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The notion that fish species form stocks

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The development of the notion that fish species form stocks (or populations) was a gradual process, taking place between 1878 and about 1930. This new concept was due to a shift from "migration thinking" to "population thinking." The relevant research during this period was primarily directed towards the intertwined practical problems of the causes of fluctuations in fisheries and the evaluation of overfishing. The development of three components of the population concept is traced: pattern, richness, and variability. The so-called racial investigations of Heincke were instrumental to the conclusion that most marine fish species comprise geographically distinct spawning populations which may intermingle during other parts of the life cycle migrations. The work of Committee A of ICES under the leadership of Hjort led to the understanding that year-class strengths within populations can be extreme and lead to population variability. The studies by Schmidt between 1917 and 1930 led to the conclusion that there are species-specific differences in numbers of populations, with European eel, for example, having a single population within the distributional limits to species, and eelpout having many populations. The work of Committee B of ICES on the overfishing problem contributed to the shift to "population thinking" by demonstrating the restricted geographic area of plaice in the North Sea, and the relatively limited abundance estimates of the exploited resource. The change in thinking had profound influences on both the studies on the over-fishing problem (1930–1950s) and the conceptual framework within which the influence of climate variability on fish recruitment has been addressed up to the present time. The research by Heincke and Schmidt had an impact on the broader scientific community, whereas the key contributions by Hjort on year-class variability do not appear to have had any influence on the development of ecological theory.

Keywords: age determination, ICES, migration, overfishing, populations, recruitment, stock structure.

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Introduction

The objective of this paper is to review the origin of "population thinking" in fisheries science from the 1870s until 1930, and the linkages between this concept and the intertwined debate on the relative roles of overfishing and hydrographic variability on fluctuations in landings from commercial fisheries. The new species concept involving population thinking within fisheries science, that which eventually became the biological species concept of Mayr (1942) and a key component of the so-called modern synthesis of evolutionary theory, emerged from the study of the causes of fluctuations in landings in coastal fisheries. As Johan Hjort stated in his 1914 classic paper (p. 1), "from the earliest times, a characteristic feature in all branches of the fishing industry has been fluctuations in the respective yields from year to year."

Sinclair (1997) has argued that the transition from "migration thinking" to "population thinking" represents a paradigm shift in the theory of fluctuations in fisheries yields, and that Committee A of ICES (which started its work in 1902) made a major contribution to the change. The shift in the conceptual framework is summarized below (modified from Sinclair, 1997, Table 1):

Before	After
"Essentialist" species concept	"Biological" species concept
Species the unit of study	Population the unit of study
Abundance relatively constant, renewal regular	Abundance highly variable, renewal irregular
Inexhaustible abundance of the species (overfishing impossible)	Finite abundance of populations (overfishing a potential factor in fluctuations)
Interannual fluctuations due to geographically variable migration of species	Interannual fluctuations due to year-class variability and migration of populations

Hjort (1914, p. 202), explaining the extant theory of 1902 on the causes of fluctuations in fisheries, stated:

> the renewal of the stock of fish took place as in the case of any human population, by means of a more or less constant annual increment in the form of new individuals.

In an introduction to a special ICES meeting on fish populations held in 1929, Hjort described the degree to which the species concept in 1902 was a constraint to understanding fluctuations in landings (Hjort, 1930, p. 5):

> When we entered upon our international collaboration 30 years ago, the biological analysis of the organisms we caught in the sea was in the main confined to the systematic determination of the various species…It was realized that the terms of species were inadequate to give a clear and orderly grasp of the phenomena…

The above quotations provide a flavour of the change in conceptual framework between 1902 and 1930.

There can be considered to be four components of "population thinking": geographic *pattern* in the populations of a species (i.e., its *richness*), the mean *abundance* levels of the component populations, and the interannual and decadal scale *variability* of abundance of these populations (Sinclair, 1988). How did this paradigm shift from "migration" to "population" thinking occur, and what was the role of ICES research activities in the change? Three of the four components are addressed in this paper.

