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Advances in herring biology: from simple to complex, coping with plasticity and adaptability

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At least two centuries of investigations on herring have been absorbed by scientific journals, and applied and fundamental research has produced groundbreaking concepts in fisheries, population biology, and marine ecology. By the 1970s, a firm understanding of herring biology formed the basis for more sophisticated research. At that point, herring populations had been delineated, and their migration patterns described. The reproduction and early stage biology were characterized in ways that could be applied to fisheries management. However, over the subsequent four decades, new approaches and technology overturned many of the earlier findings. Behavioural studies revealed a repertoire of patterns that extended the concept of schooling, and genetic analyses showed high levels of stock mixing. Application of otolith analysis to larval, juvenile and adult fish revealed the scope of plasticity in growth and life-history strategies. Developments in physiological research have revealed that herring are not "primitive", as once believed, but highly adaptable in their nutrition and metabolism. These advances fundamentally changed our view of herring, and the resulting challenge is to synthesize current knowledge to help explain the significance of adaptability and plasticity in its flexible life history.

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Introduction

Atlantic herring (*Clupea harengus*) have been the focus of applied and curiosity-driven research. Its past and continuing commercial value has determined the management needs for information on, and understanding of, many biological aspects. The study of herring populations and their dynamics, as living resources, has led to many fundamental advances in fisheries research. In fact, the history of herring research shows that many of the major concepts in fisheries ecology originated from work on this species (Sinclair and Solemdal, 1988; Stephenson, 2001; Sinclair, 2009). Even the introduction of rigorous statistical procedures of hypothesis testing into fisheries science grew out of the need to compare and distinguish different herring populations (Buchanan-Wol and Fisher, 1933).

The commercial value of the herring fisheries has motivated most of the research to define populations and quantify their dynamics. The results of this research have been regularly collated and synthesized through reviews and symposia dedicated to understanding herring population biology and its management. Questions about the recruitment mechanisms, and whether these are specific to different populations, have motivated biological research, which has produced insights into adaptations and adaptability during different life-history stages. However, the results of these investigations have not been reviewed or synthesized as frequently. What are probably the last comprehensive overviews are found in Blaxter and Holliday's (1963) review of clupeid biology and

physiology, and the collection of papers presented to the 1968 ICES Symposium on the Biology of Early Stages and Recruitment Mechanisms of Herring (Saville, 1971).

During the past four decades, applied and curiosity-driven research has produced detailed information on the ecology, adaptability and plasticity, and phylogenetic characterization of herring. New data have often subverted our original, simplistic understanding of the mechanisms and processes operating during the different life-history stages. Recent data show the importance of plasticity, and the more complex picture emerging is less amenable for synthesis and understanding, because every life-history stage would require an overview of recent research and new information first. The following examples highlight recent research advances, and attempt to set this accumulating knowledge into a context that can motivate such a new synthesis. The examples are drawn, for the most part, from studies of herring populations in the Northeast Atlantic, with apologies to the authors of the many excellent publications about populations in the Northwest Atlantic and its Pacific congener (*Clupea pallassi*).

The examples are organized here according to life-history stage, beginning with reproduction and spawning behaviour, proceeding through the egg and larva stages to processes important for juvenile herring, and returning to maturation and reproductive potential. Finallly, several phylogenetic studies are highlighted to demonstrate the relationships between evolutionary history and adaptability in herring.

Reproduction and spawning

Herring appear to be quite unique among marine fish in having a wide range of discrete spawning seasons while using very specific spawning locations. These two aspects represent the major characteristics used to name or identify the various (sub-)populations. The depth and substratum of the spawning beds may vary to some extent but, for the most part, herring spawn coastally and on offshore banks, and deposit their eggs on gravel or rocks. In this respect, Baltic and Pacific herring are notably different in that they spawn on seaweeds in the littoral or sublittoral zones.

