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Historical roots of the migration triangle

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The current theory of fish migration specifies that philopatry and population structure are inextricably linked, requiring a circuit of migration to and from localized spawning habitats. The circuit, popularized by Harden Jones as the migration triangle, has been a first principle in fisheries science since Hjort's early work demonstrating circuits of migration by Norwegian cod. The roots of the migration triangle theory are unearthed by examining a central dialectic on population attributes in fisheries science: Hjort and Dannevig's debate on the effectiveness of the cod hatching program. Resolution of this early debate led to an assumption of closed populations (philopatry) and related theory development during the 20th century (e.g., surplus yield and stock recruitment). Unresolved issues include: 1) the interaction between sea basin populations and *localformen* (e.g., fjord cod, estuarine herring, resident salmon); 2) the consequence of straying on population persistence; and 3) allopatric migration circuits within populations. While philopatry has been verified in countless studies using various "certificates of origin", recent investigations indicate that polymorphism in migration circuits and reduced philopatry can be important in the regulation of fish populations.

Keywords: contingents, life cycle, metapopulations, migration triangle, philopatry, stock concept.

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Introduction

The first principle guiding our understanding of how migration affects population dynamics is philopatry. Harden Jones (1968) codified philopatry as the migration triangle, a series of seasonal and ontogenetic migrations arranged to guarantee homing and reproduction at localized spawning grounds. The concept of philopatry has supported the assumption of closed populations and allowed important theoretical development of surplus yield and stock-recruitment relations (Smith, 1994). The underlying theory of philopatry is, in fact, quite complex, particularly in the evidence initially required to prove it. Early fisheries scientists within ICES and elsewhere had to demonstrate:

1) Spawning is restricted to a small geographical scale relative to the distribution of juveniles and adults. Active migrations link areas of adult distribution and local spawning grounds.
2) Adults return to natal spawning grounds.
3) Juveniles and adults originating from different spawning grounds can seasonally co-exist as mixed stocks.

In this essay, the roots of the migration triangle "theory" are unearthed by examining the early debate on local versus global effects of the cod hatching program. The debate was fundamental to closed population thinking that dominated fisheries science throughout most of the 20th century (Sinclair, 1988; Sinclair and Solemdal, 1988).

Entity: local versus global effects

A recurring conflict in fisheries science is the effectiveness of mass releases of cultured marine fish larvae (Secor and Houde, 1998). Solemdal *et al.* (1984) and Schwach (1998) have argued that Hjort's 1914 synthesis – the year-class paradigm and related critical period theory – was stimulated in large part by a contest between Hjort and Captain Dannevig, the progenitor of Norway's cod hatching program. Hjort sought political and economic capital from the Norwegian government, necessary for fueling his vision of modern fisheries science (Schwach, 1998). Dannevig had staked his career and the mission of the Flødevigen laboratory at Arendal on the recent technology of pisciculture and the potential of mass releases of cod larvae to enhance local stocks.

