sardine. Fish Res. 232:105723. doi: 10.1016/j.fishres.2020.105723.

Furuichi S, Yasuda T, Kurota H, Yoda M, Suzuki K, Takahashi M, Fukuwaka M. 2020. Disentangling the effects of climate and density-dependent factors on spatiotemporal dynamics of Japanese sardine spawning. Mar Ecol Prog Ser. 633:157–168. doi: 10.3354/meps13169.

Galleguillos R, Ferrada S, Canales C, Hernández C, Oliva M, González MT, Cubillos L, Niklitschek E, Toledo P. 2012. Determinación de unidades poblacionales de sardina austral entre la X y XII regiones de Chile. Concepción, Chile. IFOP. Report No.: FIP 2010-17.

Ganias K. 2008. Ephemeral spawning aggregations in the Mediterranean sardine, *Sardina pilchardus*: a comparison with other multiple-spawning clupeoids. Mar Biol. 155(3):293–301. doi: 10.1007/s00227-008-1027-7.

Garcia S. 1982. Distribution, migration and spawning of the main fish resources in the northern CECAF area. CECAF/ECAF Ser. 82(25):9. https://www.fao.org/4/p8888e/p8888e.htm

García-García LM, Ruiz-Villarreal M, Bernal M. 2016. A biophysical model for simulating early life stages of sardine in the Iberian Atlantic stock. Fish Res. 173:250–272. doi: 10.1016/j.fishres.2015.10.002.

Garrido S, Ben-Hamadou R, Oliveira PB, Cunha ME, Chícharo MA, Van der Lingen, CD. 2008. Diet and feeding intensity of sardine *Sardina pilchardus*: correlation with satellite-derived chlorophyll data. Mar Ecol Prog Ser. 354:245–256. doi: 10.3354/meps07201.

GFCM. 2009. Resolution GFCM/33/2009/2 on the establishment of geographical subareas in the GFCM area of application, amending Resolution GFCM/31/2007/2. https://www.fao.org/gfcm/data/maps/gsas/en/.

Giannoulaki M, Iglesias M, Tugores MP, Bonanno A, Patti B, De Felice A, Leonori I, Bigot JL, Tičina V, Pyrounaki MM, et al. 2013. Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages. Fish Oceanogr. 22(2):69–89. doi: 10.1111/fog.12005.

Giannoulaki M, Pyrounaki MM, Liorzou B, Leonori I, Valavanis VD, Tsagarakis K, Bigot JL, Roos D, De Felice A, Campanella F, et al. 2011. Habitat suitability modelling for sardine juveniles (*Sardina pilchardus*) in the Mediterranean Sea. Fish Oceanogr. 20(5):367–382. doi: 10.1111/j.1365-2419.2011.00590.x.

Giannoulaki M, Valavanis VD, Palialexis A, Tsagarakis K, Machias A, Somarakis S, Papaconstantinou C. 2008. Modelling the presence of anchovy *Engraulis encrasicolus* in the Aegean Sea during early summer, based on satellite environmental data. Hydrobiologia. 612(1):225–240. doi: 10.1007/s10750-008-9498-6.

Gibson GA, Baker MR, Stockhausen WT, Hinckley S, Parada C, Aydin K, Coyle KO, Hermann AJ, Hurst TP, Punt AE. 2022. Modeling in an integrated ecosystem research framework to explore recruitment in Gulf of

Alaska groundfish – Applications to management and lessons learned. Deep Sea Res 2 Top Stud Oceanogr. 197:105048. doi: 10.1016/j.dsr2.2022.105048.

Gigliotti ES, Gherardi DFM, Paes ET, Souza RB, Katsuragawa M. 2010. Spatial analysis of egg distribution and geographic changes in the spawning habitat of the Brazilian sardine *Sardinella brasiliensis*. J Fish Biol. 77(10):2248–2267. doi: 10.1111/j.1095-8649.2010.02802.x.

Gkanasos A, Schismenou E, Tsiaras K, Somarakis S, Giannoulaki M, Sofianos S, Triantafyllou G. 2021. A three dimensional, full life cycle, anchovy and sardine model for the North Aegean Sea (Eastern Mediterranean): validation, sensitivity and climatic scenario simulations. Medit Mar Sci. 22(3):653–668. doi: 10.12681/mms.27407.

Goitein R. 1978. Sardinella brasiliensis (Steindachner, 1879): estudo sobre alimentação nas regiões de Ubatuba (23°26’S), Santos (24°02’S) e Cananéia (25°01’S), Brasil [M.Sc]. São Paulo, Brasil: Instituto Oceanográfico, USP.

Goto T. 1998. Abundance and distribution of the egg of the sardine, Sardinops melanostictus, in the Japan Sea dring spring. Japan Sea Natl Fish Res Inst. 48:51–60.

Gunther KM, Baker MR, Aydin KY. 2024. Using predator diets to infer forage fish distribution and assess responses to climate variability in the eastern Bering Sea. Mar Ecol Prog Ser. 741:71–99. doi: 10.3354/meps14389.

Guraslan C, Fach BA, Oguz T. 2017. Understanding the impact of environmental variability on anchovy overwintering migration in the black sea and its implications for the fishing industry Front Mar Sci. 4:275. doi: 10.3389/fmars.2017.00275.

Gutiérrez M, Angulo J, Tarazona A, Peraltilla S, Pecquerie L, Vagner M, Sardenne F, Grados D, Espinoza P. 2022. Variations in maximum fish length, spatial distribution, biomass, and omega 3 content of anchovy (*Engraulis ringens*) off the Peruvian coast between 1998 and 2022 with repercussions on fishery management. EBUS & Humboldt Current 2022 Conference. Lima, Perú.

Gutierrez M, Castillo R, Segura M, Peraltilla S, Flores M. 2012. Trends in spatio-temporal distribution of Peruvian anchovy and other small pelagic fish biomass from 1966–2009 v. LAJAR. 40(3):633–648. doi: 10.3856/vol40-issue3-fulltext-12.

Gutiérrez M, Ñiquen M, Peraltilla S, Herrera N. 2000. Las Operaciones Eureka: una aproximación a la abundancia de anchoveta en el período 1966–1982. Bol Inst Mar Perú. 19(1–2):83–102. https://hdl.handle.net/20.500.12958/999

Hammann MG, Baumgartner TR, Badan-Dangon A. 1988. Coupling of the Pacific sardine (*Sardinops sagax caeruleus*) life cycle with the Gulf of California pelagic environment population off western North America. Cal Coop Oc Fish Inv Rep. 29:102–109. https://www.researchgate.net/publication/253535217_Coupling_of_the_Pacific_Sardine_Sardinops_sagax_caeruleus_life_cycle_with_the_Gulf_of_California_pelagic_environment

Harden-Jones FR. 1968. Fish migration. London: Edward Arnold.

Hare JA. 2014. The future of fisheries oceanography lies in the pursuit of multiple hypotheses. ICES J Mar Sci. 71(8):2343–2356. doi: 10.1093/icesjms/fsu018.

Haslob H, Rabade-Uberos S, Saborido-Rey F. 2013. Seasonal variability of fecundity and spawning dynamics of Baltic sprat. Fish Res. 138:99–109. doi: 10.1016/j.fishres.2012.08.002.

Hay DE, McCarter PB. 1997. Larval distribution, abundance, and stock structure of British Columbia herring. FJ Fish Biol. 51(sA): 155–175. doi: 10.1111/j.1095-8649.1997.tb06098.x.

Hay DE, McKinnell SM. 2002. Tagging along: association among individual Pacific herring revealed by tagging. Can J Fish Aq Sci. 59:1960–1968. doi: 10.1139/f02-141.

Hay DE. 1985. Reproductive biology of Pacific herring. Can J Fish Aq Sci. 42(1):111–126. doi: 10.1139/f85-267.

Hayashi A, Goto T, Takahashi M, Watanabe Y. 2019. How Japanese anchovy spawn in northern waters: start with surface warming and end with day length shortening. Ichthyol Res. 66(1):79–87. doi: 10.1007/s10228-018-0652-5.

Heath M, Zenitani H, Watanabe Y, Kimura R, Ishida M. 1998. Modelling the dispersal of larval Japanese sardine, *Sardinops melanostictus*, by the Kuroshio Current in 1993 and 1994. Fish Oceanogr. 7(3–4):335–346. doi: 10.1046/j.1365-2419.1998.00076.x.

Hebert K. 2020. Southeast Alaska herring stock assessment surveys. Alaska: Alaska Department of Fish and Game. Report No.: Fishery Data Series No. 20–23.

Hedgecock D, Hutchinson ES, Li G, Sly FL, Nelson K. 1989. Genetic and morphometric variation in the pacific sardine, *Sardinops sagax caerulea*: comparisons and contrasts with historical data and with variability in the Northern Anchovy *Engraulis Mordax*. Fish Bull. 87:571–653. https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/1989/873/hedgecock.pdf

Heino M, Díaz Pauli B, Dieckmann U. 2015. Fisheries-induced evolution. Annu Rev Ecol Evol Syst. 46(1):461–480. doi: 10.1146/annurev-ecolsys-112414-054339.

Hernández-Santoro C, Landaeta MF, Pizarro JC. 2019. Effect of ENSO on the distribution and concentration of catches and reproductive activity of anchovy *Engraulis ringens* in northern Chile. Fish Oceanogr. 28(3):241–255. doi: 10.1111/fog.12405.

Hilborn R, Buratti C, Díaz Acuña E, Hively D, Kolding J, Kurota H, Baker N, Mace PM, de Moor CL, Muko S, et al. 2022. Recent trends in abundance and fishing pressure of agency-assessed small pelagic fish stocks. Fish Fish. 23(6):1313–1331. doi: 10.1111/faf.12690.

Hjort J. 1914. Fluctuations in the great fisheries of Northern Europe. Rapp P-V Reun Cons Int Explor Mer. 20:1–228.

Huang M, Ding L, Wang J, Ding C, Tao J. 2021. The impacts of climate change on fish growth: a summary of conducted studies and current knowledge. Ecol Indic. 121:106976. doi: 10.1016/j.ecolind.2020.106976.

Hufnagl M, Peck MA, Nash RDM, Dickey-Collas M. 2015. Unravelling the Gordian knot! Key processes impacting overwintering larval survival and growth: a North Sea herring case study. Prog Oceanogr. 138:486–503. doi: 10.1016/j.pocean.2014.04.029.

Huggett JA, Boyd AJ, Hutchings L, Kemp AD. 1998. Weekly variability of clupeoid eggs and larvae in the Benguela jet current: implications for recruitment. S Afr J Mar Sci. 19(1):197–210. doi: 10.2989/025776198784126773.

