Aquat. Living Resour., 1988, **1**, 189-213

The development of "population thinking" in fisheries biology between 1878 and 1930

Michael Sinclair [1] and Per Solemdal [2]

[1] *Department of Fisheries and Oceans, Halifax Fisheries Research Laboratory, Halifax, Nova Scotia B3J 2S7, Canada.*
[2] *Institute of Marine Fisheries, Directorate of Fisheries, Bergen, Norway.*

Received April 11, 1988; accepted September 20, 1988.

Sinclair M., P. Solemdal. *Aquat. Living Resour.*, 1988, **1**, 189-213.

Abstract

The early debate concerning the existence of several self-sustaining populations within the distributional limits of marine species centered on Atlantic herring in the northeastern Atlantic. Fr. Heincke convincingly resolved the controversy by extensive sampling of herring and sprat for the analysis of a large number of meristic and morphometric characters, and the development of new statistical methodology (including rudimentary multivariate statistics). He initially analysed the morphological variability at different parts of the life cycle of spring—and autumn—spawning herring aggregations off Kiel. This detailed study was accompanied by somewhat less-detailed sampling of herring and sprat from other locations in the Baltic Sea, North Sea, and Norwegian coastal waters. Heincke argued that a fundamental shift in both the species concept and the mechanism of speciation was required to account for the emerging empirical observations on marine fish. His observations and conclusions on the nature of geographic variability of fish species, even though revolutionary, were accepted rapidly. The influence of his studies on fisheries research, systematics, and evolutionary biology are evaluated. In addition, the contributions of J. Schmidt and J. Hjort to population thinking are briefly addressed. It is concluded that the studies by Heincke on herring populations, as well as having a major impact on subsequent developments in fisheries biology and management (in essence the definition of management units based on geographic populations or population complexes), also had an important impact on the biometricians (Weldon, Pearson) and the development of the evolutionary synthesis in the 1920s and 1930s (through Chetverikov, Dobzhansky, and Goldschmidt). Observations on geographic patterns in populations from terrestrial systems could be generalized to the oceans on the basis of Heincke's quantitative studies on herring and sprat (and the follow-up work on other fish species).

These early investigations on the very existence of marine populations by Heincke, Hjort and Schmidt are still pertinent to recruitment research and the studies underlying the definition of management units. An historical perspective may contribute to the resolution of present topical issues involving the regulation of populations.

Keywords : Fisheries biology, historical perspective, population complexes, variability of species.

Évolution du concept de population en biologie des pêches entre 1878 *et* 1930.

Résumé

Les premiers débats sur l'existence de populations autonomes multiples à l'intérieur des limites de distribution d'une espèce ont porté sur le hareng de l'Atlantique dans le nord-est Atlantique. Fr. Heincke a tranché la controverse de manière convaincante par un échantillonnage intensif du hareng et du sprat, qui lui a permis d'analyser un grand nombre de caractères morphométriques et méristiques et de mettre au point une nouvelle méthode statistique (comprenant des statistiques à variables multiples initialement rudimentaires). Il a analysé la variabilité morphologique à différentes étapes du cycle de vie des reproducteurs de printemps et d'automne au sein d'agrégats de hareng au large de Kiel. Cette étude détaillée du hareng et du sprat provenant d'autres régions, la mer Baltique, la mer du Nord et les eaux côtières de la Norvège comprenait également un échantillonnage quelque peu allégé. Heincke fait valoir qu'une modification fondamentale aussi bien de la notion d'espèce que des mécanismes de la spéciation était nécessaire pour expliquer les nouvelles observations empiriques sur le poisson marin. Ses observations et conclusions sur la nature de la variabilité géographique des espèces de poissons, bien que révolutionnaires furent acceptées très rapidement. Les conséquences de ses travaux sur la recherche halieutique, la systématique et l'étude de l'évolution des poissons sont évaluées. De plus, l'apport de J. Schmidt et J. Hjort à la notion de population est brièvement abordé. On conclut que les études de Heincke sur les populations de harengs ont non seulement joué un rôle majeur sur les développements ultérieurs de la biologie et de la gestion des pêches (en essence, la définition des unités de gestion fondée sur les populations géographiques ou les complexes de populations, sur les spécialistes de la biométrie (Weldon, Pearson) et l'élaboration d'une synthèse de l'évolution dans les années 20 et 30 (par l'intermédiaire de Chetverikov, Dobzhansky et Goldshmidt). Les observations sur les répartitions géographiques des populations des systèmes terrestres pourraient être étendues aux océans en utilisant les études quantitatives de Heincke sur le hareng et le sprat (et les études ultérieures sur d'autres espèces de poissons). Ces premières investigations effectuées par Heincke, Hjort et Schmidt sur l'existence tangible de populations marines conservent leur pertinence pour les recherches sur le recrutement et les études nécessaires à la définition d'unités de gestion. Une analyse rétrospective des concepts et de leur évolution peut contribuer à la résolution des problèmes actuels de la régulation des populations marines.

Mots-clés : Biologie des pêches, rétrospective, populations, variabilité des espèces.

INTRODUCTION

This paper traces the development of concepts in fisheries biology, in particular the introduction of population thinking, between 1878 (the first paper by Fr. Heincke on populations of herring) to 1930 (the final paper in the series by J. Schmidt on "racial investigations" of marine fish). The development of population thinking involved the shift from the species to the population as the appropriate unit of study for many ecological questions. The term "population" is used in this paper to signify a self-sustaining group of animals which persists in a particular geographic area on ecological time scales. They are the sexually reproducing units that comprise the biological species concept, and are considered to be real entities (rather than abstractions of ecologists in relation to a particular question being posed). The term "population" has not usually been defined in this biological species concept sense in modern ecology (*see* Kingsland 1985). The population concept in fisheries biology (and population genetics, systematics, and evolutionary biology) is thus not necessarily the same as that used in modern ecology.

Even though the history of the development of population thinking as defined in the above sense has been treated in general terms (by, for example, Mayr 1982), and the contribution of this conceptual development to the evolutionary synthesis has been discussed in Mayr and Provine 1980, the specific contribution by fisheries biologists has not received historical treatment. This paper is thus an initial contribution to the history of this subject area in fisheries biology. It is also hoped that such a historical review of the development of population thinking in fisheries may contribute to resolving extant contentious issues in population biology.

The value of taking a historical perspective in carrying out scientific research has been discussed by Medawar (1979) and Picken (1960). Picken, in a somewhat apologetic tone in his introduction to *The Organization of Cells and Other Organisms*, states (p. XXXIV),

> "A knowledge of the history of changing ideas in the past, far from being a luxury, is essential as a means of accustoming us to, and preparing us for, the possibility of ideas changing in the present and the future; and it may make us the more ready to experiment in enlarging or revising our concepts; it will make us self-conscious about our habits of scientific speech; it will tend to make us aware of the gyves and manacles of language which set limits to our powers of observation."

Picken is suggesting that the recent scientific literature at any time period, and the underlying generally accepted theories, can mask one's perception of reality and set limits on what observations are made. Medawar (1979) elaborates on this point in his short book, *Advice to a Young Scientist*. He states (p. 30),

> "A most distinguished French historian, Fernand Braudel has said of history that "it devours the present". I do not quite understand what he means (those profound French epigrams, you know), but in science, to be sure it is the other way about: the present devours the past. This does something to extenuate a scientist's misguided indifference to the history of ideas."

Braudel (1981) explains what he means by this so-called epigram. He argues most effectively in the *Structure of Everyday Life* that the inertia inherent in traditions in cultural activities prevents change from happening when the materials for change are readily available. He states (p. 28), "The obstinate presence of the past greedily and steadily swallows up the fragile lifetime of men." An example provided by Braudel is the lack of development of overland transportation systems between the fifteenth and eighteenth centuries in spite of the availability of appropriate technology. In daily activities the past can dominate the present, and it is in this sense that Braudel develops his theme. In science, however, we are perhaps less influenced by the older literature; the present devours the past, as Medawar states.

Is there anything inherently dangerous with this converse that is characteristic of science? Without putting too fine a point on it, one can argue that real knowledge, in science as well as in other disciplines, cannot be achieved without an understanding of the temporal component. Why, for example, was the biological species concept accepted with such difficulty by natural historians and systematists at the turn of the century? A clear understanding of the previously accepted species concept, and the turmoil in the literature as this fundamental concept about the natural world was rejected, adds richness and significance to the new species concept that emerged. For us the bland definition of the biological species concept, which was learned by heart during introductory courses in biology, took on new meaning when considered in a historical context. It may well be that the biological species concept, and its full significance to evolutionary biology, cannot be fully understood in ahistorical terms.

Collingwood (1946) goes further in stating (p. 10), "The value of history, then, is that it teaches us what man has done and thus what man is." Paraphrasing for a science context, a historical perspective teaches us how concepts have arisen and thus a fuller appreciation of their full significance. This paper attempts to describe the development of a new concept in fisheries biology, that of populations, and the explanatory power that accompanied its acceptance by the scientific community.

HEINCKE'S CONTRIBUTION TO POPULATION THINKING

Darwin's theory of evolution of species undermined the typological species concept. After 1859, increasing emphasis was directed by naturalists toward describing the geographic patterns in variability between individuals of a species, and evaluating the significance of this variability to natural selection. This created some tension in systematics which was still largely based on the identification of the ideal type or form of each species and finding representatives for incorporation into museum collections. The transition in marine fisheries research—from considering the typological species as a useful unit of study, to recognizing persistent geographic variability in form as an important characteristic of species—occurred relatively early compared to other areas of natural history. This happened to a large degree as a result of problems in the fishing industry and resultant pressures on fisheries biologists to provide advice on the management of the exploited resources. Much of the debate in the marine fisheries literature during the mid-nineteenth century on the nature of the species was focussed on Atlantic herring. In this section we first discuss the issues that were being debated at that time. Then Heincke's contribution to the resolution of the issues is summarized using his published papers and comments on them by other fisheries biologists. Particular attention is addressed toward his thoughts on both the species concept and evolutionary biology. Finally, the impact of Heincke's research on fisheries biology and flanking disciplines is evaluated.

The herring problem prior to 1878

In the "Introduction" sections of both the 1878 and 1898 major papers on Atlantic herring, Heincke provides extensive background information on the topical research questions of that time. Variability between individuals of the same species had been repeatedly observed, first by the fishermen and subsequently documented by the naturalists, and thus its existence was well accepted. There was not, however, a concensus on the interpretation of the empirical observations.

Much of the debate in northern Europe focussed on Atlantic herring. The Swedish zoologist Nilsson (1832) in his book *Prodomus faunae ichthyologiae Skandinaviae* maintained that the species *Clupea harengus* L. comprised a large number of geographically restricted self-sustaining populations. This conclusion contradicted the extant hypothesis of that time, which was first stated in 1748 by the Englishman, Dodd, and further developed by the mayor of Hamburg, Johan Anderson, in 1748. They had proposed that herring in the northern Atlantic was highly migratory. In the spring of each year it was interpreted that herring schools migrate from Arctic waters to the diverse coastal areas of northern Europe, returning again to the polar waters in the autumn. The Dodd-Anderson polar migration theory was based on the tacit assumption that there was one vast aggregation of herring in the northern Atlantic, with no local varieties. In 1786 an American, Gilpin, extended the polar migration hypothesis to the northwestern Atlantic and further generalized that the timing and extent of migration was defined by water temperature changes. This hypothesis was generally accepted by nonspecialists until early in the twentieth century. Hjort, for example, as late as 1914 discusses it as a working hypothesis in the introduction to his classic paper on fluctuations.

In the years 1826 to 1833, Nilsson was commissioned by the Swedish government to carry out research on the coast of Bohuslan to determine the reasons for the collapse of the herring fishery in 1808.

The results of his studies were set forth in his report to the Swedish government in 1832. As stated above, he concluded that herring consists of numerous local populations which acquire their particular traits as a result of the physical character of the particular region of the ocean which they inhabit year round with a limited geographic scale of migration.

The debate which followed Nilsson's report was heated and of long duration. It was aired in public as well as in scientific circles because of the critical importance of herring fisheries to the economics of northern Europe and the implications of the two hypotheses (variants of Dodd-Anderson versus Nilsson) on fisheries management issues. If the polar migration hypothesis was valid, the local declines in landings could be interpreted to be a result of interannual differences in migration patterns rather than due to the effects of overfishing on a local population. Nilsson's hypothesis urged for local responsibility in regulating fishing effort to ensure relatively stable future landings. In addition, the alternate hypotheses on Atlantic herring population biology had implications for the advantages to be expected from hatchery-raised stocking of local areas with herring larvae, an activity which was being actively pursued in the latter half of the nineteenth century.