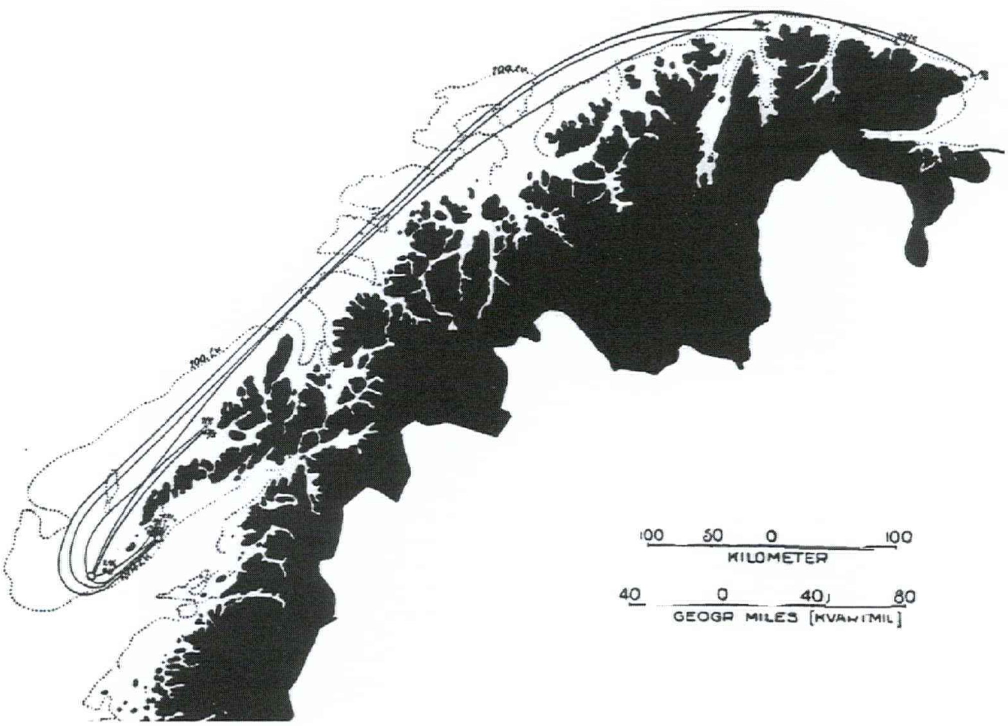


Figure 1. Migration pathways of mature cod tagged at Lofoten spawning ground and recovered on Finnmark feeding ground (Hjort, 1914, p. 103; original text: "Figure 69. Examples of long migrations made by grown cod marked at Lovoten (Moksness, Røst) end of April 1913, and recaptured off the Finmark coast end of May or early June the same year. Dates of marking and recapture indicated.").

From 1890 to 1906, 3.3 billion <5-day-old cod larvae were stocked into small fjords, sounds, and bays mostly surrounding Arendal (Solemdal *et al.*, 1984).

Today, there are various ways to mark "delicate" marine larvae to evaluate their rates of contribution and ecological effects (Tsukamoto *et al.*, 1989; Secor *et al.*, 1995). Without these technologies, Dahl tested the effectiveness of Dannevig's cod hatching program by considering scale or *entity*. Hjort and Dahl tested whether fluctuations in cod abundance (juveniles or adults) were determined locally or globally. Dannevig subscribed to local entities and effects, the corollary of the modern migration theory. That theory prescribed restricted movements inshore and offshore by numerous fish stocks (Smith, 1994) and led to expectations that 1) local fisheries result in local depletions, and 2) local releases result in local enhancement. Dahl (1909) specified the theoretical underpinning of Dannevig's program:

> the importance of the size of the waters [to enhancement] was reduced by accepting the doctrine that each area of the sea, even the smallest, possessed its own tribe of fish. These tribes were supposed to be highly local during the whole life of the individuals. They were easily injured by over-fishing and had to be replaced by the aid of man.

Over three years, local effects by enhancement were investigated by Dahl in small fjord systems, testing whether released larvae would drive abundance dynamics of larvae and juvenile cod in those waters (Table 1). (In fact, surveys of stocked fjord systems were conducted for many decades; Smith *et al.* (2002) revisited the issue of the effectiveness of the Norwegian cod stocking program based on this more complete set of surveys). In 1904, large numbers of juveniles were encountered in surveyed fjords regardless of the number of released larvae. But in 1905, the abundance of juveniles was scarce everywhere, again independent of release levels. Dahl (1909) summarized that, "The addition of artificially hatched cod larvae to a locality can nowhere be proved to have influenced the relative abundance of littoral fry in a recognisable degree."

Several explanations were given by Dahl for the lack of local effects. Eggs and larvae were observed to be entrained in surface currents and to drift in and out of fjords, indicating wide areas of distribution and intermingling of eggs, larvae, and juveniles between fjords and adjacent coastal areas. Older fish (>5 years) were

Table 1. Number of larvae ("fry") released into different fjords as part of Captain Dannevig's cod hatching program. Dahl's study on the effectiveness used "cod per haul" (number of juveniles collected using beach seines) to index juvenile abundance among years for the months of July and August. Data from Dahl (1909, p. 31).