Migration thinking

"Migration thinking" was an outgrowth of the Polar Migration Theory on Atlantic herring biology and fisheries. The theory (or story) probably had multiple origins, but was well articulated by Johann Anderson, a mayor of Hamburg, in his 1746 book (summarized recently by Wegner, 1993). The theory was ecological and was consistent with many fishery observations at the time. It addressed the timing of migration to different fishing grounds, abundance changes between years, seasonal differences in herring quality, and geographical differences in body form. The theory postulated that the home of herring (*Heerings - Heymath*) is at great depths under the northern polar ice. Excess herring migrated away from the polar ice in search of food and were pushed southward by predators. Some reproduction was thought to occur en route, with growth occurring under different oceanic conditions. This activity accounted for the differences in form of herring from place to place. Fluctuations in landings between years were explained by interannual differences in predation during the migration. The most attractive aspect of the theory was the interpretation of the progressively later seasonal differences in the time of the various fisheries from Iceland and northern Norway to the English Channel. Gilpin (1786) modified the theory to include trans-atlantic migrations from the southern end of the putative European migration to the United States, with the herring returning back to their polar "home" a year later.

The theory over time was broadened to include other fish species and generated "migration" thinking with respect to the interpretation of fluctuations in fisheries and their collapses. Thus, the ICES Committee A formed in 1902 to address the high priority problem of fluctuations in landings of commercial fisheries was called the Migration Committee. As stated by Hjort (1914, p. 2), the observations on fluctuations in yields at different locations "gave rise to the theory of *migrations* which were supposed to be of great extent, nothing being known as to where the fish were to be found during a considerable part of the year, and a plausible explanation of occasional dearth was furnished by the suggestion that the fish in such poor years neglected, wholly or in part, to visit usual grounds."

Under this explanation involving migration changes, it should be noted that fluctuations were not thought to be due to abundance differences or to the activities of fishing itself.

Population thinking: pattern

Friedrich Heincke was funded, beginning in 1875, by the German Commission for Scientific Investigations to conduct research on the herring fluctuations in the Baltic Sea. There was considerable controversy at that time concerning the explanation of the good and bad periods of the Swedish winter herring fishery off the coast of Bohuslän. The documentation on these herring periods is well summarized by Höglund (1978). Lars Nilsson of Sweden studied the herring problem during the period 1826–1833 and concluded that overfishing of local races (or populations) could be a contributing factor to the fluctuations. This interpretation was hotly contested by the Dane, Krøyer, who criticized the methodology used by Nilsson to characterize the local races (i.e., the observed morphological differences were interpreted by Krøyer to be due to age and growth differences rather than to racial features). It should be noted that Cleghorn (1854) had also interpreted fluctuations (or declines) in the herring landings off the northeast coast of Scotland as being due to overfishing. This interpretation did not make him popular with the fishing industry. It was within the context of this controversy that Heincke defined his research program in 1875. He stated the question of the fluctuations problem in the following terms (Heincke, 1878, p. 45):

> Is the species *Clupea harengus* within its range really divided into varieties which differ in their morphological characteristics? Or, are all the observable characteristics within the species dependent upon age, sex, and other factors which influence the variability...?

He focused directly on the controversy between Nilsson and Krøyer. The key point to be made here is that the debate on the role of hydrographic variability on flutuations (under the rubric of "migration thinking") led directly to research on the nature of species (i.e., the existence of geographic patterns of populations within species).

Heincke carried out his work on the morphometric and meristics of Atlantic herring in two periods. During the first period, he measured 11 characteristics from 2000 fish. This led to the Heincke 1878 and 1882 papers which focused to a large degree on the separation of spring- and fall-spawning populations off Kiel. The second period involved measures of six characteristics of 6000 fish and led to his 1898 synthesis paper. To analyse these large sets of data, he developed primitive multivariate statistics and considered that he was capable of scientifically proving his conclusions. Duncker (1899, p. 366), in a review of Heincke's classic paper, stated:

> The existence of local populations of herring is *proven* beyond a doubt. (Emphasis added.)

At the first meeting of Committee A in September 1902, Heincke stated:

> It must be regarded as *proved* that different races of herring, separated by real distinctions, exist in European seas.... It is necessary, in relation to the existence of local races, to find out the spawning areas of herring, and to determine the distribution of herring larvae in the different parts of the North Sea. (Emphasis added.)