The debate involved several camps. The extreme positions were held respectively by Nilsson (and his followers) and the Danish ichthyologist, Kröyer (and his followers). The scientific dispute between the two opposing sides was fought out not only in the essays of learned societies, notably the Swedish Academy, but also in writings of economic societies, in numerous lectures, and in the daily press. The confusion in the literature was particularly fueled by the zeal of Nilsson and his followers in oversplitting (*i. e.* identification of too many populations) and the fundamental limitations in the methodology of identifying populations (*i. e.* the essence of a variety or population could be expressed by a short diagnosis of a fully grown individual, a typological description). They carried to extremes the splitting of herring into local populations. Heincke interprets that by defining small geographic areas for each population, Nilsson was attempting to influence the government and industry to introduce conservation measures into each of the areas. Some of the descriptions of putative populations very quickly turned out to be useless. The limitations in the methodology, and the complexity of the empirical observations on herring (differences in timing of spawning between and within areas, differences in size composition and morphology), provided ample opportunity for criticism of the Nilsson hypothesis. Kröyer asserted, on the basis of comparative studies of samples of herring having extreme differences in characteristics, that the differences were not constant. He assumed that the observed differences could be explained by differences in age, sex, maturity, and nutritional state, rather than due to population differences. The overall literature was in chaos. Even though few scientists upheld the polar migration hypothesis of Dodd-Anderson in its strict form (*i. e.* homogeneity of all Atlantic herring), on essentially every issue of significance, there were strongly held contradictory opinions within the scientific community. The full flavor of the debate and the number of intermediate positions between the extremes of Nilsson and Kröyer can be garnered from the "Introduction" sections of Heincke 1878 and 1898.

There was heated debate in British scientific circles as well as in continental Europe. To a large degree it appears that the arguments were developed independently. Bertram (1865) treats the herring polar migration hypothesis somewhat distainfully. He attributes the hypothesis to Pennant rather than to either Dodd or Anderson. Pennant added a moral dimension to his statement of the hypothesis (p. 229, quoted by Bertram 1865).

> "Were we inclined to consider this migration of the herring in a moral light, we might reflect with veneration and awe on the mighty power which originally impressed on this useful body of His creatures the instinct that directs and points out the course that blesses and enriches these islands [British Isles], which causes them at certain and invariable times to quit the vast polar depths, and offer themselves to our expectant fleets... It is not from defect of food that they set themselves in motion, for they come to us full and flat, and on their return are almost universally observed to be lean and miserable."

Bertram, in 1865, was clearly aggravated by the acceptance in some circles of "this myth" (*i. e.* the polar migration hypothesis) and summarizes the recent findings that supported the existence of local populations of herring. Cleghorn (1854) independently presented an interpretation similar to Nilsson's at the Liverpool meeting of the British Association. His interpretation was based on temporal patterns in fishing effort and landings along the Scottish coast in the vicinity of Wick. Because he believed that the fluctuations in landings of herring were due to overfishing of local populations rather than to variability in "migration", according to Bertram he suffered much local persecution. Mitchell, the Belgian Consul at Leith (1862), also presented a paper to the British Association (at the Oxford meeting) on populations of herring around the coast of Scotland. His conclusions were based on differences in morphology and quality of herring spawning in different locations. Bertram, in discussing Mitchell's paper, states (p. 234).

> "A Lochfyne fish differs in appearance from a herring taken off the coast of Caithness while the latter again differs from those taken by the Dundee boats of the Isle of May. Experienced fishmongers know the different localities of the same kinds of fish... they can tell at a glance a Lochfyne *matie* [herring] from a Firth of Forth one."

The arguments on each side of the general debate, just as was the case in Germany and the Scandinavian countries, could not be convincingly resolved on the basis of the extant scientific methodology.

Heincke's research questions

It was within this context (*i.e.* a highly polarized scientific debate on the fundamental characteristics of species) that Heincke defined his research questions. He was interested in fish species in general, not just the commercially exploited resources. The argument went far beyond herring and at root was based on an inadequate species concept in systematics. The empirical observations on variability between individuals undermined the credibility of the typological or essentialistic species concept. A quote from Czerny (1857) illustrates the tension that was generated by the contradiction between observation and theory. He states in an article discussing the identifying characteristics of freshwater fish in the area around Charkov, southwestern Russia,

> "As far as I know little attention has been given to the important conclusions which may be drawn from these results, *i. e.* that many of the characteristics commonly used to identify the species of fish are subject to much greater variation than is supposed, and that *many data thought to be erroneous* are in fact correct: two areas, even adjacent ones, may show considerable variation in the identifying characteristics of the same fish species" (emphasis added).

Heincke felt that the failure to resolve the herring species/population controversy was due to the methodological approach adopted rather than a lack of zeal. What were required, in his view, were more complete descriptions of the different forms of herring and careful studies of developmental history and life-cycle distributions. Further, he felt that the shortcoming of previous studies was in part due to their narrowness of scope. The studies were too practically oriented; and because of the narrowness in the definition of the individual diverse studies, they could not hope to resolve the overall problem convincingly. In his view, some exacting fundamental work in systematics was required prior to the resolution of particular applied fisheries problems in a particular geographic area. Heincke's thoughts on the relative importance of fundamental and applied research in solving the "herring question" in 1878 are worth quoting at length (p. 45):

> "In the relatively minimal consideration of these important points, there is the methodological shortcomings of previous research, and the source of that shortcoming was the one-sided "practical" point of view from which the herring question was tackled. In almost all of the previous research one was anxiously eager not to lose sight of its great practical purpose; one feared that one might act contrary to this great purpose if one allowed oneself to be lured into purely systematical or anatomical research which must tie the explorer to his desk and divert him from the direct observation of the living animals.
>
> Even where the need for an answer to such questions became undeniably clear, such as for example with Axel Boeck, one of the most notable explorers of the field, we find only fleeting attention given to it. Boeck's attempts to find tenable differences between the varieties in their bodily characteristics, such as for example, through the measurements of dimensions, failed almost from the start. Lack of success diminished the interest in monotonous and tedious examinations; and the manifold biological and practical questions pressed into the foreground.
>
> Now, it is my belief that the search for herring varieties is one of those scientific problems where the "pursuit of practical purposes" is, for the time being, the least practical thing that one can do. Let us for once try to limit ourselves, let us forget our desire to learn about the migrations, spawning times, and varieties of herring all at once, and to the fullest extent! The last is a goal which, in view of the difficulty of the whole investigation, will not be attained in the foreseeable future.
>
> Rather, let us devote our special attention to any particular subject out of the biology of herring, and let us try to advance in a narrow area slowly, but exactly. In other words: let us, for once, proceed strictly scientifically, even at the risk of becoming one-sided."

Heincke did just that. For about 25 years he rigorously addressed what the considered to be the critical question of the day, *i. e.* a realistic characterization of the biological species.

Heincke's herring research can be considered to comprise two periods (1875 to 1882 and 1887 to 1892). In 1875 he was asked by the Commission for the Scientific Investigation of German Seas in Kiel to address the question of the existence of populations of herring. The results of his work are described in detail in the 1878 and 1882 papers entitled *Die Varietäten des Herings*. Heincke clearly states his research question in the introduction to his 1878 paper. Again, it is of interest to quote his statement in full (p. 45),

> "The question to which it shall be my task to find an answer, can be formulated thus: Is the species *Clupea harengus* within its range really divided into varieites which differ in their bodily characteristics, and which can withstand the sharpest critique of science? Or are all the observable bodily characteristics within the species such as can be shown to depend on age, sex, and other factors which influence the variability during the length of time of its existence?"

In this synthesis paper of 1898, Heincke states the research objectives of the second period of his herring studies conducted between 1887 and 1892. This second period of research was initially supported by the Berlin Academy of Science but later exclusively by the German Sea Fisheries Society. The overall aim was to overcome the weaknesses in his earlier study and address the major criticisms that had subsequently arisen in the literature. To this end, he wanted to quantify the age effect and the population effect for a given character of Atlantic herring, increase the number of characters analysed, and sample more geographic areas. Specifically, he states (p. 34),

> "1. Examination of a greater number of local forms from geographically more separate areas.
>
> 2. Of each local form examine a greater number of ready-to-spawn individuals of one and the same shoal. Only in this manner can one to be sure that the sample is a true sample of a pure local form to properly differentiate between the fall and spring herring of the Bay of Kiel. One must visit both at their spawning grounds, while they are in fully mature conditions; that means one must visit the ones in the open sea in autumn, the others in the Schlei in the spring. As I have shown to be probable, the fall and spring herring of the Bay of Kiel mix during the winter months into common shoals. It would obviously not do to try and learn the difference between the two races through an investigation of such not ready-to-spawn mixed shoals. I was temporarily not clear about how many individuals of each race were to be examined; mostly, I chose 30.
>
> 3. If possible, one should determine for one and the same local form the entire variation of body form from the larval stage to the sexually mature animal, and beyond this until the attainment of the greatest body length. In doing so, one should investigate all the used bodily characteristics for age-dependent changes (with due regard to differences in sex).
>
> 4. The number of body characteristics to be examined should be increased considerably. The combination of characteristics is to be carried to the point where individual descriptions of single herring can be attained. Special attention should be paid to such internal or external characteristics which are individual constants, such as the number of vertebrae, because these are the most convenient for the discovery of racial differences."

It is important to consider the time period during which these two major studies were carried out (the field work was carried out intermittently between 1875 and 1892). The early period pre-dates by two decades important developments in mathematical statistics. The first great formative period in mathematical statistics started in 1890 (Pearson, 1965). Pearson mistakenly identifies a paper by Weldon (1890), which shows that the distributions of four different measurements (expressed as ratio to total length) made on several populations of the shrimp *Crangon vulgaris* closely follows the Gaussian law, as "...almost certainly the first paper in which statistical methods were applied to biological types other than man." Heincke's initial work, published in 1878, predates Weldon's study by 12 years. The influence of Heincke's work on Weldon, and thus indirectly on the growth of mathematical statistics, is addressed in a following section (it is perhaps noteworthy to indicate at this point that Pearson [1967] considers that, "...the first great formative biometric period ended with Weldon's death.") Heincke (1898, p. 37) infers that he developed his own statistical approaches independent of the statistical studies of Galton on inheritance in human populations. He states,

> "I know that I could have saved myself much tedious labour if I had been fully conversant from the start about the improvements in anthropology and in statistics of the last decades. There is no doubt that the general problem of herring populations is entirely similar to that of human populations, that both can be solved only through the same methodology of research. Many applications and laws of variability that were known in anthropology I have found anew, totally independent of it. On the other hand, my labours may bring something new that is hitherto unknown to anthropologists and that constitutes progress beyond their method."

Heincke's quantative methodology

In his first study on the population of herring. Heincke made measurements of 11 characteristics on approximately 2000 specimens. His second study was more extensive, involving 65 characteristics and over 6000 specimens. To analyze the large number of observations he developed rudimentary multivariate statistics.

From the averages and coefficients of variation of the diverse characteristics, he first calculated Gaussian or Normal curves following methodology that had recently been developed in anthropology. He tested for differences between geographic populations in single characteristics by comparison of distribution curves which differed according to their means, coefficients of variation, or both. Heincke in this manner analyzed a number of characteristics which he showed to be independent of age and gender (number of vertebrae, keel scales, and fin rays). Several far-reaching conclusions were drawn (quoted in summary form from Duncker 1899, p. 366).

> "1. The existence of local populations of herring is proven beyond a doubt.
>
> 2. The populations of herring differ from one another in very many qualities, and generally in those in which the species of the genus *Clupea*

differ from one another. Only the differences between the populations are mostly, but not always, smaller than those between species.

3. As a rule, populations which are distant from one another geographically (or, better, in a physical sense that live under very different external conditions) differ more in certain qualities than do populations that live closer together. There are, however, also populations and characteristics for which the opposite can be true."

4. The curious phenomenon of seasonal [spawning] populations living side by side [not to be confused with seasonal dimorphism!] such as the autumn – and spring-spawning herring of the western Baltic.

5. The populations differ from one another as do the species, in one or more characteristics; the more noticeably so the greater the differences in the conditions under which they live. Among the most important characteristics are the number and shape of the keel scales, the number of vertebrae, and the mass of the skull. As regards to the latter, there exists among herring brachiocephalic as well as dolichocephalic populations, just as among humans.

6. The population peculiarities must be regarded as hereditary in all cases where the question could be tested. For example, the population averages of the herring of the Schlei were the same when repeatedly tested over several years. The author further concluded from the uniform results of these examinations that, "...the young brood of the herring of the Schlei, once they have grown to sexual maturity, return to the place of birth, to spawn..." there.

7. The areas in which the separate populations of herring dwell are obviously very different in extent. According to my theory, the herring as a rule do not leave these areas during their entire span of life..."