Huret M, Bourriau P, Doray M, Gohin F, Petitgas P. 2018. Survey timing vs. ecosystem scheduling: degree-days to underpin observed interannual variability in marine ecosystems. Prog Oceanogr. 166:30–40. doi: 10.1016/j.pocean.2017.07.007.

Huret M, Lebigre C, Iriondo M, Montes I, Estonba A. 2020. Genetic population structure of anchovy (*Engraulis encrasicolus*) in North-western Europe and variability in the seasonal distribution of the stocks. Fish Res. 229:105619. doi: 10.1016/j.fishres.2020.105619.

Huret M, Petitgas P, Woillez M. 2010. Dispersal kernels and their drivers captured with a hydrodynamic model and spatial indices: a case study on anchovy (*Engraulis encrasicolus)* early life stages in the Bay of Biscay. Prog Oceanogr. 87(1–4):6–17. doi: 10.1016/j.pocean.2010.09.023.

Huse G, Fernö A, Holst JC. 2010. Establishment of new wintering areas in herring co-occurs with peaks in the first time/repeat spawner ratio. Mar Ecol Prog Ser. 409:189–198. doi: 10.3354/meps08620.

Huse G. 2016. A spatial approach to understanding herring population. Can J Fish Aq Sci. 188(5817):177–188. doi: 10.1139/cjfas-2015-0095.

Hutchings L, Barange M, Bloomer SF, Boyd AJ, Crawford RJM, Huggett JA, Kerstan M, Korrûbel JL, de Oliveira JAA, Painting SJ, et al. 1998. Multiple factors affecting South African anchovy recruitment in the spawning, transport and nursery areas. S Afr J Mar Sci. 19(1):211–225. doi: 10.2989/025776198784126908.

Ibaibarriaga L, Uriarte A, Laconcha U, Bernal M, Santos M, Chifflet M, Irigoien X. 2013. Distribución espacio-temporal de la edad 1 de anchoa del golfo de Bizkaia (*Engraulis Encrasicolus)* en el momento de puesta. Sci Mar. 77(3):461–472. doi: 10.3989/scimar.03851.05C.

IBAMA. 1995. Situação do estoque da Sardinha no Litoral Sudeste e Sul do Brasil. Série Estudos - Pesca. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, Centro de Pesquisa e Extensão Pesqueira das Regiões Sudeste e Sul - CEPSUL, Itajaí, Santa Catarina, Brazil. Report. 1–41.

IBAMA 2011. Plano de gestão para o uso sustentável da sardinha-verdadeira *Sardinella brasiliensis* no Brasil Cergole M.C., Dias-Neto J. (org.). Série Plano de Gestão dos Recursos Pesqueiros, 5. Brasília (Brazil): Ibama.

ICES. 2022a. Baltic Sea ecoregion – fisheries overview. Report of the ICES advisory committee, 2022 ICES advice 2022. Copenhagen, Denmark: ICES; p. 42. doi: 10.17895/ices.advice.21646934.

ICES. 2022b. Official nominal catches 2006–2021. Ices.dk. [accessed 06 October 2023] http://ices.dk/data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx.

ICES. 2022d. ICES preliminary catches 2022. Copenhagen, Denmark: ICES.

ICES. 2023b. Baltic fisheries assessment working group (WGBFAS). ICES Scientific Reports. Copenhagen, Denmark: ICES. doi: 10.17895/ices.pub.23123768.v2.

ICES. 2023d. Working group on southern horse mackerel, anchovy and sardine (WGHANSA). ICES Scientific Reports. Copenhagen, Denmark: ICES.

ICES. 2024b. Working Group on Surveys on Ichthyoplankton in the North Sea and adjacent Seas (WGSINS; outputs from 2023 meeting). ICES Sci Rep. 6:62. doi: 10.17895/ices.pub.25212692.

ICES. 2001. Report of the study group on the herring assessment units in the Baltic Sea. ICES CM, ACFM. 10. Copenhagen, Denmark: ICES.

ICES. 2021a. Working group on acoustic and egg surveys for small pelagic fish in NE Atlantic (WGACEGG; outputs from 2020 meeting). ICES Sci Rep. 3(76):1–709. doi: 10.17895/ices.pub.8234.

ICES. 2021b. Working group on southern horse mackerel anchovy and sardine (WGHANSA). ICES Sci Rep. 3(55):1–689. doi: 10.17895/ices.pub.8138.

ICES. 2021c. International bottom trawl survey working group (IBTSWG). ICES Sci Rep. 3:201. 69 doi: 10.17895/ices.pub.8219.

ICES. 2022c. Greater North Sea ecoregion – fisheries overview. ICES advice 2022. Copenhagen, Denmark: ICES, Report No: Report of the ICES Advisory Committee.

ICES. 2023a. Working group of international pelagic surveys (WGIPS). ICES Sci Rep. 5(74):1–122. doi: 10.17895/ices.pub.23607303.

ICES. 2023c. Herring assessment working group for the area South of 62° N (HAWG). ICES Sci Rep. 5(23):837. doi: 10.17895/ices.pub.22182034.

ICES. 2024a. Second workshop on stock identification and allocation of catches of herring to stocks (WKSIDAC2; outputs from 2023 meeting). ICES Sci Rep. 6(5):67. doi: 10.17895/ices.pub.24998747.

IPIAP. 2023. Presencia de anchoveta (*Engraulis ringens*) en el Golfo de Guayaquil: crucero de prospección hidroacústica y pesca comprobatoria. Proceso de investigación de los recursos bioacuaticos y su ambiente (IRBA). p. 1–6.

Ito S. 1961. Fishery biology of the sardine, *Sardinops melanostictus* (T. & S.), in the waters around Japan. Bull Jap Sea Reg Fish Res Lab. 9:1–227.

Itoh S, Yasuda I, Nishikawa H, Sasaki H, Sasai Y. 2009. Transport and environmental temperature variability of eggs and larvae of the Japanese anchovy (*Engraulis japonicus)* and Japanese sardine (*Sardinops melanostictus*) in the western North Pacific estimated via numerical particle-tracking experiments. Fish Oceanogr. 18(2):118–133. doi: 10.1111/j.1365-2419.2009.00501.x.

Iversen SA, Zhu D, Johannessen A, Toresen R. 1993. Stock size, distribution and biology of anchovy in the Yellow Sea and East China Sea. Fish Res. 16(2):147–163. doi: 10.1016/0165-7836(93)90049-D.

Johanneson KA. 1975. Relatório preliminar das observações acústicas quantitativas sobre tamanho e distribuição dos recursos de peixes pelágicos ao largo da costa sul do Brasil Serie documentos técnicos. PDP/SUDEPE. Sao Paulo.

Kääriä J, Rajasilta M, Kurkilahti M, Soikkeli M. 1997. Spawning bed selection by the Baltic herring (*Clupea harengus* membras) in the Archipelago of SW Finland. ICES J Mar Sci. 54(5):917–923. doi: 10.1006/jmsc.1996.0204.

Kändler R. 1949. Die häufigkeit pelagischer fischeier in der ostsee als masstab für die Zu- und Abnahme der Fischbestånde. Kieler Meeresforsch. 6:73–89. https://oceanrep.geomar.de/id/eprint/55058/

Kanstinger P, Peck MA. 2009. Co-occurrence of European sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicolus*) and sprat (*Sprattus sprattus*) larvae in southern North Sea habitats: Abundance, distribution and biochemical-based condition. Sci Mar. 73(1):141–152. doi: 10.3989/scimar.2009.73s1141.

Kaplan IC, Koehn LE, Hodgson EE, Marshall KN, Essington TE. 2017. Modeling food web effects of low sardine and anchovy abundance in the California Current. Ecol Modell. 359:1–24. doi: 10.1016/j.ecolmodel.2017.05.007.

Kasai A, Sugimoto T, Nakata H. 1997. The dependence of yearly recruitment of Japanese sardine *Sardinops melanostictus* on Survival in the Kuroshio-Oyashio Transition Region. Fish Sci. 63(3):372–377. doi: 10.2331/fishsci.63.372.

Kelly C, Michelsen FA, Kolding J, Alver MO. 2022. Tuning and development of an individual-based model of the herring spawning migration. Front Mar Sci. 8:754476. doi: 10.3389/fmars.2021.754476.

Keyse MD, Lawson TD. 2023. Alaska Peninsula-Aleutian Islands Management Area commercial herring fishery management strategy. Alaska: Alaska Department of Fish and Game, Report No.: 4K23-06.

Kim J, Kim S, Choi Y, Lee J. 2006. Evidence of density-dependent effects on population variation of Japanese sardine (*Sardinops melanostictus*) of Korea. Fish Oceanogr. 15:345–349. doi: 10.1111/j.1365-2419.2006.00413.x.

Kim J, Lo NCH. 2001. Temporal variation of seasonality of egg production and the spawning biomass of Pacific anchovy, *Engraulis japonicus*, in the southern waters of Korea in 1983–1994. Fish Oceanogr. 10(3):297–310. doi: 10.1046/j.1365-2419.2001.00175.x.

Kondo K. 1969. Ecological studies of life pattern of the Japanese anchovy *Engraulis japonicus* (Houttuyn). Bull Tokai Reg Fish Res Lab. 60:29–81.

Kondo K. 1988. On the mode of distribution and migration of the Japanese sardine, Sardinopls melanostictus (Temminck & Schelegel), at high level stock size. Bull Tokai Reg Fish Res Lab. 124:1–33.

Koslow JA, Davison P, Lara-Lopez A, Ohman MD. 2014. Epipelagic and mesopelagic fishes in the southern California current system: ecological interactions and oceanographic influences on their abundance. J Mar Sys. 138:20–28. doi: 10.1016/j.jmarsys.2013.09.007.

Krause J, Ruxton G. 2002. Living in groups. Oxford: Oxford University Press.

Kristiansen T, Jorgensen C, Lough RG, Vikebo F, Fiksen O. 2009. Modeling rule-based behavior: habitat selection and the growth-survival trade-off in larval cod. Behav Ecol. 20(3):490–500. doi: 10.1093/beheco/arp023.

Kurtz FW. 1999. Dinâmica larval de Sardinella brasiliensis (Steindachner, 1879) (Teleostei, Clupeidae) na região sudeste do Brasil e implicações no recrutamento [PhD]. São Paulo, Brasil: Universidade de São Paulo.

Lamb PD, Hunter E, Pinnegar JK, van der Kooij J, Creer S, Taylor MIP, Lamb CD. 2019. Cryptic diets of forage fish: jellyfish consumption observed in the Celtic Sea and western English Channel. J Fish Biol. 94(6):1026–1032. doi: 10.1111/jfb.13926.