It would appear that not all scientists were convinced that the analyses resulted in scientific proof. Murray and Hjort (1912), in *Depths of the Ocean* (p. 758), stated:

> Another important series of investigations was inaugurated by Heincke...to characterize variations...and he found the relations between these dimensions to be so characteristic that he *supposed* the herring to be subdivided in various races... (Emphasis added.)

There are two interesting "sidebars" from the Heincke papers. The first is the new interpretation of the Bohuslän herring periods. Herring reappeared off Bohuslän in the winter of 1877 (the beginning of the 1877–1906 period). Heincke sampled the fishery and determined that they most resembled herring that spawn on Jutland Bank in the southern North Sea. Thus, the research question on the Bohuslän periods was reformulated to involve the causes of decadal-scale variability in geographic location of the overwintering migration of the Jutland Bank spawning population.

The second point of interest was the Darwinian context of Heincke's herring observations. They were considered to indicate the process of speciation in action, a hot topic at the time within evolutionary studies. In 1894, Galton proposed to the Royal Society of London the formation of a Committee to Conduct Statistical Enquiries on Measurable Characteristics of Plants and Animals (in short the Evolution Committee). It was established with a research fund of £100. Most of the fund went to a study by Weldon on the morphometrics of herring that spawn off Plymouth. The justification for the study was based on the early Heincke papers. The results (involving meristic and morphometric measures of 1900 fish) analysed by Pearson were never published because they failed to illustrate bimodal distributions in the characteristics measured, as might be expected because the samples were all from a single spawning group. For a discussion of the influence of Heincke's work on evolutionary biology, see Sinclair and Solemdal (1988, pp. 203–206).

The herring investigations of Heincke prior to the formation of ICES eventually had a revolutionary influence on thinking about the geographic pattern of populations within species. Schmidt (1917, p. 325) stated:

> Local races (populations) have... been shown to exist in quite a number of fish species. Most important of all...are Heincke's (1898) herring investigations. From a *mere chaos* Heincke succeeded in furnishing...a basis for all future investigations in this field. (Emphasis added.)

Somewhat surprisingly, however, the changing species concept initiated by Heincke at the turn of the century does not appear to have influenced interpretations of fluctuations in landings by the broader scientific community. The acceptance of geographic pattern in populations did not in itself lead to a change in thinking about interannual and decadal-scale variability in abundance; rather, it would be the work of Committee A to make that link.

Population thinking: variability

The so-called Migration Committee, or Committee A, was established by ICES in 1902 to address the economic problem of fluctuations in the great fisheries (herring and cod in particular). This problem was one of the main reasons for the founding of the Council. The initial members of the Committee were:

Dr Johan Hjort, Bergen, Convener
Professor D'Arcy W. Thompson, Dundee
Mr Walter Garstang, Lowestoft
Professor Fr. Heincke, Helgoland

Dr N. Knipowitsch, St Petersburg
Dr C. G. J. Peterson, Copenhagen
Dr H. C. Redeke, Den Helder
Dr P. P. C. Hoek (General Secretary of ICES)

Additional members after 1902 included Dr E. W. L. Holt, Professor G. Gilson, and Dr F. Trybom. This was a very powerful international committee of young scientists. Two oceanographers (Otto Pettersson and Bjorn Helland-Hansen) also participated in the meetings and resultant research programmes. The leadership of Johan Hjort proved to be of critical importance to fulfilling their remit. Hjort was already well respected by his international peers as being capable of leading research on this practical problem. In the report of the British delegates following the 1902 founding meeting (Anon., 1903), C. S. Moncrieff and D'Arcy Thompson stated:

> Dr. Hjort, an eminent Norwegian savant, was appointed chairman of the first Committee. No better appointment could have been made. He has a *practical* knowledge of the subject possessed by no other member of the council… (Emphasis added.)

That Hjort was 33 years of age at the time reflects the youth and youthful enthusiasm of the scientists drawn into ICES in its formative years.

