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Contribution to the Theme Section 'Latest advances in research on fish early life stages'

INTRODUCTION

Research on early life stages of fish: a lively field

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ABSTRACT: The first weeks in life are crucial for the fate of fish. During this period, fish show large dispersal rates and suffer from massive mortality due mainly to predation. Intrinsic and extrinsic processes (growth rates, advection, behavior, diseases) affect this mortality and have profound consequences on populations. For a century now, describing the distribution, physiology and dynamics of fish early life phases has been the focus of intense research, building a solid community of scientists that met at the 43rd Annual Larval Fish Conference, held in Palma, Spain, 21–24 May 2019. The present Theme Section consists of 19 papers that are a sample of the research presented at the conference. The papers are organized around 5 main topics: (1) mortality estimation and process understanding, (2) parental effects on larval fish ecology, (3) larval settlement to juvenile grounds, (4) early life stages of fish within food webs, and (5) contribution of early life stages of fish to assessment and management. Contributions to this Theme Section focus on hot topics as well as old paradigms; the latter continue to elicit much research work, which has benefited from recent advances in technology.

KEY WORDS: Growth · Ichthyoplankton · Settlement · Mortality · Parental effects · Physiology · Predator–prey interactions · Recruitment · Simulation modelling

1. INTRODUCTION

The study of the early life history of fishes in ecology is characterized by the specific eco-morpho-physiological features of early fish life stages. These demand specific gear required for field sampling, taxonomic knowledge for identification, specific types of sample analyses, and holistic information gathered on external drivers. All of these, as well as a recognition of the important role early life stages play in the dynamics of fish populations, have led to both technological and conceptual breakthroughs. Results from studies on early fish life stages have also played an important role in other research fields such as biomedicine (e.g. Teame et al. 2019) and aquaculture (e.g. Rønnestad et al. 2013). The study of early life stages of fish roots deeply in the ecological realm and has been pivotal in promoting interdisciplinarity, linking physical oceanography, fisheries research and conservation science (Govoni 2005, Houde 2008) as well as globally connecting ecosystems, removing national boundaries (Ramesh et al. 2019).

This Theme Section (TS) originates from the American Fisheries Society's Early Life History Section which held its 43rd Annual Larval Fish Conference in Palma, Spain, 21–24 May 2019. The contributed works cover a wide variety of topics ranging from theoretical and quantitative advances in fundamental processes (molecular and behavioral ecology, growth/mortality, trophodynamics), to practical management applications. We grouped these contributions into 5 topics, although some papers crossed topics: (1) mortality estimation and process understanding, (2) parental effects on larval fish ecology,

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(3) settlement from pelagic larval to demersal juvenile habitat, (4) early life stages of fish within food webs and (5) early life stages of fish in stock assessments and management. The key messages of each of the 19 contributions are contextualized in this framework.

2. MORTALITY ESTIMATION AND PROCESS UNDERSTANDING

Estimating natural mortality is a difficult task in the early life stages of fish due to the inherent challenges of sampling prey and predators of young fish at adequate temporal and spatial scales (Govoni 2005, Houde 2008). Growth and size-at-age in early life stages of fish appear to be positively related to survivorship (see Pepin 2016), but others have reported contradicting results (e.g. Litvak & Leggett 1992), and solid evidence is not easy to obtain. Fennie et al. (2020, this TS) explored this long-lasting problem through direct analysis of otoliths of juvenile rockfish *Sebastes maliger* consumed by Coho salmon *Oncorhynchus kisutch* versus concurrently caught survivors. They provide evidence that consumed fish were smaller, slower-growing at capture, and younger than their surviving counterparts. Gleiber et al. (2020, this TS) analyzed predator–prey dynamics at fine spatial scales (cm to m) and found that high prey densities at small scales correlate with recent growth, particularly in slow-growing species such as wrasses, whereas fast-growing tuna *Katsuwonus pelamis* may depend on a higher density of prey averaged over the sampling area. They also reported that growth-selective mortality was stronger at high predator densities, although the direction of the selection was species-specific. These relationships, however, appear to be system-specific and cannot be generalized. For example, Axler et al. (2020b, this TS) used highly spatially and temporally resolved data to conclude that, in a plume system, high prey density can actually be associated with lower growth and physiological condition of early stages of fish. One of the possible reasons for this observation could be the detrimental effect of high turbidity and turbulence on feeding success (Axler et al. 2020b). Ferreira et al. (2020, this TS) showed that the concurrent consideration of spatial and temporal overlap between prey (copepods) and predators (young Northeast Arctic cod *Gadus morhua*) at adequate resolution explained a significant proportion of cod survival. This type of research requires detailed datasets but is a promising approach to analyze the Match-Mismatch hypothesis (Hjort 1914, Cushing 1967,1990, Ferreira et al. 2020). In an exploration of bird guts as biological samplers of fish otoliths, Khamassi et al. (2020, this TS) found that selective mortality of slow-growers occurred in Atlantic mackerel *Scomber scombrus* up to 3 mo of age, indicating that selection processes can extend well beyond the larval period.