Year	Søndeled Fjord		Helle Fjord		Sandnes Fjord		Støle Fjord		Kristiania Fjord	
	Larvae released	Cod per haul	Larvae released	Cod per haul	Larvae released	Cod per haul	Larvae released	Cod per haul	Larvae released	Cod per haul
1904	33.5×10^6	33.7	0	10.9	0	49	0	112	20×10^6	10.8
1905	33×10^6	11.4	10×10^6	1.5	0	4.1	0	2.7	20×10^6	1.9

not observed in fjords, and mark-recapture experiments showed that younger cod sometimes migrated out of the studied fjords. High abundance of littoral juveniles in fjords seemed to be independent of same-year abundance of larvae and younger pelagic-stage juveniles. In conclusion, Dahl (1909) felt it "just to consider the fish stock of a considerable stretch of coast as belonging to or common to the whole of the area."

How might this and other investigations (Hjort and Dahl, 1906) of the cod hatching program have served as signposts for Hjort? Certainly Hjort's genius in applying human censusing methodology to fishes "was big with possibilities" (Smith, 1994). Fisheries science was also the beneficiary of an extremely strong 1904 cod year class that provided such compelling evidence that it could not be ignored by Hjort and his colleagues. It could also be argued that the entity of fluctuation – not the fjord, but the entire Norwegian coast in 1904 – provided Hjort with a critical spatial domain that permitted projection of decadal cycles due to year-class fluctuations.

By rejecting local effects, Hjort was by no means accepting the historical concept of the polar sea theory. Indeed, much of Hjort's 1914 thesis was devoted to rebutting the idea of single, large, panmictic populations of herring and cod. Hjort ably refuted conjecture of deep cryptic cod under polar icecaps by showing that the lower temperature thresholds for cod would curtail such behavior. Then, through distribution studies on ripe and recently spent adults, eggs, and larvae, Hjort and his collaborators demonstrated that spawning grounds for both species were, in fact, much more restricted than the spatial extent of adults and juveniles (Schmidt, 1909; Hjort, 1914). Because adults do not reside the entire year in proximity to spawning grounds, it was necessary to assume that seasonal migrations bring adults to local spawning grounds. In ground-breaking work, Hjort (1909) confirmed such seasonal migrations by tagging spring-spawning cod off the Lofoten Islands and recapturing them in the summer hundreds of kilometers away in the Barents Sea (Figure 1). For spring herring, Hjort and his colleagues used "certificates of origin" – unique optical patterns of scale annuli – to chart the seasonal migrations to and from principal spawning grounds (Hjort, 1914). Using these same certificates of origin as evidence, Hjort (1914, p. 16) argued forcefully that different stages or sizes of herring located in different regions are in fact members of the same population:

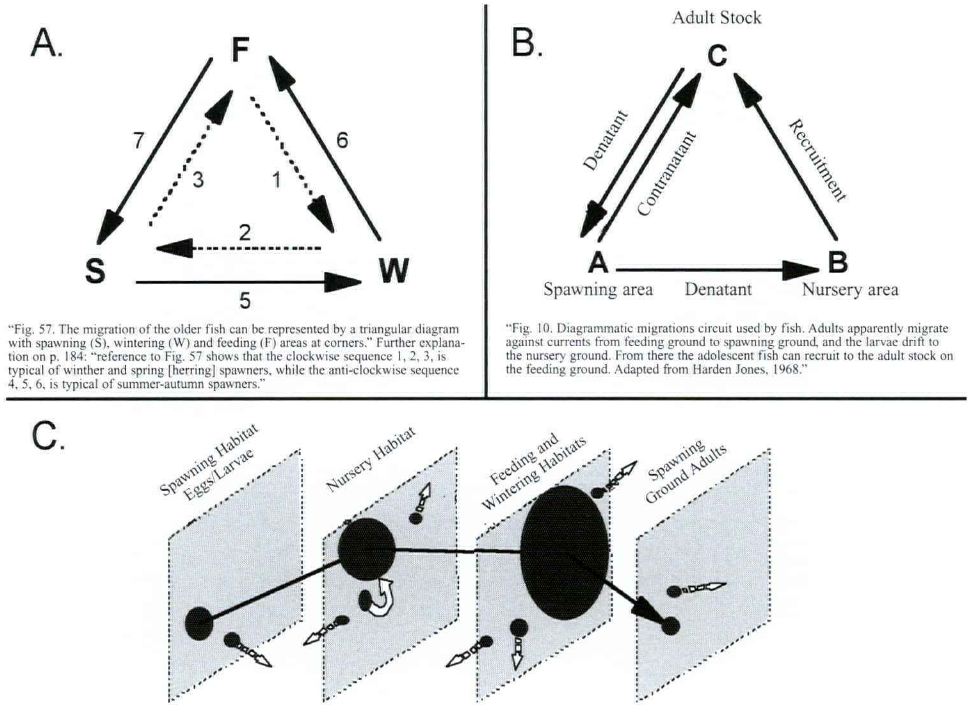
> Small herring and fat herring are thus immature fish, the large and spring herring being mature; it would therefore be natural to consider all four classes as representing different stages of size, development, and age in one and the same race of fish.

