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REVIEW

Larval trophic ecology of small pelagic fishes: a review of recent advances and pathways to fill remaining knowledge gaps

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ABSTRACT: Early life stages constitute a bottleneck for most fish populations, particularly for small pelagic fish (SPF), for which the interannual variability in recruitment strength is very high, and recruits frequently constitute the bulk of the population biomass. Finding the right prey (in terms of size and quality) during these early stages is critical for recruitment success. In this work, we synthesize the available literature on the trophic ecology of the early life stages of SPF, particularly clupeiforms. Works published during the last decade (2013–2022, 37 papers) were compared to those published previously (1920–2012, 107 papers). Gut content analysis of field-caught larvae is still the most commonly used technique (44%), while the use of biomarkers (e.g. stable isotopes and fatty acid composition), molecular tools (e.g. metabarcoding) and multitrophic approaches has increased in the last decade. Significant new knowledge was gained recently, such as that on larval feeding rates and behavior through laboratory experiments for species kept in culture (e.g. Atlantic herring, Pacific and Atlantic sardines), but some old challenges remain, such as the high vacuity rates of field-caught larvae. Lastly, we provide recommendations for future studies, such as the use of complementary techniques, the importance of studying ontogenetic shifts, the use of metabarcoding for analyzing the diet of early larvae that depend on microplankton, and the identification of prey with high taxonomic resolution. Such studies are essential to better understand larval growth and survival at sea, and thus to better understand and predict SPF population dynamics.

KEY WORDS: Larval fish · Diet · Gut content · Food availability · Trophodynamics

1. INTRODUCTION

Larval survival is a bottleneck for most marine fish populations; therefore, identifying bottom-up and top-down drivers impacting recruitment success remains an active field in fishery science (Llopiz et al. 2014, Arevalo et al. 2023, Ferreira et al. 2023, Hinchliffe et al. 2023, Moyano et al. 2023). The impact of prey availability on larval dynamics has been studied for more than a century, since Hjort (1914) postulated the critical period hypothesis. This hypothesis suggests that if larvae cannot find the proper prey (abundance, type) when they transition into exogenous feeding, they will experience strong starvation-related mortality, leading to a weaker than average year-class. Several extensions to this hypothesis were

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proposed in the following decades (e.g. match–mismatch, stable ocean; Lasker 1978, Cushing 1990), expanding the critical period beyond the first feeding phase and emphasizing the importance of hydrodynamics, such as upwelling strength and wind stress, on larval trophodynamics (Houde 2008). Many of these seminal hypotheses have focused on small pelagic fish (SPF) (e.g. Hjort 1914, Lasker 1978, Cury & Roy 1989), which respond quickly to environmental forcing, having a boom-and-burst strategy and high interannual variability in recruitment success (Cury et al. 2000, Peck et al. 2021). Testing these hypotheses in the field is not an easy task, and the link between larval trophodynamics and recruitment has been supported in some cases (e.g. Murphy et al. 2012), but not others (e.g. Irigoien et al. 2009). These results led Robert et al. (2014) to suggest that our ability to detect a 'critical period' linked to recruitment success is hampered by the low taxonomic resolution of our knowledge of prey preference, and it was possible to confirm the influence of larval food availability on recruitment variability only in those cases when prey preference was known with sufficient resolution. In fact, most statistically significant relationships found between larval vital rates and prey availability were based on a detailed knowledge of diet and prey preference (Robert et al. 2014).

Traditionally, the diet of larval fish has been investigated by examining their gut contents under a microscope (Garrido & van der Lingen 2014). This method is relatively simple, but has major limitations, such as the need for an expert taxonomist, and prey degradation of larvae preserved in formaldehyde (one of the most common fixatives), that precludes the visualization and/or identification to species level of some prey (e.g. soft-bodied organisms such as protists and jellyfish). The limitations of gut content analysis for SPF larvae are even larger than for most other fish groups, since their long and straight gut leads to a very high degree of regurgitation and defecation at capture and fixation (van der Lingen et al. 2009, Garrido & van der Lingen 2014). As a consequence, the feeding incidence (i.e. the number of larvae with at least one prey in the gut) is generally very low in most SPF larval diet studies. The largest effort to collect gut content information in clupeoid larvae to date was done for the Pacific sardine *Sardinops sagax* by Arthur (1976), who analyzed more than 10 000 larval guts and found prey in less than 25% of them. Nevertheless, while the high percentage of empty stomachs implies that a very large sample size is necessary to obtain meaningful results, gut content analysis provides valuable information on diet composition, namely the relative contribution of different prey types to the diet.

More recently, other methods beyond visual gut content analysis, such as stable isotopes and fatty acids, have helped explore longer-term trophodynamics in the wild (Garrido & van der Lingen 2014). New emerging methods linked to the fast development of genetics and the '-omics' are also a promising step change in the study of larval diets, as they are able to provide a high taxonomic resolution even with highly degraded gut contents (Hirai et al. 2017). Laboratory experiments have also contributed to shed light on feeding rates and feeding behavior of SPF larvae, such as the ontogenetic changes in maximum prey size and preference, and on foraging behavior (e.g. Munk 1992, Friedenberg et al. 2012, Caldeira et al. 2014). The data obtained from controlled laboratory experiments have been used to parameterize dispersal and feeding models aiming at describing and eventually predicting the relationship between environmental conditions and larval dynamics (Hufnagl et al. 2015).

Trophic ecology of SPF and larval fish has been the focus of several reviews over the past few decades. Two previous studies synthesized the existing information on the trophic ecology of sardine and anchovy species individually throughout the life cycle (van der Lingen et al. 2009, Garrido & van der Lingen 2014). These reviews acknowledged that there was significantly more information available on the trophic ecology of SPF juvenile and adult stages than larvae, for which there were some species at that time with a complete lack of information (e.g. *S. sagax* and *Engraulis encrasicolus* in the Benguela system). Other general reviews on larval fish diets across multiple families (Peck et al. 2012, Llopiz 2013) have also provided significant insights on SPF species. SPF larvae are pause-and-travel predators, and their diets are initially limited by mouth gape and prey behavior (Hufnagl & Peck 2011). Copepod eggs and nauplii have been identified as the main prey of clupeoids, which had the lowest median feeding incidences (<40%) across all studied fish families (Peck et al. 2012, Llopiz 2013). Phytoplankton and protozoans (<200 µm) also contribute to clupeoid diets, as first shown by Hardy (1924), particularly during first-feeding, but the magnitude of their contribution is still unclear. Having SPF larvae reared under laboratory conditions has contributed to advance our knowledge on prey type, size and behavior, namely to assess the contribution of protists (i.e. unicellular algae and protozooplankton) particularly for SPF species with smaller size-at-hatch (Theilacker & McMaster 1971, Huntley 1989, Illing et al. 2015).

Considering the rapid evolution of different techniques to study trophic ecology, the present study synthesizes the current knowledge on SPF larval trophodynamics, almost a decade after the last available reviews, revisiting their recommendations and expanding to other species of Clupeiformes. While previous reviews focused on information collected species by species, here we conduct a comparative analysis of the information available by species and by method, identifying the information that can be obtained from different approaches and identifying gaps in knowledge that still exist, and the most promising methods for improving the knowledge of SPF larval trophic ecology in future efforts.