The scope of activities of Committee A was broad and took place at shelf and basin scales. Heincke urged the Committee to conduct studies on the geographic patterns of egg and larval distributions of the commercially important species. That he made this proposal in the context of the "fluctuations problem" infers that he, at least, had grasped by 1902 the connection between population thinking and temporal variability in landings. No doubt he was very much on his own with this vision.

Otto Pettersson (and others) supported the simultaneous co-measurement of oceanographic properties (i.e., temperature and salinity) and egg and larval distributions with the expectation that the observed geographical patterns in spawning locations in relation to physical properties would lead to insights into the causes of variable migration patterns (and thus the causes of the fluctuations in the fisheries on spawning aggregations). The geographic scale of the egg and larval studies was enormous, stretching from Iceland to Spain and from the coastal areas to the deep sea. The results were published by Damas (1909) and Schmidt (1909). The fixed stations and lines for oceanographic properties that were organized by the Hydrographic Committee provided synoptic views of seasonal hydrographic distributions. The port sampling of groundfish in the North Sea fisheries complemented the programme that had already been established by Norway to estimate the changing size composition of the various fisheries (herring, cod, and haddock). Owing to the influence of Heincke, fish aging studies were initiated in the Bergen Laboratory which made it possible to estimate the annual age composition of the landings from the port sampling program of length measurements. Dahl (1907) presented some of the first herring ageing methodology using fish scales.

In sum, the work of Committee A was multidisciplinary in nature at a range of spatial scales (from coastal inlets to ocean basins). It involved a wide range of fish species both commercial and non-commercial. The biological studies involved all the life history stages and were well integrated with the oceanographic research initiatives. This was the GLOBEC (Global Ocean Ecosystem Dynamics) of the turn of the century, with a focus on a major practical problem facing the Member Countries (i.e., the fluctuations in the "great fisheries" of northern Europe).

The synthesis work on the research results of Committee A studies (1902–1906) done by the biologists Schmidt and Damas, and the oceanographer Pettersson led to a modification of the Migration Theory which did not involve "population thinking." Schmidt (1909) articulated the new conceptual framework in the most detail when he stated (p. 11):

> The fishes…vary greatly in their sensitiveness towards external conditions (temperature, salinity, depth) during the different stages of their life. They are most sensitive at the spawning season, and thus we find that they undertake long wanderings in order to obtain certain definite external conditions whilst spawning.…The result is that 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 fertilization and thus reproduction of the *species*. (Emphasis added.)

This modified Migration Theory by Schmidt could be entitled the Super Sensitivity before Sex (SSS) theory. The interpretation infers that interannual and decadal changes in oceanographic properties of particular sensitivity to fish during their sexual reproduction generates differential geographic patterns in spawning and thus fluctuations in landings at particular locations. The new hypothesis is stated in relation to species rather than races.

Damas (1909) supported the SSS interpretation and stated (p. 222, translated from French):

> The reproduction of adults at the most restricted locations possible is evidently favourable to reproduction in that it augments the chances of fertilization.… This aggregating behaviour requires a special instinct and particularly a highly developed sensitivity. We must agree with Johannes Schmidt that, at this period in life, the fish are influenced by differences in pressure, salinity and temperature to which they are usually fairly indifferent. We abstain from explaining this phenomenon of which its existence appears obvious to us…

These two quotes indicate the struggle that the young scientists encountered in the interpretation of their results of the Committee A activities. Perhaps it is this struggle that Schmidt (1917) referred to above as the "mere chaos" of interpreting the results under "migration thinking."

In summary, by the end of the initial five-year programme of Committee A of the Council, there had not really been much progress on the practical problem of interpreting fluctuations in the great fisheries. There was a modified hypothesis which did not generate much explanatory power. ICES (1909) provided a summary of the work of Committee A under the title "Some practical questions in light of the results obtained". Five questions relating to the remit of the Committee were discussed. Population variability was not hinted at. Furthermore, ICES General Secretary Hoek (1913), in his 1912 summary of the first decade of ICES work, suggested that limited progress had been made. As General Secretary, of course, Hoek put a positive spin on what must have been seen as disappointing progress on the fluctuations problem when he wrote:

> and although the problem of fluctuations cannot yet be regarded as solved, the earlier vague conjectures as to the occurrence and migration of the fish (cod) have taken a clearer and more certain form. The migrations of each species have their peculiarities, which has been especially necessary to learn.