Hjort and early ICES scientists moved from the essentialist viewpoint commonly held by fishermen of that day that each different local type of herring would reproduce its own, to a more dynamic one based on migration. Here were the rudiments of the migration triangle and the pursuit of evidence thereof (Schmidt, 1909, p. 11):

> ...the spawning fish, on account of their much more definite cravings after certain external factors, are brought together on a much smaller area than that over which the species is ordinarily distributed, i.e., a congregation of individuals takes place, which is presumably of importance for fertilisation and thus the reproduction of the species. In great contrast to this stands the dispersion of the individuals over much greater, in physical regards often very dissimilar areas, which arises from the drift of the pelagic fry from the spawning places, and which naturally amongst other things has the advantage of procuring better conditions as to food for each individual during growth than if they had all remained at the spawning places.

Having now recognized the complex life cycles of North Atlantic fishes and the geographical scale over which they occur, Hjort still needed to address the issue of entity. Which and how many spawning shoals were relevant to cycles of population change? The dominant effect of the 1904 year class on cod and spring herring landings throughout Norway and the North Atlantic (excluding the North Sea) directed Hjort's attention to basin-scale entities (Hjort, 1914, p. 29):

> The fact that such small samples taken at such a distance apart (200 miles), should exhibit so great a similarity as regards composition in point of age, can only be regarded as marvelous. The only possible explanation seems to be, that the shoals [taken throughout the Norwegian Sea] were in reality perfectly homoge-



"Fig. 57. The migration of the older fish can be represented by a triangular diagram with spawning (S), wintering (W) and feeding (F) areas at corners." Further explanation on p. 184: "reference to Fig. 57 shows that the clockwise sequence 1, 2, 3, is typical of winther and spring [herring] spawners, while the anti-clockwise sequence 4, 5, 6, is typical of summer-autumn spawners."

"Fig. 10. Diagrammatic migrations circuit used by fish. Adults apparently migrate against currents from feeding ground to spawning ground, and the larvae drift to the nursery ground. From there the adolescent fish can recruit to the adult stock on the feeding ground. Adapted from Harden Jones, 1968."

"Fig. 1. Migration triangle in a diffusive environment. Each pane represents a cross-sectional profile of spatial occurence (for example, horisontal and vertical access of each pane could represent latitude and longitudes). Panes arranged left to right to show ontogenetic pattern of migration. Mean migration circuit is shown by the bold line. Centroids exhibit dispersion of the population aggregations. Open arrows indicate possible migration fates of vagrant aggregations. Note that collapsing all panes into a single framework would cause the mean migration curcuit to circumscribe a migration triangle (sensu Harden Jones 1968)."

Figure 2. Evolution in depiction of Harden Jones Migration Triangle. A. Harden Jones (1968); B. Cushing (1982); C. Secor (1999). Figures are all redrawn. Original text from figure legends presented below each panel.

> neous in this respect; that the samples examined were thus representative of the stock as a whole...

In addition, it can be argued that Hjort and Dahl's experience in fjords investigating local dynamics of eggs, larvae, and juvenile cod led them to consider populations as more global entities (Schwach, 1998).

> When the young bottom stages grow up many miles distant from the places where the eggs and larval stages developed, any purely local result from the liberation of the larvae cannot be expected, and... when the existence of great variations in the drift of the larvae and in the quantitative occurrence of the year-groups up to several years old have been proved, all these conditions and phenomena must possess dimensions which far exceed the limits of human, practical endeavours (Hjort, 1909, p. 150).