2. MATERIALS AND METHODS

The emphasis of this review is to highlight the advances in knowledge on the trophic ecology of SPF (here considered to be taxa within the Order Clupeiformes) larvae during the last decade (2013–2022) in comparison to earlier studies, which is tightly linked to the emergence and/or consolidation of new methodological approaches. For this, we conducted a semi-structured literature review using the following search string in ISI Web of Knowledge (3 October 2022):

'(fish AND larva*) AND (feeding OR diet) AND (Sprattus OR sprat OR Engraulis OR anchovy OR Sardina OR sardine OR pilchard OR Sardinops OR Anchoa OR Clupea OR herring OR anchoveta OR clupei* OR 'small pelagic*') NOT (aquaculture).'

This search string resulted in 862 studies starting in 1972. Many studies were excluded after reading the title, abstract and/or complete paper, leading to a total of 92 studies to be evaluated in this review. Laboratory experiments focusing specifically on feeding ecology (diet composition, trophic position, spatial and temporal variability of feeding) were included in the analysis, but those just focusing on RNA/DNA and/or enzymatic analysis were excluded. Modeling studies exploring larval foraging behavior were not included. Search results missed several references mainly from the period before 1990, so 52 studies (36 prior to 1990) were added, including those used in previous reviews and compilations of diet studies of early life stages of fish and SPF in particular (Hufnagl & Peck 2011, Llopiz 2013, Garrido & van der Lingen 2014, Robert et al. 2014). A total of 144 studies from 1920 until 2022 were analyzed in this study. For each study, the species, system (e.g. NW Atlantic, Gulf of Mexico) and the method used (e.g. lab experiment, stomach content, biomarkers including stable isotopic analysis [SIA] or molecular methods) were recorded (Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m14543_supp1.pdf).

In order to investigate the type of information made available for each species/system, manuscripts included in this review were classified in 13 categories of type of data: (1) diet composition of the type of prey; (2) diet composition of size of prey; (3) diel feeding intensity, (4) selectivity, (5) feeding, growth and/or survival with different food levels; (6) feeding, growth and/or survival with different temperature levels; (7) ingestion rates; (8) foraging behavior; (9) digestion rates; (10) $\delta^{15}N$ - trophic level; (11) trophic position; (12) food source; (13) resource partitioning.

In the case of studies that reported data of stomach content analysis of SPF larvae (63 articles), the proportion of prey items consumed by each species was compiled. Numerical percentage (%N; contribution by number of a type of prey group in relation to the total number of prey; Hyslop 1980), frequency of occurrence (%FO; number of stomachs sampled in which a given prey was found versus the total number of stomachs sampled) and index of relative importance of prey (%IRI; Pinkas et al. 1971) were recorded for 48 out of 63 papers where gut contents of 19 SPF species were visually inspected (Table S2 and Supplement 2, www.int-res.com/articles/suppl/m14543_supp2.xlsx. To compare the proportion of prey groups in the guts between different studies, the percentage by number (%N) was used whenever available, given that it was the most commonly used metric. For those studies where %N was not reported (12 articles), the %FO rescaled to 100% (8 articles) or the %IRI (4 articles) was used for further analysis. Although the 3 indices differ, considering the low number of studies using gut content analysis of SPF larvae worldwide, we considered it important to include all studies in the analysis. Each prey was assigned to a set of predefined taxonomic groups to standardize the reported diets, creating a database of 20 species with 53 prey groups (Table S2). To examine differences in diet between species, mean diet composition was estimated. We found studies that reported a single averaged diet, or one averaged diet by sampling site, by year/season or by developmental stage/size. To unify the database (Table S2), the mean diet for each species was first obtained for each study and then for each species. Temporal or spatial comparisons of diets across different studies were not possible due to the low amount of information available.

A total of 18 out of 48 studies that reported stomach content data also included data for different larval size classes. Using those works, dietary information

was recorded by larval size and analyzed to explore potential ontogenetic changes of larval feeding preferences. Larval size classes reported were not consistent across studies. Therefore, to aggregate the information from different studies, we classified the larvae in 3 size categories: small, medium and large. The size range for each species was based on the information reported in the different studies and does not necessarily follow developmental milestones (e.g. pre-flexion or post-flexion); therefore, the stage-dependency changes in diet must be interpreted with caution (Table S3).

3. RESULTS

A total of 144 studies on the feeding ecology of SPF were compiled in this review, 37 of which were published after 2013 (Fig. 1). A constant rate of 3–4 studies was published per year from the mid-1980s to present, suggesting a proportional decrease in the contribution of larval trophic studies in relation to the increasing number of works studying SPF identified by Peck et al. (2021).

While the number of studies per year included in the present compilation was similar before and after 2013, the methods employed for studying larval feeding changed substantially (Fig. 1). Gut content analysis via microscopic identification of prey was the most common method used in both periods (45% before 2013 vs. 44% after 2013), mainly data of prey composition by prey type followed by prey size (Table S4 and Supplement 2). The proportion of studies using biomarkers, such as stable isotopes and fatty acids, as well as molecular methods, significantly increased in the last decade (8 vs. 25% for biomarkers, and 1 vs. 8% for molecular methods). On the other hand, the contribution of laboratory studies decreased by half (46% before vs. 22% after 2013). It is worth noting that all studies in the recent decade used only 1 method at a time, while there are some examples of studies using a combination of gut content analysis and other techniques, such as fatty acid biomarkers (Chicharo et al. 2012) and epifluorescence (Fukami et al. 1999) in the first period analyzed.

During the last decade, studies on SPF larval diets have covered new biogeographic regions, such as Patagonia and South Africa, and increased in other regions such as the Mediterranean Sea (Fig. 2). Nevertheless, the NE Atlantic remains the most studied region, which is reflected in the distribution of studies per species (Fig. 3). Atlantic herring *Clupea harengus* is still the most studied species in the last decade, followed by European sardine *Sardina pilchardus*. Northern anchovy *Engraulis mordax* was the second most studied species before 2013, but there are no recent studies in the last decade. Since 2013, there have been studies on species not investigated before, such as Araucarian herring *Strangomera bentincki* and Falkland sprat *Sprattus fuegensis*.

Atlantic herring was the species with the largest number of trophic studies and broader diversity of data on trophic ecology (10 out of 13 information categories), closely followed by northern anchovy (9 out of 13) and European sardine (7 out of 13) (Table 1; Table S1). Larvae from these 3 species have been successfully reared in the laboratory. Most studies on Atlantic herring used gut content analysis and laboratory experimentation, providing a detailed understanding of the diet composition, prey size preference

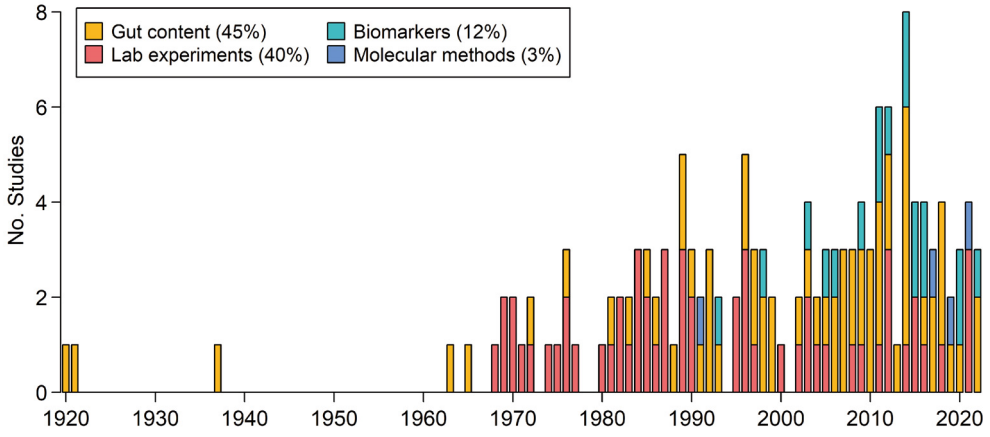

Fig. 1. Summary of studies on larval diet of small pelagic fishes by year of publication. Studies are color-coded by methodology used (gut contents, biomarkers, lab experiments or molecular methods). The contribution (%) of each method to the total number of studies is indicated in the legend