The existence of local populations was thus proven by statistical analysis of single characteristics. The second task was to identify membership of individual herring to specific populations. Heincke accomplished this by the method of combined characteristics, which he invented. The crux of the method was the calculation, for an individual herring, of the relative deviations from the averages of the various characteristics of diverse populations. The population for which the deviations raised to the square yield the least sum is the population to which the individual belongs; or if it represents a new population, the one to which it is most closely related. This application of rudimentary multivariate statistics for the identification of individuals to populations was a major accomplishment. Quantitative methodology was rarely used in either natural history or systematics. Heincke (1898, p. 72/73) states this aversion to quantative methodology in strong terms,

"Most of our morphologists have a pronounced aversion toward measurements and numbers. This aversion is understandable because many of them have no mathematical sense, and no schooling in mathematics. The aversion is admissible when it is a manner of gaining a quick overview about the manifold varieties of organic forms, and is pardonable when the pleasure of the composing artist in the beauty and variety of forms and in his fanciful conceptions is greater than the sense for exploration of the analytical scholar; but this aversion toward measurement and numbers, which at times is heightened into contempt, is incomprehensible, inadmissible, and unpardonable when the scholar demands that his labours be regarded as a contribution to the knowledge of the true laws of nature."

The surprise to Heincke and the scientific community was that variability in most morphological characteristics was distributed following Gaussian curves and thus followed the laws of probability. Because of this, populations could be identified by the use of single characteristics, and individual membership by his method of least squares of combined characteristics.

The analysis, however, did not lead to the complete rejection of the typological species concept, but rather to its elaboration. It is very clear from his publications that the limitations of the typological species concept were a predominant concern. This is discussed in some detail in the next section. The empirical observations led to the conclusion that the individuals of a spawning population are in each of their characteristics, as well as in the combination of all of them, the manifestation by chance of an "ideal type" which is defined by the average values for that particular population.

The new method of combined characteristics was applied to several topical fisheries problems. The method was somewhat limited by the lack of statistical descriptions of many of the spawning populations in the northeastern Atlantic. Most of Heincke's sampling had been carried out in the Baltic and North Seas. Of special interest was his application of the method to the resolution of the source of the herring which overwinter off the coast of Bohüslan, Sweden. The overwintering aggregations were largely missing from this area from 1808 to 1877/78. It was the cyclical disappearance of the so-called Bohüslan overwintering herring that led to the initial study by Nilsson (1832), commissioned by the Swedish government. In 1887, Heincke identified overwintering herring caught in this fishery as being closest morphologically to those spawning in the northeastern North Sea on the Jutland Bank. Following this analysis he undertook a cruise to the Jutland Bank in August 1889 to more adequately sample the spawning population. The results were consistent with his preliminary conclusion. Ready-to-spawn herring of the Bohüslan characteristics were caught in large numbers on Jutland Bank. Heincke's study in this way contributed to an improved statement of the Bohüslan fishery problem (*i. e.*, what causes the temporal fluctuations in the geographic location of overwintering of Jutland Bank herring?). G. Ekman and O. Pettersson found that the horizontal and vertical structure of water masses in the Skagerrak off the coast of Bohüslan varied both seasonally and annually. The overwintering migration of Jutland Bank herring to the Skagerrak was interpreted to be a function of water mass characteristics. Subsequently, Pettersson (1914) interpreted the cyclic appearance of overwintering herring off the Bohüslan coast as an availability problem caused in part by ocean climate changes, in particular the 18.6-year tidal cycle.

Heincke also used his method to formally refute the Dodd-Andersson polar migration theory applied to the herring caught off the shores of Great Britain in summer and fall.

Heincke's contribution to systematics

A recurrent theme that occurs throughout Heincke's work is his acute dissatisfaction with the Linnaean typological species concepts. In his first (1878) paper on herring he notes (p. 67), "Der Variationsumfang in den meisten Eigenschaften des Herings muss nach unsern gewöhnlichen systematischen Vorstellungen sehr bedeutend gennant werden." ["The range of variation of the characteristics of herring must be called very large according to our habitual systematic notions."] In his 1880 paper on pipefish populations he states (p. 329), "So sicher es demnach ist und nicht anders sein kann, das Localracen existiren, so reicht doch unsere gegenwärtige Kenntniss dieser Art und vor allem die bishern von den Autoren geübte Methode der Beschreibung nicht aus, die wirkliche Form dieser Localracen zu erkennen." ["Despite the fact that we can be sure that local populations exist, our present knowledge of the species and especially the method of description used up until now are inadequate for identifying the characteristics of these local populations."] In sum, the systematics methodology itself inhibited a realistic geographic description of variability in form that would allow analysis of population structure. The emphasis of the methodology for identifying typological species was on characteristics of mature individuals which did not show much variability. Heincke, 1898 (p. 90/91) describes the effect of this approach as follows.

> "In so far as he... searches out the few characteristics of a group of individuals which from a certain age onwards remain individually constant and rejects all others, he renounces all intellectual grasp of specific forms, but merely builds a system for the schematic serializing of species into an artificial framework which, at best, might be suitable for a museum. It is the task of science to discover the true differences between individuals, and these differences are found in all the parts and characteristics of the body. There are differences in the cycle of life, not differences in rigid, unchangeable forms."

He further argues that (p. 11),

> "The reason for this constant failure to observe and describe this natural phenomenon [*i. e.* existence of geographically limited populations of fish species], which does actually exist—and so with the local forms of herring—was not in any way a result of lacking qualifications of the researchers, who on the contrary were equally distinguished in genius, perseverence, and diligence. The true reason lay in the inadequate tools of research, and particularly in the incompleteness, indeed in the utter uselessness of the method of systematic description—a method that has governed the zoological sciences into the most recent of times, and to some extent still governs them. The dogma of the constant characteristics of the species and its varieties, the belief that these characteristics, and through them the nature of those systematic categories could be grasped through the description of a few so-called typical individuals... this method was utterly incapable, even in the hands of a Nilsson, of bringing to light that which the genius of the researcher sensed and believed."

The typological method is summarized by Heincke (p. 14) using the descriptions of herring by Günther (who had been particularly careful to use essentially all the existing literature),

> "*Clupea harengus*
>
> The height of the body is approximately the same as the length of the head. The lower jaw protrudes; the upper jaw extends to just below the middle of the eyes. An elongated, oval cluster of minute teeth is found on the tongue and the vomer; teeth in the palate, when existing, are minute. Gill arches are fine, and closely spaced, about as long as the eye. The ventral fins are under the middle of the dorsal fins. Thirteen keel scales are behind the ventral fins. The operculum is without radiating stripes. No black shoulder spots are visible."

The distinctive features, however, proved to be difficult to use in the field. The method assumed that the distinctiveness of a species could be described by a limited number of supposedly typical, sexually mature specimens, and that the characteristics chosen were constant within the species. Heincke's extensive sampling demonstrated that the life-cycle morphological variability itself, and its geographic pattern, was of interest in the definition of a species. He strongly focussed the attention of both systematics and natural historians on the variability of individuals and the very existence of populations. Similar observations were made by systematists working on terrestrial animals. The combined literature challenged the usefulness of the typological species concept.

Goldschmidt (1940) captures the excitement generated within the university system in Germany as results such as these became available in the literature. He states (p. 27),

> "I remember distinctly the *shock* which it created in my own taxonomic surroundings (I was an ardent coleopterologist at that time) when Matschie claimed that the giraffes and African mammals had many different subspecific forms characteristic for different regions which he could recognize with certainty; when Kobelt claimed that the mussel *Anodonta fluviatilis* was different in each river or brook; when Hofer stated that each Alpine lake contained a different race of the fish *Coregonus;* or when Heincke claimed the same for herring" (emphasis added).

Such observations contributed to the new species concept (the Rassenkreis of Rensch in the early 1930's in German and the so-called biological species concept popularized by Mayr shortly afterwards in English). *See* Mayr 1942 (Chapter 1) for a discussion of the shift in emphasis in systematics that occurred as data accumulated on the geographic variability in morphology within a species. Goldschmidt (1939) indicates that Heincke's detailed work on herring predated the taxonomic reform by several decades. Goldschmidt states (p. 31),

> "I might mention one such case [the requirement for a statistical approach in defining populations] in order to show that a conception very similar to the rassenkreis concept had been arrived at in a very different way prior to that taxonomic reform. The herring in the North Sea forms large schools which are found in definite localities and travel to definite spawning grounds. These localities are different over the whole area inhabited by the species, and each area has a different constant race which, however, cannot be distinguished by ordinary taxonomic methods. Only a biometric study of a series of variable characters like number of vertebrae, number of keeled scales, and about sixty others, and their evaluation by biometric methods, permitted Heincke (1897-98) to find the constant racial differences. Since that time similar work with identical results had been performed by many ichthyologists..."

Heincke's analysis of the nature of the species (*i.e.* usually comprised of groups of relatively isolated populations) led him to conclude forcefully that the population should be the unit of study in natural history, not the species. He states (p. 42),

> "Does it not teach us that the starting point of all our systematic and biological research must no longer be the species, but the local form?"

Finally, Heincke recognized the critical importance of a realistic species concept on the development of evolutionary biology. This realization appears to have occurred early in his research career at the time he was asked in 1875 by the Commission for Investigation of German Waters in Kiel to address the question of the actual exsitence of populations of herring. It is of interest to quote at length his thoughts in 1898 of the development of his new method for the systematic description of species and populations which was published in the 1878 and 1882 papers. Evolutionary theory was at the forefront of his study from the very beginning (p. 13/14, 1898),

> "I succeeded in developing this method not only through thorough analysis of the variability of numerous marine and freshwater fish, whose results I published later in different articles (115-117), but especially through comparative study of the various publications on the variability of the wild and domesticated organisms with the inclusion of man, in particular the works of Darwin himself. I recognized that the old method, handed down by Linné, of systematic description for the recognition of the natural diversity of form and its laws, is completely insignificant. It fails completely where it is a matter of differentiating between closely related species, and of recognizing the great variety of forms in which one and the same widely distributed type may appear. Yet a firm foundation of evolutionary theory can be erected only on a knowledge of these matters. I was astounded that eminent followers and advocates of the theory of evolution and of Darwinism still made use of Linné's old tool of methodological representation, in order to demonstrate the inconstancy and changeability of species. However, they fail to notice that the species concept with which they are working is a completely inadequate term for the individual groups that really exist in nature. As created according to the old method, this concept appeared to me to a more-or-less worthless abstraction, which could not prove anything either for or against the theory of evolution. Indeed I entertained serious doubts as to whether the presently reigning form of the theory of evolution, the theory of gradual transmutation of the species by natural selection, is a proper expression for the description of the actual occurrences in nature. After all, this theory is itself tailored according to the dated concept of species, which it aims to destroy."

The issues so clearly identified in the above-quoted paragraph, which represents Heincke's thoughts as a young scientist as early as the 1870's (less than 20 years after the publication of the *Origin of Species* by Darwin), were central to the prolonged debate which preceeded the evolutionary sunthesis (which did not take place until the 1930's). The changing species concept itself played a major role in the elaboration of Darwinism on route to the synthesis. Heincke's research on herring and other fish played a significant role in this process (his influence on Weldon, Chetverikov, and Dobzansky, for example, is documented in Section: Impact of Heincke's research).

In retrospect it is difficult to fully comprehend the tension and difficulties that occurred in the scientific community as the new description of nature arose (*i.e.* from an emphasis on essences and constancy to an emphasis on individual and group variability and change). Deep-rooted cultural perceptions of reality were forced to change by the overwhelming evidence that was accumulated by systematists and natural historians. This event in intellectual history involved metaphysics as much as natural history. Goldschmidt uses the word "shock" to describe the impact of these observations on species within the university community. Heincke himself indicates that the transition in concepts was not an easy one. He states in concluding his Chapter 4 (1898 paper) that there was still considerable uncertainty about the number of populations of herring and their geographic patterns because of limitations in his initial sampling program (*i.e.* for the 1878 and 1882 papers). In addition, however, there was undertainty due to his difficulty in giving up the essentialistic species concept. He states (p. 21).

> "...but most importantly, I myself have still not completely shed the restrictions of the old systematics."

It is not clear that this difficulty refers to his thoughts in 1875-1882 (the time period dealt with in Chapter 4), or his thoughts at the time they were written (1898). Nevertheless, Heincke did not fully give up essentialism, within his metaphysical approach to his work. This is clear from his treatment of the new species concept in Chapter IX of his introduction to the 1898 paper.

In this final chapter of the introduction he deals with results that he considered to be of general significance, in particular in relation to evolutionary theory. He begins the chapter with a discussion of new systematics. He stresses that a knowledge of variability is an essential foundation for any theory of descent. This knowledge is to be acquired by a detailed description of the actual quantitative differences between individuals (in measures and counts). From this empirical basis an improved methodology in systematics would be possible. He states that there are countless spatially separate forms—the individuals—which are unequally different from one another and which can be combined into groups of increasing order according to their degrees of difference. He argues that these groups are as sharply differentiated morphologically as are the individuals. Just as the individuals are real, so are the groups (*i.e.* population, species). To the degree that these groups are correctly recognized, they describe the natural system. This view of nature and systematics is a very different one than that defined by Darwin who did not consider species to be real units in nature.