Many recent advances in our knowledge result from technological improvements in observation and measurement. Initially, herring were assumed to spawn in schools, in response to seasonal, environmental signals. Remote observation techniques, especially acoustics, do not only show schooling and vertical migration, but also demonstrate that the composition of spawning schools changes over time as new fish arrive at spawning grounds and spent fish leave (Axelsen *et al.*, 2000; Skaret *et al.*, 2003). Individual females leave the spawning schools with one or more males to deposit their eggs on different sites within a particular spawning ground. Males follow closely and release ribbons of milt that are heavier than water and sink to fertilize newly spawned eggs (Aneer, 1982). In Pacific herring, sperm release is triggered directly by female pheromones signalling that a female is in the process of releasing eggs (Carolsfeld *et al.*, 1997).

Egg–sperm interactions at fertilization are complex. The sperm of Pacific herring is activated only in the presence of eggs (Pillai *et al.*, 1994), and spermatozoa show distinct search patterns to locate the the micropyle to achieve fertilization (Yanagimachi *et al.*, 1992). In Atlantic herring, sperm is activated on contact with seawater, although not all spermatozoa activate simultaneously: there are waves of activity that can persist over several hours (Evans and Geffen, 1998; Geffen, 1999). Sperm motility and fertilization success vary between pairs of fish, and individual males may achieve quite different fertilization rates for eggs from different females, and vice versa. For the most part, variations attributable to paternal contributions are not included in fishery-dynamics models. Nash *et al.* (2008) incorporated male variability by adjusting the total egg production of Northeast Arctic cod to reflect potential fertilization success resulting in slightly different recruitment patterns. However, similar analyses have not yet been applied to herring.

Eggs and larvae

Herring serve as a good model species for studies of parental, or epigenetic, effects, because individual eggs can easily be followed throughout development and sampled just prior to hatching (Geffen, 2002). Characteristics of the eggs and newly hatched larvae have revealed both maternal and paternal effects. Paternal effects are evident in larva size at hatching (Panagiotaki and Geffen, 1992; Evans and Geffen, 1998), as well as in characteristics related to growth and metabolic potential such as protein

(Bang *et al.*, 2006) and otolith size (Hoie *et al.*, 1999). Paternal effects have not yet been traced to particular characteristics of individual males, although Evans and Geffen (1998) suggested that they may relate to differences in fish size or age constituting consecutive spawning cohorts. Maternal factors are clearly demonstrated in egg size, which translates into differences in larval size at hatching (Blaxter and Hempel, 1963; Morley, 1998; Morley *et al.*, 1999).

A perennial question has been "Why are there so many herring populations, and why are they so different?" The life-history strategy appears to be so flexible that this species can produce viable eggs at virtually all times of year. This means that the eggs and larvae are adapted to the varied seasonal conditions of temperature, light, hydrographic conditions, predator fields, and food availability. Fish eggs and larvae are normally considered to be closely adapted to meet specific seasonal conditions (match–mismatch; Cushing, 1990). The challenge has been to explain the recruitment processes in a way that matches the patterns observed in the different herring populations (Cushing, 1975; Sinclair and Tremblay, 1984).

How can herring eggs and larvae survive in all seasons? Egg sizes differ between spawning populations (see below) as well as between individual females (Almatar and Bailey, 1989). These differences lead directly to differences in larva size at hatching (Morley *et al.*, 1999). However, embryonic metabolism appears to be less subject to interactive effects between egg size and temperature in herring than in other fish species (Pepin *et al.*, 1997; Benoit and Pepin, 1999; Fox *et al.*, 2003b). Despite the population-specific differences in egg size, which may or may not be related to spawning season (e.g. winter vs. autumn spawners), the temperature-dependent development and metabolic rates are remarkably similar. For example, herring eggs utilize the same amount of oxygen throughout development, irrespective of temperature (Overnell, 1997; Overnell and Batty, 2000). Genetic adaptation to local conditions may have been replaced or superseded by the plasticity of eggs and yolk-sac larvae because metabolic fitness is constant over a range of temperature.