Lasker R. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the Northern anchovy. *Engraulis mordax*. 36:1–99. https://repository.library.noaa.gov/view/noaa/5695

Le Bourg B, Bănaru D, Saraux C, Nowaczyk A, Le Luherne E, Jadaud A, Bigot JL, Richard P. 2015. Trophic niche overlap of sprat and commercial small pelagic teleosts in the Gulf of Lions (NW Mediterranean Sea). J Sea Res. 103:138–146. doi: 10.1016/j.seares.2015.06.011.

Le Moan A, Gagnaire PA, Bonhomme F. 2016. Parallel genetic divergence among coastal-marine ecotype pairs of European anchovy explained by differential introgression after secondary contact. Mol Ecol. 25(13):3187–3202. doi: 10.1111/mec.13627.

Le Roy D, Giraldo C, Travers-Trolet M. 1988. CGFS: channel ground fish survey. Cruise report: doi: 10.18142/11.

Lecomte F, Grant WS, Dodson JJ, Rodriguez-Sanchez R, Bowen BW. 2004. Living with uncertainty: genetic imprints of climate shifts in East Pacific anchovy (*Engraulis mordax*) and sardine (*Sardinops sagax*). Mol Ecol. 13(8):2169–2182. doi: 10.1111/j.1365-294X.2004.02229.x.

Leonori I, Tičina V, Giannoulaki M, Hattab T, Iglesias M, Bonanno A, Costantini I, Canduci G, Machias A, Ventero A, et al. 2021. History of hydroacoustic surveys of small pelagic fish species in the European Mediterranean Sea. Medit Mar Sci. 22(4):751–768. doi: 10.12681/mms.26001.

Lett C, Roy C, Levasseur A, van der Lingen CD, Mullon C. 2006. Simulation and quantification of enrichment and retention processes in the southern Benguela upwelling ecosystem. Fish Oceanogr. 15(5):363–372. doi: 10.1111/j.1365-2419.2005.00392.x.

Lima A, Garrido S, Riveiro I, Rodrigues D, Borges R, Angélico MMP, Gonçalves EJ, Peck MA, 2022. Seasonal approach to forecast the suitability of spawning habitats of a temperate small pelagic fish under a high-emission climate change scenario Front Mar Sci. 19:956654. doi: 10.3389/fmars.2022.956654.

Lima ARA, Baltazar-Soares M, Garrido S, Riveiro I, Carrera P, Piecho-Santos AM, Peck MA, Silva G. 2022. Forecasting shifts in habitat suitability across the distribution range of a temperate small pelagic fish under different scenarios of climate change. Sci Total Environ. 804:150167. doi: 10.1016/j.scitotenv.2021.150167.

Lima ID, Castello JP. 1995. Distribution and abundance of South-west Atlantic Anchovy spawners (*Engraulis anchoita*) in relation to oceanographic process in the southern Brazilian shelf. Fish Oceanogr. 4(1):1–16. doi: 10.1111/j.1365-2419.1995.tb00057.x.

Limborg M, Pedersen JS, Hansen JH, Tomkiewicz J, Bekkevold D. 2009. Genetic population structure of European sprat (*Sprattus sprattus* L.): differentiation across a steep environmental gradient in a small pelagic fish. Mar Ecol Prog Ser. 379:213–224. doi: 10.3354/meps07889.

Lindeberg MR, Baker MR, Dickson DMS, Kimmel DG, Ormseth OA, Strom SL, Suryan RM. 2022. Long-term monitoring and integrated research – understanding ecosystem processes in the Gulf of Alaska. Deep Sea Res. 206:105208. doi: 10.1016/j.dsr2.2022.105208.

Lindegren M, Checkley DM, Rouyer T, MacCall AD, Stenseth NC. 2013. Climate, fishing, and fluctuations of sardine and anchovy in the California current. Proc Natl Acad Sci USA. 110(33):13672–13677. doi: 10.1073/pnas.1305733110.

Litz MN, Heppell SS, Emmett RL, Brodeur RD. 2008. Ecology and distribution of the northern subpopulation of Northern Anchovy (*Engraulis mordax*) off the US West Coast. Cal Coop Oc Fish Inv Rep. 49:167–182. https://www.academia.edu/18890252/Ecology_and_distribution_of_the_northern_subpopulation_of_northern_anchovy_Engraulis_mordax_off_the_US_west_coast

Lluch-Belda D, Crawford RJM, Kawasaki T, Maccall AD, Parrish RH, Schwartzlose RA, Smith PE. 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. S Afr J Mar Sci. 8(1):195–205. doi: 10.2989/02577618909504561.

Lo NCH, Green Ruiz YA, Cervantes MJ, Moser HG, Lynn RJ. 1996. Egg production and spawning biomass of Pacific sardine (*Sardinops sagax*) in 1994, determined by the daily egg production method. Calif Coop Oc Invest Rep. 37:160–174. https://calcofi.com/publications/calcofireports/v37/Vol_37_Lo_etal.pdf

Lowerre-Barbieri S, Catalán IA, Frugård Opdal A, Jørgensen C. 2019. Preparing for the future: integrating spatial ecology into ecosystem-based management. ICES J Mar Sci. 76(2):467–476. doi: 10.1093/icesjms/fsy209.

Lowerre-Barbieri S, DeCelles G, Pepin P, Catalán IA, Muhling B, Erisman B, Cadrin SX, Alós J, Ospina-Alvarez A, Stachura MM, et al. 2017. Reproductive resilience: a paradigm shift in understanding spawner-recruit systems in exploited marine fish. Fish Fish. 18(2):285–312. doi: 10.1111/faf.12180.

MacCall AD. 1990. Dynamic geography of marine fish populations Oceanography WSGF. Seattle (WA): University of Washington Press.

Macdonald JI, Logemann K, Krainski ET, Sigurðsson Þ, Beale CM, Huse G, Hjøllo SS, Marteinsdóttir G. 2018. Can collective memories shape fish distributions? A test, linking space-time occurrence models and population demographics. Ecography. 41(6):938–957. doi: 10.1111/ecog.03098.

MacKenzie B, Ojaveer H. 2018. Evidence from the past: exploitation as cause of commercial extinction of autumn-spawning herring in the Gulf of Riga, Baltic Sea. ICES J Mar Sci. 75(7):2476–2487. doi: 10.1093/icesjms/fsy028.

Mahe JC, Laffargue P. 1987. EVHOE evaluation halieutique ouest De L'Europe. France: IFREMER.

Malavolti SARA, De Felice A, Costantini I, Biagotti I, Canduci G, Grilli F, Marini M, Tirelli V, Borme D, Caputo Barucchi V, et al. 2018. Distribution of *Engraulis encrasicolus* eggs and larvae in relation to coastal oceanographic conditions (a south-western Adriatic Sea case study). Medit Mar Sci. 19(1):180–192. doi: 10.12681/mms.14402.

Mantzouni I, Somarakis S, Moutopoulos DK, Kallianiotis A, Koutsikopoulos C. 2007. Periodic, spatially structured matrix model for the study of anchovy (*Engraulis encrasicolus*) population dynamics in N Aegean Sea (E. Mediterranean). Ecol Modell. 208(2–4):367–377. doi: 10.1016/j.ecolmodel.2007.05.021.

Martinez Barrio A, Lamichhaney S, Fan G, Rafati N, Pettersson M, Zhang H, Dainat J, Ekman D, Höppner M, Jern P, et al. 2016. The genetic basis for ecological adaptation of the Atlantic herring revealed by genome sequencing. Elife. 5:e12081. 1–32. doi: 10.7554/eLife.12081.

Massé J, Uriarte A, Angélico MM, Carrera P. 2018. Pelagic survey series for sardine and anchovy in ICES subareas 8 and 9 – Towards an ecosystem approach. Towards an ecosystem approach ICES. Coop Res Rep. 332:1–268. doi: 10.17895/ices.pub.4599.

Matsuura LY. 1998. Brazilian sardine (*Sardinella brasiliensis*) spawning in the southeast Brazilian Bight over the period 1976–1993. Rev Bras Oceanogr. 46(1):33–43. doi: 10.1590/S1413-77391998000100003.

Matsuura Y, Spach HL, Katsuragawa M. 1992. Comparison of spawning patterns of the Brazililan sardine (*Sardinella brasiliensis*) and anchoita (*Engraulis anchoita*) in Ubatuba region, southern Brazil during 1985 through 1988. Bol Inst Oceanogr. 40(1–2):101–115. doi: 10.1590/S0373-55241992000100009.

Maynou F, Olivar MP, Emelianov M. 2008. Patchiness and spatial structure of the early developmental stages of clupeiforms in the NW Mediterranean Sea. J Plankton Res. 30(8):873–883. doi: 10.1093/plankt/fbn048.

Maynou F, Sabatés A, Ramirez-Romero E, Catalán IA, Raya V. 2020. Future distribution of early life stages of small pelagic fishes in the northwestern Mediterranean. Clim Change. 161(4):567–589. doi: 10.1007/s10584-020-02723-4.

Mbaye BC, Brochier T, Echevin V, Lazar A, Lévy M, Mason E, Gaye AT, Machu E. 2015. Do *Sardinella aurita* spawning seasons match local retention patterns in the Senegalese-Mauritanian upwelling region? Fish Oceanogr. 24(1):69–89. doi: 10.1111/fog.12094.

McBride RS, Somarakis S, Fitzhugh GR, Albert A, Yaragina NA, Wuenschel MJ, Alonso-Fernández A, Basilone G. 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. Fish Fish. 16(1):23–57. doi: 10.1111/faf.12043.

McGowan DW, Branch TA, Haught S, Scheuerell MD. 2021. Multi-decadal shifts in the distribution and timing of Pacific herring spawning in Prince William Sound. Alaska Can J Fish Aq Sci. 78:1611–1627. doi: 10.1139/cjfas-2021-0047.

McGrath A, Hermes J, Moloney C, Roy C, Cambon G, Herbette S, van der Lingen CD. 2020. Investigating connectivity between two sardine stocks off South Africa using a high resolution IBM: retention and transport success of sardine eggs. Fish Oceanogr. 29(2):137–151. doi: 10.1111/fog.12460.

McGurk MD, Paul AJ, Coyle KO, Ziemann DA, Haldorson LJ. 1993. Relationships between prey concentration and growth, condition, and mortality of pacific herring *Clupea pallasi*, larvae in an alaskan sub-arctic embayment. Can J Fish Aquat Sci. 50(1):163–180. doi: 10.1139/f93-019.

McKeown NJ, Carpi P, Silva JFE, Healey AJ, Shaw PW, van der Kooij J. 2020. Genetic population structure and tools for the management of European sprat (*Sprattus sprattus*). ICES J Mar Sci. 77(6):2134–2143. doi: 10.1093/icesjms/fsaa113.