Heincke then defines in some detail his concept of populations, species, and the process of speciation. The description of a spawning population, however, includes reference to random deviations from an ideal type. He states (p. 372 from Duncker 1899),

> "1. The family (population) as a systematic grouping of the first order.
>
> The family is a group of individuals which live at the same place and under the same conditions, have the same habits, and which because of immediate cross-breeding and procreation are related to each other directly by blood... Morphologically, the single individuals of a family are only the accidental manifestations of an *ideal type*, represented by the averages of all individuals... All individuals, however, deviate in the combination of all their characteristics, taken as 'whole' equally from the *ideal type* of the family" (emphasis added).

Thus, there is a residual typological component in Heincke's new systematics. His thoughts on the lack of importance of reproductive isolation as part of the species concept appear to result from his preoccupation with morphology. He states (p. 376 from Duncker 1899),

> "5. The kind, or species
>
> This category is the second level in the natural system. It is a grouping of the most similar families. At the same time it is purely a morphological concept, because the formerly valid criterion that all its individuals must be capable of reproducing with one another to create permanently fertile offspring can no longer be maintained... Just as the families are more differentiated than their individuals, so also are the species more strongly differentiated than the families composing them. The magnitude of the difference is the measure of the breadth of the individualizing organic boundary separating the groupings of the nature system."

This latter definition of species is not too clear without consideration of his concept of speciation, which is addressed in the next section.

Heincke's contribution to evolutionary biology

As discussed above, Heincke considered that a more accurate definition of the species concept, which included a description of the range of individual variability and of geographic population patterns, was essential to an improved understanding of evolution and the putative role of natural selection in this process. From the beginning of his herring studies in 1875 it is clear that he was very much influenced by Darwin's *Origin of Species* (1859). The concept of evolution itself was accepted without question throughout his studies. However, there are changes in his support for the importance of natural selection in evolution, from initial doubts in the 1878 herring paper to strong criticism in this 1898 paper. It was the empirical results themselves on the nature of the nature of the observed variability that generated this changing point of view. In his 1898 paper he goes so far as to propose in skeleton form an alternate mechanism of adaptation and speciation. His contribution to evolutionary biology was recognized as being substantial by his peers in fisheries biology (Duncker, 1899; Kyle, 1899; Redeke, 1912, for example) but does not appear to have been evaluated seriously by the broader scientific community. This is not due to a lack of exposure of his work, because the systematics component of his papers (the empirical observations and his quantitative method of analysis) have been widely cited within the literature that contributed to the evolutionary synthesis in the 1920's and 1930's. It must be concluded that his specific thoughts on problems with natural selection were not widely accepted, either at the time of their publication or subsequently.

In summarizing Heincke's thoughts on evolutionary theory it is important to recognize the meaning of the term "natural selection" during the time period 1878 to 1898. It was not used then in the same sense as in the last few decades (as an aside, even today "natural selection" means quite different processes to different scientists [Endler 1986, Chapter 1]). During the latter half of the nineteenth century, "natural selection" implied intense intraspecific competition as suggested in the alternate expressions "survival of the fittest" and "struggle for existence." Darwin's metaphor of the wedge (p. 119) visually implied such a process,

> "The face of Nature may be compared to a yielding surface, with ten thousand sharp wedges packed close together and driven inwards by incessant blows, sometimes one wedge being struck, and then another with greater force."

Also because of the accepted concept of blended inheritance (which rapidly damped out variability between individuals), and the then estimated relatively short time span of the existence of the earth, it was hypothesized that evolution must be rapid and thus the process of natural selection should be intense. The empirical results on variability within and between populations described by Heincke did not, in his view, provide support that intense competition was generating the observed patterns. Other natural historians and systematists who were describing population patterns came to similar conclusions concerning the lack of support for natural selection (*i.e.* Gulick, 1872; 1888 on land snails).

Heincke (1878) devotes a specific section ("Stellung zum Darwinismus," p. 118-122) to evolutionary questions. He considers that section to constitute a critique both for and against Darwin's theory of descent. It is beautifully written and provides evidence of his penetrating mind and a rigorous scientific approach to natural history. With obvious admiration for Darwin and Haeckel (the author of the biogenic law), he critically discusses their theories in relation to his empirical results. References are made to other evolutionary biologists such as Weismann and Naegeli. This is pretty exciting stuff to be found in a fisheries journal. Heincke was 26 years old in 1878, and in his own words had married, "...the most beautiful girl in Kiel" (Bückmann, 1982). He evidently was working with great energy and had no lack of confidence concerning the significance of his study on herring to the major intellectual issues of that time. Darwin (1859, p. 454) states that when the views, "...on the origin of species, or when analogous views are generally admitted, we can dimly foresee that there will be a considerable *revolution* in natural history." Heincke's work must be considered part of that revolution.

The observation that the differences between populations of the same species are of the same type as those between species of the same genera (*i. e.* herring and sprat) provided strong field evidence for gradualism (and thus Darwinism). However, the nature of the variability between individuals and populations (and the coexistence of these animals while sharing a common environment) led Heincke to question the role of intraspecific competition (or struggle for existence) in generating the morphological differences observed between spawning populations. He states (1878, p. 119),

> "Let it be admitted that natural selection does exist—and I cannot deny it, I am convinced that it is a most important factor in the formation of species—then there still is nothing to compel me to think of it as being active in the manner in which most disciples of Darwin imagine it to be: as a strict culler of the minutest useful or harmful characteristic. On the contrary, the facts contradict such a conception. Why, so do I ask, did natural selection let things go so far that the different characteristics of a variety of herring, which surely are to be the largest part dependent on geographical range, are already present in the same magnitude in two animals of the same locality, or of one and the same swarm?"

Heincke subsequently explores several thought experiments based on both the empirical results on herring and sticklebacks, and on the concept of natural selection. He concludes (p. 120),

> "As soon as I try to use, as an explanatory principle, natural selection in the form in which most Darwinians have interpreted it, I run into contradictions of this kind."

Heincke also finds difficulty in fitting his new observations on variability in nature to the concept of perfect adaptation that was being promoted at that time. He states (p. 120),

> "Can one, in such cases, still speak in the usual way of the perfect adaptation of a certain characteristic to the conditions of life? Is it still

permissible to ascribe to even a quite small, minute deviation, such a value that it must necessarily have been taken into account by natural selection?

I openly answer: no! and I will not be a party in turning and twisting the discovered facts so as to make them fit into the assumption of natural selection."

Heincke was obviously not seduced by the adaptationist approach which has been labelled by Bateson in 1909 and Gould and Lewontin 1979 as the Panglossian Paradigm. Unlike many of his contempories, he would rather change the theory to fit the empirical observations than to dream up hypothetical advantages for morphological features.

By 1898 his objections to natural selection as the mechanism of evolution had become firmly cemented and somewhat better articulated. In addition he was prepared to propose some alternate mechanisms. At the base of his dissatisfaction was the depiction of a new reality (a fundamental change in the recognition of the nature of the real world). The new species concept, based on detailed observations on herring and other animal species, stressed the opposite features of essentialism (the individuality rather than the type). In Heincke's view, this new perception on the natural world required a modified mechanism to explain its evolution.

His views on systematics and evolution are presented in the final chapter (IX) entitled "Ergebnisse von allgemeinener Bedeutung" (Results of General Significance) of the introduction (or preface) to the 1898 paper (the "Introduction" section itself consists of 136 pages, paginated in Roman numerals). We summarize Heincke's major points on evolution in that chapter from Duncker's (1899) extensive review. After stating in considerable detail his suggested approach to a new natural systematics (which in essence is an early version of the biological species concept of Mayr [1942] or the Rassenskries of Rensch [1929]) Heincke discusses his views on variability (we have not, however, documented whether Heincke's analysis of herring influenced Rensch or Mayr in the development of the new systematics). He disagrees with the interpretation that individual and population variability indicates speciation in action. At that time the expression "a species varies" had been taken to mean that it was in the process of transformation (note again that the rate of evolution and thus the intensity of natural selection were hypothesized to be high). Heincke in contrast stresses that variability is an intrinsic function of organic life, a *condition* of imperfect inheritance and different environmental effects, rather than evidence of the *process* of speciation. He states (p. 374 of Duncker 1899).

"The individual variability, however great it may be, is thus neither a proof of the transformation of a species, nor a cause of or a means there to... It is merely a function of organic life as such."

He distinguishes between the Gaussian distribution in the measures of morphological characteristics (which he defines as variability) and a directed change in the mean of a characteristics through time (which he defines as variation). Variability is considered to be an intrinsic condition of organic life, variation a process. Heincke does not consider that natural selection (as it was used in the scientific literature at that time to imply "struggle for survival") was the mechanism generating either the "variability" or the "variation." He argues that adaptation and speciation are caused by changes in the physical conditions of life. A first step toward a better explanation of speciation should involve studies of the mutual influences of organic forms on one another and of the effects of changing physical conditions. He proposes a general law that populations, species, and genera are restricted to particular geographical areas, the inference being that the changing physical geography itself is critical to the mechanisms of evolution. He argues that geographic isolation provides opportunities for evolution by providing new physical conditions of life. Although not well developed, he uses the concept of allopatric speciation (p. 375 of Duncker, 1899).

"Just as the boundaries separating populations change through contraction, expansion, newly springing into being, or vanishing, so too do new conditions of life and therewith new populations appear. On this, isolation is an important factor, but not in itself, but in so far as it offers new conditions of life. Expansion of the natural boundaries probably means an increase, and contraction a decrease in the number of individuals within the population. If the spatial boundary between two populations vanishes completely then cross-breeding will take place and result in the formation of a new population, which does not at all have to resemble its original two populations. Cross-breeding between two populations, however, is possible only if they are not too differentiated. Too great a differentiation between the original populations may be the reason why the ability to procreate of successful crossings of different species, already ceases at a very early ontogenetic stage."

The process of expansion and contraction of populations of species, and the possibility of both isolation and merging, has many of the elements of models of speciation that were to develop in the 1930's and 1940's by Wright, Dobyhansky, and Mayr. By that time the term "natural selection" had taken on a new meaning. Even today it is not clear what the role of natural selection is in speciation (*i.e.* the origin of reproductive isolation).

Given Heincke's emotional rejection of this terminology (*i.e.* "natural selection"), it appears to have been a culturally loaded term as much as a scientific term during the late 1800's. He states (p. 375 from Duncker, 1899).

> "For me, it is clear that such phenomena operating with the struggle for survival and with natural selection can never be explanations of the transformation of organisms and their wonderful adaptations; and that it is only a mechanical reconstruction of organic forms after one has first divided them into an arbitrary number of smaller parts... The struggle for survival and natural selection are not forces at all, but are only subjective forms of contemplation by man; inadequate words taken from our sensory notions and our inner feelings, to express certain mutual relationships of the organisms towards one another."

Heincke ends this long introduction by stressing that the key to an understanding of the origin of species lies in the study of the role of the changing physical conditions of life on speciation. The emphasis is on physical geography, rather than on intense competition. Natural selection meant the latter process at that time, and Heincke rejected it in this narrow definition as not a sufficient explanation of the new patterns in nature that were being described. The evolutionary synthesis of the 1930's and 1940's resolved Heincke's dilemma, in part by a clarification of the two components of evolution (speciation and adaptation) and by reducing the role of natural selection in speciation. In addition the term "natural selection" gradually changed its meaning from "intraspecific competition for survival" to "changes in gene frequencies through time" (*see* Endler, 1986, Chapter 1, for detailed definition).

Impact of Heincke's research

The publication of all three of Heincke's major papers on the existence of populations of herring (1878, 1882 and 1898) had major impacts on fisheries research. The papers were also influential on other biological disciplines (natural history, systematics, evolutionary biology, and statistics). The impacts on fisheries research are summarized first.

Impact on fisheries research

As already indicated, the herring literature was in chaos at the time Heincke started his research in 1875. None of the major contentious issues could achieve any degree of consensus, and the extant methodology was probably incapable of permitting further progress. His first two papers, even though they clarified the issues and focussed the discussions, did not fully resolve the fundamental debate. There were still two major camps after 1882. However, the 1898 paper (in reality a book) seems to have completely resolved the central issue (*i. e.* the existence of geographically restricted spawning populations of herring). The conclusions do not appear to have been questioned in the subsequent literature. This is remarkable given the intensity of opposing views prior to publication. The paper, almost instantly, became a classic and was reviewed in glowing terms by Dunker (1899). The magnitude of its impact is illustrated by Schmidt (1917) who stated.

> "Local races [populations] have in course of time been shown to exist in quite a number of fish species. Most important of all in my opinion, are Heincke's herring investigations collected in the comprehensive 'Naturgeschichte des Herings,' 1898. From a *mere chaos* Heincke succeeded, by his admirable and systematic work in furnishing not only a basis for all future investigations in this field; he also succeeded through the study of a single species, the herring, in revealing so many important features —quite unexpected in part—as to occurrence and relationship of various races, that subsequent investigations with other species have in a certain degree only amounted to a repetition of Heincke's results" (emphasis added).