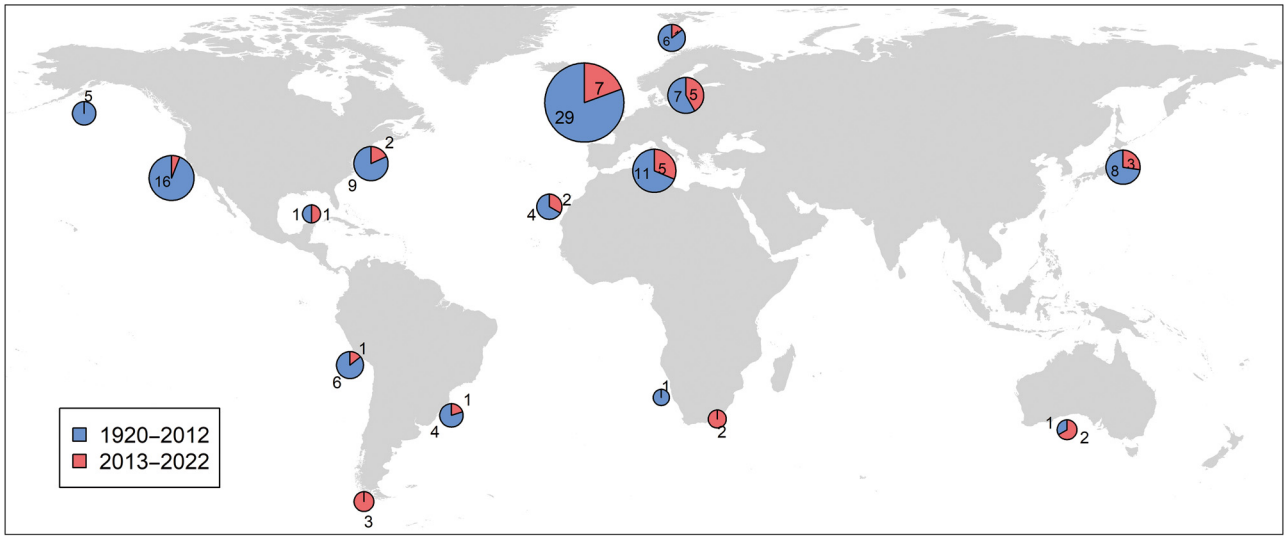

Fig. 2. Number of studies on larval diets of small pelagic fish published during 2 time periods (1920–2012 and 2013–2022) in 16 different biogeographic regions. Pie chart size reflects the number of studies, which are indicated numerically for each period inside each pie. Note that the location of each circle often represents a much broader region (e.g. one or more large marine ecosystems)

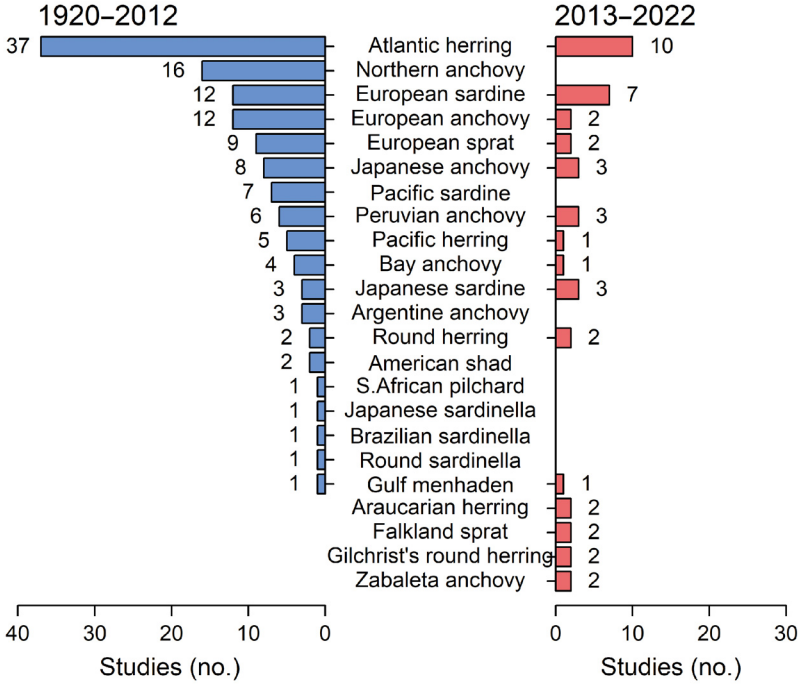

Fig. 3. Number of larval diet studies published on various species of small pelagic fish within 2 time periods (1920–2012 and 2013–2022)

and foraging behavior (e.g. Busch 1996, Denis et al. 2016, Illing et al. 2018). However, SIA, gut fluorescence and fatty acid biomarkers were only used in 1 study each, reflecting a lack of information on trophic level, trophic position and resource partitioning for this species. No work has yet used molecular techniques to study the diet of Atlantic herring. For northern anchovy, an impressive amount of work, especially laboratory work, was done around the 1970s on California Current SPF, but several questions remained open, such as the ontogenetic shifts in diet composition of the larvae, which could benefit from new techniques such as metabarcoding that still have not been used for this species. So far, detailed data obtained by new methods, particularly SIA, on trophic position and resource partitioning have mostly come from species in the Mediterranean Sea and Australian waters (Table 1).

3.1. Gut content analysis

Gut content analysis of field-caught larvae provides valuable information of the diet composition, diel feeding periodicity and prey selectivity (when compared to plankton availability in the water). In our query, a total of 63 studies analyzed gut contents of SPF larvae. The proportion of studies reporting prey at higher taxonomic resolution has increased, with 78%

Table 1. Number of studies providing information classified in 13 categories per region and species. EBUS: eastern boundary upwelling system. 'Some data': information not sufficient to describe other classes of information represented here

