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Who captures the marks for the Petersen estimator?

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Summary. We examine the claim that the well-known Petersen estimator which is used in population size estimation was not in fact used by the scientist after whom it is named. We show how, in the early years of the last century, the modern use of the Petersen estimator grew from that of the fishing coefficient. Contending with the somewhat conflicting claims that were made at the time, and what by modern standards is poor referencing of sources, we investigate where the credit lies for these concepts, and the principles and protocols which support them. We assess also how far attributions of credit were affected by practical considerations, and the history of the estimator by the nature of the problems being pursued. We identify scientists whose early work on marking and estimating fish populations deserves more credit than it has received.

Keywords: Fishing coefficient; Lincoln index; Mark–recapture; Population size; Stock assessment; Tagging

1. Introduction

Of the various estimators of population size based on recapture data, the Petersen estimator appears to have been the earliest. To obtain the estimate, M animals from a closed population of unknown size N are captured, marked, released and allowed to mix freely with the rest of the population. A random sample of size n is then taken, and the number m of marked animals is observed. The rationale of the Petersen estimator of N, which is given by $\hat{N} = Mn/m$, is that, under suitable assumptions, the ratio m/n of marked animals in the sample should closely approximate the corresponding ratio M/N for the whole population.

The Petersen estimator, which is equivalent to the dual system estimator that is used in human population studies (e.g. Brown *et al.* (2006)), is simply a ratio estimator, a concept that was used well before the time of the Danish fisheries scientist C. G. Johannes Petersen (1860–1928). Cormack (1968) noted that such an estimate was used by Laplace (1786) to estimate the population of France, and Ricker (1975), page 75, acknowledging E. S. Pearson, noted the earlier such usage by Graunt in 1662 to estimate that of London (Graunt, 1964).

By the 1950s, the estimator $\hat{N}$ had been long associated with Petersen. Chapman (1952) said that Petersen 'used the tag and sample method to enumerate a plaice population', citing Petersen (1896) as evidence. A more careful assessment, however, appeared in the same year. Bailey (1952) reported that, from 1889, Petersen used records of the proportions of marked fish that had been recaptured to study their growth and migration, and, from 1894, to estimate their mortality. Bailey noted that Petersen's method of estimating relative abundance from length–frequency graphs did not provide estimates of the total population size. Bailey's belief was that the first use of recapture data for such estimation was made by Lincoln (1930). It is indeed accepted

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that, independently of earlier work and of each other, the estimator was derived by Lincoln (1930) for estimating the wild-fowl population of North America and by Jackson (1933) for estimating the abundance of tsetse flies in Tanganyika. The first of these uses accounts for its designation as the Lincoln index in the ecological literature. The estimator was also used by Pearse (1923) to estimate numbers of turtles in part of Lake Mendota, Wisconsin. Although Pearse provided no specific reference for the estimator, Petersen was among the researchers whom he cited.

Le Cren (1965), however, reported that, 13 years before Lincoln, the Norwegian fisheries scientist Knut Dahl had used the Petersen estimator to estimate the number of trout in two small tarns near Bergen (Dahl, 1917). The English translation (Dahl (1919), page 19) gave a clear description of how to evaluate the estimator. It reads,

> 'The theory of calculation is shortly this. If I have marked 100 trout and distributed them evenly, and if I then fish and capture 150 trout, of which 50 prove to have been marked, I have taken half of the marked fish. Considering the marked fish as representative of the stock I should consequently have taken half the stock of the tarn and the total number contained should be about 300 fish.'

Le Cren, believing that Dahl would have known Petersen's work well, added

> 'it would appear that this quotation confirms that Petersen did not in fact calculate total populations from marked fish and that Dahl was the first to use this method'.

The fact that Dahl judged it appropriate to explain how to calculate the estimate does offer some support for this conclusion. However, Dahl described (page 18) the 'marking of fish as a means of estimating the stock' as

> 'the idea that originally prompted Dr C. G. Johs. Petersen in his famous experiment with the plaice of the Limfjord'.

This may imply that Petersen did not produce such estimates based on the Limfjord plaice experiment, but it leaves unproven whether he had decided *how* to produce the estimate, or whether or not he did so for some later experiment. It is also possible that, unknown to Dahl, the estimator had been previously used by someone other than Petersen. Cormack (1968) qualified Le Cren's position, asserting that 'Although Petersen did not use this estimate he has the prior claim in advocating its use'.