Chaos was replaced by order, at least in conceptual terms. There was still considerable uncertainty concerning the numbers of populations, their precise location of spawning, the extent of their migrations, and the degree to which they intermingled before and after spawning. Heincke's 1898 paper encouraged fisheries biologists to consider the population as the unit of study, rather than the species. His contribution was particularly timely as the first planning meeting for international marine research was held in 1899 in Stockholm, and the International Council for the Exploration of the Sea (ICES) was subsequently founded in 1902. The new international research thrusts in fisheries biology were defined to a major degree on the basis of this paradigm shift. As a result, remarkably rapid progress in understanding the processes involved in generating variability in landings was achieved in the first decade of ICES research.

Hjort (1930) in his introductory address to the Special Meeting of ICES on recruitment fluctuations in London in 1929 clearly states the importance of this transition from the species to the population as the essential unit of study (as well as its key role in making progress on the recruitment question). He states (p. 5),

> "When we entered upon our international collaboration 30 years ago [*i. e.* 1899], the biological analysis of the organisms we caught in the sea was in the main confined to the systematic determination of the various species... However, as the work advanced, the demand for a more refined biological analysis and morphological classification became urgent. It was realized that the terms of species were inadequate to give a clear and orderly grasp of the phenomena in the large field covered by the international cooperation, and that recourse had to be taken to the conception of races or tribes [populations] as more natural and convenient morphological and biological units... *it is a matter of the greatest importance for all our*

> *researches and deliberations that the existence of these races and their geographical area of distribution have been revealed*" (emphasis added).

It was Committee A (Fish Migrations) of ICES which directed this research on population patterns. In the first meeting of Committee A in September 1902 Heincke, in a discussion of the general research approach to be taken by the Committee, stated (p. 95),

> "It must be regarded as *proved* that different races of herrings, separated from one another by real distinctions, existed in European seas... It was further necessary—and indeed in the first place, and in relation to the existence of local races—to find out the spawning grounds of the herring, and to determine as exactly as possible the distribution of the herring larvae in the different parts of the North Sea" (emphasis added).

Such a program was initiated for herring as well as gadoids in the northeastern Atlantic under the guidance of Committee A and Hjort's chairmanship. Population thinking thus rapidly became incorporated into fisheries research.

> Murray and Hjort (1912) in *Depths of the Ocean* state (p. 758),
>
> "Another important series of investigations was inaugerated by Heincke, who endeavoured to employ the methods of anthropology by recording various dimensions in order to characterize variations in growth peculiar to a species in different areas of the sea. Heincke measured the length and height of body, length of head, etc. in a great number of herrings from various marine areas, and he found the relations between these dimensions to be so characteristic that he *supposed* the herring to be subdivided into various races, each constituting a peculiar type of growth" (emphasis added).

Even though there is a difference in emphasis between *proved* and *supposed* by respectively Heincke (in his 1902 quote) and Hjort (in his 1912 quote), the direction of research taken by Committee A on herring and gadoids was strongly influenced by population thinking. Hjort's (1929) quotation suggests that the paradigm shift in fisheries biology occurred over some years. We would suggest the time period 1899 (the beginning of international cooperative research) to 1913 (Hjort's lecture at ICES on fluctuations, which is to be discussed in a section to come). It may have taken somewhat longer for population thinking to reach the fisheries laboratories in North America. Needler (1987), in a recent sketch of the early research activities at the St. Andrews Biological Station, New Brunswick, Canada (first few decades of this century), indicates that the population concept took some time to fully permeate the local scientific community. He states, referring to the 1920s and 1930s.

> "Many concepts very familiar to us had not yet emerged. The existence of more or less distinct populations or 'stocks' of the same species and many concepts of population dynamics were not yet imagined."

The two fisheries issues of substance that generated discussion of the requirement for an international research organization to study the oceans were: 1) the general problem of fish migrations (which encompassed the problem of fluctuations between years in landings), and 2) the overfishing problem. The Committee structure (Committee A dealt with fish migrations, and Committee B with overfishing) reflects the prominence of these two issues. The term "migration" at that time encompassed a broader subject area than usually associated with the term in its modern usage. It included the mystery of where do fish of different species come from when they appear in coastal waters off diverse northern European nations at different times. Also, the vagaries of migrations were thought to generate the interannual and decadal variability in landings in particular fishing areas. The polar *migration* theory for herring, which was discussed above, provides an example of the scope of the term in relation to geographic source and variability. The term in this usage predates the shift from species to the population as the unit of study. In fact the discovery and generalization of the existence of geographically restricted populations and variability in their age structure in a certain sense solved the "migration problem" as the term implied at that time. The migration problem encompassed or addressed interannual fluctuations in landings in particular fishing areas. The variability was interpreted as being due to changes in migration patterns of typological species. The discovery that populations of fish are restricted to specific geographic areas throughout their life cycles (and subsequently that variability in abundance of populations is due to year-class size variability) indicated that interannual fluctuations in landings were in some cases largely due to population fluctuations within a fishing area rather than due to changes in migration patterns. In this sense, then, the introduction of population thinking solved (or at the very least markedly modified) the "migration" problem. Heincke was one of a handful of fisheries biologists who formulated the research program for ICES (in 1899 at the Stockholm conference). He had already made great progress in resolving the migration problem for herring, and encouraged similar work on other species of commercial importance. Studies of egg and larval distributions were considered to be crucial to addressing the "migration" question to the degree that they contributed to the identification of the geographic patterns in spawning populations.

The explanatory power provided by Heincke's research is indicated by his comments on Schmidt's early work on eel morphometrics and meristics. Schmidt had observed no differences between adult eels from rivers throughout Europe, and reported these results to ICES in 1913. The Minutes state (Appendix D, p. 108),

> "Geheimrat Heincke observed that his experience had, in general, shown him that 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 presumed that the conditions on its spawning grounds were uniform."

It was on the basis of this kind of argument that it was concluded that studies of egg and larval distributions would contribute to the identification of populations.

Hjort (1943), during the war, wrote a summary of ICES work during the 40-year period 1902 to 1942. In a section entitled "Races and Populations" (p. 14-15) he identifies the role of Heincke in the initiation of population thinking in fisheries biology.

> "In the majority of species, perhaps in all, groups are formed which so to speak divide the distribution area of the species among themselves and which irrespective of size-classes, live separate from each other. They are called races... The German scientist Heincke raised these problems by his years of investigations into the natural history of herring... Subsequent investigations have confirmed and augmented these observations, not only with regard to herring but also as regards many other species...
>
> Out of this view of the geographical limitation of the races to definite areas there gradually arose the important conceptions connected with the words 'population' and 'stock', which denote a group of individuals distinct from all others both geographically and biologically. Thus we speak, for instance, of a herring population and a cod population off the west and north coast of Norway that are different from the cod and herring populations of the North Sea and the Baltic. The experimental proofs of the correctness of this view have been obtained by *marking experiments*... In experimental investigations of this kind the term 'population' gradually came to be used as an expression for the conception of a collective group of animals, and this in turn led on to using all the ideas and research methods that in the theory of human population had developed into the Science called 'population statistics'" (emphasis in original).

The links from Heincke's herring work, which was essentially completed in 1898, to the development of population thinking within ICES are clearly enunciated in the above quotation by Hjort. From the fisheries biology literature during this time period (1898 to 1930), most contributions to the population question start with or include a discussion of the importance of Heincke (1898). Schmidt (1917), in his first paper in the series on "racial investigations", indicates that his starting point was based on Heincke's classic study. The work is not just cited but identified as the contribution that clarified the issues, introduced new methodology, and generated research initiatives on other fish species. The context within which the work was cited suggests that the research was influential both within Germany (on Duncker and Redeke, for example) and in other northern European nations (Kyle and Schmidt, for example). Hjort's (1943) identification of Heincke's role (in the above quotation) supports this conclusion. Further study, however, using archival material (rather than just the scientific literature), is required to fully establish the degree to which the influence of Heincke was a direct one. The work on populations eventually led to the definition of management units, taking into consideration the geographic patterns in populations. Heincke's impact on fisheries research has been enormous and in recent years largely unrecognized.

Impact on other disciplines

Heincke's colleagues in Germany recognized that the impact of the herring studies should be felt beyond fisheries biology itself. Duncker (1899), for example, in his review of the 1898 paper, states (p. 363),

> "Prof. Dr. Fr. Heincke, Director of the Biological Institute of Helgoland, published the first part of his treatise in August of last year, under a title which seems to presume an interest in a narrow speciality of zoology. Yet, the work is of fundamental scientific importance, and far transcends the boundaries of zoology. This work – the result of the author's labours through several decades – contains not only new and important insights into the specialty defined by its title, but also conclusions of the most significant sort; reflections which were not forced ad hoc, as it were, under the influence of this or that scientific fad of the day, but which spontaneously pressed themselves upon the author in the course of his tedious and manifold investigations, and which will hardly remain without reverberations."

We will argue that the herring studies had a substantive impact on the so-called biometricians in England (in particular on Weldon and Pearson), the population geneticists in continental Europe (Chetverikov, Goldschmidt), and indirectly the systematists in Germany (Rensch, Mayr).

The Royal Society formed in 1894 a committee to conduct statistical enquiries on measurable characteristics of plants and animals. The need for such a committee was proposed by F. Galton. His interest was in applying statistical methods to topical problems in evolutionary biology. He was actively encouraged by W. F. R. Weldon in his proposal. Weldon's early interests in the application of quantitative methods to evolutionary problems and his interactions with Galton are described in some detail by K. Pearson (1906).

During Weldon's extended *Wanderjahre* (defined by Pearson as the period from 1882 to 1890), following the Tripos at Cambridge, a new phase in his ideas began. Like Heincke, he was stimulated by Darwinism as a student and did his initial research on embryology. Weldon travelled widely in continental Europe, but it is not certain that he became aware of Heincke's herring work (the 1878 and 1882 papers) during this transition period. Pearson (1906) notes that,

> "Lent and May terms, 1888, were spent as usual in Cambridge, but June to December were given up to Plymouth, with a brief Christmas holiday in Munich. And here we must note the beginning of a new phase in Weldon's ideas. His thoughts were distinctly turning from morphology to problem in variation and correlation."

The following year the book *Natural Inheritance* by Galton was published, which introduced Weldon to statistical methodology in relation to evolutionary questions. He visited Dresden in September of that year, and it is noteworthy in relation to his ability to learn of new developments in science that he was fluent in German. At Plymouth in 1890 Weldon started his study on morphometrics of *Crangon vulgaris*, a decapod crustacean. Two papers on variability in measurable characters resulted (Weldon 1890; 1892). Given his fluency in German, and wide travel in continental Europe during his *Wanderjahre*, it is probable but not documented that he was aware of Heincke's herring work prior to the initiation of his study on *Crangon* in 1890. Pearson (1906) states that these, "...two papers [by Weldon] were epoch-making in the history of the science, afterwards called biometry." Weldon received samples of *Crangon vulgaris* from P. P. C. Hoek of Den Helder, Holland, prior to 1892 (Weldon, 1892). Hoek was a colleague of Heincke and during the years 1888 to 1890 had carried out a study on the distinctness of herring spawning in Zuider Zee. Even if Weldon's first work on biometrics was not stimulated by Heincke, he was certainly aware of the herring studies by January 1894.

Weldon's papers on quantitative analysis of form on decapods had brought him in touch with Galton. As his work on the use of statistics in the study of natural selection expanded, it was felt that a committee structure might lead to more rapid progress of the field. According to Pearson (1906), the idea, "...was first discussed informally by R. Meldola, Francis Galton, and Weldon at a meeting held on December 9, 1893, at the Savile Club." A proposal was subsequently made to the Royal Society to form a committee, "...for the purpose of conducting enquiry into the variability of organisms." The proposal was accepted and the first meeting was held on January 25, 1894. Galton was chairman, and Weldon acted as secretary. Only two others participated in this initial meeting (F. Darwin and R. Meldola). The committee was formally entitled "Committee for Conducting Statistical Inquiries Into the Measurable Characteristics of Plants and Animals." It became known as the Evolution Committee.

In the minutes of the first meeting, the deliberations of the Council of the Royal Society relative to the Evolution Committee were reproduced,

> "Read a letter from Mr. F. Galton suggesting the desirability of appointing a Committee for conducting statistical inquiries into the Measurable Characteristics of Plants and Animals.
>
> Resolved. That the following gentlemen be appointed a Committee for that purpose, with power to add to their number: —Mr. Galton (Chairman), Mr. F. Darwin, Prof. Macalister, Prof. Meldola, Prof. Poulton, Prof. Weldon.
>
> Resolved that £50 be granted from the Donation Fund to the above Committee to pay initial expenses and that the Committee be recommanded to apply to the Government Grant Committee for any further sum they may think necessary."

At this meeting Weldon, "...explained the reasons why the herring appeared to be a suitable subject for a first investigation." The suggestion was approved, and the conduct of the observations was left in his hands.