"Migration thinking" was alive and well in ICES in 1912 and the above quotations from the three syntheses of Committee A's work (ICES, 1909, 1913) provide compelling evidence that the concept of year-class variability in geographically restricted populations had not been articulated. That would not occur until Hjort presented his 1914 paper entitled "Fluctuations in the great fisheries of northern Europe" in which he stated his "most important results" as "the existence of an intimate relation between the fluctuations in the numerical value of the stock of fish and the yield of the great fisheries."

The key change to "population thinking" was that fluctuations in landings were due to temporal variability in abundance within populations. Under "migration thinking," fish abundance was considered to be relatively constant, with fluctuations in landings due to variable "wanderings." Hjort's second key finding was that "the renewal process…is of a highly irregular nature."

This was a fundamental shift in perspective that was generated by the observations on variable year-class strengths in herring and cod populations. In addition, Hjort noted that the variability was induced during the early life history stages, his so-called Critical Period hypothesis. This hypothesis, which today is considered to be one of Hjort's claims to fame, was somewhat of an afterthought, or second-order contribution, of the long paper.

This *tour de force* paper was instantly recognized by the broader marine science community. Allen (1914), in a review of the paper published in *Nature*, stated:

> There can be little doubt that this report by Dr. Hjort will mark an epoch in the history of scientific investigations. If the arguments upon which its conclusions are based successfully withstand the *test of criticism*, there has been established a method of predicting the probable future course from year to year of some of our most important fisheries.… (Emphasis added.)

Just as in the case of Heincke's earlier herring investigations, this emphasis on scientific proof through quantitative analyses is of interest. Marine science at this time included enhanced standards of proof and tests of criticism. The review in *Nature* in addition highlighted the economic value expected from the potential of forecasting future landings from populations of long-lived fish species under moderate levels of exploitation. This aspect of the paper must have pleased the Council, given the tenuous nature of funding five-year programmes to address practical problems on fisheries. The work of Committee A, under the leadership of Hjort, after a delay of several years, did fulfil the initial remit. Fluctuations in landings were interpreted as being due to population variability.

The explanatory power of this new conceptual framework generated, over time, new studies to provide forecasts of fisheries trends. Hjort again provided the new vision. He stated (1930, p. 8):

> A biological service must be organized for the regular observation of the age distribution in the stock, and of the relative numerical strength of year-classes. It will be something like the meteorological service which records the weather and weather prospects. In the organization of this biological observation, the International Council will have a task which, in itself, will repay all the work and expense that its existence during the past thirty years has occasioned.

The paradigm shift to "population thinking" and the notion that fish form stocks which fluctuate over time owing to environmental variability and fishing pressure were prerequisites to the provision of scientific advice on fisheries management.

In his 1914 paper, however, Hjort was not optimistic that there would be increases in understanding of the ultimate causes of year-class variability. He stated (p. 210) that there was:

> little reason to believe that continued investigation as to the *causes* of the fluctuations in the numerical value of year classes will be of any great immediate practical significance….A final solution of the problem of fluctuations in the fishery by any permanently valid formula must be regarded as an impossibility and all such assertions as to the discovery of such a solution may safely be relegated to the sphere of pure imagination. (Emphasis added.)

By 1926, however, he was somewhat more optimistic and encouraged multidisciplinary studies involving oceanography, meteorology, and fish biology on the problem of the causes of year-class variability. It would take several decades before this category of research was actively promoted by ICES (1980s to the present GLOBEC programme).

Thus, by the 1920s, attributable in large part to the activities of ICES, it was generally recognized that fluctuations in fisheries landings could be due to the influence of climate variability on year-class strengths of geographically restricted populations. The critical period of Hjort (1914, 1926) inferred that both advective losses of eggs and larvae from the appropriate distributional area for the stock, and zooplankton availability at the first-feeding stage of larval development, could contribute to the observed dramatic differences in year-class strengths. "Migration thinking" with respect to the fluctuations problem was history. That is not to say that interannual and decadal-scale migrations were not considered important in fisheries fluctuations. Rather, such changes in migration were conceptualized within the framework of "population thinking".

