

Theme Session H

What do fish learn in schools? Life cycle diversity within populations, mechanisms and consequences

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Overview

Depleted fish stocks, degraded habitats and uncertainty in forecasts of future ecosystem states emphasize the need to include the conservation of life-cycle diversity, population connectivity, balanced population structure and associated population resilience as objectives for fisheries management. Life-cycle diversity within populations and knowledge transfer between generations are increasingly recognized as factors that can influence population resilience and thus fishery and habitat recovery actions. Although life-cycle diversity is seen as being a common feature across numerous fish taxa, mechanistic concepts and demonstrative studies explaining the role of this diversity and its persistence are nascent. Concepts that were represented in this session include genetic polymorphism, partial migration, and social transmission of learned behaviours. Further, relatively little attention has been focused on the consequences of this diversity in particular for population resilience to perturbation (e.g., fishing, climate), spatial management strategies and recovery plans.

Presentations

Contributions (16 platform and 10 posters) addressed all thematic areas envisaged for this session and represented diadromous and marine species ranging from boreal freshwater systems to Asian estuaries to Patagonia to the Gulf of Mexico to the North Sea. Unfortunately, our scheduled sessions were considerably compromised by failed projector technology in the Paris Room, which resulted in (1) the first speaker giving his entire presentation without visual aids, (2) considerably reordering of talks, (3) rushed talks without time for questions, and (4) cancellation of discussion and poster presentation periods of our schedule. We wish to commend participants, who persisted throughout talks despite these difficulties. Attendance was quite high reaching over 120 in the small room. Presenters were good natured about the changes and fortunately well prepared as it was critical that talks should not go beyond 15 minutes each.

Presentation Synopsis

Below we summarize each portion of the session which was thematically organized into (1) Genetics and Movement; (2) Migratory v. Resident Forms; (3) Population Structure: Is Behaviour Necessary? (4) Population Structure: Importance of Behaviour; and (5) Population Properties and Management. We then conclude with perspective on cross-cutting themes and future activities related to the theme of population life cycle organization.

Case studies on genetics and movements were developed to emphasize likely population structuring in three divergent taxa: beaked redfish (H:01), Atlantic bluefin tuna and blue marlin (H:12); and Atlantic cod and whiting (H:13). A large synthesis on microsattelite genetic analysis, phenotypic traits, fatty acid profiles, and otolith and parasite natural tags supported an ICES working group consensus that beaked redfish exhibited reproductive isolation in the North Atlantic between deep pelagic, shallow pelagic, and Icelandic Slope regions. These depth-defined stocks were believed to have colonized from the Pacific as recently as 4000 years ago; as such the species could serve as a model for the understanding biological organization along the contingent to species continuum. In contrast to the more retentive life cycles of beaked redfish, large pelagic species use the Gulf of Mexico alternatively as a spawning “pit-stop” (bluefin tuna) or to complete their life cycles (blue marlin). A contingent of blue marlin resident to the Gulf represents a new discovery made with application of electronic tagging and otolith chemistry. The case study for Atlantic cod and whiting suggested that alternative life cycle closure mechanisms may be operating in the North Sea and in UK Atlantic shelf waters. Increased genetic differentiation in Atlantic cod in the southern North Sea corresponds with persistent frontal systems that could favour larval retention. Elsewhere, cod showed no differentiation and it was suggested that this was due to strong advective currents in the northern North Sea and UK Atlantic shelf waters. Thus, it would seem that for the same species, either larval retention or entrainment could lead to natal homing and life cycle closure.

The session benefited by a state of the art review of partial migration in anadromous salmonids (H:06) and two possible instances where partial migration may be operating for Atlantic cod (H:14 and H:15). Systems of partial migration included mating systems that cause disruptive selection for size polymorphisms and/or frequency dependent polymorphisms, and resource polymorphisms of that can result in alternate lifetime migration and trophic behaviours. The theory of threshold reaction norms with genetically determined switch points was supported through a review of directed experiments, and four criteria were erected for partial (aka “condition dependent”) migration: (1) co-existence of migratory tactics that are not genetically distinct; (2) expression of phenotypes that are related to individual threshold conditions; (3) genetic variance in the trait response to the threshold; and (4) differentiation in threshold reaction norms among populations. The interplay between colonization and partial migration remains unstudied, but is of considerable interest in understanding metapopulation structure and persistence. This topic was also highlighted in poster contributions, where fishing pressure (H:18) and climate change (H:23) could select for certain traits associated with partial migration, resulting in biased or lost life cycles.

Partial migration was suggested to explain three migratory types of Atlantic cod, long recognized in the Gulf of Maine and Canadian maritimes: cod that show directed shelf migrations resulting in natal homing, resident individuals, and dispersive cod that show low rates of natal homing. Resident and migratory forms were linked with varying energetic traits, levels of maturity and productivity, trophic ecology, position in the water column, and ecomorphology. In particular, striking differences in coloration – red and olive cod – have been noted for decades. Importantly, marine protected habitats that emphasize more shoal coastal or sea mount habitats could inadvertently bias the resident life cycle

over the migratory one. Although evidence is mounting for partial migration in these cod populations, definitive studies remain lacking. A contributed poster (H:19) indicated that divergent ecotypes of Icelandic cod may represent separate sub-populations.

