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Contribution to the Theme Section 'Small pelagic fish: new research frontiers'

INTRODUCTION

Small pelagic fish: new frontiers in ecological research

Myron A. Peck[1], Ignacio A. Catalán[2], Susana Garrido[3], Ryan R. Rykaczewski[4], Rebecca G. Asch[5], Jan R. McDowell[6], Elliott L. Hazen[7], Isaac C. Kaplan[8]

[1]Royal Netherlands Institute for Sea Research (NIOZ), Department of Coastal Systems, PO Box 59, 1790 AB Den Burg, The Netherlands

[2]Mediterranean Institute for Advanced Science, IMEDEA (UIB-CSIC), Miquel Marqués 21, 07190 Esporles, Illes Balears, Spain

[3]Portuguese Institute for Marine and Atmospheric Science (IPMA), Rua Alfredo Magalhães Ramalho 6, 1449-006 Lisbon, Portugal

[4]NOAA National Marine Fisheries Service, Pacific Islands Fisheries Science Center, 1845 Wasp Blvd., Honolulu, Hawaii 96818, USA

[5]East Carolina University, Department of Biology, 101 East 10th Street, Greenville, North Carolina 27858, USA

[6]College of William and Mary, Virginia Institute of Marine Science (VIMS), Gloucester Point, Virginia 23062, USA

[7]NOAA National Marine Fisheries Service, Southwest Fisheries Science Center, 99 Pacific St. Suite 255A, Monterey, California 92037-1508, USA

[8]NOAA National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, Washington 98112, USA

ABSTRACT: Populations of small pelagic fish (SPF), such as sardines, anchovies and herrings, support some of the largest marine fisheries globally and are critical for trophic transfer in large marine ecosystems and food security, particularly in low- to medium-income countries. Marked changes in population size, shifts in distribution on multiple time scales, and impacts on their populations from other pressures (e.g. overfishing, climate change) pose large challenges to sustainably manage these resources to avoid the serious socioeconomic and ecological impacts of population collapses. The ecology and management of SPF was discussed in an international symposium in Lisbon, Portugal, attracting participants from 38 countries and 6 continents. This Theme Section includes 18 research contributions examining SPF from 6 different ecological regions alongside 3 global analyses. These studies, including a wide range of topics from parasitology, behavior and trophodynamics to growth and spawning, provide important new knowledge that will improve science-based advice and tools needed for sustainable, ecosystem-based management of these resources. This symposium was an important milestone for a global working group and sowed the seeds for continued, globally coordinated research efforts on the role of SPF in complex socio-ecological systems.

KEY WORDS: Small pelagic fish · Forage fish · Environmental drivers

1. INTRODUCTION

Small pelagic fish (SPF) are key to the trophodynamic structure and function of many aquatic food webs by transferring energy from lower to upper trophic levels (Pikitch et al. 2012). These fishes form about 30% of total global catches with Peruvian anchovy *Engraulis ringens* being the largest fishery worldwide (FAO 2022). Given their ecological and economic importance, and the fact that they display

*Corresponding author: myron.peck@nioz.nl

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marked and often rapid shifts in distribution and abundance (Essington et al. 2015, Checkley et al. 2017), revealing the processes impacting their population dynamics has been an active area of research for decades (Checkley et al. 2009, Peck et al. 2021).

Coordinated, international efforts to advance knowledge of SPF ecology and population dynamics started in the early 1980s under the auspices of the Fisheries and Agriculture Organization (FAO) and the Intergovernmental Oceanographic Commission (IOC), including a global research symposium (Sharp & Csirke 1983a,b, Csirke & Sharp 1984). Following that symposium, Small Pelagic Fish and Climate Change (SPACC) became an active working group (Checkley et al. 2009) within the International Geosphere-Biosphere programme 'GLOBEC' (Global Ocean Ecosystem Dynamics) that concluded in 2008. Symposia in Nantes, France (Peck et al. 2014) and Victoria, Canada (Alheit & Peck 2019, Alheit et al. 2019) re-ignited formal international collaboration on the ecological and socio-economic drivers of change in SPF, leading to the formation of a PICES-ICES working group (WG43/WGSPF) in 2019. This working group organized the most recent international symposium on SPF which convened in Lisbon, Portugal, from 7–11 November 2022.