McQuinn I. 1997. Metapopulations and the Atlantic herring. Rev Fish Biol Fish. 7:297–329. doi: 10.1023/A:1018491828875.

Menard J, Leon JM, Bell J, Neff L, Clark K. 2022. Annual management report Norton Sound–Port Clarence Area and Arctic–Kotzebue management areas. Anchorage (USA): Alaska Department of Fish and Game, Fishery Management Report N° 22–27.

Mhlongo N, Yemane D, Hendricks M, van der Lingen CD. 2015. Have the spawning habitat preferences of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) in the southern Benguela changed in recent years? Fish Oceanogr. 24(S1):1–14. doi: 10.1111/fog.12061.

Miller DCM, Moloney CL, van der Lingen CD, Lett C, Mullon C, Field JG. 2006. Modelling the effects of physical-biological interactions and spatial variability in spawning and nursery areas on transport and retention of sardine *Sardinops sagax* eggs and larvae in the southern Benguela ecosystem. J Mar Syst. 61(3–4):212–229. doi: 10.1016/j.jmarsys.2005.03.007.

Milligan SP. 1986. Recent studies on the spawning of sprat (*Sprattus sprattus* L.) in the English Channel. Fish Res, Tech Rep. 83:1–18. https://www.cefas.co.uk/publications/techrep/tech83.pdf

Moll D. 2018. Contribution of coastal nursery areas to the spring-spawning population of Atlantic herring (Clupea harengus) in the Western Baltic Sea [PhD]. Hamburg, Germany: University of Hamburg.

Montes I, Zarraonaindia I, Iriondo M, Grant WS, Manzano C, Cotano U, Conklin D, Irigoien X, Estonba A. 2016. Transcriptome analysis deciphers evolutionary mechanisms underlying genetic differentiation between coastal and offshore anchovy populations in the Bay of Biscay. Mar Biol. 163(10):205. doi: 10.1007/s00227-016-2979-7.

Moraes L. 2012. Ecologia espacial da sardinha verdadeira (Sardinella brasiliensis Steindachner 1879): padrões relacionados à variabilidade atmosférica e oceânica no Atlântico Sudoeste [PhD]. São José dos Campos. Brazil: National Institute for Space Research.

Moraes LE, Gherardi DFM, Katsuragawa M, Paes ET. 2012. Brazilian sardine (*Sardinella brasiliensis* Steindachner, 1879) spawning and nursery habitats: spatial-scale partitioning and multiscale relationships with thermohaline descriptors. ICES J Mar Sci. 69(6):939–952. doi: 10.1093/icesjms/fss061.

Moraes LE, Paes E, Garcia A, Möller O, Jr, Vieira J. 2012. Delayed response of fish abundance to environmental changes: a novel multivariate time-lag approach. Mar Ecol Prog Ser..456:159–168. doi: 10.3354/meps09731.

Morello EB, Arneri E. 2009. Anchovy and sardine in the adriatic sea-an ecological review. Oceanogr Mar Biol. 47:209–256. https://www.taylorfrancis.com/chapters/edit/10.1201/9781420094220-8/anchovy-sardine-adriatic-sea-ecological-review-betulla-morello-enrico-arneri

Moreno P, Claramunt G. 2022. Expansion and contraction of the *Engraulis ringens* spawning area in northern Chile. SCIMAR. 86(4):e045–e045. doi: 10.3989/scimar.05284.045.

Moron G, Galloso P, Gutierrez D, Torrejon-Magallanes J. 2019. Temporal changes in mesoscale aggregations and spatial distribution scenarios of the Peruvian anchovy (*Engraulis ringens*). Deep Sea Res II: Top Stud Oceanogr. 159:75–83. doi: 10.1016/j.dsr2.2018.11.009.

Motos L. 1996. Reproductive biology and fecundity of the Bay of Biscay anchovy population (*Engraulis encrasicolus* L.). Sci Mar. 60(2):195–207. https://scimar.icm.csic.es/index.php/secId/8/IdArt/238/

Moyano M, Illing B, Akimova A, Alter K, Bartolino V, Börner G, Clemmesen C, Finke A, Gröhsler T, Kotterba P, et al. 2023. Caught in the middle: bottom-up and top-down processes impacting recruitment in a small pelagic fish. Rev Fish Biol Fish. 33:55–84. doi: 10.1007/s11160-022-09739-2.

Moyano M, Rodríguez JM, Benítez-Barrios VM, Hernández-León S. 2014. Larval fish distribution and retention in the Canary Current system during the weak upwelling season. Fish Oceanogr. 23(3):191–209. doi: 10.1111/fog.12055.

Muelbert JH, Acha M, Mianzan H, Guerrero R, Reta R, Braga ES, Garcia VMT, Berasategui A, Gomez-Erache M, Ramírez F. 2008. Biological, physical and chemical properties at the Subtropical Shelf Front Zone in the SW Atlantic Continental Shelf. Cont Shelf Res. 28(13):1662–1673. doi: 10.1016/j.csr.2007.08.011.

Muko S, Ohshimo S, Kurota H, Yasuda T, Fukuwaka M. 2018. Long-term change in the distribution of Japanese sardine in the Sea of Japan during population fluctuation. Mar Ecol Prog Ser. 593:141–154. doi: 10.3354/meps12491.

Munk P, Huwer B, Van Deurs M, Kloppmann M, Sell A. 2024. Spatial separation of larval sprat (*Sprattus sprattus*) and sardine (*Sardina pilchardus*) related to hydrographical characteristics in the North Sea. Fish Oceanogr. 33(1):e12656. doi: 10.1111/fog.12656.

Munk P. 1993. Differential growth of larval sprat *Sprattus sprattus* across a tidal front in the eastern North Sea. Mar Ecol Prog Ser. 99(1–2):17–27. doi: 10.3354/meps099017.

Muradian ML, Branch TA, Moffitt SD, Hulson P-JF. 2017. Bayesian stock assessment of Pacific herring in Prince William Sound. PLoS One. 12(2):e0172153. doi: 10.1371/journal.pone.0172153.

Nakata H, Funakoshi S, Nakamura M. 2000. Alternating dominance of postlarval sardine and anchovy caught by coastal fishery in relation to the Kuroshio meander in the Enshu-nada Sea. Fish Oceanogr. 9(3):248–258. doi: 10.1046/j.1365-2419.2000.00140.x.

Nash R, Dickey-Collas M. 2005. The influence of life history dynamics and environment on the determination of year class strength in North Sea herring (Clupea Harengus L.). Fish Oceanogr. 14(4):279–291. doi: 10.1111/j.1365-2419.2005.00336.x.

Niino Y, Furuichi S, Kamimura Y, Yukami R. 2021. Spatiotemporal spawning patterns and early growth of Japanese sardine in the western North Pacific during the recent stock increase. Fish Oceanogr. 30(6):643–652. doi: 10.1111/fog.12542.

Nishida K, Yasu A, Nanjo N, Takahashi M, Kitajima S, Ishimura T. 2020. Microscale stable carbon and oxygen isotope measurement of individual otoliths of larvae and juveniles of Japanese anchovy and sardine. Estuar Coast Shelf Sci. 245:106946. doi: 10.1016/j.ecss.2020.106946.

Niu M, Wang J. 2017. Variation in the distribution of wintering anchovy *Engraulis japonicus* and its relationship with water temperature in the central and southern Yellow Sea. Chin J Ocean Limnol. 35(5):1134–1143. doi: 10.1007/s00343-017-6134-1.

Norcross BL, Brown ED, Foy RJ, Frandsen M, Gay SM, Kline TC, Mason DM, Patrick EV, Paul AJ, Stokesbury KDE. 2001. A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound. Alaska Fish Oceanogr. 10(s1):42–57. doi: 10.1046/j.1054-6006.2001.00040.x.

Nyuji M, Takasuka A, Okada M. 2022. Variation in reproductive parameters of round herring in the Pacific coastal waters of Japan. J Sea Res. 187:102247. doi: 10.1016/j.seares.2022.102247.

O'Toole MJ, Crous HB. 1989. A new net for sampling juvenile stages of pelagic fish. S Afr Shipp News Fishg Ind Rev. 44(4):37–39.

Ohshimo S, Nagatani H, Ichimaru T. 1997. Growth of 0-age Japanese sardine *Sardinops melanostictus* in the waters off the western coast of Kyushu. Fish Sci. 63(5):659–663. doi: 10.2331/fishsci.63.659.

Okunishi T, Ito S, Hashioka T, Sakamoto TT, Yoshie N, Sumata H, Yara Y, Okada N, Yamanaka Y. 2012. Impacts of climate change on growth, migration and recruitment success of Japanese sardine (*Sardinops melanostictus*) in the western North Pacific. Clim Change. 115(3–4):485–503. doi: 10.1007/s10584-012-0484-7.

Okunishi T, Yamanaka Y, Ito, S. 2009. A simulation model for Japanese sardine (*Sardinops melanostictus*) migrations in the western North Pacific. Ecol Modell. 220(4):462–479. doi: 10.1016/j.ecolmodel.2008.10.020.

Olivar MP, Catalán IA, Emelianov MF, De Puelles ML. 2003. Early stages of *Sardina pilchardus* and environmental anomalies in the Northwestern Mediterranean. Estuar Coast Shelf Sci. 56(3–4):609–619. doi: 10.1016/S0272-7714(02)00210-X.

Olivar MP, Salat J, Palomera I. 2001. Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. Mar Ecol Prog Ser. 217:111–120. doi: 10.3354/meps217111.

Ormseth OA, Baker MM, Hopcroft RR, Ladd C, Mordy CW, Moss JH, Mueter FJ, Shotwell SK, Strom SL. 2019. Introduction to understanding ecosystem processes in the Gulf of Alaska. Deep Sea Res 2 Top Stud Oceanogr. 165. 2:1–6. doi: 10.1016/j.dsr2.2019.06.019.

Ortega-Cisneros K, de Moor CL, Cochrane K. 2024. Linking the movement of South African sardine and anchovy to environmental variables using a model of intermediate complexity. Fish Res. 275:107001. doi: 10.1016/j.fishres.2024.107001.

Ospina-Álvarez A, Bernal M, Catalán IA, Roos D, Bigot J-L, Palomera I. 2013. Modeling fish egg and spatial distribution from acoustic data: a step forward into the analysis of recruitment. PLoS One. 8(9):e73687. doi: 10.1371/journal.pone.0073687.

Ospina-Alvarez A, Catalán IA, Bernal M, Roos D, Palomera I. 2015. From egg production to recruits: Connectivity and inter-annual variability in the recruitment patterns of European anchovy in the northwestern Mediterranean. Prog Oceanogr. 138:431–447. doi: 10.1016/j.pocean.2015.01.011.