3. PARENTAL EFFECTS ON LARVAL FISH ECOLOGY

Some researchers assert that there may be adaptive value in fish producing eggs and larvae with different traits stemming from differences in parental characteristics (genetic or phenotypic) (e.g. Riveiro et al. 2004, Eilertsen et al. 2009). The so-called parental effects continue to drive much research that is exemplified by 3 papers in this TS. Planas et al. (2020, this TS) provided the first estimates of the trophic enrichment factors in a seahorse. They showed how diet isotopic signature can be transferred to newborns, suggesting an income–capital continuum pattern for parent-egg transmission. García-Fernández et al. (2020, this TS) detected maternal effects on the reproductive output of southern stock of the European hake *Merluccius merluccius*. A clear effect of spawning seasonality was found on the number and quality of eggs produced, likely mediated by differences in maternal size and condition. Larval morphometrics also differed between seasons but, in this case, the drivers could be a combination of environmental factors and maternal effects (García-Fernández et al. 2020). The capacity of larval Atlantic herring *Clupea harengus* to cope with a wide range of salinities was tested by Berg et al. (2020, this TS) with respect to genetic and environmental (acclimation) factors. While larvae were highly adaptable to different ambient salinities (based on salinity-specific respiration rate measurements), this plasticity was apparently not affected by parental genetic origin or salinity acclimation.

4. LARVAL SETTLEMENT TO JUVENILE GROUNDS

The variability in the arrival of pelagic early stages of fish to coastal habitats and their landing to the seafloor (settlement) has been a cornerstone in the analysis of recruitment potential (Levin 1994). Faillettaz et al. (2020, this TS) analyzed temporal and spatial pre-settlement dynamics using light traps in the northwestern (NW) Mediterranean Sea over 3.5 yr. They demonstrated that settlement was highly spatially variable at both monthly and annual scales, with a strong influence of the lunar phase; these findings are similar to those found in the settlement of larvae in tropical systems (e.g. Robertson 1992, Doherty 2002). Jørgensen et al. (2020, this TS) studied why 2 sympatric populations of juvenile Atlantic cod *Gadus morhua* that hatched at similar times but in different places show consistent differences in body growth in their shared juvenile habitat. Although back-calculated growth was slightly different between cod ecotypes during their pelagic larval life, growth differences were greatest during the settlement phase for unknown reasons, thus supporting the key role of settlement processes in shaping the dynamics of a population. Behavioral analyses at individual to higher organizational levels can also provide insights into settlement variability, and fish behavioral ecology is a lively area of study (e.g. Jørgensen et al. 2014). In a series of flume experiments, Vicente et al. (2020, this TS), showed that non-naïve larval sand-smelt *Atherina presbyter* actively selected water from locations with which they were familiar or where conspecifics had been dwelling, adding to the few studies demonstrating important effects of chemical cues (presumably for orientation in the wild) on early stages of temperate species (e.g. Díaz-Gil et al. 2017, Fobert & Swearer 2017). Another fundamental trait of larval behavior that drives survival and geographical persistence of populations is swimming ability. Maximum swimming velocity (Ucrit), usually measured in the laboratory, was found by Leis (2020, this TS) to correlate poorly with observed field swimming velocities, and no straightforward conversion was satisfactory, which suggests caution when using Ucrit-related velocities to infer dispersal patterns.