Region	Species	Diet—type of prey	Diet—size of prey	Diel feeding intensity	Selectivity	Foraging behavior	Ingestion rates	Digestion	Growth/survival—food level	Growth/survival—temp.	δ^{15}N—trophic level	Trophic position	Food source	Resource partitioning
Arctic Sea	*Clupea harengus*	1												
Australia	*Sardinops sagax*										1		1	
Baltic Sea	*C. harengus*	2	1	1	4	2	2		1					
	Sprattus sprattus	3	1	1	3				1					
Benguela EBUS	*Engraulis encrasicolus*								1	1				
	Sardinops ocellata								1					
California EBUS	*Clupea pallasii*	1												
	Engraulis mordax	3	1	1	4	4	6	1	9	1				
	S. sagax	1	1	1										
Cary Current	*E. encrasicolus*	1	1	1										
	Sardina pilchardus					2	2		2	1				1
Cary EBUS	*E. encrasicolus*	2												
	S. pilchardus	3			1									
Gulf of Mexico	*Brevoortia patronus*	2	1											
	Etrumeus teres	1	1											
Humboldt EBUS	*Engraulis ringens*	6	3	1							1	1	1	
	S. sagax	5	2	1										
Japan	*Engraulis japonicus*	5	2	1	2									1
	E. teres	1												
	Sardinella zunasi	1												1
	Sardinops melanostictus	2												1
Kuroshio	*E. japonicus*	1												
	S. melanostictus	1												
Mediterranean Sea	*E. encrasicolus*	8	3	5	7						1		1	1
	S. pilchardus	4	2	3	2						3	1	1	1
	Sardinella aurita	1	1	1										
NE Atlantic	*C. harengus*	13	3	3	8	3	2	1	12		1		1	
	E. encrasicolus	1	1	1	2				1					
	S. pilchardus	3	1	1					1					
	S. sprattus	5		1	1									
NE Pacific	*C. pallasii*	1			1	1			1					
North Sea	*S. pilchardus*	1	1											
	S. sprattus	1			1									
Norwegian/ Barents Sea	*C. harengus*					2	2	1	4	1				
NW Atlantic	*Alosa sapisissima*								2					
	Anchoa mitchilli				3	3	2		2					
	C. harengus	3	3	1	2									
NW Pacific	*C. pallasii*	1				1	1	1	1					
	E. japonicus	2	1		1						2		2	1
	E. teres	1			2						1		1	1
	S. melanostictus	2	1		2						1		1	1
Patagonia	*E. ringens*	2	1	2	1									
	Sprattus fuegensis	2		1										
	Strangomera bentincki	2		1										
South Africa	*Gilchristella aestuaria*	1	1		1						1		1	
SW Atlantic	*Anchovia clupeoides*	2												
	Engraulis anchoita	3	2											
SW Pacific	Clupeidae	1			1									
	Engraulidae	1			1									
	E. japonicus	1												

of studies reporting prey at the species level in the period 2013–2022 compared to 32% in the period 1991–2012 (Fig. S1). A total of 48 out of the 63 studies were included in our comparative analysis of diet composition, after removing studies where diet was not numerically reported or only partially reported, and those that only found empty stomachs. A major problem reported when analyzing gut contents of SPF larvae is a high vacuity rate. Feeding incidence was estimated in 60 out of 63 studies. Most studies found >40% of the analyzed larvae with empty guts, but 2 studies reported >99% (Costalago & Palomera 2014, Bernal et al. 2020). The percentage of empty guts was larger for smaller larvae (60% of studies had >60% empty guts for larvae <10 mm) (Fig. 4). For larger larvae (>15 mm), the percentage of empty guts was variable, but the probability of finding at least one prey in the gut (30% of studies report <20% of empty guts) was higher than for small larvae.

SPF larvae are typically omnivorous feeders, with most of the energy derived from zooplankton, particularly copepods (Fig. 5; Table S2 and Supplement 2). Most studies comparing larval diet with food availability have identified important differences in prey selectivity throughout ontogeny, probably related to the increase in mouth gape and swimming/feeding abilities. Prey that were positively selected were mostly different life stages of calanoids, followed by harpacticoid copepods (e.g. Voss et al. 2009, Catalan et al. 2010). When taking into consideration the

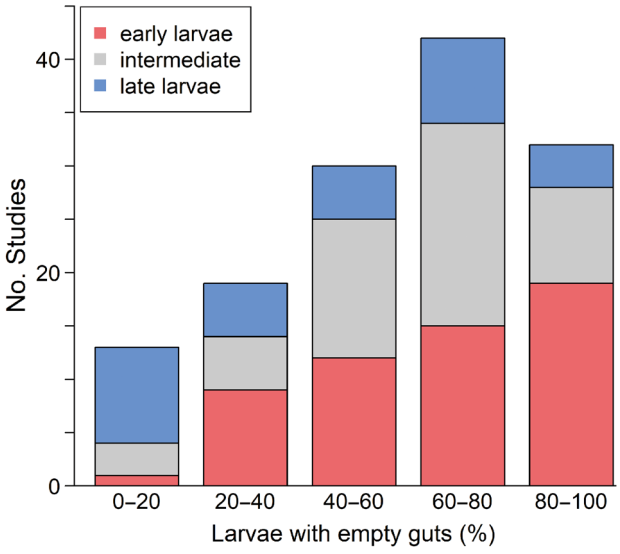

Fig. 4. Proportion of larvae with empty guts (as % of total larvae analyzed) reported in different gut content studies. Larval stage is indicated (red, early larvae; grey, intermediate larvae; blue, late larvae)

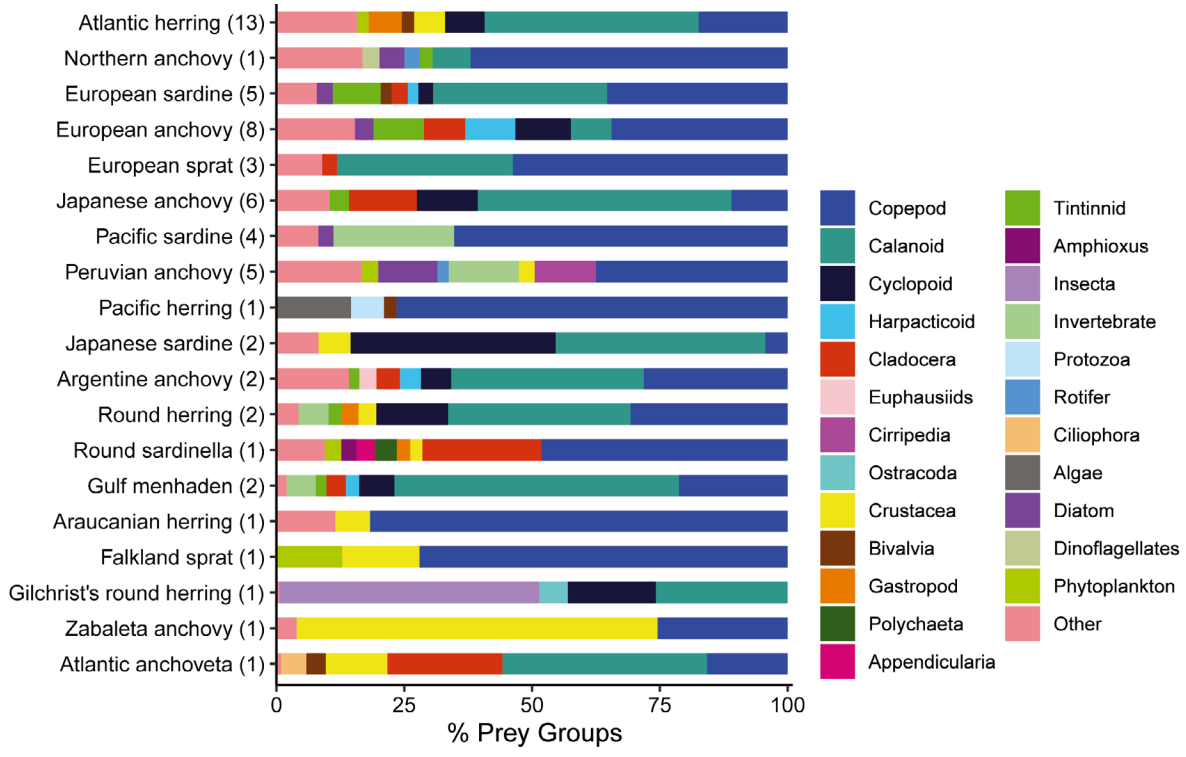

Fig. 5. Mean contribution of each prey group to the diet of 20 larval species of small pelagic fish. Prey groups contributing less than 2% to the total diet of the species are aggregated as 'Other'. Number of studies included in each species is indicated in brackets

family, species or copepod developmental stages (eggs, nauplii, copepodites and adults), diet varied significantly across species (Tables S2 & S3 and Supplement 2). Specifically, the order Calanoida was numerically the most important in the diet of Atlantic herring, Zabaleta anchovy *Anchovia clupeoides* (Lima & Barletta 2016), Gulf menhaden *Brevoortia patronus* (Chen et al. 1992, Hoover et al. 2022), Atlantic anchoveta *Cetengraulis edentulus* and the Japanese anchovy *Engraulis japonicus*, representing 40–55% of the of the total number of prey (Fig. 5). For Japanese sardine *Sardinops melanostictus*, cyclopoids were as important as calanoid copepods (Yasue et al. 2011, Okazaki et al. 2019). Harpacticoid copepods were described in the diet of European anchovy *E. encrasicolus*, European sardine, Gulf menhaden and capelin *Mallotus villosus*, but in a low proportion (2–11%).