The symposium 'Small pelagic fish: new frontiers in science for sustainable management' attracted 289 participants from 38 countries and 4 international organizations (PICES, ICES, FAO and NPFC). Scientists came from 6 continents: Australia (5), Africa (17), Europe (168), Asia (36), North America (48), and South America (15), with 47 participants being from developing countries. The symposium was nearly gender-balanced (47% female, 53% male), with a substantial portion (44%) of the attendees being early-career researchers. The participation of many of these young scientists from around the world was facilitated by the generous support of more than 20 co-sponsors (with the primary international organizers being PICES, ICES, and FAO).

The symposium was organized around 7 themes: (1) trophodynamics, (2) life cycle closure, (3) population- and ecosystem-level phenological shifts and tipping points, (4) responses to climate variability and change at long time scales, (5) progress in monitoring and surveys, (6) management strategies safeguarding marine ecosystem services, and (7) social-ecological analyses and sustainability. There were also 6 workshops on topics ranging from specific measurement techniques (e.g. daily egg production method) to equitable harvesting of SPF. In total, there were 278 presentations: 14 plenary talks, 7 invited and 173 contributed talks, and 84 posters. Contributions to Themes 1–4 were published within this Theme Section, while research within Themes 5–7 were published separately in a Special Issue of the Canadian Journal of Fisheries and Aquatic Sciences (Rooper et al. 2024b). Taken together, the papers stemming from the 2022 symposium, and published in these 2 collections, have advanced fundamental knowledge not only of the ecology and environmental drivers of SPF populations, but also of the management tools and impacts of changes in SPF on vulnerable human communities.

2. ECOLOGICAL DRIVERS OF SPF

2.1. Trophodynamic processes

Global syntheses have attempted to quantitatively compare the multiple roles of SPF as predators, prey and fisheries targets. For instance, Pikitch et al. (2014) assembled 72 global food web models to estimate both the landed value of SPF and their supporting value to harvested species at higher trophic levels. The research in this Theme Section advances this type of analysis from local to global scales, incorporating important nuances including cannibalism, spatio-temporal variation, and ontogenetic shifts in diets, in some instances elucidated by novel quantitative and molecular techniques. Ruzicka et al. (2024 in this Theme Section) took a global approach by assembling a database of 199 models that use Ecopath and related food web modeling frameworks. Those authors found that SPF accounted for 43% of total fish production, and 18% of global catches. As forage, SPF also supported 34% of total fisheries catch, and >15% of energy flowing to top predators, such as marine mammals and birds. At a local scale within the Northern Peru Current Ecosystem, Luján et al. (2024 in this Theme Section) conducted rigorous uncertainty analyses of the trophodynamic OSMOSE model, finding that parameter uncertainty for species such as euphausiids and Humboldt squid *Dosidicus gigas* strongly impacted the projected biomass of species including Peruvian anchovy and mackerels. In a second, local-scale example, a new diet database (Bizzarro et al. 2023) and spatio-temporal modeling (Thorson 2023) allowed Wells et al. (2024 in this Theme Section) to investigate spatial variation in diets of Pacific hake *Merluccius productus* and Chinook salmon *Oncorhynchus tshawytscha* within the California Current Ecosystem. This high-resolution approach allowed an understanding of long-observed patterns in diets, such as patchy and episodic bouts of cannibalism by

Pacific hake, and diet variation stemming from productivity shifts related to El Niño. Similarly, Gunther et al. (2024 in this Theme Section) used a diet database for 4 groundfishes in the Eastern Bering Sea to yield information on the spatial distribution and habitat preferences of 5 species of forage fish. In this case, and other recent studies (e.g. Gaichas et al. 2024), predators were used as 'samplers' of a dynamic seascape with spatiotemporal variations in species abundance and distribution.