A note by Weldon in support of his application for a grant was submitted to the Royal Society (Appendix 1). Even though he is not particularly complementary toward Heincke's use of statistics in the 1882 paper, and the classification procedure, he is obviously very excited about the empirical observations (in particular the degree of variability [Point 1], the fact that the characters are dimorphic [Point 2], and that the variability between spawning groups also existed during the early life history stages [Point 5]). Heincke himself recognized that his sample size was small and rectified this difficulty in his subsequent work. The more detailed study (1898) reinforced his initial conclusions. The critical observation from Weldon's point of view was the dimorphic character of the variability and thus the inference that speciation in action under natural selection was being observed by Heincke. An illustration taken from Heincke's 1882 paper showing morphological differences between separate populations spawning in Kiel Bay was appended to Weldon's application (*fig.* 1). He wished to describe the same phenomena in British waters in a more rigorous manner. It is surprising that the 1878 paper on herring by Heincke is not referred to in the application.

At the second meeting held on July 6, 1894, it was reported that Galton had been successful in acquiring a further £50 from the Government Grant Committee (giving the Evolution Committee a total budget of £100). It was agreed that £50 be placed to the credit of Weldon for his herring study. He reported that about 1000 herrings from the Plymouth area had

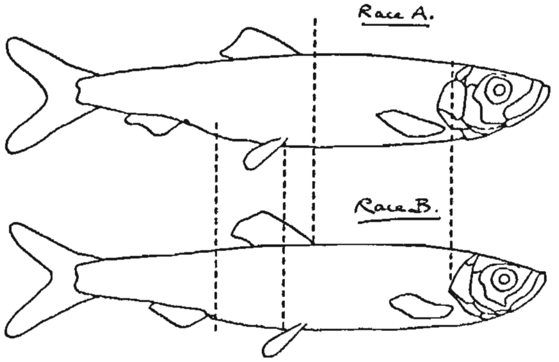

Figure 1. — Illustration of representatives of two populations of herring spawning in the vicinity of Kiel (appended to Weldon's 1894 application to the Royal Society for funding).

been measured. At the third meeting on November 15, 1894, a further £25 was paid to Weldon (thus 75% of the total budget was spent on the herring problem).

"It was reported that about 1900 herrings had been measured; and after considering the time and cost involved, it was resolved that the measurements be stopped after rather more than 2000 measurements, and that Mr. Weldon communicate the results of the measurements to the Committee."

The results of the herring investigation were never published. The reasons for this are discussed by Pearson (1906). Pearson indicates that,

> "One of the first subjects to be taken up by the new Committee was to test whether the method of resolution into two Gaussian curves, which suggested dimorphism in the Naples crabs, would be helpful in confirming a similar dimorphism said to exist in the herring. Several thousand herrings arrived at University College, a measurer was trained to deal with them, and the variability of a wide series of characters determined. The distributions came out skew, and Weldon was intensely hopeful that statistical evidence of dimorphism would be forthcoming. Instead of this, the analysis showed dimorphic Gaussian components to be impossible. This result was a great disappointment to him, and, I believe, to the Committee. I could never understand why. A most extensive and valuable series of measurements had been made, which in themselves were well worth publishing. It had been shown that simple dimorphism of a Gaussian kind certainly did not hold for these herrings; in all probability it was a typical case of skew frequency, which would have been most valuable as adding to the known instances, and aiding statisticians eventually to classify such occurrences. But Weldon, and, I presume, the Committee were disheartened, they had been searching for dimorphism and had not found it. The herring data were put on one side by Weldon, and as far as I know have never been published. It is much to be hoped that they may some day be resuscitated from the archives of the Committee (16)."

The herring data, unfortunately, are not archived at the Royal Society, and thus have not been "resuscitated". The degree to which Weldon was disappointed by the analysis of the results is indicated in a letter by him to Galton (March 6, 1895), quoted by Pearson (1965). Weldon adds in a footnote to the letter,

> "The Herring, which makes a skew curve are very heterogenous... I have not the figures at hand, because I sent them to Pearson, as a basis for his curve; but he says that '*the material is homogenous, with skew variation about one mean.*' I don't believe it!" (emphasis in original).

The correspondence also indicates that Weldon's scientific methodology did not involve the rejection of null hypotheses but rather the search for support of a preferred hypothesis.

The reasons for the "failure", of the study, in hindsight, are obvious. Heincke compared the distribution in measurable characteristics between two or more spawning populations. Weldon took samples from a single spawning population (so-called Plymouth herring). One would not expect to observe a dimorphic distribution of characters within a spawning population.

Even though this particular study of the Evolution Committee dead-ended, the work by Heincke contributed to the initial thoughts of the Committee and perhaps contributed partially to its formation. As an aside, the Evolution Committee had an eventful history within British evolutionary circles, and played an unfortunate role in the bitter debate between the Mendelians under Bateson and the Biometricians under Weldon and Pearson (Provine, 1971).

Heincke's herring studies also had an impact on the development of the so-called new systematics (see quote by Goldschmidt, above) and the evolutionary synthesis. S. Chetverikov, the Russian evolutionist, who is recognized as having a major impact on the synthesis both due to his 1926 classic paper and his influence on the Russian school of population genetics (in particular through Th. Dobzhansky), was aware of Heincke's work. For example, he discusses it in relation to evidence for geographic and seasonal isolation between populations in his 1926 contribution (p. 179),

> "Thus, undoubtedly, there exists *isolation in time*... In this connection, the best studied example is our common herring (*Clupea harengus* L.) which is subdivided into several colonies living in one place but separated from each other by difference in time of their egg-laying (fall and spring-spawning herrings). As the classical investigation of Heincke (1898) have shown, these separate colonies, isolated in time,

vary among themselves in mean values of a whole series of characters, and making use of the method of 'combined deviations', developed by the same author, it is possible to assign each separately caught specimen, entirely by its morphological characters, to one or another of these 'seasonal' races with a high degree of probability."

Dobzhansky (1937), in his book *Genetics and the Origin of Species*, refers in a similar manner to Heincke's herring work (p. 141),

> "In some species of fish, given to large-scale migrations, a differentiation of the population into local subgroups had been demonstrated. For herring (*Clupea harengus*) a penetrating analysis of this problem was first made by Heincke (1898), and since then has been corroborated by newer investigations (Scheuring 1929-30, Schnakenbeck 1931, and others). The herring is one of the fish that comes for purposes of reproduction, to shore waters, while the young lead a pelagic life in the open sea. Among the herrings of the North Atlantic, North Sea, and the Baltic, there exist separate strains differing from each other in the place and the season of the breeding, the paths of the yearly migration, and also in morphological characters. The latter differences are usually small, the variation limits for the different strains overlap, but the averages are distinct. Heincke has shown that if proper statistical methods (the least-square method) are applied, the strains are distinguishable even in single individuals. Every strain is, then, a separate breeding community, and deserves the name of 'elementary race' suggested by Heincke."

Two other major book contributions to the evolutionary synthesis (Mayr, 1942; Rensch, 1959) also use the emprical observations on herring populations as part of the evidence for the existence of geographic patterns in populations, but quote secondary review sources rather than the original work by Heincke.

In sum, the detailed empirical observations in variability in measurable characters of herring, and the quantitative statistical analysis that led to the conclusion that geographic populations exist, have been repeatedly cited in the major contributions to the evolutionary synthesis. Heincke provided the best marine evidence for the existence of geographic patterns in populations. It is in this sense, as well as his statistical approach to the problem at a time when quantitative methods were rarely used in natural history, that his work contributed to the development of "new systematics" and the evolutionary synthesis. Again, it is not just that Heincke's research papers were cited, but what was said about his work in comparison to other papers when it was cited. Chetverikov, Dobzhansky, and Goldschmidt each refer to Heincke's least-square method and highlight the results in some detail. From the overall literature on geographic patterns in populations, Heincke's contribution was considered to be amongst the best work. However, his thoughts on the difficulties with natural selection, and his emphasis on the role of changes in physical geography on the speciation process, appear to have been completely ignored.

SCHMIDT'S CONTRIBUTION TO POPULATION THINKING

As stated earlier, Committee A of ICES addressed the general problem of "fish migration" (which in actually meant the determination of geographic patterns in spawning populations of commercially important species). A major international research thrust was made to describe the spawning locations of gadoids in the northeastern Atlantic from Spain to Iceland. The method used was egg and larval surveys. The collections were made from 1903 to 1907, and the results were analysed and published in a single massive report comprising two parts by respectively Damas (1909) and Schmidt (1909). Damas, a Belgian, worked in J. Hjort's laboratory in Bergen; and J. Schmidt, a Dane, at the Carlsberg Institute in Copenhagen.

The major conclusions that were drawn from this impressive study were that: (1) spawning locations differed between gadoid species; (2) within the distributional limits of a species, spawning occurred in several precise locations; and (3) the geographic areas of spawning were very small compared to the distributional area of the species.

Damas did not continue with his studies on gadoids, but did make some major contributions to zooplankton ecology. His career was unusually short, and we have not discovered why. Schmidt, in contrast, pursued the population problem aggressively during most of his research career. Much of his research was published in serial form ("Racial Studies" in fishes I to X, from 1917 to 1930). He took a comparative approach, studying geographic population patterns in a number of species. He demonstrated with the combined use of meristics and morphometrics, egg and larval surveys, and breeding experiments that, like Atlantic herring, most species are comprised of a number of geographically defined populations. However, he demonstrated a marked difference between species in the number of populations. *Zoarces viviparus*, a coastal species which is viviparous, has many discrete populations. Atlantic cod has a moderate number. Yet the Atlantic eel was argued to consist of a single breeding population (*i. e.* panmictic). Thus, population richness (*i. e.* numbers of populations per species) was shown to be highly variable between species. Schmidt (1930) speculated that events during the early life history were critical to this difference between species in geographic patterns in populations.

In sum, Schmidt's "Racial Studies" of fishes generalized for all marine fish species the conclusions drawn by Heincke (1898) on the existence of discrete spawning populations of Atlantic herring. In addition, he demonstrated that population richness is species specific, and that morphological difference between populations is in part genetically based.

His impact on fisheries biology was major. By generalizing the conclusions of Heincke, he completed the transition within this field to population thinking. His studies on eels, in particular, were highly topical. Heincke predicted, on the basis of a lack of morphological variability between eels in the rivers of Europe, that eels shared a similar or the same spawning area. The search for that spawning area was dramatic, and was, followed by the ICES community with great interest. In addition, Schmidt's breeding studies on *Zoarces* sp. contributed to the development of what Mayr (1982) has called ecological genetics. We have not documented the degree to which Heincke directly influenced the research of Schmidt. They participated in annual meetings together at ICES for many years. Heincke was one of the major proponents of Schmidt's first major study on the gadoids (published in 1909) but is not cited in the text. Schmidt (1917), in his first paper on racial studies, discusses Heincke's 1898 classic in glowing terms. Also, Schmidt used Heincke's method in general terms. On this basis it is inferred that Heincke was influential but not demonstrated. Future work on Schmidt's motivation in starting the series on racial studies would be most useful to establish Heincke's role.

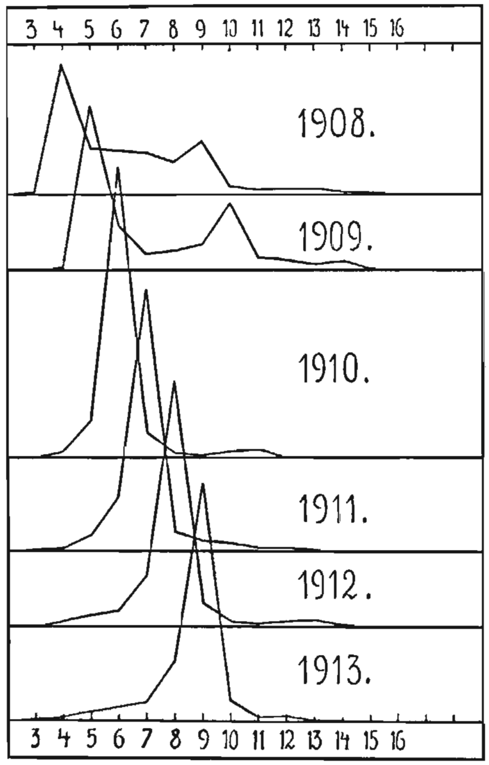

Figure 2. — Percent frequency distribution of age composition of landings of herring off the coast of Norway from 1908 to 1913 (from Hjort, 1914). The 1904 age class dominated the fishery throughout this time period.

HJORT'S CONTRIBUTION TO POPULATION THINKING

Hjort's overall contribution to fisheries biology, oceanography, fisheries management, and internationalism in marine research was enormous. In this paper we restrict ourselves to only those aspects of his contribution that relate to the development of population thinking.

In 1902 when ICES began its research program on fisheries biology, it is doubtful that Hjort was convinced of the generality of Heincke's 1898 conclusions about the existence of discrete populations of marine fish. This is suggested by the summary of Heincke's work in Hjort's book with Murray in 1912 (quoted in section: Impact of Heincke's research). However, in the reviews by Hjort in 1930 and especially in 1945, he indicates that the ICES community rapidly incorporated Heincke's ideas and built upon them. Hjort himself played a major role in this process.