Besides copepods, other secondary prey significantly contributed to larval feeding such as other crustaceans, Ciliophora, Bivalvia and Cladocera. For example, in round sardinella *Sardinella aurita* and Atlantic anchoveta, Cladocera constituted more than 20% of the diet, but this was not a common prey group in the diet of other SPF larvae (Morote et al. 2008). Less detectable zooplankton groups such as appendicularians represented 2–3.6% of the diet of European anchovy and round sardinella (Morote et al. 2008, 2010, Chícharo et al. 2012). Gilchrist's round herring *Gilchristella aestuaria* (Strydom et al. 2014), mostly found in estuaries in South Africa, had the most contrasting diet with other SPF species, with insects as the main prey (50.8%). Microplankton (e.g. diatoms, dinoflagellates and tintinnids) were present in the gut of most species analyzed but represented a small fraction of prey.

SPF larvae are selective visual feeders, and prey catchability improves with larval development (Bernal et al. 2020). In the studies reviewed here, 18 reported ontogenetic changes in diet composition for 10 species. Microplankton, invertebrate eggs, copepod eggs and nauplii were the main prey for small and medium larval sizes (Fig. 6), whereas the contributions of copepodites, adult copepods, cladocera and other larger zooplankton prey groups were mostly important for the diet of large larvae (Fig. 6; Table S3).

3.2. Experimental studies

Laboratory experimentation provides valuable information on larval trophic ecology that would be difficult or impossible to obtain from the wild. This includes valuable parameters for modeling and bioenergetic estimations, such as ingestion, digestion, growth and survival rates for different food types and food levels; observation and quantification of foraging behavior; and food preference or selectivity. Laboratory experiments investigating the trophic ecology of early life stages of SPF started in the late 1960s and early 1970s. Three species were the main target of these early studies and have remained among the most studied species to date: Atlantic herring, northern anchovy and European sardine (Fig. 3). Atlantic herring larvae were one of the first to be reared under controlled conditions, likely because it is easier to obtain fertilized eggs from this species by strip-spawning (Blaxter 1968). The intense research for the other 2 species is linked to the establishment of a broodstock in captivity that allowed the induction of spawning by manipulating temperature and/or food, resulting in a stable source of high-quality eggs. For northern anchovy, the broodstock at the NOAA Southwest Fisheries Center led to 12 papers on larval feeding dynamics in the 1970s and 1980s (e.g. Hunter 1976, Theilacker 1987), while the European sardine broodstock in Portugal has led to several papers since 2010 (e.g. Caldeira et al. 2014, Garrido et al. 2021). Fertilized eggs collected from the wild have been another regular source of fish larvae for experimentation, for species such as bay anchovy *Anchoa mitchilli* (e.g. Houde & Shekter 1980), European sardine (Blaxter 1969) or Cape anchovy *Engraulis capensis* (Brownell 1983).

Nearly half of the laboratory studies compiled here (44%) used natural zooplankton as a food source to culture fish larvae, occasionally supplemented with artemia (*Artemia salina*) nauplii (10%) (Houde & Shekter 1980, Rodriguez-Murillo et al. 1989). Using natural prey assemblages allowed the investigation of selectivity and prey preference, focusing on metazoan prey (e.g. Checkley 1982) or protists (e.g. Lasker 1975, Friedenberg et al. 2012). Some laboratory experiments were specifically designed to test the importance of protists during first feeding, and responses are species-specific. For example, northern anchovy first-feeding larvae grew well when fed the dinoflagellate *Gymnodinium* spp., but not with copepod nauplii (Lasker et al. 1970, Huntley 1989), while Atlantic herring larvae increased their window of opportunity for first feeding in the presence of algae or the dinoflagellate *Oxyrrhis marina*, but still needed copepod nauplii to grow successfully (Illing et al. 2015). Based on this knowledge, several follow-up studies have used cultured copepod nauplii (sometimes in combination with dinoflagellates) as the