Intra-guild competition and predation, as well as cannibalism can be important processes controlling SPF populations (Peck et al. 2021). Fonseca et al. (2024 in this Theme Section) revised estimates of gastric evacuation rates of European sardine *Sardina pilchardus* that had consumed different prey, including fish eggs. Their refined estimates indicated that sardine may cannibalize 2–16% of their eggs. European sardine can also exert substantial predation pressure by consuming eggs of European anchovy *Engraulis encrasicolus*. Veríssimo et al. (2024 in this Theme Section) applied novel molecular techniques to further quantify egg predation by SPF, reporting strong evidence of cannibalism by sardines, as well as intraguild predation with sardine consuming eggs of anchovy and a sparid. Garrido et al. (2024 in this Theme Section) reviewed the information available on the trophic ecology of SPF larvae and proposed new research directions. They described how a combination of old and new techniques has helped better understand larval diets, such as the identification of highly digested organisms in guts (gelatinous zooplankton, teleost eggs) by DNA metabarcoding. Jacobson et al. (2024 in this Theme Section) reviewed information regarding trophically-transmitted parasites, highlighting how parasites can provide relevant information on long-term feeding history of SPF and the identification of predators not detected by traditional diet analysis.

2.2. Life cycle closure: advances in process understanding

Studies by Maathuis et al. (2024 in this Theme Section), Thorvaldsen et al. (2024 in this Theme Section), Berg et al. (2024 in this Theme Section), and van der Kooij et al. (2024 in this Theme Section) collectively underscore the critical importance of understanding the spatial variability and life cycle closure of SPF in the face of environmental change and human impacts. Maathuis et al. (2024) provided a detailed examination of SPF behavior in a tidal channel, revealing the dynamic use of a migration corridor to shallow-water nursery grounds, especially for juvenile Atlantic herring *Clupea harengus* and European sprat *Sprattus sprattus*. Their innovative use of echosounder technology showcased the seasonal variability in SPF abundance and vertical distribution, emphasizing the need for high-resolution monitoring to understand the spatial nuances of SPF life stages. Thorvaldsen et al. (2024) expanded on this theme by exploring the 3D movement patterns of mesopelagic fishes. By highlighting the variability in movement strategies between juvenile and adult stages and across different environmental conditions, their research challenges conventional models of predator-prey interactions and underscores the significance of individual-level behaviors in ecological modeling. Berg et al. (2024) contributed to this dialogue with their groundbreaking study on the growth plasticity of Atlantic herring under varying light and temperature conditions. Their findings not only demonstrate the adaptability of herring to different environmental regimes but also provide insight into the potential impacts of climate change on growth and maturation strategies of SPF. Finally, van der Kooij et al. (2024) offered a perspective on the broader implications of climate change through their study of a shift in the distribution of European anchovy. The observed expansion and increased spawning activity of European anchovy in the English Channel was not observed a decade earlier (Petitgas et al. 2012), highlighting the complex interactions among genetic distinctiveness, environmental drivers, species distribution, and the adaptiveness of SPF life history strategy. Together, the results of these studies advocate for a nuanced approach to fisheries management and conservation strategies, taking into account the detailed spatial and temporal patterns of SPF life stages to ensure their resilience and sustainability in a rapidly changing world.