Ospina-Alvarez A, Vásquez SI, Catalán IA, Lowerre-Barbieri S, Arteaga M, de Juan, S. 2022. A reproductive resilience index for pelagic fish in the southern Humboldt Current Large Marine Ecosystem. Can J Fish Aquat Sci. 79(12):2138–2159. doi: 10.1139/cjfas-2021-0263.

Palomera I, Olivar MP, Salat J, Sabatés A, Coll M, García A, Morales-Nin B. 2007. Small pelagic fish in the NW Mediterranean Sea: an ecological review. Prog Oceanogr. 74(2–3):377–396. doi: 10.1016/j.pocean.2007.04.012.

Palomera I. 1991. Spawning of anchovy *Engraulis encrasicolus* in the Northwestern Mediterranean relative to hydrographic features in the region. Mar Ecol Prog Ser. 79:215–223. doi: 10.3354/meps079215.

Parada C, Colas F, Soto-Mendoza S, Castro L. 2012. Effects of seasonal variability in across-and alongshore transport of anchoveta (*Engraulis ringens*) larvae on model-based pre-recruitment indices off central Chile. Prog Oceanogr. 92:192–205. doi: 10.1016/j.pocean.2011.07.015.

Parada C, Mullon C, Roy C, Fréon P, Hutchings L, van der Lingen CD. 2008. Does vertical migratory behaviour retain fish larvae onshore in upwelling ecosystems? A modelling study of anchovy in the southern Benguela. Afr J Mar Sci. 30(3):437–452. doi: 10.2989/AJMS.2008.30.3.1.635.

Parada C, van der Lingen CD, Mullon C, Penven P. 2003. Modelling the effect of buoyancy on the transport of anchovy (*Engraulis capensis*) eggs from spawning to nursery grounds in the southern Benguela: an IBM approach. Fish Oceanogr. 12(3):170–184. doi: 10.1046/j.1365-2419.2003.00235.x.

Parada CE. 1999. Influencia de factores físicos en la variabilidad interdiaria de la distribución de estados tempranos de Engraulis ringens en el Golfo de Arauco [MsC]. Concepción, Chile: Universidad de Concepción.

Parmanne R, Rechling O, Sjöstrand B. 1994. Status and future of herring and sprat stocks in the Baltic Sea. Dana. 10:29–59.

Patel R, Roy S, Capuzzo E, van der Kooij J. 2023. Seasonality of diet overlap among small pelagic fish in the waters southwest of the UK. Mar Ecol Prog Ser. 708:101–123. doi: 10.3354/meps14260.

Patterson K. 1992. Fisheries for small pelagic species: an empirical approach to management targets. Rev Fish Biol Fisheries. 2(4):321–338. doi: 10.1007/BF00043521.

Patti B, Torri M, Cuttitta A. 2020. General surface circulation controls the interannual fluctuations of anchovy stock biomass in the Central Mediterranean Sea. Sci Rep. 10(1):1554. doi: 10.1038/s41598-020-58028-0.

Payne MRC, Hatfield EM, Dickey-Collas M, Falkenhaug T, Gallego A, Gröger J, Priscilla L, Llope M, Munk P, Röckmann C, et al. 2009. Recruitment in a changing environment: the 2000s North Sea herring recruitment failure. ICES J Mar Sci. 66(2):272–277. doi: 10.1093/icesjms/fsn211.

Payne MR, Danabasoglu G, Keenlyside N, Matei D, Miesner AK, Yang S, Yeager SG. 2022. Skilful decadal-scale prediction of fish habitat and distribution shifts. Nat Commun. 13(1):2660. doi: 10.1038/s41467-022-30280-0.

Peck MA, Alheit J, Bertrand A, Catalán IA, Garrido S, Moyano M, Rykaczewski RR, Takasuka A, van der Lingen CD. 2021. Small pelagic fish in the new millennium: a bottom-up view of global research effort. Prog Oceanogr. 191:102494. doi: 10.1016/j.pocean.2020.102494.

Peck MA, Dutz J, Voss R 2012. A lasting legacy for the Baltic and North Sea GLOBEC Germany program. Prog Oceanogr. 107:1–2. doi: 10.1016/j.pocean.2012.08.002.

Peck MA, Reglero P, Takahashi M, Catalán IA. 2013. Life cycle ecophysiology of small pelagic fish and climate-driven changes in populations. Prog Oceanogr.116:220–245. doi: 10.1016/j.pocean.2013.05.012.

Pegau SW, Aderhold DR. 2021. Herring research and monitoring synthesis. Synthesis report. Cordoca (AK): Exxon Valdez Oil Spill Trustee Council Restoration Project; Report No.: 14120111).

Pennino MG, Coll M, Albo-Puigserver M, Fernández-Corredor E, Steenbeek J, Giráldez A, González M, Esteban A, Bellido JM. 2020. Current and future influence of environmental factors on small pelagic fish distributions in the Northwestern Mediterranean sea. Front Mar Sci. 7:00622. doi: 10.3389/fmars.2020.00622.

Perea A, Peña C, Oliveros-Ramos R, Buitrón B, Mori J. 2011. Potential egg production, recruitment, and closed fishing season of the Peruvian anchovy (*Engraulis ringens*): implications for fisheries management. Cienc Mar. 37(4b):585–601. doi: 10.7773/cm.v37i4B.1827.

Petitgas P, Alheit J, Peck MA, Raab K, Irigoien X, Huret M, van der J, Pohlmann K, Wagner T, Zarraonaindia C, et al. 2012. Anchovy population expansion in the North Sea. Mar Ecol Prog Ser..444:1–13. doi: 10.3354/meps09451.

Petitgas P, Doray M, Huret M, Massé J, Woillez M. 2014. Modelling the variability in fish spatial distributions over time with empirical orthogonal functions: anchovy in the

Bay of Biscay. ICES J Mar Sci. 71(9):2379–2389. doi: 10.1093/icesjms/fsu111.

Petitgas P, Magri S, Lazure P. 2006. One-dimensional biophysical modelling of fish egg vertical distributions in shelf seas. Fish Oceanogr. 15(5):413–428. doi: 10.1111/j.1365-2419.2006.00409.x.

Petitgas P, Renard D, Desassis N, Huret M, Romagnan JB, Doray M, Woillez M, Rivoirard J. 2020. Analysing temporal variability in spatial distributions using min-max autocorrelation factors: sardine eggs in the bay of biscay. Math Geosci. 52(3):337–354. doi: 10.1007/s11004-019-09845-1.

Petitgas P, Rijnsdorp AD, Dickey-Collas M, Engelhard GH, Peck MA, Pinnegar JK, Drinkwater K, Huret M, Nash RDM. 2013. Impacts of climate change on the complex life cycles of fish. Fish Oceanogr. 22(2):121–139. doi: 10.1111/fog.12010.

Petitgas P, Secor DH, Mcquinn I, Huse G, Lo N. 2010. Stock collapses and their recovery: mechanisms that establish and maintain life-cycle closure in space and time. ICES J Mar Sci. 67(9):1841–1848. doi: 10.1093/icesjms/fsq082.

Pikitch E, Boersma PD, Boyd IL, Conover DO, Cury P, Essington T, Heppell SS, Houde ED, Mangel M, Pauly D, et al. 2012. Little fish, big impact: managing a crucial link in ocean food webs. Lenfest Ocean. p. 108. https://www.lenfestocean.org/~/media/legacy/lenfest/pdfs/littlefishbigimpact_revised_12june12.pdf

Pikitch EK, Rountos KJ, Essington TE, Santora C, Pauly D, Watson R, Sumaila UR, Boersma PD, Boyd IL, Conover DO, et al. 2014. The global contribution of forage fish to marine fisheries and ecosystems. Fish Fish. 15(1):43–64. doi: 10.1111/faf.12004.

Pinsky ML, Jensen OP, Ricard D, Palumbi SR. 2011. Unexpected patterns of fisheries collapse in the world's oceans. Proc Natl Acad Sci U S A. 108(20):8317–8322. doi: 10.1073/pnas.1015313108.

Plirú A, van der Kooij J, Engelhard GH, Fox CJ, Milligan SP, Hunter E. 2012. Sprat feeding behaviour, selective predation, and impact onplaice egg mortality. ICES J Mar Sci. 69(6):1019–1029. doi: 10.1093/icesjms/fss081.

Politikos D, Rose K, Curchitser E, Checkley D, Rykaczewski R, Fiechter J. 2021. Climate variation and anchovy recruitment in the California Current: a cause-and-effect analysis of an end-to-end model simulation. Mar Ecol Prog Ser. 680:111–136. doi: 10.3354/meps13853.

Politikos D, Somarakis S, Tsiaras KP, Giannoulaki M, Petihakis G, Machias A, Triantafyllou G. 2015. Simulating anchovy's full life cycle in the northern Aegean Sea (eastern Mediterranean): a coupled hydro-biogeochemical-IBM model. Prog Oceanogr. 138(B):399–416. doi: 10.1016/j.pocean.2014.09.002.

Politikos DV, Huret M, Petitgas P. 2015. A coupled movement and bioenergetics model to explore the spawning migration of anchovy in the Bay of Biscay. Ecol Modell. 313:212–222. doi: 10.1016/j.ecolmodel.2015.06.036.

Polte P, Kotterba P, Moll D. 2017.

Prodanov K, Mikhailov K, Daskalov G, Maxim C, Chashchin A, Arkhipov A, Shlyakhov V, Ozdamar E. 1997. Environmental management of fish resources in the Black Sea and their rational exploitation. Studies and Reviews of the General Fisheries Council for the Mediterranean. Rome, Italy: FAO.

Punt AE, Butterworth DS, de Moor CLD, Oliveira JAA, Haddon M. 2016. Management strategy evaluation: best practices. Fish Fish. 17(2):303–334. doi: 10.1111/faf.12104.

Quinci EM, Torri M, Cuttitta A, Patti B. 2022. Predicting potential spawning habitat by ensemble species distribution models: the case study of European anchovy (*Engraulis encrasicolus*) in the strait of Sicily. Water. 14(9):1400. doi: 10.3390/w14091400.

Quintela M, Kvamme C, Bekkevold D, Nash RDM, Jansson E, Sørvik AG, Taggart JB, Skaala Ø, Dahle G, Glover KA. 2020. Genetic analysis redraws the management boundaries for the European sprat. Evol Appl. 13(8):1906–1922. doi: 10.1111/eva.12942.