Population thinking: richness

Schmidt (1909) observed that spawning locations differed markedly between groundfish species. Also, within the overall distributional limits of each species studied, spawning occurred in precise locations. Finally, the geographic areas of spawning were observed to be very small compared with the distributional limits of the species. These results were unexpected, showing a degree of spatial heterogeneity that was beyond anything that previous studies had suggested.

Schmidt carried out an extensive research programme over the next two decades on population (or racial) studies. A series of ten papers entitled "Racial investigations" were published in the *Comptes-rendus des travaux du Laboratoire Carlsberg* between 1917 and 1930. Much of his research was funded by the Carlsberg beer company, following his marriage to the daughter of the company owner. Schmidt reported on a continuum of population richness. The eelpout species *Zoarces viviparus* comprised many populations in coastal waters (Schmidt, 1917). Atlantic cod is characterized by a moderate number of populations, spawning both in coastal embayments and fjords as well as on offshore banks (Schmidt, 1930). After many years of investigation, Atlantic eel was concluded to have a single spawning population within the distributional limits of the species (i.e., the species is panmictic; see Schmidt, 1922).

Schmidt (1930), as did Heincke, speculated that events during the early life history stages were critical to species-specific levels of population richness. The minutes of a 1913 ICES meeting (Appendix D, p. 108) stated:

> Geheimrat Heincke observed that his experience had, in general, shown him that a species could fall into a great number of races. The origin of these races was connected with the difference in the conditions prevailing on the spawning grounds, and even in the youngest stages racial distinctions could be observed. As the eel exhibited no differentiation in its species, it was to be presumed that the conditions on its spawning grounds were uniform.

This quotation indicates explanatory power that Heincke derived from "population thinking". It would be over a decade of extensive research before the single spawning area of Atlantic eel, of relatively uniform conditions, would be discovered in the Sargasso Sea (Schmidt, 1922).

Conclusions

Sinclair (1997) has characterized the change in conceptual framework on the interpretation of fisheries fluctuations as a paradigm shift. However, the development of "population thinking" was a gradual process taking place over several decades. As such perhaps, the term "paradigm shift" (in the sense of Kuhn, 1962) is appropriate for the 1914 conceptual change in the interpretation of fisheries fluctuations, but not for the overall transition from "migration" to "population" thinking (1878 to about 1930). There were several steps in the process. The concept of fish species comprising geographically distinct races, populations, or stocks was initiated in a rigorous manner by Heincke (1898). It is stressed again that this revolutionary species concept at the time arose from a research programme on the fisheries fluctuations problem and the role that overfishing might play. Heincke was the leader of studies on geographic patterns of populations of commercial fish species. His studies (which were generated to solve the fluctuations problem) did not, however, lead to broad acceptance that the existence of populations explained in any way the causes of fluctuations. The results did eventually change the geographical scale of the fluctuations problem (from ocean-basin scale to the area of the population in question).

The concept of year-class variability was defined by Hjort (1914), no doubt based on significant input from his research team of Dahl, Damas, and Helland-Hansen (see Solemdal, 1997, for a more literary interpretation of the genesis of this new concept). Solemdal's interpretation is that Hjort may have been the last of the Bergen team to be convinced that fisheries fluctuations are generated in large part by year-class variability!

The concept of species-specific differences in numbers of populations (or population richness) was developed by Schmidt (1917–1930). He did not use the term "richness," but was searching for a general hypothesis to interpret the empirical observations on species-specific differences in the number of populations. We attribute this development in the history of ideas to three dominant scientists: Heincke for pattern, Schmidt for richness, and Hjort for variability. This interpretation could be criticized for overemphasis on the "big men" of science, with insufficient credit to the broader scientific community of ICES and, in the case of Hjort, of the very able and independent thinking staff that he had assembled. However, our review of the literature does lead to the conclusion that the individual contributions by these ICES leaders were significant in the development of the "notion that fish species form stocks".