5. EARLY LIFE STAGES OF FISH WITHIN FOOD WEBS

Understanding and quantifying the role of developing fish within food webs is hampered by several difficulties, including sampling prey and predators at appropriate spatial and temporal scales (Guiller & Gee 1988, Holliday et al. 2003) as well as sampling and identifying the consumed prey (e.g. Hay 1981, von Herbing et al. 2001). Four papers in this TS explored trophic relationships of fish early life stages. Swieca et al. (2020, this TS) used an *in situ* ichthyoplankton imaging system (*IS*IIS) to discover how larval fish, their prey and their predators coincide at small spatial scales in and around a river plume modulated by tides in the Northern California Current. Not only remarkably high concentrations of larval fish and their prey, but also their predators co-occurred in this system compared to offshore locations. The authors described complex patterns of overlap, suggested high patchiness in rates of growth and potential survival, and recommended further investigation of species-specific fine-scale interactions. Using the same image-based approach and incorporating artificial intelligence to classify plankters, Axler et al. (2020a, this TS) analyzed the physics governing a coastal river-dominated system. Their results — showing that the trophic environment of larvae is dominated by the physics of river discharge and winds — set the basis for further studies of the influence of coastal discharges on fish production. In the equatorial and tropical Atlantic, Contreras et al. (2020, this TS) analyzed the trophic dynamics, including ingestion rates, of key transforming and juvenile mesopelagic fish that migrate to the surface at night to feed. They found no resource partitioning among these species but suggested that migrating to this top layer may reduce spatial competition for resources with respect to other species/stages with deeper depth distribution. Trophic pathways of larval fish in Northern Patagonia were explored by Bernal et al. (2020, this TS) using stable isotopes. The authors suggested food partitioning between larvae of several species as well as changes in trophic level of the larval assemblage over the seasons. Also, they reported that larval carbon isotopic signature may reflect the seasonally changing origin of carbon source detected in the particulate organic matter.

6. EARLY LIFE STAGES OF FISH IN ASSESSMENTS AND MANAGEMENT

Studies on early stages of fish have long been used to estimate population size and changes, as well as to understand the processes behind those changes (Govoni 2005). The potential of such estimates to support assessment models and management decisions, however, is not yet fully developed, and further applications should be explored. The potential links between climate-responsive variables and fish propagules were explored by Thaxton et al. (2020, this TS) through an analysis of phenological changes in larvae of 10 fish species in the east coast of the

USA during almost 3 decades. The phenology of ingress to an estuary was found to be advanced (but with different magnitudes) in response to increasing sea surface temperature and delayed in response to stronger northerly winds. The authors suggested that, within the current climate projections, the average time of ingress to the estuary might advance from weeks to months. A key determinant for understanding population dynamics is mortality, often determined through trophic-mediated impacts which lead to predation pressure. A new tool to assess larval survival was presented by Raya et al. (2020, this TS). Their new 'box-balance model' enables the partitioning of larval mortality estimates to either the trophic environment or the mesoscale hydrodynamic conditions. The model, applied to 2 small pelagic fish in the NW Mediterranean Sea, suggested that survival of larval European anchovy *Engraulis encrasicolus* is favored by retention/dispersion mechanisms, whereas round sardinella *Sardinella aurita* would not adapt so well, despite being a tropical species theoretically favored by a warming Mediterranean Sea. Finally, an exercise by Ospina-Alvarez et al. (2020, this TS) demonstrated how graph theory can be applied to a small-scale network of Marine Protected Areas to analyze the emergent properties of a connectivity network. Using an example of coastal fish in the NW Mediterranean Sea, they explored how important different biological parameters are for connectivity, and — based on increasing levels of information (from simple geographic distance to spawning properties) — how this frame can be used to explore the current and alternative configuration of networks that fulfill conservation or fisheries-related goals.

7. CONCLUSIONS

The studies presented in this TS are representative of current topics in research on early life history of fishes. Core questions in fisheries oceanography persist, but new technologies and increased computing power are allowing researchers to answer these questions, for example, by better resolving spatial and temporal scales relevant for the study of early stages of fish. The studies collected in this TS are examples of how technological advances have paved the way for much larger, more rapid and more refined sampling and analyses, helping researchers better tackle hot topics in early life stage research such as adaptive capacity, response to long-term changes (both historically and in the future), and small-scale interactions.

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