Blaxter and Holliday (1963) described laboratory investigations from the 1800s that examined embryonic development (Brook, 1885, 1886; Kupffer, 1878) and the effects of temperature on development (Meyer, 1878). Early-feeding studies on larvae from artificially fertilized eggs have also been reported using natural zooplankton as food (Ford, 1929; Schach, 1939). Important advances in laboratory investigations have been made possible through Blaxter's (1955, 1956, 1957, 1968) development of protocols for reliable fertilization, incubation, and rearing, as well as for keeping juvenile herring in captivity (Blaxter and Holliday, 1958). Since then, studies of physiology, growth, feeding, behaviour, and responses to environmental conditions have been conducted in laboratory tanks and large mesocosms. The results underscore how adaptable herring can be in its growth, feeding, and behaviour (Munk and Kiorboe, 1985; Utne-Palm, 2004). At the same time, they show considerable plasticity in both physiology and form, which helps to explain the observed physical differences between populations, such as in vertebral counts and body shape (Blaxter, 1957; Johnston *et al.*, 1998; Temple *et al.*, 2000).

Growth of herring larvae is sensitive to both temperature and to feeding conditions. Unlike many other marine species, herring larvae can survive long periods of little or no growth. This ability may be part of the explanation for their survival when spawned in seasons of low productivity (Johannessen *et al.*, 2000). However, size, growth rate, and condition affect both swimming behaviour and vulnerability to predation in laboratory experiments (Williams *et al.*, 1996; Skajaa *et al.*, 2004). As with other species, older, well-fed herring larvae are more responsive to predator attacks and have faster escape speeds.

The results from laboratory experiments have supported extensive modelling exercises testing the responses to a wide variety of environmental conditions (Gallego *et al.* 1996; Fiksen *et al.*, 1998; Fiksen and Folkvord, 1999). Field investigations indicate that herring larvae indeed demonstrate a wide repertoire of swimming and feeding behaviour, with a marked vertical migration component (Fortier and Leggett, 1983; Lazzari *et al.*, 1993). The distributions of herring larvae are influenced by water-mass features (Heath *et al.*, 1991), as well as food concentrations and light intensity (Munk *et al.*, 1989).

The larvae of late autumn- and early winter- (October–February) spawning herring forage in a prey field that differs both in concentration and composition from those of the spring and summer spawners appearing in more productive seasons. It appears an obvious question to ask what the winter-spawned larvae feed upon, but studies of their diets are few compared with those of spring- and

summer-spawned larvae. Diet preferences change in relation to larval size and ontogeny, and comparisons between seasons indicated similar preferences in the laboratory (Checkley, 1982), but significant differences in large outdoor mesocosms (Gamble *et al.*, 1985). In general, autumn-spawned larvae are smaller and consume smaller copepods such as cyclopoids (Gamble *et al.*, 1985), or microzooplankton such as ciliates, dinoflagellates, and tintinnids when other small zooplankton types are less abundant (de Figueiredo *et al.*, 2005).

In the late 1970s, otolith increment analysis was developed to estimate the age of fish larvae, and was applied with mixed success to herring studies. Townsend and Graham (1981) and Lough *et al.* (1982) constructed length-at-age curves for the Gulf of Maine, and Moksness *et al.* (1987) analysed increment counts to determine the age and growth of Norwegian spring-spawned larvae. However, Geffen (1982) found that increment counts did not correspond well with age, based on known-age larvae in tanks and in outdoor mesocosms. Otolith growth slows under poor conditions (Folkvord *et al.*, 2000), and narrow increments may be difficult to detect (Campana *et al.*, 1987), although a pattern of narrowing increments may be used as an indicator of likely ageing problems and of a poor-growth history (Folkvord *et al.*, 2004). However, slow growth may also cause increments to fuse into single, wider increments that are hard to distinguish from usual growth increments. This is particularly common during the first two weeks after hatching (Folkvord *et al.*, 2004), but also later (Fox *et al.*, 2003a).