In contrasting sets of talks, we asked whether learned behaviour (entrainment) was needed to explain population structure. The first set of talks under this topic developed alternative models based upon the larval retention hypothesis (H:24), parapatric spawning (H:08), and simple rules of school organization and thermal response (H:16). Along the SW Nova Scotia coast, analysis of long-term ichthyoplankton surveys supported the view of stable larval retention areas over a two decade period. This occurred despite long larval durations by Atlantic herring (7 months) and loss of the large spawning aggregation that historically used Trinity Bay. The persistence of larval retention areas despite the loss of a major spawning unit drew discussion on the issue of which level of biological organization was relevant to metapopulation conservation in herring. Similarly, putative larval retention areas in the inner fjords of Patagonia were described for southern hake and hoki (Poster H:22). Using otolith as natural tags for samples dating back over 50 years, the complex stock structure of Celtic Sea herring was explained in terms of parapatric spawning components. These components differentially contributed to stock mixing over the entire regions due to changing productivity of autumn and winter spawning components. In the first of two talks on school behaviours (see also H:04), Icelandic capelin individuals were modelled as interacting particles that had simple rules of attraction and repulsion respective to each other, advective flow, and thermal tolerance. The model reproduced the observed large-scale cyclonic spawning migration circuit around Iceland. A fascinating property that emerged was the capacity of large schools to efficiently detect and respond to thermal gradients over >km scales; the school essentially creating a "temperature map." This capability was evident in acoustic assessment of schooling Peruvian anchovy (poster H:21), which showed temperature-directed schooling behaviours.

The role of behaviour as a mechanism of population structuring was considered by a series of four presentations in which individual processes produce group-level phenomena. Multispecies analysis of spatial distributions on Georges Bank (H:07) suggested that after accounting for occupancy-abundance relationships, species are occupying fewer locations than they used to, possibly resulting from habitat destruction and fragmentation. Loss of habitat may explain some shifts in migratory behaviours. Overwintering of sand eels was modelled as a behaviour that is adapted to minimize metabolic costs or predation in suboptimal conditions (H:05). Model results indicated that the onset and termination of feeding were critical in relationship to the spring bloom. Overwintering behaviour was also investigated for Norwegian spring-spawning herring (H:11). Major changes in migration patterns of herring occurred when the age structure of the stock had relatively few old adults and a relative abundance of first-time spawners, offering a compelling case of apparent entrainment. When there were few adults, substantial changes in the location of overwintering occurred and persisted over multiple years. A review of several case studies (H:09) built on the theme of distinct changes in migratory patterns associated with demographic conditions. The approach of the review was to use case studies of stock collapse as opportunities to investigate the entrainment hypothesis, in which group-level phenomena are produced by individual-level behaviours. Case studies included

the decolonizations of herring on Georges Bank (essentially by a single year class) and Aberdeen Bank, loss of the typical migration pattern of California sardine when the adult stock collapsed, and the failure of recovery for the offshore spawning group of northern cod.

The final portion of the session was focussed on population properties and management. The consequences of population structure and connectivity were demonstrated using age-structured simulations with alternative behaviours and connectivities (H:02). Three population scenarios were simulated to emulate white perch in the Chesapeake Bay, herring in the Celtic and Irish Seas and Gulf of Maine cod. Common population properties among the three systems were that resident components confer stability whereas dispersive components confer productivity, and connectivity tended to increase variability in stock size. Another simulation was focussed on population structure and connectivity of yellow perch in Lake Michigan yellow perch (H:03). Simulations had alternative recruitment scenarios, with and without regime shifts; pooled or separate stock-recruit functions and source-sink relationships. The conclusion was that spawning components should be conserved, because source-sink dynamics are difficult to identify.

Addressing the main subject of the theme session, "what do fish learn in schools?" each premise of the entrainment hypothesis was considered during the session. The entrainment hypothesis requires 1) interactive behaviour, 2) learning and 3) long-term memory for individual fish to respond to their neighbours, learn a new behaviour and remember that behaviour during the next annual migration cycle and in the following years. The mathematical modelling of repulsion and attraction (H:16) illustrated interactive schooling behaviour. Learned behaviours were clearly demonstrated in the context of behavioural modifications after interactions with fishing gear (H:04). Long term retention has also been demonstrated by fish responding to artificial sounds associated with feeding years later (C. Glass, post-session discussion). Therefore the entrainment hypothesis should be considered along with alternative mechanisms, such as natal homing or partial migration, to explain population structure. Such mechanistic understanding will help to form the most appropriate form of conserving population productivity and persistence.