As the first chairman of Committee A on Fish Migrations, Hjort was instrumental in the definition of research questions and their relative priority. Even at the young age of 33, Hjort had gained an international reputation and thus wielded considerable influence as Chairman. His growing reputation is reflected in the report of the British delegates (C. S. Moncrieff and D'Arcy Thompson) attending the first meeting of ICES in Copenhagen to the British government. They state (p. 93),

> "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, and in the voyages of research made by him during the last two years he has added largely to the fishery resources of his country, as was mentioned in the report of the Christiania Conference of 31st May, 1901."

He personally worked with Damas during his ICES joint study (with Schmidt) on gadoid egg and larval distributions. He also directed the overall Norwegian programs on cod and herring biology that were part of the work of Committee A. His personal research contribution to the population question is the 1914 classic publication, which was presented verbally at an evening lecture during September 1913 at the 12th Statutory Meeting of ICES. It is our view that the major contribution of this paper has been misrepresented in the recent literature. The paper is widely cited because of the critical-period hypothesis (*i. e.* year-class variability is a function of critical events during the early life-history stages). We would argue that the major contribution to fisheries research at the time of publication was the convincing demonstration that variability in landings at particular fishing areas was due to the very existence of geographically persistent age-structured populations characterized by highly variable year-class abundances. The demonstration was convincing in part because of the ability to track the exceptionally large 1904 year class of "Atlantoscandian" herring as it passed through the Norwegian fishery (*figure* 2). The tracking was made

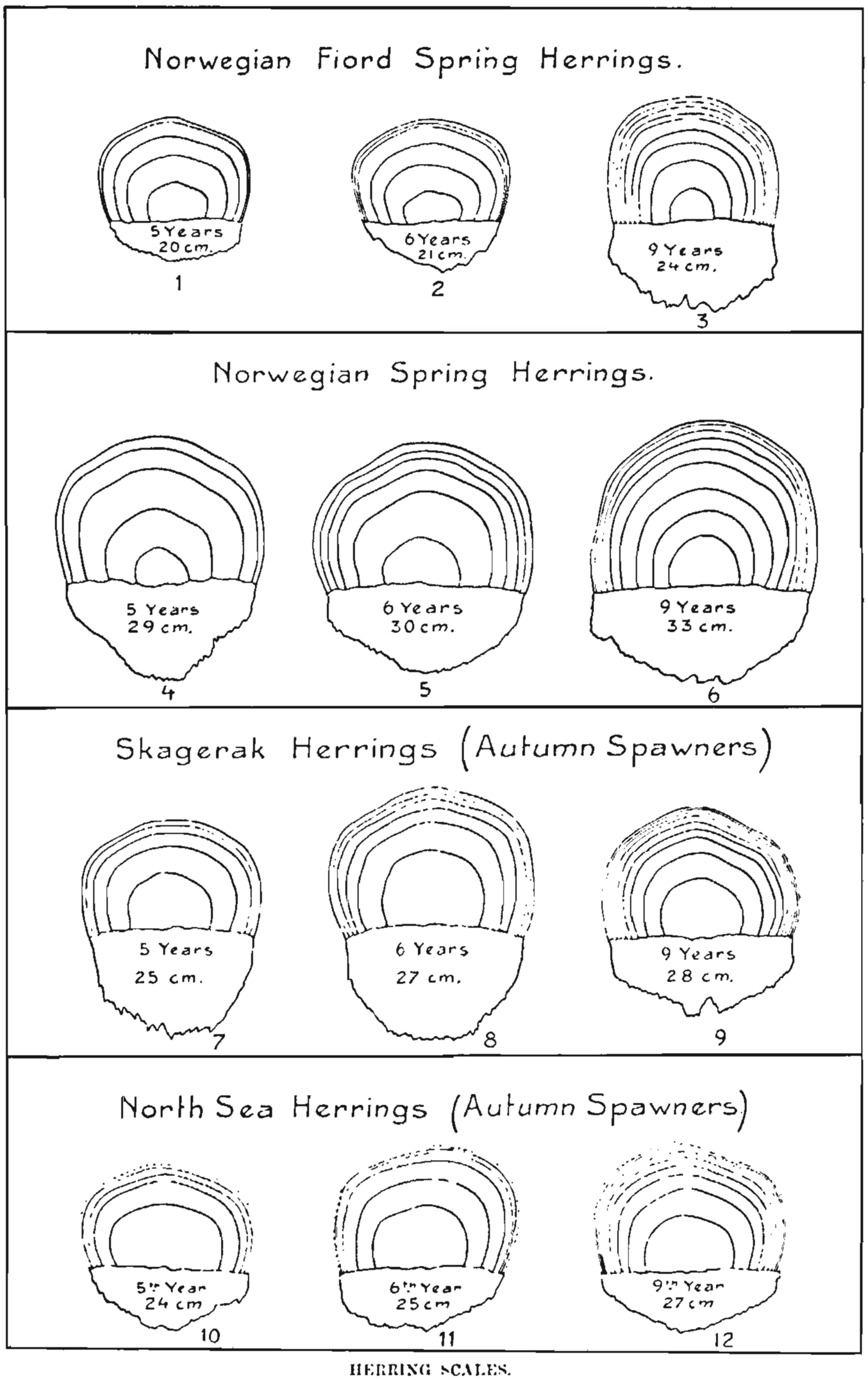

Figure 3. — Illustration of scales of herring of different ages and geographic areas (from Dahl, 1907). This aging method permitted the decomposition of landings into age classes (see *figure* 2).

possible by the development of an aging method for herring (*figure* 3). An important observation was that the relative abundance of a year class of herring was defined prior to being exploited by the fishery. Similar conclusions could be drawn from other studies on cod and haddock. Thus, Hjort generalized that events during the early life-history stages prior to availability to the fishery are critical to recruitment variability.

Large catches were thus interpreted as a function of abundant year classes of geographically persistent populations, rather than to the vagaries in migration of pan-oceanic species. In essence, Hjort demonstrated the explanatory power of population thinking. The critical-period hypothesis was somewhat of an afterthought, albeit a highly significant one.

If generally accepted, Hjort's age-structured population hypothesis to account for variability in landings provided the possibility of predicting future catch levels (*i.e.* from prerecruit surveys). His hypothesis was substantiated after several years of intense debate with Thompson, and has become so well established that it is difficult to imagine the excitement that must have occurred at publication. A modern-day parallel would be the increase in understanding that has arisen concerning the physical mechanisms causing El Niño. Population thinking, with the new methodology of aging, generated impressive explanatory power. A second example in Hjort's 1914 paper was the explanation of the interannual variability in relative yields of cod liver oil (as a function of age composition).

The aging method alone was not sufficient to generate the breakthrough. Hjort recognized that sampling of the age structure of the landings would generate vital statistics on the *population*. Ruud (1948) decribes the origin of this idea as follows,

> "While preparing plans for a scheme of accident insurance for Norwegian fishermen it occurred to Hjort that the methods and principales which were followed in drawing up the statistics of population could be adopted in studies of the stocks of fish, and in a lecture delivered before the International Council in 1907 he outlined a program for such investigations."

Smith (1987) indicates that ICES did not follow-up on Hjort's proposal until many years later. Hjort himself, however, instigated a sampling program for the age composition of Norwegian landings. It was this data set on cod and herring which permitted Hjort to develop his age-structured population hypothesis to account for variability in landings.

The 1914 paper is a tour de force and indicates Hjort's breadth as a scientist and his critical approach. As an aside he demonstrates that the physical oceanographers were sampling the Norwegian Current inadequately, which led to aliasing of their results. He also criticized Helland-Hansen's sunspot hypothesis accounting for cod liver oil variability. He brought together all the available methods and data (aging, port sampling, egg and larval surveys, tagging, plankton dynamics, and physical oceanography) toward the resolution of the interannual variability in landings problems. Much like Heincke's 1898 paper, it became a classic very quickly. The paper was reviewed by E. J. Allen in *Nature* (Allen, 1914). He stated,

> "There can be little doubt that this report by Dr. Hjort will *mark an epoch in the history of scientific fishery investigation.* 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, which should be of the utmost value both to those engaged practically in the fishing industry and to those responsible for fishery administration" (emphasis added).

As already indicated, the paper is cited in the recent literature with reference to the critical-period hypothesis which address the causes of interannual variability in year-class abundance. In fact, it is really two hypotheses; the first involves food-chain interactions (specifically, variable mortality between years due to the variable timing of spawning and timing of phytoplankton blooms); the second involves the direct affect of variable advection of eggs and larvae away from their appropriate distributional area for the population. These two hypotheses continue to define much of the research being carried out on the recruitment problem.

Hjort (1926), in the first issue of the *Journal du Conseil*, reviewed the field of fisheries fluctuations. It is clear from the review that the ICES scientific community considered the recruitment problem to have two components: (1) species are composed of discrete populations, and (2) recruitment to these populations varies. They were searching for general laws of nature to account for the definition of both the species-specific geographic patterns in populations and the regulation of abundance for a particular population. He states (p. 30-31),

> "... an attempt has been made to determine the spawning areas of the principal fish, plaice, herring, cod, haddock, to define the spawning migrations, the nurseries where the young fish develop, etc. It is hoped it may in this way be possible to find *the general laws for the appearance of biological groups...*" (emphasis added).

The quotation suggests that the ICES scientific community were, during this time period (1902 to 1926), interested in the broader question of population regulation, not just the fisheries management applications. They sought for an understanding of the "general laws" causing geographic population patterns and the variability in abundance of these populations with time. Population thinking was fully accepted by the fisheries biology community by 1930. Hjort had contributed to this rapid acceptance, or shift in perspective, by demonstrating its explanatory power and usefulness to the management of fisheries resources.

DISCUSSION

This paper has traced the development within marine fisheries biology of a single concept (that of populations), and the associated emergence of a new perspective on geographic patterns in the natural world (population thinking). The development within fisheries biology is argued to be part of a larger intellectual trend involving an increasing emphasis on variability and evolution. As such, the development of population thinking within fisheries biology had a metaphysical component. Reading the original studies, such as Czernay (1857) and Heincke (1898), as well as commentaries on this literature as it was assimilated by the scientific community (Goldschmidt, 1940), suggests that the shift in perspective on nature (or the shift in metaphysics) was a wrenching process. It is difficult to imagine after the fact how naturalists actually viewed the organic world prior to this paradigm shift. Nevertheless, it is clear that the naturalist did see static entities. The more complete description of variability in form in the natural world weakened the essentialistic perspective which emphasized the ideal type. Empirical observations in this case made necessary the development of new concepts. The period from about 1880 to 1930, during which naturalists and systematists assimilated population thinking, must be considered as a dramatic shift in our collective perception of reality. It was indeed the "revolution" that Darwin had predicted.

Heincke represents an interesting stage in this shift from the typological species concept of Linnaeus to modern population thinking. Although he clearly rejected the concept of a typological uniformity of species, he nevertheless gives the impression of a rather typological conceptualization of his "constant local forms". As Heincke himself stated, "I myself have still not completely shed the restrictions of the old systematics". This analysis of Heincke's herring papers suggests that the shift in the species paradigm could not be done in a single step.

Surprisingly, population thinking in the sense defined by Mayr (1982) and explored here in fisheries biology has not influenced modern ecology (Kingsland, 1985). In contrast, population thinking had a central role in the development of population genetics (largely influenced by Chetverikov, Dobzhansky and Wright) and the evolutionary synthesis (see Mayr, 1982 for an extensive review).

The shift from essentialism to population thinking occurred in all fields of systematics but appears to have had a more widespread effect on the working scientist in fisheries than has been the case in other components of ecology. Population thinking, and the definition of management units on the basis of geographically persistent spawning populations, was accepted and used by most European fisheries biologists by the 1920's. Part of the reason for this rapid incorporation of the new concept was its importance to fisheries management.

Heincke's research, and that of Nilsson before him, was generated by applied problems given very high priority by governments in northern Europe. Fluctuations in the fisheries landings influenced dramatically the whole economy of some nations, and the well-being of the coastal communities. Heincke, Schmidt, and Hjort were each stimulated by applied problems. Good scientists working in applied research led to increases in understanding at a fundamental level and generated impressive explanatory power. The lesson is topical for today. Applied research obviously does not necessarily mean trivial research.

The impact of population thinking on fisheries biology and fisheries management was far reaching and occurred relatively rapidly. The classic papers of Heincke (1898) and Hjort (1914) generated new orientations in research. Redeke (1912) reviewed the research on geographic population patterns that followed Heincke's contribution and that used his quantitative approach. An ICES Special Meeting was held in 1928 to review the advances on "Racial Investigations of Fish" (Rapp. Proc.-Verb. Réun. 54). The next year at London, ICES sponsored a so-called Biological Meeting to review progress on "Fluctuations in the Abundance of the Various Year-Classes of Food Fishes" (Rapp. Proc.-Verb. Réun. 65). As a result of this latter meeting, the Council nominated special rapporteurs to summarize the state of the art on fluctuations in recruitment for cod, haddock, plaice, herring, sprat, and sardine (Rapp. Proc.-Verb. Réun. 68). This interrelated series of special meetings and review volumes during 1928 and 1929 on respectively the very existence of discrete populations (or races) and the variability in year classes of such geographically defined spawning groups indicates the dual nature of the recruitment problem. Hjort (1930) explicitly links the two aspects of the problem as well as the two special meetings. It was to a large degree the contributions of Heincke and Hjort which generated the research reviewed during these meetings.