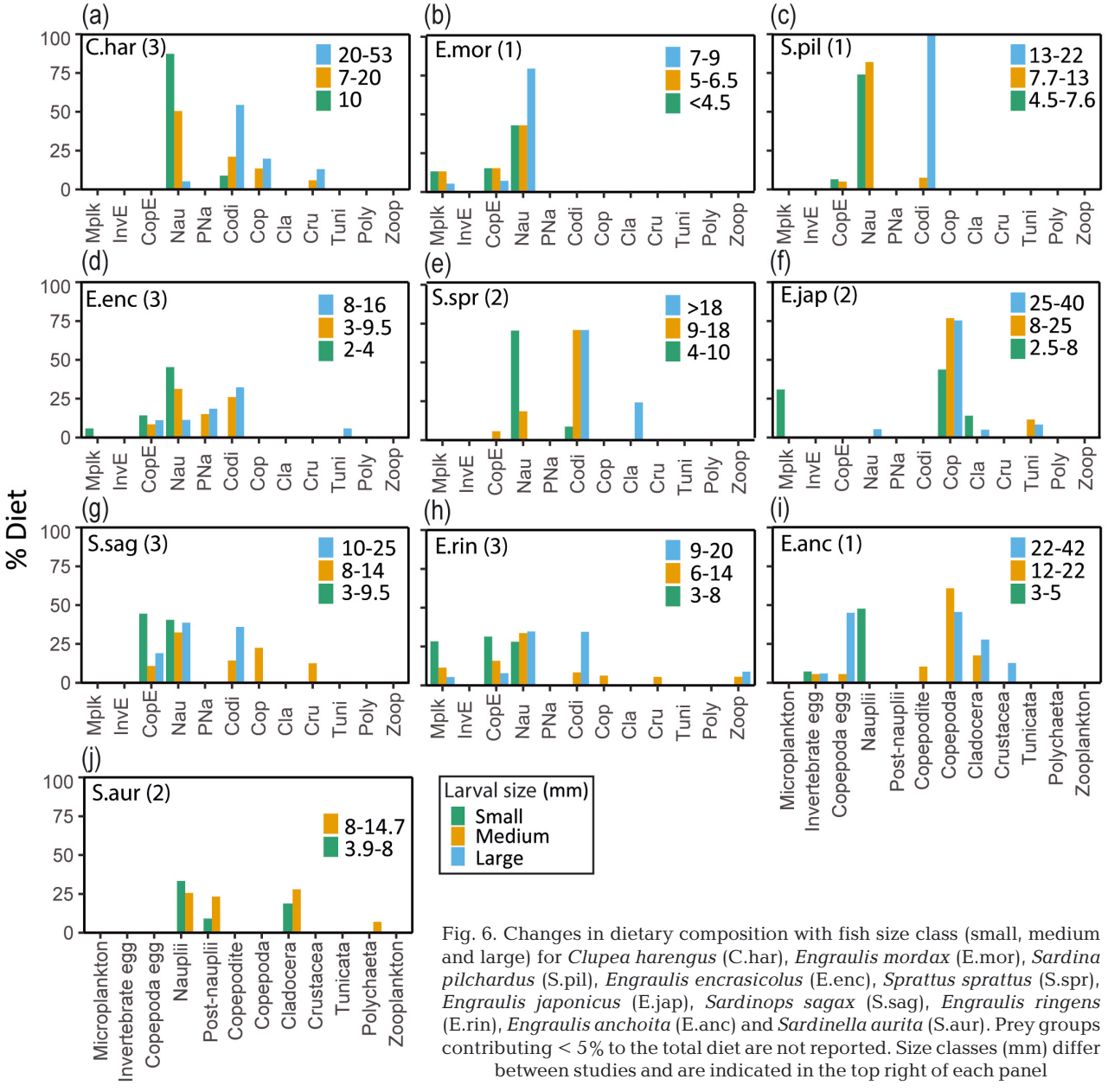

Fig. 6. Changes in dietary composition with fish size class (small, medium and large) for *Clupea harengus* (C.har), *Engraulis mordax* (E.mor), *Sardina pilchardus* (S.pil), *Engraulis encrasicolus* (E.enc), *Sprattus sprattus* (S.spr), *Engraulis japonicus* (E.jap), *Sardinops sagax* (S.sag), *Engraulis ringens* (E.rin), *Engraulis anchoita* (E.anc) and *Sardinella aurita* (S.aur). Prey groups contributing < 5% to the total diet are not reported. Size classes (mm) differ between studies and are indicated in the top right of each panel

main food source in their experiments (11 of 52 studies) (e.g. Munk & Kiørboe 1985, Kiørboe et al. 1987, Illing et al. 2015), rather than diets limited to rotifers and/or artemia (8 of 52 studies).

Beyond testing for different prey types and levels required to successfully rear larvae in captivity, laboratory experiments have provided vital information on the ontogenetic changes in prey size requirements and feeding rates. Atlantic herring is arguably the best studied species in this regard, and information is available on optimal and maximum prey size (Peck et al. 2012). Substantial work has been done to study the foraging behavior of this species (e.g. ingestion and attack rates, handling time) and how it is impacted by the density of food (Kiørboe et al. 1985, Munk & Kiørboe 1985), type of food (Busch 1996), temperature (Illing et al. 2018, Allan et al. 2022) and turbulence (MacKenzie & Kiørboe 1995), among other factors. This extensive knowledge on foraging behavior, together with that gained from gut content analysis from wild larvae (see Section 3.1), have promoted the development of modeling approaches that can help identify key periods during ontogeny when larvae are more prone to starvation, as well as the major environmental drivers impacting larval growth and survival (e.g. Fiksen & Folkvord 1999, Hufnagl & Peck 2011).

The present review shows that there has been a decrease in the number of studies (n = 8) published during the last decade that have specifically addressed feeding dynamics or foraging behavior using laboratory experiments, compared to the intense work carried out between the 1960s and 1990s (Fig. 1). These 8 studies investigated the effect of prey level on ingestion rates and somatic and otolith growth of European sardine (Caldeira et al. 2014, Garrido et al. 2021), and changes in foraging behavior under different temperatures and prey level scenarios in Atlantic herring (Illing et al. 2015, Allan et al. 2022).

3.3. Biomarkers (stable isotopic composition, fatty acids and others)

The use of SIA of $\delta^{15}N$ and $\delta^{13}C$ to study the trophic ecology of SPFs started in 1998 analyzing ontogenetic shifts of the trophic ecology of adult Japanese anchovy (Lindsay et al. 1998). This method is now being widely used in food web research, and provides information of the relative trophic level of a given organism (using $\delta^{15}N$) and source production (using $\delta^{13}C$). Contrasting to stomach content analysis that only provides a 'snapshot' of a given consumer's diet, SIA reflects the assimilated diet over a temporally longer time, which depends on the turnover rate of the tissue analyzed (for adult sardines it was estimated from 40 to 80 d in fish muscle tissue; Bode et al. 2007). The high vacuity rate that characterizes most SPF species and some ontogenetic stages does not affect SIA, which thus makes it a good complementary technique to gut content analysis to derive information of trophic level, diet composition, selectivity and resource partitioning. The number of papers using SIA to study the trophic ecology of SPF larvae is very low, compared to studies using SIA for juveniles and adults (see Garrido & van der Lingen 2014 for papers on sardine and anchovy until 2012), and equal between the 2 periods analyzed in this review (n = 6). Nearly half of the studies compiled here were conducted on sardine and anchovy species collected in the Mediterranean Sea.

SIA has advanced our knowledge on the ontogenetic changes in trophic position of SPF larvae for several species, via changes in $\delta^{15}N$ (i.e. an increase in $\delta^{15}N$ can be interpreted as an increase in trophic level). For example, an ontogenetic increase in $\delta^{15}N$ was shown for European sardine (Laiz-Carrión et al. 2011, Quintanilla et al. 2020) and for Pacific sardine in the East Australian Current (Uehara et al. 2005). In the Kii Channel off Japan, the increase in $\delta^{15}N$ with larval ontogeny was more significant for Pacific round herring and Japanese sardine than for the Japanese anchovy (Yasue et al. 2014). In the Mediterranean Sea, SIA revealed that the trophic position ($\delta^{15}N$) of European sardine late larvae was significantly lower than that of juveniles and adults, whereas values were similar between European anchovy life stages (Costalago et al. 2012). In the North Sea, Atlantic herring larvae of different body sizes fed at the same trophic level (similar $\delta^{15}N$) but on different prey (different $\delta^{13}C$) (Bils et al. 2022).

Besides showing ontogenetic and inter-species variability in trophic level, SIA has contributed to identify seasonal and spatial changes in the diet of SPF larvae and trophic overlap between species. Particularly, higher trophic position and higher feeding specialization was described for European anchovy larvae from less productive regions of the Mediterranean Sea (Quintanilla et al. 2015). Strong trophic overlap between Japanese anchovy, Japanese sardine and Pacific round herring was described in the Kii Channel, Japan (Yasue et al. 2014). For Peruvian anchovy larvae off the Humboldt Current, seasonal differences in the trophic position were more noticeable than spatial differences (Castro et al. 2020).

All SIA studies on SPF larvae to date have used bulk SIA. This type of analysis has uncertainties associated with defining the isotopic baseline and the variability in trophic discrimination factors, which can lead to errors when estimating trophic position of organisms in the wild. A recent approach that may help overcome the key shortcomings of bulk SIA is compound-specific nitrogen SIA on amino acids (CSIA-AA). This method provides $\delta^{15}N$ values of source and trophic AAs in the same sample, which allows estimating trophic position without the need for sampling the baseline separately, and the variability in the trophic position across species, areas and seasons (Miyachi et al. 2015, Whiteman et al. 2019, Giménez et al. 2023). This method has not yet been used for SPF larvae.