The debate about otolith increment formation in herring larvae has continued, and even scanning-electron microscopy studies have failed so far to resolve the question of "missing rings" (Fox *et al.*, 2003a). Daily increment formation is irregular in yolk-sac and first-feeding larvae, but the development of vertical migration behaviour and associated feeding rhythms entrain a daily pattern, leading to detectable increments (Geffen, 1982).

Because the relationship between increment number and age of larvae is still uncertain, most authors applying this technique to study growth in the wild are careful to consider wide confidence limits for age estimates, or to restrict the application to late larvae. Few recent studies rely on age determination of herring larvae using micro-increments because of the discrepancies sketched. Nevertheless, patterns in increment width can provide valuable information about larva growth in response to temperature and feeding (Fey, 2005). In general, otolith increment width decreases with decreasing growth rate, so periods of slower growth can be identified. This pattern has been used to separate spring- and autumn-spawned larvae, first along the Norwegian coast (Moksness and Fossum, 1991), and more recently for populations in the Irish and Celtic seas (Brophy and Danilowicz, 2002). Otolith size is also a good indicator of metabolic rate and potential for growth in herring larvae (Bang *et al.*, 2006, 2007).

Juveniles

Studies of juvenile herring are primarily concerned with predation, feeding, and mixing. Because of the considerable variation in life-history characteristics, the term "juveniles" is ambiguous. If the stage stretches from metamorphosis to first maturity, then the term encompasses different age ranges in different populations. Older larvae form patches and to some extent follow each other, but schooling (behaviour suggesting a super-individual) becomes more apparent after metamorphosis (Gallego *et al.*, 1995). Metamorphosis also marks the time when herring become facultative filter-feeders, switching between filtering and biting depending on light intensity and prey density (Batty *et al.*, 1990).

The major research questions raised for the juvenile stage involve the movements of larvae from spawning to nursery grounds, the extent of mixing with juveniles from other populations, and the eventual mechanisms that operate so that they join the adults of the populations from which they originated as soon as they are ready to reproduce. Juveniles may travel considerable distances, as demonstrated directly through tagging studies (Morrison and MacDonald, 1986; Molloy *et al.*, 1993). Using a variety of techniques, the movements of juvenile herring between basins can be traced, and mixtures of herring from different spawning populations may be detected within the same nursery areas. Techniques that have been applied successfully to determine the origin of juveniles include morphometrics (Jorgensen *et al.*, 2008), parasite prevalence (Campbell *et al.*, 2007), and otolith analyses such as increment width patterns (Moksness and Fossum, 1991; Brophy and Danilowicz, 2002; Clausen *et al.*, 2007), otolith shape (Burke *et al.*, 2008), and chemical composition (Brophy *et al.*, 2003). In contrast, population genetics have not been able to detect consistent differences among

populations and the patterns emerging so far produce a confusing picture (Grant, 1984; Dahle and Eriksen, 1990; Jorstad, 2004; Jorgensen *et al.*, 2008).

McQuinn (1997a) applied the meta-population concept to herring to reconcile empirical evidence and a background of apparently conflicting hypotheses (member/vagrant hypothesis of Sinclair and Iles, 1989, vs. the dynamic-balance hypothesis of Smith and Jamieson, 1986) in seeking to explain the patterns of population structure. This concept reconciles the observed distinctness of different populations, the existence of both natal homing and straying by individuals, and the varying extent of genetic differentiation among populations. Essentially, McQuinn's (1997a) "adopted-vagrant" hypothesis proposes that mixing between populations during the juvenile stage is an adaptive life-history strategy that favours colonization and is a response to variations in population abundance. Individual herring may mature and spawn within their natal population (Brophy *et al.*, 2006), or may join other populations that spawn in the same season at another location or in a different season at the same location (Almatar and Bailey, 1989; McQuinn, 1997b). Taken together, these studies provide clear evidence that both options are available, fuelling the debate about whether herring actually show natal homing. Natal homing is probably too restrictive a term in this respect, and some form of learning (social transmission) has been invoked to explain the way that young herring are adopted into a specific population during first maturation and spawning (McQuinn, 1997a). In any case, all available evidence shows that individuals return to the same spawning ground in the same season where and when they first spawned (Wheeler and Winters, 1984), so establishing an annual spawning pattern. The notions of "recruiting" and "being led astray" are anthropomorphisms, but they may well describe one of the mechanisms of mixing between different groups.