It has long been appreciated that the conditions for the valid use of the Petersen estimator are demanding. Cormack (1968), page 464, even referred to a 'universal lack of faith in the assumptions'. The basic estimator requires a closed population in which marked animals do not lose their marks and suffer no greater natural mortality. Those captured must be correctly classified as marked or unmarked, and, crucially, every animal must have the same chance of recapture. Hilborn and Walters (1992), page 175, indicated that they could not recommend tagging studies for estimating the abundance of fish populations unless 25% or more of the population could be marked.

Nevertheless, as Schwarz and Seber (1999) showed, there is still extensive use by ecologists of the Petersen estimator and its variants. Seber (1982) gave details of the bias reducing versions of the estimator due to Chapman and to Bailey. Seber also discussed the stratified Petersen estimator, which was designed for use when greater homogeneity is provided by stratification in time or space. Assuming equal numbers of release and recovery strata, he presented Darroch's derivation of the maximum likelihood estimators of the capture probabilities in each stratum and the probabilities of transitions between strata. The resulting estimator of the total population size is a sum of Petersen-type estimators within each stratum. Ricker (1975), page 75, described as widely adopted the practice that had begun with Petersen of using marked fish to compute rates of exploitation and total populations. His detailed account covered, in particular, adjustments to the Petersen estimator for various failures of the closure assumption as well as methods for experiments with multiple samples. Much of modern fish stock assessment is not based on mark–recapture, but Quinn and Deriso (1999) discussed its use in a range of contexts, including estimation of migration, natural mortality and age composition. Pine *et al.* (2003) recommended the use of closed population procedures, such as the Petersen estimator, in short-term studies in which the closure assumption can be met. Schwarz and Taylor (1998) reviewed developments of the stratified Petersen approach.

As far as we are aware, Le Cren's rather tentative suggestion that Dahl was the first to use the estimate remained unchallenged until Buckland *et al.* (2000) claimed that the international group of scientists studying the problem of overfishing in the North Sea was using recapture data to estimate abundance at least as early as 1913. The present paper seeks to validate that claim, and to investigate how the modern usage of the Petersen estimate emerged from the methodologies that were developed before the First World War.

Before 1914, many of the main fisheries scientists in the countries around the North Sea co-operated closely. Much of their work is, in some senses, well recorded. Some of the documents were published in more than one language or translation, or by more than one organization. The history is nevertheless difficult to unravel, since, by modern standards, referencing of sources was often poor. This would not have caused problems at the time as they met frequently and were well versed on each other's work. There was also a strong element of practicality in their co-operation in tackling the urgent problem of declining fish stocks, and the agreed programme of action was perhaps the most important part of the minutes of the meetings. An impression of selfless co-operation would, however, be misleading. Different methodologies were vigorously promoted, and routine competition between scientists was heightened at times by national rivalries. Many of the participants were often struggling to obtain financial support from their respective Governments, and the need not to understate one's contribution was as great as it is today.

2. The origins of marking

Over the last century a very wide range of methods has become available for marking or tagging fish. Indeed Rounsefell and Everhart (1953) listed 19 materials from which external tags had been made, nine for tags which pierced the tissue, and seven, including cadmium plating, for internal tags. A selection of the designs was shown in the illustrated review of Jakobsson (1970), who also described identification of stocks by using blood-groups, parasites and methods which he regarded as unconventional such as the use of dyes, tattooing and sonic and subcutaneous tags. Since then a major role has been played by internal tags, particularly the coded wire tag and the passive integrated transponder tag. Coded wire tags are used extensively. In particular, millions of young salmon each year are thus tagged before being released into the Pacific Ocean. Passive integrated transponder tags provide a non-destructive means of identification as they can be read without removing the tag. Overviews of current tagging methods are given by Thorsteinsson (2002) and Nickum *et al.* (2004).

In contrast, when Petersen became the Director of the Danish Biological Station in 1889, tagging technology was in its infancy. Marking and recapturing of fish had, however, been taking place for many years, albeit to learn about their migration and biology rather than to estimate their abundance. Cormack (1968) noted that, according to Walton in 1653 (Walton, 1953), the life history of salmon was investigated by Sir Francis Bacon (1561–1626), who marked fish by 'tying a riband ... in the tail'. In the 19th century, marking became increasingly common in Scotland.

> 'Mackenzie of Ardross in 1823 attached brass wires to the tails of salmon and grilse kelts. The late Duke of Atholl used copper wire and a copper label the size of a halfpenny in marking Tay fish, and between 1850 and 1863 obtained interesting recaptures, although the copper ... is reported to have caused considerable laceration'

(Calderwood (1908), page 57). Jakobsson (1970) attributed the first successful large scale tagging to C. G. Atkins, who tagged Atlantic salmon in Maine in 1873.