Raab K, Nagelkerke LAJ, Boerée C, Rijnsdorp AD, Temming A, Dickey-Collas M. 2012. Dietary overlap between the potential competitors herring, sprat and anchovy in the North Sea. Mar Ecol Prog Ser. 470:101–111. doi: 10.3354/meps09919.

Ramírez F, Shannon LJ, van der Lingen CD, Julià L, Steenbeek J, Coll M. 2022. Climate and fishing simultaneously impact small pelagic fish in the oceans around the southernmost tip of Africa Front Mar Sci. 9:1031784. doi: 10.3389/fmars.2022.1031784.

Rasmus Nielsen J, Lundgren B, Jensen TF, Stæhr K-J. 2001. Distribution, density and abundance ofthe western Baltic herring (*Clupea harengus*) in the Sound (ICES Subdivision 23) in relationto hydrographical features. Fish Res. 50(3):235–258. doi: 10.1016/S0165-7836(00)00220-4.

Renfree JS, Beittel A, Bowlin NM, Erisman BE, James K, Mau SA, Murfin DW, Sessions TS, Stierhoff KL, Vasquez L, et al. 2023. USA. Report on the summer 2022 California current ecosystem survey (CCES) (2207RL), 27 June to 30 September 2022, conducted aboard NOAA ship Reuben Lasker, fishing vessels Lisa Marie and Long Beach Carnage, and uncrewed surface vehicles. California: NOAA. Report No.: Technical Memorandum NMFS-SWFSC-678. [accessed 2024 April 25] doi: 10.25923/66p9-hc28.

Rijavec L, Amaral JC. 1977. Distribuição e abundância de peixes pelágicos na costa sul e sudeste do Brasil Programa de Pesquisa e Desenvolvimento Pesqueiro do Brasil. Brasília. Ministério da Agricultura – Superintendência do Desenvolvimento da Pesca. Série Documentos Técnicos 24. 86 pp.

Robinson JPW, Mills DJ, Asiedu GA, Byrd K, Mancha M, Cohen PJ, Fiorella KJ, Graham NAJ, Macneil MA, Maire E, et al. 2022. Small pelagic fish supply abundant and affordable micronutrients to low- and middle-income countries. Nat Food. 3(12):1075–1084. doi: 10.1038/s43016-022-00643-3.

Röckmann C, Dickey-Collas M, Payne MRV, Hal R. 2011. Realized habitats of early-stage North Sea herring: looking for signals of environmental change. ICES J Mar Sci. 68(3):537–546. doi: 10.1093/icesjms/fsq171.

Rodriguez JM, Moyano M, Hernandez-Leon S. 2009. The ichthyoplankton assemblage of the Canaries–African coastal transition zone: a review. Prog Oceanogr. 83(1–4):314–321. doi: 10.1016/j.pocean.2009.07.009.

Rodríguez-Climent S, Angélico MM, Marques V, Oliveira P, Wise L, Silva A. 2017. Essential habitat for sardine juveniles in Iberian waters. Sci Mar. 81(3):351–360. doi: 10.3989/scimar.04554.07A.

Roel BA, Hewitson J, Kerstan S, Hampton I. 1994. The role of the Agulhas Bank in the life cycle of pelagic fishes.

S Afr J Sci. 90:185–196. https://journals.co.za/doi/pdf/10.10520/AJA00382353_4633

Roel BA, O'Brien CM, Basson M. 2004. Management options for the Blackwater herring, a local spring-spawning stock in the Thames Estuary. ICES J Mar Sci. 61(3):297–307. doi: 10.1016/j.icesjms.2004.02.001.

Rose KA, Cowan JH, Jr, Winemiller KO, Myers RA, Hilborn R. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish Fish. 2(4):293–327. doi: 10.1046/j.1467-2960.2001.00056.x.

Roy C, Cury P, Fontana A. 1989. Stratégies spatio-temporelles de la reproduction des clupéidés des zones d'upwelling d'Afrique de l'Ouest. Aquat Living Resour. 2:21–29. doi: 10.1051/alr:1989003.

Rykaczewski RR, Dunne JP, Sydeman WJ, García-Reyes M, Black BA, Bograd SJ. 2015. Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. Geophys Res Lett. 42(15):6424–6431. doi: 10.1002/2015GL064694.

Sabatés A. 1990. Distribution pattern of larval fish populations in the Northwestern Mediterranean. Mar Ecol Prog Ser. 59:75–82. doi: 10.3354/meps059075.

Saccardo SA, Rossi-Wongtschowski CLDB, Cergole MC, Bittencourt MM. 1988. Age and growth of the southeastern Brazilian sardine, *Sardinella brasiliensis,* 1981–83. Bol Inst Oceanogr. 36(1–2):17–35. doi: 10.1590/S0373-55241988000100003.

Sakamoto T, Komatsu K, Shirai K, Higuchi T, Ishimura T, Setou T, Kamimura Y, Watanabe C, Kawabata A. 2019. Combining microvolume isotope analysis and numerical simulation to reproduce fish migration history. Methods Ecol Evol. 10(1):59–69. doi: 10.1111/2041-210X.13098.

Sakamoto T, Takahashi M, Chung M-T, Rykaczewski RR, Komatsu K, Shirai K, Ishimura T, Higuchi T. 2022. Contrasting life-history responses to climate variability in eastern and western North Pacific sardine populations. Nat Commun. 13(1):5298. doi: 10.1038/s41467-022-33019-z.

Sakuma KM, Field JC, Mantua NJ, Ralston S, Marinovic BB, Carrion CN. 2016. Anomalous epipelagic micronekton assemblage patterns in the neritic waters of the California Current in spring 2015 during a period of extreme ocean conditions. Cal Coop Ocean Fish Inv Rep. 57:163–183. https://swfsc-publications.fisheries.noaa.gov/publications/CR/2016/2016Sakuma2.pdf

Santos AMP, Nieblas AE, Verley P, Teles-Machado A, Bonhommeau S, Lett C, Garrido S, Peliz A. 2018. Sardine (*Sardina pilchardus*) larval dispersal in the Iberian upwelling system, using coupled biophysical techniques. Prog Oceanogr.162:83–97. doi: 10.1016/j.pocean.2018.02.011.

Saraux C, Van Beveren E, Brosset P, Queiros Q, Bourdeix J-H, Dutto G, Gasset E, Jac C, Bonhommeau S, Fromentin J-M. 2019. Small pelagic fish dynamics: a review of mechanisms in the Gulf of Lions. Deep Sea Res 2 Top Stud Oceanogr.159:52–61. doi: 10.1016/j.dsr2.2018.02.010.

Šaškov A, Šiaulys A, Bučas M, Daunys D. 2014. Baltic herring (*Clupea harengus* membras) spawning grounds on the Lithuanian coast: current status and shaping factors. Oceanologia. 54(4):789–804. doi: 10.5697/oc.56-4.789.

Schismenou E, Giannoulaki M, Valavanis VD, Somarakis S. 2008. Modeling and predicting potential 1spawning habitat of anchovy (*Engraulis encrasicolus*) and round sardinella (*Sardinella aurita*) based on satellite environmental information. Hydrobiologia. 612(1):201–214. doi: 10.1007/s10750-008-9502-1.

Schmidt J, Van Damme CJ, Röckmann C, Dickey-Collas M. 2009. Recolonisation of spawning grounds in a recovering fish stock: recent changes in North Sea herring. Sci Mar. 73(S1):153–157. doi: 10.3989/scimar.2009.73s1153.

Schneider F, Schwingel PR. 1999. Estudo preliminar da ecologia Trófica da *Sardinella brasiliensis* na Costa Sudeste do Brasil. Notas Técn FACIMAR. 3:67–72. https://periodicos.univali.br/index.php/bjast/article/view/2472

Schwartzkopf BD, Dorval E, James KC, Walker JM, Snodgrass OE, Porzio DL, Erisman BE. 2022. A summary report of life history information on the central subpopulation of Northern Anchovy (*Engraulis mordax*) for the 2021 stock assessment. California: NOAA Tech Memo NMFS SWFSC. 659. doi: 10.25923/0fyc-t888.

Secor DH. 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fish Res. 43(1–3):13–34. doi: 10.1016/S0165-7836(99)00064-8.

Sewall F, Norcross B, Vollenweider J, Heintz R. 2019. Growth, energy storage, and feeding patterns reveal winter mortality risks for juvenile Pacific herring in Prince William Sound, Alaska, USA. Mar Ecol Prog Ser. 623:195–208. doi: 10.3354/meps13013.

Shelton PA, Armstrong MJ, Roel BA. 1993. An overview of the application of the daily egg production method in the assessment and management of anchovy in the southeast Atlantic. Bull Mar Sci. 53:778–794. https://www.researchgate.net/publication/233631925_An_Overview_of_the_Application_of_the_Daily_Egg_Production_Method_in_the_Assessment_and_Management_of_Anchovy_in_the_Southeast_Atlantic

Shepherd CS, Haught S. 2019. Pacific herring aerial surveys and age, sex, and size processing in the Prince William Sound Area, 2018–2021. AK (USA). Report No.; Regional Operational Plan ROP.CF.2A.2019.05. Juneau (AK): Alaska Department of Fish and Game Regional Operational Plan.

Shimura T, Yamamoto J, Morimoto H, Ohshimo S, Shimoyama S, Sakurai Y. 2008. Maturation and spawning of the Japanese anchovy in the Sea of Japan off the Torrori coast during spring. Bull Jap Soc Fish Oceanogr. 72:101–106.

Shvetsov F, Kozlovsky A, Rudneva A. 1995. The structure of Baltic sprat population as a base for the assessment of the stock. Copenhagen: ICES. Report No. CM 1995/J:14.

Silva A, Garrido S, Ibaibarriaga L, Pawlowski L, Riveiro I, Marques V, Ramos F, Duhamel E, Iglesias M, Bryère P, et al. 2019. Adult-mediated connectivity and spatial population structure of sardine in the Bay of Biscay and Iberian coast. Deep Sea Res 2 Top Stud Oceanogr. 159:62–74. doi: 10.1016/j.dsr2.2018.10.010.

Silva A, Skagen DW, Uriarte A, Massé J, Santos MB, Marques V, Carrera P, Beillois P, Pestana G, Porteiro C, et al. 2009. Geographic variability of sardine dynamics in the Iberian Biscay region. ICES J Mar Sci. 66(3):495–508. doi: 10.1093/icesjms/fsn225.

Simmonds J, Mannnini A, Vasilakopoulos P. 2017. Scientific, technical and economic committee for fisheries (STECF)-Mediterranean stock assessments 2017 part I (STECF-17-15).

Luxembourg: Publications Office of the European Union. doi: 10.2760/897559.