ICES did play a dominant role in this change in thinking. In spite of the fact that Heincke's key papers predated the formation of ICES, the concept became accepted and generalized within the ICES community (from 1902 to the 1920s). The work of Committee A provided much of the initial empirical observations (e.g., Schmidt, 1909; Damas, 1909) and the port sampling data that eventually led to the synthesis papers on population variability and richness.

The impact of "population thinking" on ICES has been enormous. It was a prerequisite to the conceptual developments on the theory of overfishing. The work of Committee B on overfishing under the leadership of Garstang, and then Heincke, reinforced the population concept. Smith (1994) traced these events in considerable detail. The studies on catch rates of plaice by Heincke in the North Sea led to the conclusion that fishing mortality was surprisingly high, and also led Garstang to hypothesize that regular migrations occurred within a limited geographical area. This conclusion was confirmed by high rates of tag recovery (Garstang, 1912) and a surprisingly low estimate of the total number of spawning plaice from an egg and larval survey by Buchanan-Wollaston (1923), as described by Smith (1994, pp. 143–152). The work of Committee B, and the follow-up committees after 1906, complemented that of Committee A. The fluctuations problem and the overfishing problem were interwoven in a manner that did not become clear until the 1920s.

The "notion that fish species form stocks" with a number of year classes was a prerequisite (perhaps unstated) of the theory of fishing as developed in a sequential manner by Russell (1931), Hjort *et al.* (1933), Graham (1935), Schaefer (1954), and Beverton and Holt (1957). The title of the latter book, *On the Dynamics of Exploited Fish Populations*, indicates that the population was the unit of study for the analysis of overfishing.

"Population thinking," as developed within ICES up to 1930, also defined the research agenda on recruitment variability in an oceanographic context. Gran's work on the seasonal cycle of phytoplankton growth in relation to mixed layer dynamics (Gran and Braarud, 1935) was framed in a quantitative manner by Sverdrup's critical-depth model (Sverdrup, 1953). This led to Cushing's (1975) match–mismatch hypothesis on year-class variability, an elegant rephrasing of one component of Hjort's 1914 critical-period hypothesis. Sinclair (1988) emphasized the second component of Hjort's hypothesis (i.e., advective losses from the population area) in his member-vagrant interpretation of recruitment variability. All of the above work was done within the ICES framework. It is perhaps no exaggeration to conclude that the ideas of Heincke, Hjort, and Schmidt on "population thinking" have redefined the research agenda on recruitment variability up to the present time.

The impact of "population thinking" of fisheries on the broader scientific community has been uneven. Heincke influenced the development of the biological species concept of Mayr (1942), which was a cornerstone of the so-called Modern Synthesis of evolutionary biology (see Mayr, 1982, for a history of the "synthesis," and Sinclair and Solemdal, 1988, for a summary of Heincke's role). Schmidt was a key early contributor to ecological genetics. Paradoxically, the research contribution of Hjort has been essentially ignored in the development of ecological theory on populations. Kingsland (1985) provided a scholarly history of population biology which was devoid of "population thinking" in the sense developed in fisheries science by ICES and that incorporated into the Modern Synthesis of evolution (i.e., geographically distinct populations of a "biological species concept"). In recent years, however, geographical patterns of populations have become a central component of ecological theory. These more recent developments do not appear to have been influenced by the early ICES development of the "notion that fish species form stocks." It would have been interesting to trace, in the more recent literature, how these concepts were drawn into modern ecological theory, and to what developments this aspect of ICES work may have pointed the way. This implies that improved emphasis on communication of ICES science to the broader scientific community should be an objective of the future.

Smith (1994) provided an historical analysis of the gradual development of the quantitative theory of under- and overfishing. His synthesis, however, did not identify the essential role of "population thinking" as a prerequisite, or unstated assumption, of the overfishing concepts. Sinclair (1997) and Sinclair and Solemdal (1988) did not identify the stepwise nature of the transition from "migration thinking" to "population thinking." We believe that the present summary is a better representation of the complex history of ideas of the "notion that fish species form stocks".

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