Fatty acid biomarkers provide information on trophic interactions in aquatic habitats because they are transferred largely unmodified from prey to predator tissues (Dalsgaard et al. 2003). This way, fatty acids and fatty acid ratios can provide complementary information of ontogenetic, spatial and seasonal variability in dietary composition, and can detect a wide range of different prey groups, including protozoans. Like SIA, fatty acid biomarkers give an indication of prey consumed over an extended period and represent food assimilated, not just ingested, contrary to gut content analysis. More importantly, fatty acid composition gives important information of lar-

val nutritional condition because essential fatty acids are crucial to marine fish larval development and survival (Sargent et al. 1997). Fatty acid biomarkers were used to study SPF trophic ecology of field-caught larvae in only 9 studies, and 2 of them used this technique in combination with gut content analysis. Most of these studies were conducted on European anchovy and European sardine in the Atlantic and Mediterranean Sea (e.g. Riveiro et al. 2003, Costalago et al. 2011). These studies identified zooplankton as the main prey for late larvae, while Prymnesiophyceae markers were found in the gut of early larvae, although the authors proposed that these were ingested indirectly via protozoan prey (Rossi et al. 2006, Costalago et al. 2011). In addition, fatty acids were used to study larval diet for sprat and herring in the Baltic Sea and northern anchovy in the California Upwelling system in just 1 study each (Håkanson 1993, Paulsen et al. 2014, Peters et al. 2015).

Immunochemical detection of protist ciliate prey in northern anchovy larval guts was carried out in laboratory feeding experiments (Ohman et al. 1991). Even at very low food concentrations (0.8 prey ml^{-1}), ciliate antigens were detected in the guts, whereas visual inspection failed to detect the prey. This method allows estimation of the time spent to detect and ingest prey after contact, which was surprisingly high in this study (>2 h for first contact for early larvae) and digestion rates, by estimating the amount of time for the immunoreactive gut content to decrease. Similarly, gut epifluorescence was used as a proxy for ingestion rates for Atlantic herring and European sardine, as well as for several SPF species off Japan, namely the Japanese anchovy, Japanese sardinella *Sardinella zunasi* and Japanese sardine (Fukami et al. 1999, Becognee et al. 2009, Denis et al. 2016). This technique allowed the identification of ontogenetic shifts in diet composition and spatial variability in diet related to food availability. Despite the importance of protists for several species of fish larvae, Fukami et al. (1999) found none in Japanese anchovy guts. Although this method can lead to valuable information of diet composition, ingestion and digestion, as described above, and particularly for prey such as ciliates that are not detected by visual inspection, it has seldom been used to study SPF larval diets.

3.4. Emerging molecular approaches

Molecular approaches applied to diet analysis can achieve high taxonomic resolution compared to traditional methods, even for damaged samples or prey lacking morphologically discernable characteristics (Hirai et al. 2017). Studies using molecular techniques to analyze SPF diets are still scarce, especially for larval stages. Multiplex PCR was used to describe the diet of larval European sardine in the SW Mediterranean (Yebra et al. 2019). This method detected prey in the guts during the entire diel cycle, although no prey was visually detected in the guts of larvae collected at night. Flagellates and copepods (the most abundant zooplankton groups in the water) represented the most abundant zooplanktonic prey in larval guts, suggesting opportunistic feeding behavior. Using eukaryotic metagenetics, the diet of early postlarvae of Japanese sardine and Pacific round herring were described and compared (Hirai et al. 2017), showing that the diet of both species was similar, and mainly dependent on early life stages of copepods, although protists and gelatinous organisms, not detected by visual inspection, were occasionally very abundant in the guts.

DNA metabarcoding analysis of the cytochrome oxidase I gene has been recently used to investigate Pacific herring *Clupea pallasii* diet in the San Francisco Estuary (Jungbluth et al. 2021). Herring prey included abundant copepods from the estuary in their diet, but also some unexpected prey such as cnidarians. Moreover, several copepod species that could not be identified to species using morphology were identified using DNA. In order to exclude most of the non-target gene sequences, the authors used a strict sequence classification and size-based exclusion and suggested re-sequencing fish guts targeting an additional gene (e.g. 18S rRNA) to identify a broader range of taxonomic groups in the fish diets, and to reduce the incidence of empty guts that are so common in SPF.

4. DISCUSSION

Based on our review, the last decade has brought significant advances in the understanding of the trophic ecology of SPF larvae, namely of the importance of easily digested prey such as protozoans and gelatinous organisms, of the ontogenetic, spatial and temporal variability in diet composition and of feeding rates derived from laboratory experiments that have been used to inform larval dispersal models (e.g. Hirai et al. 2017, Garrido et al. 2021, Bils et al. 2022). Research has mostly focused on species with high commercial value, and the observed trends in research efforts likely respond to changes in stock status. For example, intense research on northern

anchovy larval diets (both in the field and laboratory) occurred in the 1970s (Fig. 3, Table S5) linked to the increased biomass of this species and an anomalous low biomass of Pacific sardine (Peck et al. 2021). Similarly, larval diets and feeding dynamics of European sardine have significantly increased in the last decade coinciding with a historical population size minimum (Garrido et al. 2017). New geographical regions and species have been investigated in the field, and new species are increasingly being cultured in the laboratory (e.g. Peruvian anchovy, Pacific sardine); therefore, improved knowledge of larval diets and foraging behavior is expected in the upcoming years.

Gut content analysis is still the most common method to study the trophic ecology of SPF larvae, despite the challenge of dealing with very high vacuity rates for most species, and low prey diversity associated with rapid digestion of several potentially important prey types such as protists. In fact, microplankton such as phytoplankton species and tintinnids are seldom found in stomachs and, if present, they occur in low numbers. These species may play an important role in the diet of SPF larvae, particularly for the first weeks of life, due to their high densities at sea and high content of essential fatty acids, and also due to the poor mobility of early larvae (Sargent et al. 2002, Tocher 2003, Peck et al. 2012, Perez & Fuiman 2015). Emerging methods that are helping, at least partially, to overcome this problem are molecular techniques, such as DNA metabarcoding. With these techniques, high taxonomic resolution can be obtained, even with damaged prey that cannot be identified by visual inspection.

Molecular methods are promising in the study of SPF larval diets, but also have limitations. First, one of the most challenging aspects of eukaryotic metabarcoding is to obtain reliable identification of prey DNA sequences; however, the available data are improving rapidly, which will enhance the quality of data produced by genetic methods applied to diet studies (Bucklin et al. 2011). Second, life stages of prey cannot be identified, which is important because not only food availability (density and prey composition) but also the size/development stage of available prey influence the diet and feeding mode used by the larvae (Buskey et al. 1993) Third, molecular methods have mostly been used to provide presence/absence information, but metabarcoding can be applied semi-quantitatively to estimate relative abundance of organisms within a sample. Particularly for the planktivorous adult European sardine and sprat, the method used (18S rRNA) was able to reconstruct relative abundances among taxa but only for samples dominated by a few taxa (Albaina et al. 2016). More recently, studies have shown that the 18S rRNA amplicon fits well with the carbon biomass of phytoplankton groups determined using microscopy (Andersson et al. 2023). Therefore, given the importance of having a quantitative understanding of the diet composition in terms of type and size of prey organisms, we emphasize the need to continue visual analysis of gut contents of SPF larvae, despite its shortcomings (time-consuming, dependent on trained taxonomist, high degree of vacuity). Sampling protocols could be improved to reduce regurgitation, for example, by using light traps instead of plankton nets. Ideally, gut content analysis would be complemented with biomarkers and molecular approaches, following the multi-proxy approach currently recommended for larger fish (Nielsen et al. 2018, Bachiller et al. 2020). Combining molecular tools with traditional microscopy observations allows the exploration of the full diversity of the prey spectrum. Such a combination would allow quantitative information on prey contributions via gut content analysis (albeit at a lower taxonomic resolution) together with highly detailed presence/absence data from metabarcoding to be obtained. This combination is recommended for future fish trophic studies for all life stages (Albaina et al. 2016).