Siple MC, Koehn LE, Johnson KF, Punt AE, Canales TM, Carpi P, de Moor CL, Oliveira D, Gao JAA, Jacobsen J, et al. 2021. Considerations for management strategy evaluation for small pelagic fishes. Fish Fish. 22(6):1167–1186. doi: 10.1111/faf.12579.

Sjöblom V, Parmanne R. 1980. Sprat off the coast of Finland in 1977 and 1978. Annales Biologique. 35:200–203.

Skagseth Ø, Slotte A, Stenevik EK, Nash RDM. 2015. Characteristics of the Norwegian coastal current during years with high recruitment of Norwegian spring spawning herring (*Clupea harengus* L.). PLoS One. 10(12):e0144117. doi: 10.1371/journal.pone.0144117.

Slotte A. 1999. Effects of fish length and condition on spawning migration in Norwegian spring spawning herring (*Clupea harengus* L). Sarsia. 84(2):111–127. doi: 10.1080/00364827.1999.10420439.

Smith PE. 2005. A history of proposals for subpopulation structure in the Pacific sardine (*Sardinops sagax*) population off western North America. Cal Coop Oc Fish Inv Rep. 46:75–82. https://calcofi.org/downloads/publications/calcofireports/v46/Vol_46_Smith_History_Of_Subpopulation_Structure.pdf

Somarakis S, Ganias K, Siapatis A, Koutsikopoulos C, MacHias A, Papaconstantinou C. 2006. Spawning habitat and daily egg production of sardine (*Sardina pilchardus*) in the eastern Mediterranean. Fish Oceanogr. 15(4):281–292. doi: 10.1111/j.1365-2419.2005.00387.x.

Somarakis S, Tsoukali S, Giannoulaki M, Schismenou E, Nikolioudakis N. 2019. Spawning stock, egg production and larval survival in relation to small pelagic fish recruitment. Mar Ecol Prog Ser. 618:113–136. 617. doi: 10.3354/meps12642.

Soto-Mendoza S, Parada C, Castro L, Colas F, Schneider W. 2012. Modeling transport and survival of anchoveta eggs and yolk–sac larvae in the coastal zone off central-southern Chile: assessing spatial and temporal spawning parameters. Prog Oceanogr .95:178–191. 92–doi: 10.1016/j.pocean.2011.07.001.

Spalding M, Fox H, Allen G, Davidson N, Ferdaña Z, Finlayson M, Halpern B, Lombana JM, Lourie A, Martin S, et al. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience. 57(7):573–583. doi: 10.1641/B570707.

Spondylidis S, Giannoulaki M, Machias A, Batzakas I, Topouzelis K. 2023. Can we actually monitor the spatial distribution of small pelagic fish based on sentinel-3 data? An example from the North Aegean Sea (Eastern Mediterranean Sea). Front Mar Sci. 10:1117704. doi: 10.3389/fmars.2023.1117704.

STECF. 2013. Assessment of black sea stocks (STECF 13-XX). Ispra: Scientific, technical and economic committee for fisheries. p. 1–429.

Stenevik EK, Hølleland S, Enberg K, Høines Å, Salthaug A, Slotte A, Vatnehol S, Aanes S. 2022. Predicting density-dependent somatic growth in Norwegian spring-spawning herring. ICES J Mar Sci. 79(4):1340–1352. doi: 10.1093/icesjms/fsac057.

Stiti DJS. 2022. Spatiotemporal variation in the density distribution of sprat (Sprattus sprattus). Hardangerfjorden and sognefjorden [MSc]. Bergen, Norway: University of Bergen.

Stokesbury KDE, Kirsch J, Patrick E, Norcross BL. 2002. Natural mortality estimates of juvenile Pacific herring in Prince William Sound. Alaska. Can J Fish Aq Sci. 59:416–423. doi: 10.1139/f02-017.

Stratoudakis Y, Coombs S, Lago De Lanzós A, Halliday N, Costas G, Caneco B, Franco C, Conway D, Santos · M, Begoña Silva A, et al. 2007. Sardine (*Sardina pilchardus*) spawning seasonality in European waters of the northeast Atlantic. Mar Biol. 152(1):201–212. doi: 10.1007/s00227-007-0674-4.

Suhara M, Mori Y, Mihara Y, Yamamoto M, Kawabata A, Takahashi M, Katsukawa Y, Katayama S, Yamashita Y, Kawamura T, et al. 2013. Comparison of reproductive traits of Japanese anchovy *Engraulis japonicus* among sea areas around Japan. Nippon Suisan Gakk. 79(5):813–822. doi: 10.2331/suisan.79.813.

Suzuki KK, Yasuda T, Kurota H, Yoda M, Hayashi A, Muko S, Takahashi M. 2018. Spatiotemporal variations in the distribution of round herring eggs in the East China and Japan Seas during 1997–2013. J Sea Res. 142:1–10. doi: 10.1016/j.seares.2018.09.003.

Swalethorp R, Landry MR, Semmens BX, Ohman MD, Aluwihare L, Chargualaf D, Thompson AR. 2023. Anchovy boom and bust linked to trophic shifts in larval diet. Nat Commun. 14(1):7412. doi: 10.1038/s41467-023-42966-0.

Sydeman WJ, Dedman S, García-Reyes M, Thompson SA, Thayer JA, Bakun A, MacCall AD. 2020. Sixty-five years of northern anchovy population studies in the southern California current: a review and suggestion for sensible management. ICES J Mar Sci. 77(2):486–499. doi: 10.1093/icesjms/fsaa004.

Szuwalski CS, Britten GL, Licandeo R, Amoroso RO, Hilborn R, Walters C. 2019. Global forage fish recruitment dynamics: a comparison of methods, time-variation, and reverse causality. Fish Res. 214:56–64. doi: 10.1016/j.fishres.2019.01.007.

Takahashi M, Nishida H, Yatsu A, Watanabe Y. 2008. Year-class strength and growth rates after metamorphosis of Japanese sardine (*Sardinops melanostictus*) in the western North Pacific Ocean during 1996–2003. Can J Fish Aquat Sci. 65(7):1425–1434. doi: 10.1139/F08-063.

Takahashi M, Watanabe Y, Kinoshita T, Watanabe C. 2001. Growth of larval and early juvenile Japanese anchovy, *Engraulis japonicus*, in the Kuroshio-Oyashio transition region. Fish Oceanogr.10(2):235–247. doi: 10.1046/j.1365-2419.2001.00160.x.

Takahashi M, Watanabe Y, Yatsu A, Nishida H. 2009. Contrasting responses in larval and juvenile growth to a climate-ocean regime shift between anchovy and sardine. Can J Fish Aquat Sci. 66(6):972–982. doi: 10.1139/F09-051.

Takasuka A, Kubota H, Oozeki Y. 2008. Spawning overlap of anchovy and sardine in the western North Pacific. Mar Ecol Prog Ser. 366:231–244. doi: 10.3354/meps07514.

Takeshige A, Miyake Y, Nakata H, Kitagawa T, Kimura S. 2015. Simulation of the impact of climate change on the egg and larval transport of Japanese anchovy (Engraulis japonicus) off Kyushu Island, the western coast of Japan. Fish Oceanogr. 24(5):445–462. doi: 10.1111/fog.12121.

Talbot GB. 1973. The california sardine-anchovy fisheries. Trans Am Fish Soc. 102(1):178–187. doi: 10.1577/1548-8659.

Teles-Machado A, Peliz S, Plecha S, Garrido S. 2024. Came with the flow: how anomalous currents can bring small pelagic fish to new areas. Mar Ecol Prog Ser. 741:289–300. doi: 10.3354/meps14526.

Teske PR, Emami-Khoyi A, Golla TR, Sandoval-Castillo J, Lamont T, Chiazzari B, McQuaid CD, Beheregaray LB, van der Lingen CD. 2021. The sardine run in southeastern Africa is a mass migration into an ecological trap. Sci Adv. 7(38):eabf4514. doi: 10.1126/sciadv.abf4514.

Thiaw M, Auger PA, Ngom F, Brochier T, Saliou F, Diankha O, Brehmer P. 2017. Effect of environmental conditions on the seasonal and inter-annual variability of small pelagic fish abundance off North-West Africa: the case of both Senegalese sardinella. Fish Oceanogr. 26(5):583–601. doi: 10.1111/fog.12218.

Thompson AR, Auth TD, Brodeur RD, Bowlin NM, Watson W. 2014. Dynamics of larval fish assemblages in the California Current System: a comparative study between Oregon and southern California. Mar Ecol Prog Ser. 506:193–212. doi: 10.3354/meps10801.

Tičina V, Ivančić I, Emrić V. 2000. Relation between the hydrographic properties of the northern Adriatic Sea water and sardine (*Sardina pilchardus*) population schools. Period Biol. 102(1):181–192. https://www.academia.edu/52080210/Relation_between_the_hidrographic_properties_of_the_northern_Adriatic_Sea_water_and_sardine_Sardina_pilchardus_population_schools

Tiedemann M, Slotte A, Nash RDM, Stenevik EK, Kjesbu OS. 2021. Drift indices confirm that rapid larval displacement is essential for recruitment success in high-latitude oceans. Front Mar Sci. 8:1–13. doi: 10.3389/fmars.2021.679900.

Tiernan A, Elison T, Sands T, Head J, Vega S, Neufeld G. 2020. Bristol bay area annual management report. Anchorage (USA). Fish Man Rep. No.: 21–16. https://www.adfg.alaska.gov/FedAidPDFs/FMR21-16.pdf

Tojo N, Kruse GH, Funk FC. 2007. Migration dynamics of Pacific herring (*Clupea pallasii*) and response to spring environmental variability in the southeastern Bering Sea. Deep Sea Res 2 Top Stud Oceanogr. 54(23–26):2832–2848. doi: 10.1016/j.dsr2.2007.07.032.

Toresen R, Skjoldal HR, Vikebø F, Martinussen MB. 2019. Sudden change in long-term ocean climate fluctuations corresponds with ecosystem alterations and reduced recruitment in Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae). Fish Fish. 20(4):686–696. doi: 10.1111/faf.12369.

Torri M, Corrado R, Falcini F, Cuttitta A, Palatella L, Lacorata G, Patti B, Arculeo M, Mifsud R, Mazzola S, et al. 2018. Planktonic stages of small pelagic fishes (*Sardinella aurita* and *Engraulis encrasicolus*) in the central Mediterranean Sea: the key role of physical forcings and implications for fisheries management. Prog Oceanogr. 162:25–39. doi: 10.1016/j.pocean.2018.02.009.

Tourre YM, Lluch-Cota SE, White WB. 2007. Global multi-decadal ocean climate and small-pelagic fish population. Environ Res Lett. 2(3):034005. doi: 10.1088/1748-9326/2/3/034005.