The impact of Heincke, Hjort, and Schmidt on scientific disciplines outside fisheries biology has been mixed. Heincke's work was widely read by systematists and evolutionary biologists. His research, on herring in particular, described in a quantitative manner the geographic patterns in populations of a marine species. This work complemented that being done in terrestrial and freshwater habitats (such as Gulick, 1872; 1888 and Coutagne, 1895). Heincke's papers were cited and discussed in some detail by Chetverikov, Dobzhansky, and Goldschmidt, who were three of the leading evolutionary biologists during the 1920's and 1930's. Heincke's thoughts on the problems with natural selection, however, which was an attack on Neodarwinism, were essentially ignored.

Schmidt's experimental work on genetic versus environmental effects on morphological variability between populations of *Zoarces* sp. was also an important contribution to ecological genetics (as reviewed by Mayr, 1982).

Hjort's classic paper on fluctuations (1914) does not appear to have had an impact outside of fisheries biology and fisheries management. This is surprising given that Hjort was internationally renowned, lectured extensively overseas (such as the 1934 Huxley Memorial Lecture at the Imperial College of Science and Technology, London), and was awarded honorary degrees in both England (Cambridge and London) and the United States (Harvard). His research on the causes of fluctuations in recruitment to geographically defined populations has not to our knowledge been influential to ecology or other flanking disciplines. It appears that the population thinking that revolutionized fisheries biology had no impact on the development of modern ecology (see Kingsland, 1985 and McIntosh, 1985 for two recent histories on the development of ecology). Rather, the impacts outside fisheries biology of the work on population thinking between 1878 and 1930 were on population genetics and evolutionary biology.

Acknowledgements

We thank S. P. LeBlanc for her excellent contribution to the preparation of the manuscript, and E. Hill for providing the German translation. The reviews by E. Mills, E. Mayr, J. Muelbert and J.-P. Troadec were most helpful. E. M. Thomasson, the ICES librarian, was most helpful in introducing us to relevant material form his own research on Heincke and Hjort.

REFERENCES

Allen E. J., 1914. Fluctuations in the yield of sea fisheries. *Nature*, 93, 672-673.

Bateson W., 1909. Heredity and variation in modern lights. *In*: *Darwin and Modern Science*, A. C. Seward Ed., Cambridge Univ. Press, London.

Bertram J. G., 1865. The Harvest of the Sea. John Murray, London: 519.

Braudel F., 1981. The Structures of Everyday Life. Harper and Row, New York: 623.

Bückmann A., 1982. Letter to E. M. Thomasson, ICES Librarian, on Fr. Heincke.

Chetverikov S. S., 1926. On certain aspects of the evolutionary process from the standpoint of modern genetics. *J. Explt. Biol.* (Russian) A2: 3-54. [English trans. (1961). Proc. Amer. Phil. Soc. 105: 167-195].

Cleghorn J., 1854. On the fluctuations in the herring fisheries. Brit. Assoc. Adv. Sci. 24: 124.

Collingwood R. G., 1946. The Idea of History. Oxford Univ. Press, Oxford: 339.

Coutagne, G., 1895. Recherches sur le polymorphisme des mollusques de France. Mémoire publié par la Société d'Agriculture, Sciences et Industrie de Lyon, France.

Czernay A., 1857. Beobachtungen über das Variieren der Artkennzeichen der Süsswasserfische der Umgelbend von Charkov. *Bull. Soc. Imp. Natur.* Moscou, 30, 227-249.

Damas D., 1909. Contribution à la biologie des gadidés. Rapp. P.-v. Cons. int. Explor. Mer 10 (pt. 3): 1-277.

Dahl K., 1907. The Scales of herring as a means of determining age, growth and migration: Report of the Norwegian Fisheries and Marine Investigations, **2**, 1-36.

Darwin C., 1859. The Origin of Species (first edition). Penguin English Library Issue, 1982, 476.

Dobzhansky Th., 1937. Genetics and the Origin of Species. Columbia Univ. Press, New York, 364.

Duncker G., 1899. Fr. Heincke, Naturgeschichte des Herings. *Kritisches Referat. Biol. Centralbl.*, 19, 363-383.

Endler J. A., 1986. *Natural Selection in the Wild.* Princeton Univ. Press, Princeton, 336.

Goldschmit R., 1940. *The Material Basis of Evolution.* Yale Univ. Press, New Haven, 436.

Goud S. J., R. C. Lewontin, 1979. The spandrals of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proc. Royal. Soc. London*, B205, 581-598.

Gulick J., 1872. Diversity of evolution under one set of external conditions. *J. Limn. Soc. Lond.* (Zool.) 2.

—, 1888. Divergent evolution through cumulative segregation. *J. Limn. Soc. Lond.* (Zool.), 20.

Heincke Fr., 1878. Die Varietäten des Herings I. Jahresb. Komm. Unt. d. Deutsch. *Meere in Kiel*, 4-6, 37-132.

—, 1880. Die *Gobiidae* und *Syngnathidae* der Ostsee nebst biologischen Bemerkungen. Archiv für Naturgesch, 156, 301-353.

—, 1882. Die Varietaten des Herings II. Jahresb. Komm. Unt. d. Deutsch. *Meere in Kiel*, 7-11, 1-86.

—, 1898. Naturgeschichte des Herings I. Die Lokalformen und die Wanderungen des Herings in den europäischen Meeren. Abh. d. Seef. Ver. 2, S. cxxxvi u. 128 S.

Hjort J., 1914. Fluctuations in the great fisheries of northern Europe. *Rapp. P.-v. Cons. int. Explor. Mer*, 20, 1-228.

—, 1926. Fluctuations in the year classes of important food fishes. *J. Cons.*, **1**, 1-38.

—, 1930. Fluctuations in the abundance of the various year classes of food fishes. 1. Introductory address. *Rapp. P.-v. Cons. int. Explor. Mer*, 65, 5-9.

—, 1945. International exploration of the sea. *Rapp. P.-v. Cons. int. Explor. Mer*, **115**, 3-19.

Kingsland S. E., 1985. Modeling Nature. Univ. of Chicago Press, Chicago, 267.

Kyle H. M., 1899. An extension of the method of treating variations with examples and certain conclsuions. *Nat. Sc.*, **15**, 410-422.

Mayr E., 1942. Systematics and the Origin of Species. Columbia Univ. Press, New York, 334 p.

—, 1982. The Growth of Biological Thought. Harvard Univ. Press, Cambridge, 487.

Mayr E., W. B. Provine, 1980. The Evolutionary Synthesis. Harvard Univ. Press, Cambridge, 487.

McIntosh R. P., 1985. The Background of Ecology: Concept and Theory. Cambridge Univ. Press, 383.

Medawar P. B., 1979. Advice to a Young Scientist. Harper and Row, New York, 109.

Moncrieff C. S., D. W. Thompson. 1902. Report of the British delegates attending the meeting of the International Council held at Copenhagen in July 1902.

Needler A. W. H., 1987. The St. Andrews heritage. *St-Andrews Biol. Sta. Newsletter*, **1**, 1-2.

Pearson E. S., 1965. Some incidents in the early history of biometry and statistics 1890-94. *Biometrika*, **52**, 3-18.

Pearson E. S., 1967. Some reflexions on continuity in the development of mathematical statistics, 1885-1920. *Biometrika*, **54**, 341-355.

Pearson K., 1906. Walter Frank Raphael Weldon, 1860-1906. *Biometrika*, **5**, 1-52.

Pettersson O., 1914. Climatic variations in historic and prehistoric time. Svenska Hydr.-Biol. Kommissionens Skrifter 5:26 p.

Picken K., 1960. The Organization of Cells and Other Organisms. Oxford Univ. Press. London, 629.

Provine W. B., 1971. The Origins of Theoretical Population Genetics. Univ. of Chicago Press, Chicago, 201.

Redeke H. C., 1912. Ueber den Gegenwaertigen stnad unserer kenntnis von den Rassen der Wichtigsten Nutzfische. *Rapp. P.-v. Réun. Cons. Perm. int. Explor. Mer.*, 14, 31 p.

Rensch B., 1929. Das Prinzip Geographischer Rassenkreise und das Problem der Artbildung. Borntraeger Verl., Berlin.

—, 1959. Evolution Above the Species Level. John Wiley, New York, 419.

Ruud J. T., 1948. Johan Hjort, in memorium. Norwegian Whaling Gazette, November issue.

Schmidt J., 1909. The distribution of the pelagic fry and the spawning regions of the gadoids in the north Atlantic from Iceland to Spain. *Rapp. P.-v. Cons. int. Explor. Mer*, **10** (pt. 4), 1-229.

—, 1917. Racial investigations. I. *Zoarces viviparus* L. and local races of the same. Comptes-rendus des travaux du Lab. Carlsb., 13, 279-396.

—, 1930. Racial investigations. X. The Atlantic cod (*Gadus callaricus* L.) and local races of the same. C. R. trav. Lab. Carlsb., **18**, 1-71.

Smith T. D., 1987. Stock assessment methods: The first 50 years. *In* J. Gulland (ed.) *Fish Population Dynamics.* Wiley and Sons.

Weldon W. F. R., 1890. The variations occurring in certain decapod crustacea. 1. *Crangon vulgaris. Royal Soc. Proc.*, 47, 445-453.

—, 1892. Certain correlated variations in *Crangon vulgaris. Royal Soc. Proc.*, 51, 2-21.

APPENDIX 1

Note by Prof. Weldon, in support of his grant application to the Royal Society on the part of the Evolution Committee in 1894.

"In attempting to study the processes of animal modification, it is important to choose, as a subject of investigation, some species in which a fairly rapid process of modification is in operation at the present time. The following reasons are offered in support of the belief that the common herring is such a species.

The variation of the herring has been studied by the officers of the Fisheries Board for Scotland, and by Dr. Heincke of Kiel. The observations of Heincke are of importance for the present purpose.

The measurements upon which Heincke's observations are based are very rough, so that the whole range of adult variation (which is considerable) falls, in the case of certain organs, within three of the units of measurement employed; while the number of specimens examined is statistically inadequate.

Heincke's results may be summarised as follows:

(1) The herring in the Gulf of Kiel vary especially in six characters, namely:

Length of Head.

Distance from Snout to root of Dorsal Fin.

Distance from Snout to root of Pelvic Fin.

Distance from Snout to root of Anus.

Length of Ventral Fin.

Time and Place of Breeding.

(Herring breed chiefly either in Spring, when they spawn in shallow, more brackish water, or in Autumn, where they spawn in deeper, saltier water).

(2) These characters are imperfectly correlated, as the herring is dimorphic with respect to each of them. Heincke attempts to separate the Kiel herring into three structurally distinct groups,—a group A, a group B, and an intermediate group M. The "type" of A and B is drawn in the diagram [see Figure 1]; but the correlation between the characters measured is so loose that "typical" individuals are rare; and Heincke's method of classifying individuals into one or other of his groups is quite artificial.

Group		Percent of population
Group A.	*Autumn breeders*	13.0
	Spring breeders	18.4
	Intermediate	11.0
Groups B.	*Autumn breeders*	3.0
	Spring breeders	36.0
	Intermediate	7.4
Group M.	*Autumn breeders*	0.7
	Spring breeders	8.0
	Intermediate	2.5
		100.0

(3) The structure of these groups is only imperfectly correlated with the breeding habit. Heincke's table of the percentage composition of Kiel herrings shows this; but the table is based on less than 300 individuals, and therefore needs revision:

(4) The percentage of A and B herring differs in different places; for example in certain parts of Scotland the herring belong almost entirely to the B type, while in the Channel the A and B type are more nearly equal in numbers than in Kiel.

(5) These characters are probably affected by Natural Selection. Heincke makes an attempt to estimate the variability throughout life, which is based on very insufficient data; but such evidence as he does bring forward creates a strong presumption that variability, with respect to the characters referred to, is greater in the larvae than in the adult.

(6) The foregoing statements are sufficient to serve as a basis for extended statistical investigation. Their importance is increased by Heincke's statement that a precisely similar series of variations is found in the *Sprat*, and by the fact that the *Pilchard* is known to be variable.

We have therefore three common, cheap, and easily obtainable species of one genus, all living in the same area, and all exhibiting variations of considerable extent in characters which can easily be measured. The parallels in between the variations of two, at least of these species, besides its interest on other grounds, has this great advantage, that any general conclusion which may be drawn from observations on one species can be readily checked by reference to the other."

Heincke's results are published in "Die Varietäten des Herings II" (Heincke, 1882).