Adult maturation and fecundity

The study of maturity and reproduction has proceeded almost entirely in the context of determining the reproductive potential, primarily for stock assessment and estimating recruitment. It is difficult to study reproduction in the laboratory, and most studies are restricted to field observations rather than using a direct experimental approach. Herring is usually considered to be a "single-batch spawner", with all oocytes ovulated at the same time. The dynamics of oocyte maturation have been debated, however, especially given the differences in spawning season among populations. Herring are thought to regulate fecundity through resorption (atresia) of oocytes during the maturation cycle (Bowers and Holliday, 1961), although this has not yet been confirmed experimentally. Experimental studies represent a real challenge because it is difficult to establish populations that mature and reproduce in captivity. In what was probably the first successful experiment, Ma *et al.* (1998) tested the effects of feeding ration on oocyte number and size over a 1.5 year period, sampling individual herring at frequent intervals over an entire reproductive maturation cycle. Oocyte size was not affected by feeding treatment, but the number of developing oocytes was related to the condition, or the nutritional status, of the individual female.

In the Northeast Atlantic, autumn-, winter-, and spring-spawning herring proceed through the early stages of gonad maturation during the same season in tandem with summer feeding (Bowers and Holliday, 1961; Iles, 1964). Summer/autumn spawners proceed directly to final maturation and spawn, whereas the oocytes of winter/spring-spawning fish continue to grow over the next few months. This is a mechanism that can produce the observed differences in egg size in separate herring populations (Blaxter and Hempel, 1963), although Almatar and Bailey (1989) and Ma *et al.*, (1998) argue that egg size differences are more likely to result from different temperature and feeding regimes experienced by separate groups and/or populations.

Larger herring seem to mature and spawn earlier than smaller fish (Iles, 1961; Kjesbu, 1994), and early evidence suggested that separate spawning cohorts appear on spawning grounds, fish of different ages making up separate spawning waves; this is especially so for Pacific herring (Ware and Tanasichuk, 1989). Slotte *et al.* (2000) studied the age and size composition of spawning schools of Norwegian spring-spawning herring and concluded that larger fish are the first to spawn, but that there was no continuous changeover to smaller fish as the season progressed. Fish that were spawning for the first time were the last to spawn, perhaps the result either of later maturation or slower maturation.

The large amount of data on fecundity and the maturation schedule across different populations has provided a valuable basis for recent theoretical investigations and meta-analyses. The energetic costs of migration and spawning may lead individual fish to skip spawning, especially in their second year

of maturity (Rideout *et al.*, 2005). Engelhard and Heino (2006) claimed that this phenomenon could affect as much as 47% of Norwegian spring-spawning herring during their year after first spawning, depending on growth and condition. This corresponds to 10% of the mature fish in any given year (Engelhard and Heino, 2006) and, as an example, would represent an unaccounted biomass of 1.2 million tonnes based on the 2008 spawning-stock biomass (SSB; ICES, 2008). Other explanations for the predicted extent of skipped spawning, which was based on indirect evidence, are likely to be errors in age estimation (Baulier and Heino, 2008), or mixing of non-spawning immature fish within spawning groups (Engelhard and Heino, 2006).