It is important to recognize that while Hjort believed local entities were insignificant, he recognized basin-scale differences in population dynamics within herring and other species. Remarking on the pervasiveness of 1904 environmental forcing on year-class strength among species in Norwegian and North Atlantic waters, Hjort was careful to point out different demographics for summer-spawning North Sea herring. Abundance of these fish was driven by a strong 1906 year class.

The merging of Hjort's year-class paradigm with Heincke's early work on North Sea races has been highlighted in recent historical treatments on population thinking in fisheries science (Sinclair, 1988; Sinclair and Solemdal, 1988). Hjort devoted considerable discussion to the topic of race (Hjort, 1914, pp. 47–56), but Hjort was reluctant to accept the essentialist viewpoint of numerous local races (i.e., stationary forms) without supporting migration studies (Hjort, 1914, p. 56):

> Not until we have ascertained where all the different stages are to be found is it possible to determine the extent of the area of distribution of the race, and define the geographical limits which separate one race from another.

Further, Hjort (1914, p. 48) casts races as Linnean entities: "The idea of race is based upon that of an ideal type" and introduces probable biases in Heincke's taxonomy (Hjort, 1914, p. 49):

> By far the greater number of qualities which Heincke has examined have, however, been found to vary with age and growth. At the time when Heincke carried out his investigations, no method of determining the age of herring was known; he was therefore unable to make comparisons between individuals of equal age with full certainty of accuracy.

These are fairly severe criticisms of work conducted by a colleague who had earlier (1902–1907) (Schwach, 1998) assisted Hjort in the development of novel methods of ageing fish, upon which Hjort's year-class paradigm would depend. It is also noteworthy that in the large compendium of studies by ICES Committee A, mostly directed at cod (Hjort *et al.*, 1909), there was no reference made to Heincke's work on herring races, despite his membership on that committee. Indeed, vertebral counts were given for cod and other fishes collected on various fishing grounds, not as an indication of stock structure, but as an aid to species identification (Schmidt, 1909). Hjort's 1914 thesis followed suit, omitting racial considerations for Norwegian cod stock dynamics. As an antagonist of local effects in the debate on the cod hatching program, Hjort may have been disinclined to accept the concept of relatively stationary races as proposed by Heincke. The apparent conflict between Heincke's essentialism (stationary local races) and Hjort's dynamism (migrating basin-scale populations) deserves further scholarship on the correspondence and interactions between these two great scientists.

As final evidence of a strong shift from Heincke's static *lokalformen* to basin-scale systemic entities, the following quote is presented (Hjort, 1914, p. 60):

> for the present, we must in all probability suppose that roughly speaking, the southern part of the North Sea is one of the largest and most important growth centres for the young of the great spawning shoals of ocean herring in the North Sea. The enormous numerical superiority of the ocean form as compared with the coast varieties should in itself suffice to warrant the supposition that the young of the former race make up a considerable portion of the total young stages found in the North Sea and Skagerrak.

In this early contest with Dannevig over local effects, Hjort won. (It is noteworthy that the issue of the interaction between local and sea basin stocks of cod persists – see Harden Jones (1968); Fevolden and Pogson (1997); Jakobsen (1987); Smith *et al.* (2002).) Captain Dannevig (1841–1911) did not live to see Hjort's classic 1914 synthesis, but as the protagonist in this dialectic, he played an invaluable role (Solemdal and Sinclair, 1989). Surprisingly, the Flødevigen cod hatching program continued until 1971 (Solemdal *et al.*, 1984), a near pariah of modern fisheries science (Schwach, 1998). The year-class paradigm was established (Hjort and Lea, 1914), and within the ICES fisheries science community, local entities were overshadowed by basin-scale studies of populations for decades to come.

Philopatry and the concept of closed homogeneous stocks

The concept of systemic entity, described by Ferré (1996) as a bounded biological unit that maintains structure and function despite changing environmental conditions, is useful in considerations of Hjort's early work. The mechanism that defines the systemic entity in Hjort's concept of populations is philopatry, commonly referred to in fisheries science as the parent stream theory (Harden Jones, 1968). Philopatry permitted populations to be thought of as bounded entities that maintained function and structure (i.e., the unit stock concept). Each entity responded uniquely to the environment (Hjort's year-class paradigm), entities did not interact with other entities (philopatry), and members of single entities were homogeneous in biological attributes (assumption supporting later theories on surplus yield and stock recruitment).