Tsagarakis K, Machias A, Somarakis S, Giannoulaki M, Palialexis A, Valavanis VD. 2008. Habitat discrimination of juvenile sardines in the Aegean Sea using remotely sensed environmental data. Hydrobiologia. 612(1):215–223. doi: 10.1007/s10750-008-9500-3.

Tsikliras AC, Antonopoulou E, Stergiou K. 2010. Spawning period of Mediterranean marine fishes. Rev Fish Biol Fisheries. 20(4):499–538. doi: 10.1007/s11160-010-9158-6.

Tugores P, Giannoulaki M, Iglesias M, Bonanno A, Tičina V, Leonori I, MacHias A, Tsagarakis K, Díaz N, Giráldez A, et al. 2011. Habitat suitability modelling for sardine *Sardina pilchardus* in a highly diverse ecosystem: the Mediterranean sea. Mar Ecol Prog Ser. 443:181–205. doi: 10.3354/meps09366.

Uriarte A, Prouzet P, Villamor B. 1996. Bay of Biscay and Ibero Atlantic anchovy populations and their fisheries. Sci Mar. 60(2):237–255.

Urtizberea A, Fiksen Ø, Folkvord A, Irigoien X. 2008. Modelling growth of larval anchovies including diel feeding patterns, temperature and body size. J Plankton Res. 30(12):1369–1383. doi: 10.1093/plankt/fbn090.

Valdés L, Bode A, Latasa M, Nogueira E, Somavilla R, Varela MM, González-Pola C, Casas G. 2021. Three decades of continuous ocean observations in North Atlantic Spanish waters: the RADIALES time series project, context, achievements and challenges. Prog Oceanogr. 198:102671. doi: 10.1016/j.pocean.2021.102671.

Valencia-Gasti JA, Durazo R, Weber ED, Mcclatchie S, Baumgartner T, Lennert-Cody CE. 2018. Spring spawning distribution of Pacific sardine in US and Mexican waters. Cal Coop Oc Fish Inv Rep. 59:79–85. https://calcofi.org/downloads/publications/calcofireports/v59/Vol59-Valencia-etal_79-85.pdf

van der Kooij J, McKeown N, Campanella C, Boyra G, Doray M, Santos M, Silva JF, Huret M. 2024. Northward range expansion of Bay of Biscay anchovy into the English Channel. Mar Ecol Prog Ser.741:217–236. doi: 10.3354/meps14603.

van der Lingen CD, Coetzee JC, Hutchings L. 2002. Temporal shifts in the spatial distribution of anchovy spawners and their eggs in the southern Benguela: implications for recruitment. Plymouth (UK): Report of a GLOBEC-SPACC/IDYLE/ENVIFISH workshop on Spatial Approaches to the Dynamics of Coastal Pelagic Resources and their Environment in Upwelling Areas GLOBEC Report No: 16: 46–48.

van der Lingen CD, Coetzee JC, Hutchings L. 2010. Overview of the KwaZulu-Natal sardine run. Afr J Mar Sci. 32(2):271–277. doi: 10.2989/1814232X.2010.501581.

van der Lingen CD, Huggett JA. 2003. The role of ichthyoplankton surveys in recruitment research and management of South African anchovy and sardine. In Browman HI, Skiftesvik AB, editors. Oslo (Norway): BIG FISH BANG. (26th Annual Larval Fish Conference). p. 303–343.

van der Lingen CD, Hutchings L, Merkle D, Van Der Westhuizen JJ, Nelson J. 2001. Comparative spawning habitats of anchovy (Engraulis capensis) and sardine (Sardinops sagax) in the Southern Benguela upwelling ecosystem.Kruse. In: Bez GH, Booth N, Dorn A, Hills MW, Lipcius S, Pelletier RN, Roy D, Smith C, Witherell SJD, editors. Spatial processess and management of marine populations. 17(Symposium on Spatial Processes and

Management of Marine Populations). Fairbanks (USA): U. Alaska Sea Grant. p. 185–209.

Vásquez S, Salas C, Nuñez S, Soto-Mardones L, Letelier J, Arteaga M, Catica C, Sepúlveda A, Cisterna L, Gretchina A, et al. 2016. Estimación de índices de reclutamiento basados en variables y modelos biofísicos de pelágicos pequeños de la zona centro sur de Chile: Fase II. Informe final FIPA 2014–35. Instituto de Investigación Pesquera; p. 153.

Vazzoler AE de M, Ngan PV. 1976. Electrophoretic patterns of eye-lens proteins of *Sardinella brasiliensis* (Steindachner, 1879) off Brazilian coast. Revue Trav Inst Pêches Marit. 40(3–4):781–786.

Vazzoler AEAdM, Rossi-Wongtschowski CLDB, Braga FMdS 1987. Estudos sobre estruturai ciclo de vida e comportamento de Sardinella brasiliensis (STEINDACHNER, 1879) na área entre 22°S e 28°S, Brasil. 4, Crescimento: aspectos quantitativos. Bol Inst Oceanogr. 35(1):53–63. doi: 10.1590/S0373-55241987000100007.

Ventero A, Marcos I, Iglesias M. 2021. Acoustic evidences of the beginning of anchovy (*Engraulis encrasicolus*) schooling in the Northern Alboran Sea (Mediterranean Sea). Fish Res. 239:105950. doi: 10.1016/j.fishres.2021.105950.

von Nordheim L, Kotterba P, Moll D, Polte P. 2018. Impact of Spawning Substrate Complexity on Egg Survival of Atlantic Herring (*Clupea harengus*, L.) in the Baltic Sea. Estuaries Coasts.41(2):549–559. doi: 10.1007/s12237-017-0283-5.

von Westernhagen H, Dethlefsen V, Bade T, Wosniok W. 2002. Species assemblages of pelagic fish embryos in the southern North Sea between 1984 and 2000. Helgol Mar Res. 55(4):242–251. doi: 10.1007/s10152-001-0089-4.

Voss R, Clemmesen C, Baumann H, Hinrichsen HH. 2006. Baltic sprat larvae: coupling food availability, larval condition and survival. Mar Ecol Prog Ser. 308:243–254. doi: 10.3354/meps308243.

Voss R, Dickmann M, Schmidt JO. 2009. Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in the German Bight North Sea. Oceanologia. 51(1):117–138. doi: 10.5697/oc.51-1.117.

Voss R, Köster FW, Dickmann M. 2003. Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fish Res.63(1):97–111. doi: 10.1016/S0165-7836(02)00282-5.

Vrooman AM, Paloma PA, Zweifel JR. 1981. Electrophoretic, morphometric, and meristic studies of subpopulations of northern anchovy. Calif Fish Game. 67:39–51.

Vrooman AM. 1964. Serologically differentiated subpopulations of the Pacific sardine (*Sardina caerulea*). J Fish Board Can. 21(4):691–701. doi: 10.1139/f64-062.

Walker ND, Ouréns R, Ball JE, van der Kooij J, Uriarte A, White J, Carpi P, Schuchert P, Nash RDM. 2023. Defining sustainable and precautionary harvest rates for data-limited short-lived stocks: a case study of sprat (*Sprattus sprattus*) in the English Channel. ICES J Mar Sci. 80(10):2606–2618. doi: 10.1093/icesjms/fsad061.

Wallace PD, Pleasants CA. 1972. The distribution of eggs and larvae of some pelagic fish species in the English channel and adjacent waters in 1967 and 1968. ICES. CM.8:0–12.

Ware DM, Schweigert JF. 2001. Metapopulation structure and dynamics of British Columbia herring. Canada: CSAS. [accessed 2024 April 25]. http://www.dfo-mpo.gc.ca/csas/.

Ware DM, Tanasichuk RW. 1989. Biological basis of maturation and spawning waves in Pacific herring. Can J Fish Aq Sci. 46(10):1776–1784.

Watanabe Y, Zenitani H, Kimura R. 1995. Population decline of the Japanese sardine *Sardinops melanostictus* owing to recruitment failure. Can J Fish Aquat Sci. 52(8):1609–1616. doi: 10.1139/f95-154.

Watanabe Y, Zenitani H, Kimura R. 1996. Offshore expansion of spawning of the Japanese sardine, *Sardinops melanostictus*, and its implication for eggs and larval survival. Can J Fish Aquat Sci. 53(1):55–61. doi: 10.1139/f95-153.

Weber ED, Chao Y, Chai F, McClatchie S. 2015. Transport patterns of Pacific sardine *Sardinops sagax* eggs and larvae in the California Current System. Deep Sea Res 1 Oceanogr Res Pap. 100:127–139. doi: 10.1016/j.dsr.2015.02.012.

Weber W. 1974. Prediction of herring catches in the Western Baltic Sea. Rapp P-v Reun Cons Int Explor Mer. 166:150–151.

Xing Q, Huaming Y, Haiqing Y, Sun P, Liu Y, Ye Z, Li J, Tian Y. 2020. A comprehensive model-based index for identification of larval retention areas: a case study for Japanese anchovy *Engraulis japonicus* in the Yellow Sea. Ecol Indic. 116:106479. doi: 10.1016/j.ecolind.2020.106479.

Yasuda T, Kitajima S, Hayashi A, Takahashi M, Fukuwaka, M. 2021. Cold offshore area provides a favorable feeding ground with lipid-rich foods for juvenile Japanese sardine. Fish Oceanogr. 30(5):455–470. doi: 10.1111/fog.12530.

Zarrad R, José-Maria R, Francisco A, Aymen C, Othman J, Hechmi M. 2020. Larval fish community composition and distribution of the central-southern Mediterranean under summer and winter conditions. Acta Ichthyol Piscat. 50(3):313–324. doi: 10.3750/AIEP/02957.

Zarraonaindia I, Iriondo M, Albaina A, Pardo MA, Manzano C, Grant WS, Irigoien X, Estonba A. 2012. Multiple SNP markers reveal fine-scale population and deep phylogeographic structure in European anchovy (*Engraulis encrasicolus* L.). PLoS One. 7(7):e42201. doi: 10.1371/journal.pone.0042201.

Zwolinski JP, Demer DA, Macewicz BJ, Mau SA, Murfin DW, Palance D, Renfree JS, Sessions TS, Stierhoff KL. 2017. Distribution, biomass and demography of the central-stock of northern anchovy during summer 2016, estimated from acoustic-trawl sampling. NOAA technical memorandum NMFS; NOAA-TM-NMFS-SWFSC. 572.

Zwolinski JP, Emmett RL, Demer DA. 2011. Predicting habitat to optimize sampling of Pacific sardine (*Sardinops sagax*). ICES J Mar Sci. 68(5):867–879. doi: 10.1093/icesjms/fsr038.