2.3. Understanding population- and ecosystem-level shifts: from seasonal timing to tipping points

Changes in reproductive timing can lead to tipping points and shifts in ecosystem dynamics if different trophic levels exhibit seasonal asynchrony. Moreover, understanding reproductive timing of SPF is key for determining if there is a mismatch between fisheries-independent surveys and seasonal fish biomass in an ecosystem. As a result, developing predictive capacity in this arena will be beneficial to fisheries-based ecosystem management. This topic was explored by Ferreira & Neuheimer (2024 in this Theme Section) who examined the thermal time of Pacific herring *Clupea pallasii* spawning across 6 regions of British Columbia, Canada. They reported that latitudinal variation in spawning times can be well explained by cumulative degree days across the reproductive season of this species. A second article addressed the environmental variables that influence the distribution and timing of 5 stocks of Pacific herring spawning in British Columbia considering a wider diversity of variables (Rooper et al. 2024a in this Theme Section). The location of spawning was consistent across years, suggesting that spatial dynamics were less influenced by environmental variability, with stock biomass having a greater influence on spawning distribution. For seasonality of spawning, Rooper et al. (2024a) also found that degree days, day length, and salinity were the most prominent factors influencing timing.

2.4. Responses to climate variability and change at decadal to centennial time scales

Knowledge of processes responsible for temporal and spatial shifts in the productivity of SPF have stemmed from both statistical analyses of long-term time series of fish abundance or traits and environmental factors, as well as from coupled hydrodynamic, ecosystem, and individual-based modeling of SPF early life stages (Peck et al. 2021). In this Theme Section, we present both types of studies, which were conducted in Iberian waters and NW Pacific waters, to provide new knowledge on decadal shifts in productivity and the influence of climate variability on SPF populations.

Nishikawa et al. (2024 in this Theme Section) used a lower-trophic-level ecosystem model coupled to an ocean circulation model to investigate oceanographic impacts on the food web that supports Japanese sardine *Sardinops melanostictus*. Time series of mesozooplankton biomass, one of the key forage groups for SPF, are rare. However, coupling physical circulation and plankton models can help to bridge the gap between observed physical variability and fisheries. Modeled zooplankton biomass in the region was associated with deviations from the sardine stock-recruitment curve. Working in Iberian waters, Teles-Machado et al. (2024 in this Theme Section) simulated larval dispersal of European anchovy, finding that episodes of anomalous, intense ocean currents during periods of high spawning activity can lead to the colonization of new areas. In that study, the direction and intensity of connectivity at the early life stages between areas changed significantly with time.

Decadal comparisons were made by Takahashi et al. (2024 in this Theme Section) on the growth and hatching times of juvenile Japanese jack mackerel *Trachurus japonicus* between the 1960s–1970s and 2000s–2010s. Juveniles in the more recent period hatched, on average, about a month earlier and their somatic growth was faster than juveniles in the former period, suggesting a climate-driven phenological shift and impact on size-at-age. In northern Iberian waters, Ferreira et al. (2024 in this Theme Section) statistically compared periods before (2001–2009) and after (2010–2020) a dramatic shift to higher recruitment and fisheries catches of European anchovy. Ferreira et al. (2024) reported that recruitment was strongest during years when months of peak spawning coincided with weaker upwelling events, lower salinity, and higher precipitation. Increased anchovy recruitment not only corresponded to oceanographic conditions favoring onshore larval retention but also to years with low abundance of European sardine, suggesting that anchovy benefitted from decreased foraging competition and egg mortality via predation in accordance with the diet analyses of Veríssimo et al. (2024).

3. CONCLUSIONS

This international symposium provided a productive forum for exchange of research, ideas and knowledge on SPF dynamics around the world, from freshwater (e.g. African lakes) to marine habitats. The articles published here and in a sister volume (Rooper et al. 2024b) demonstrate the vibrant collaboration, strong advancements in state-of-the-art tools and techniques, as well as the remaining challenges to robust, ecosystem-based fisheries management of these critical ecological, economic and cultural resources. The ICES-PICES working group on SPF, currently with 131 members from >20 countries, plans to continue to foster international cooperation and collaboration, including future symposia, to push forward the science of sustainable and equitable management of SPF.

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