In his compendium of fish migration studies, Harden Jones (1968) reviewed the parent stream theory for Pacific salmon. Huntsman (1937a, 1937b), a chief antagonist of the theory, was skeptical about the >3000 km global ambits from the North Pacific Ocean near the Aleutian Islands to localized spawning reaches in low-order streams of North America. In response to the prevalent dogma of homing instincts, Huntsman (1937a) argued,

> I have failed to find a clear case of a salmon returning to its natal river from a distant place in the sea, that is, away from the neighbourhood of the river mouth. Admittedly this is a difficult thing to prove, since we must be sure of three things from the individual fish: (1) which is its natal river? (2) where it has been in the sea, and (3) that it is again in its river.

Harden Jones (1968) provided ample circumstantial support for the parent stream theory, reviewing decades of tagging studies on wild and hatchery-produced salmon (e.g., Foerster, 1936; Rich, 1937; Pritchard, 1939). Experimental research proved that imprinting to natal waters included both olfaction and hereditary components (Hasler and Scholz, 1983; Stabell, 1984; Quinn and Tolson, 1986; McIsaac and Quinn, 1988). The degree of philopatry in Pacific salmon (often >95%) and their behavioral and physiological repertoire used to accomplish migration circuits (Quinn and Dittman, 1990) still leaves fishery scientists awestruck. It was no wonder that anadromous salmon have figured dominantly in migration theory: "In temperate seas fish usually return to the same spawning ground each year at the same season, much as do Pacific salmon" (Cushing, 1995, p. 86). Conversely, Harden Jones (1968, p. 185) was careful to point out,

> Homing could be a disadvantage when fish persist in returning to spawn in an area or on a ground where conditions have become unfavourable to the survival of eggs... The only biological insurance against this is

a satisfactory level of straying and a multiplicity of spawning grounds, whose contribution to the population as a whole would change as environmental conditions varied.

A corollary to closed migration circuits is sympatry. Here, sympatry represents the idea that 1) individuals within the same population engage in an identical migration circuit, and 2) individuals of two or more populations may overlap in migration circuits. Hjort and his team expended considerable effort to develop certificates of origin to demonstrate migration circuits, but also to segregate individuals from different stocks in the Norwegian and North Seas.

> ...it is therefore of greatest importance to ascertain whether it may not be possible, when once a comprehension of the races has been obtained, to discover some more easily discernible distinctive marks by which to determine to which race the single individuals belong, and properly sort the mixed samples. (Hjort, 1914, p. 51).

This issue of sympatry is synonymous with the mixed-stock problem that has led to emphasis on certificates of origin in fisheries science (e.g., Waldman, 1999).

The migration triangle

In its original conception, the Harden Jones migration triangle depicted only seasonal migrations (Figure 2). In illustrating the concept of hydrographic containment, Cushing (1975, 1982) substantially modified the migration triangle to depict an ontogenetic migration circuit; this has since been erroneously ascribed to Harden Jones (by Sinclair, 1988; Cushing, 1995; Secor, 1999). Still, the ontogenetic migration triangle faithfully represents the first principle of philopatry that underlies population thinking in 20th century fisheries science.

In this, the 21st century, it is expected that scientists will begin to relax migration theory assumptions related to philopatry and sympatry in their considerations of those systemic entities most useful to management. During the past decade, increased considerations of the role of straying in salmon and other species have been observed (Quinn, 1993; McQuinn, 1997; Ray, 1997) that may lead to a renaissance of research related to regulation of genetic resources structured as metapopulations (Hanksi and Gilpin, 1997; Policansky and Magnuson, 1998). Regarding the assumption of population homogeneity, divergent migrations within populations by contingents have recently been addressed as a mechanism that imparts persistence to populations. Hjort (1914) provided the first definition of "contingent" as a group of juvenile "fat" herring inhabiting the Nordland feeding grounds (Norwegian coastal waters, south of Lofoten Islands) for several years. This group, representing a distinct migration circuit, was later found to mix with individuals from other contingents on spawning grounds. Contingents may represent important phenotypic modes of response, whereby populations or metapopulations persist in the face of spatial variation in habitat (Secor, 1999).

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