Biomarkers can provide substantial information on trophic history, complementing the short-term diet information obtained through gut content analysis (either via microscopy or molecular methods). While fatty acids and SIA have been used in SPF larval trophic studies, they have rarely been complemented with other metrics. Fatty acids are relevant not only as biomarkers of certain types of ingested prey, including phytoplankton species, but also to evaluate prey quality. As abundantly shown in aquaculture studies, essential fatty acids are important to larval survival, particularly during the early development. Therefore, fatty acid analysis can help us understand the relationship of food quality and larval survival. SIA comparisons across studies in this review were difficult, since no baseline data were included, or it was difficult to obtain proper baselines because there was high temporal variability in the $\delta^{15}N$ at the base of the food web. For this reason, trophic positions are difficult to estimate with bulk-SIA, and comparisons between species, areas and years are impaired. The use of CSIA-AA is increasing as a technique that may allow inter-specific, temporal and spatial comparisons of trophic position across studies. However, proper values of diet–tissue discrimination factors obtained from laboratory studies or empirically determined are still needed, given that inappropriate dis-

crimination factor values can generate inaccuracies in isotope model outputs, and consequently in the interpretation of dietary studies (Caut et al. 2009).

The potential for studying larval trophic ecology resulting from the successful acclimatization of SPF in the lab is high, and both old and new studies have successfully filled gaps in knowledge on feeding rates and larval behavior, and obtained valuable species-specific parameters for modeling dispersal and survival of fish larvae (e.g. Urtizberea et al. 2008). Presently, more research groups are able to successfully culture small pelagics, and new species are also starting to be cultured in the laboratory, such as Peruvian anchovy *Engraulis ringens* (Rioual et al. 2021), Pacific sardine (Dorval et al. 2011) or Patagonian sprat *Sprattus fuegensis* (Leal et al. 2017), which may lead to more larval studies derived from laboratory experimentation. However, SPF acclimatization and larval experimentation is highly demanding, particularly in terms of manpower, and for this reason, previous efforts tended to be limited in time, such as what was observed for the northern anchovy in the 1970s. Laboratory experiments can shed light on assimilation efficiency, which is still largely understudied. For example, using radiolabeled food allows tracking assimilated prey, and using potential prey species available in the wild may allow identifying key prey for SPF, including microplankton species (Conceição et al. 2007). Unfortunately, the challenge of high vacuity rates also occurs under laboratory conditions. In this case, sharply decreasing the temperature of the tanks before capture has been observed to strongly reduce defecation and regurgitation and can help to improve the results of prey selectivity studies and determine ingestion rates (S. Garrido unpubl. data). However, it should only be done close to capture, as this method decreases the assimilation rates. The species that was most studied via laboratory experimentation is the Atlantic herring. While there are still knowledge gaps in the feeding dynamics of Atlantic herring, we believe this is a good case study that exemplifies the benefits of detailed foraging parameters obtained under laboratory experiments to later investigate bottom-up drivers impacting larval survival and thus recruitment in the wild (e.g. Hufnagl et al. 2015, Moyano et al. 2023).

Beyond the methods used to study trophic ecology of SPF larvae, there are some general aspects on how to report results that are important to mention. First, most studies analyzing larval feeding in individuals of different sizes reported that diet significantly changed with ontogeny. These results underscore the importance of reporting diet for different larval sizes and the need to specify not only the prey group ingested, but also the stages (e.g. egg, nauplii and adult). Despite the recommendation of increasing the taxonomic resolution of prey (Llopiz 2013, Robert et al. 2014), a major constraint in comparing studies during the review process was the lack of data reported in table format. Embracing the findability, accessibility, interoperability and reusability (FAIR) principles for scientific data management and stewardship (Wilkinson et al. 2016), we encourage making raw data available if possible, or at least mean values (or other central tendency estimates) and dispersal estimates reported in figures, to allow future inter-study comparisons.

The present review revealed temporal and geographic differences in SPF larval trophic studies. The most studied species (Atlantic herring, European sardine and anchovy, northern anchovy) correspond to key commercial stocks in the northern hemisphere. Important SPF stocks also exist in the southern hemisphere (particularly in the Humboldt and Benguela ecosystems), but research on SPF larval feeding has concentrated on the northern hemisphere species. Intense research periods for each species coincide with strategic interests in the stock due to the low status of the stock (e.g. European anchovy in the early 2000s or European sardine in the 2010s; Table S1) or renewed interest in the stock due to the decrease in others (e.g. northern anchovy in the 1960s–1970s). During these periods of more intense research, significant knowledge has been gained on larval diets in the wild via gut content analysis (and more recently trophic position via SIA/fatty acids for European sardine and anchovy). Moreover, this interest has encouraged the establishment of rearing methods that have provided important information on foraging behavior, predator–prey dynamics and prey preference, which later allowed the creation of individual-based models to explore larval growth and survival in the sea (e.g. European sardine: Santos et al. 2018; European anchovy: Teles-Machado et al. in press; Atlantic herring: Hufnagl & Peck 2011). Despite advanced knowledge on the trophic ecology of these well-studied species, it is still difficult to use information of larval modeling directly to support fisheries management, given the non-stationary nature of the relationships between larval survival and the variability of environmental drivers and the complex, intertwined interactions with other recruitment drivers. For example, temperature and prey availability were incorporated in the assessment of Gulf of Riga herring, but were discarded after some years (ICES 2021). Given the ecosystem-based fish-

eries management focus of most agencies globally, it is essential to maintain regular sampling of larval diets to understand food web changes and their potential cascading effects.

5. CONCLUSIONS AND FUTURE DIRECTIONS

Substantial work has been done in recent years on the trophic ecology of SPF larvae, although several questions remain open, most importantly: What prey do larvae depend on, particularly at first feeding? What is the importance of easily digested prey such as phytoplankton, microzooplankton or jellyfish for SPF larval diet? Are SPF larvae specialized feeders or does the diet vary significantly in space or time? Is intraguild competition during the larval stage a relevant mechanism for SPF larval survival?

Our main recommendations for future studies on trophic ecology of SPF to address these questions, that include some from past works that are still valid in the present, are:

(1) Use complementary techniques to study larval feeding, combining gut content analysis with fatty acid biomarkers, stable isotopes and/or laboratory experiments (van der Lingen et al. 2009, Garrido & van der Lingen 2014), and also molecular techniques;

(2) Increase the taxonomic resolution of prey (Llopiz et al. 2014) and include information on their developmental stage (e.g. copepod egg, nauplii, copepodite, adult);

(3) Investigate the role of phytoplankton and protists in the diet of SPF larvae (Peck et al. 2012), particularly for the first weeks of life when mortality rates are very high and feeding abilities of the larvae are very poor;

(4) Include ontogenetic information of the trophic information collected, since diet changes dramatically with larval developmental milestones, such as the development of fins and notochord flexion;

(5) Use compound-specific SIA or include baseline information in bulk-SIA studies, allowing the trophic position of the larvae to be determined, and different species/systems to be compared;

(6) Make the raw diet data (e.g. mean and dispersion estimates) available, embracing the FAIR principles for scientific data management and stewardship (Wilkinson et al. 2016).

Although some of the old challenges remain, the development of new techniques (such as DNA metabarcoding and CSIA-AA) brings hope for the new decade to investigate diets in early larvae and assess the role of phytoplankton and soft-bodied organisms into larval diets. Such accurate knowledge of the relationship between prey fields and larval feeding success is essential to advance our knowledge on the trophic ecology of SPF, and better understand the impact of plankton variability in the recruitment success for SPF. Given their key trophic role in pelagic ecosystems around the world and their commercial importance, such knowledge is highly valuable for contributing to the sustainable management of SPF stocks.

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