Herring research, and insights into the evolution of fish

Fishery science may be the most compelling motivation for herring research, but herring is also an important model in physiology, development, and evolutionary research. The species belongs to an important group for studies of fish evolution, the Clupeomorpha, which are one of the five basal teleost lineages (the others are Osteoglossomorpha, Elopomorpha, Ostariophysi, and Protacanthopterygii [Inoue *et al.*, 2001]). Some authors place the origin of Atlantic and Pacific herring in the Pliocene (5–1.8 million years ago [mya]; Grant and Bowen, 1998), although the earliest fossil records for the genus *Clupea* are from the Eocene (Gaudant, 1991), as cited in FishBase (Froese and Pauly, 2008). Morphology-based systematics produced a series of phylogenetic analyses with conflicting conclusions about the relative relationships between the majors groups of the Clupeomorpha (herrings), the Elopomorpha (eels), and other basal teleosts (Ostariophysi and Protacanthopterygii). Recent work using molecular systematic methods has resolved the relationships between the different groups, providing evidence of a closer linkage between the Clupeomorpha and the Ostariophysi, and a much more distant relationship between the Clupeomorpha and the Elopomorpha (Inoue *et al.*, 2001).

Adaptations in the vitellogenin genes active during gonad maturation are found in clupeids, and were pivotal in the evolution and diversification of fish. Teleosts evolved in fresh water and first recolonized the oceans during the Jurassic. The Clupeomorpha appeared 200–240 mya and still contain fresh-water, anadromous, and marine species. Spawning in seawater produces an osmotic challenge for gametes, because oocyte hydration requires absorption of water against an osmotic gradient. The biochemical process accomplishing this is the degradation of yolk proteins (from vitellogenins) to free amino acids that, with inorganic ions, alter the osmotic balance and lead to the inflow of water for hydration (Kristoffersen and Finn, 2008). The important role of vitellogenin has been established through studies of herring eggs, and molecular phylogenetic comparisons of vitellogenin genealogy (Finn and Kristoffersen, 2007). The Elopomorpha have a similar mechanism to accomplish oocyte hydration, one which evolved independently.

The relevance of phylogenetic studies extends to the more applied concerns of fishery science, especially in modelling species and population responses to human activities. Rochet *et al.* (2000) modelled the responses of different life-history traits to fishing pressure, and evaluated whether there was a phylogenetic component to the ability of different species to withstand fishing pressure. In general, the phylogenetic component was strongly expressed through life-history strategies. Herring, together with other clupeiforms, are characterized by a low fecundity at first maturation but an associated steep increase in fecundity with increasing size. As they are relatively small fish, they do not compensate for heavy fishing mortality with greater fecundity initially, so are more susceptible to collapse than other groups such as gadoids or flatfish (Rochet *et al.*, 2000). However, they have a potentially fast population growth rate that results in rapid rebuilding or recovery when adult mortality drops.

Discussion

Herring research has been very productive, and the consequent advances in knowledge have contributed considerably to a broader understanding of general biological and ecological tenets. Recent detailed studies of biological processes have discounted many of the earlier views of the species' biology, derailing attempts at a simple synthesis. Instead of answering questions, we have discovered new ones. The populations defined initially by morphology and spawning characteristics (season and grounds) do not correspond well to observed genetic structure or differentiation. Fuelled

by the discrepancy, traditional stock concepts have been redefined to help explain the relationships between separate herring populations (McQuinn, 1997a), and the practical problems of managing a natural resource with poorly defined units continues to be an important issue (Kell *et al*., 2009; Reiss *et al*., 2009).

Questions on growth and mortality have been addressed thanks to an ability to maintain and manipulate captive populations, especially in the early life history. The ensuing results have required a re-appraisal of tolerance, plasticity, and adaptability, and have helped to explain how herring are successful across a variety of environmental conditions. Direct observations in the wild have benefited greatly from advances in acoustic and video techniques, and those observations have produced a more detailed picture of herring behaviour and communication. The enhanced understanding of the phylogenetic position of the group underpins the recent advances in knowledge, and contributes to predictions of their response to exploitation and environmental variability.

The information collected through recent studies reveals a complex population structure of herring, and demonstrates that the high level of adaptability must be a fundamental trait. Adaptability and plasticity is observed throughout the different life-history stages. Once, the picture was simple; now, with more data available, the picture proves to be more complex. However, despite the obvious need to synthesize the available information for a better understanding, a single unifying explanation for all observed herring patterns is still elusive.

Acknowledgements

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Running headings

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