An international conference was held in Stockholm in 1899 to discuss a proposed joint programme of hydrographic and biological research in the North Sea (Conference Internationale pour l'Exploration de la Mer, Stockholm, 1899). Filip Trybom (1850–1913), one of the Swedish representatives, noted (page 43) that, over the previous 10 years, Norway and possibly other countries had followed Britain in marking salmon, and Denmark had 'of late years' been marking plaice. Trybom advocated experimental tagging of fish as the best way to reach reliable conclusions on migration, growth and spawning seasons. He noted the presence of 'some most distinguished gentlemen ... of unquestionable renown as specialists on this subject', two of whom appear to have been Petersen and Thomas Wemyss Fulton (1855–1929), the Superintendent of Scientific Investigations of the Scottish Fisheries Board. For the conference did indeed back the

> 'experimental marking and liberation of fish, for instance of plaice, on as large a scale as possible and over extensive areas; for example, as carried out by Dr. C. G. Joh. Petersen and Dr T. W. Fulton and others'

(Conference Internationale pour l'Exploration de la Mer (1899), page 35).

The pace of international research on fishing quickened after the first meeting in 1902 of the International Council for the Exploration of the Sea, which was then known by its French title, the Conseil Permanent International pour l'Exploration de la Mer (CPIEM). In the early years at least, the primary goal was to understand the biology of the fish, with some members seeing tagging as a useful approach. Hjort and Petersen (1905) wrote,

> 'This method has been brought into use, chiefly by the Danish biological station, and has led to extraordinarily great results so far as plaice is concerned'.

Johansen (1928a) gave the credit specifically to Petersen. He wrote that

> '... with his comprehensive marking experiments in the Cattegat, in the early summer of 1889, he is recognised as the first to employ marking experiments with fish in the sea, on an extensive scale, with a practical object in view'.

It is noteworthy that, as with fish, early marking experiments with birds focused on learning the biology rather than estimating population size. Again a pioneering role was played by a Dane. In this case it was a school-teacher in Viborg, Hans Christian Cornelius Mortensen (1856–1921). He made the first use of individual numbered rings in the study of bird migration, initially that of starlings (Preuss, 2001). Thomson (1913) reported that the method of bird-marking had been

> 'successfully used on the Continent, notably in Denmark and in Germany, for several years, but had not been known in the British Isles previous to 1909 except on a small and restricted scale'.

Thomson indicated that birds were marked to 'afford data of value to students of migration'. Ricker (1975) indicated that the first abundance estimation for birds was the work of Lincoln (1930) with water-fowl.

3. Petersen's contributions and subsequent fisheries methodology

Whether or not Petersen actually used recapture data to estimate total population size, he was certainly interested in estimating the total fish stock in the Limfjord. Petersen (1896), page 17, said

> 'We can in various ways *approximately calculate the number of fish in these waters*, a thing which, as far as I know, has never been attempted in the sea, except by *Hensen*, who tried to make out the number of grown-up plaice in the western parts of the Baltic Sea, by counting all the eggs of plaice floating there in the spawning time'.

(Both here and below, italicized words in quotations appear as in the original paper.)

Although it does not prove that he appreciated that it implied an estimate of total population size, Petersen certainly understood, and may have been the first to enunciate, the underlying principle of the Petersen estimate, namely the assumption that the proportion of marked fish in the sample reflected that in the population as a whole. Just as importantly, he offered an experimental protocol that was designed to make it valid. For, as Cormack (1968) noted, Petersen (1896), page 21, said

> 'when we spread the labelled fish over the whole fishing-ground, we may with some reason suppose that, proportionally, as many of the unlabelled fish which are living there will be caught as those that are labelled'.

Moreover his goal in adopting this procedure, given in the opening words of the same sentence, was to 'have a better opportunity of seeing how intense the fishery is'.

From a fisheries perspective, Petersen's pioneering work on age determination (Smith (1994), pages 79–80) may be judged more influential than his use of mark–recapture given the later dominance of methods that are based on catch-at-age data. Rozwadowski (2002) described how, before 1914, further such work by Johan Hjort and Einar Lea showed the extent to which fluctuations in catch were caused by variations in year–class sizes due to varying survival rates of young fish. Knowledge of year–class sizes led to successful catch predictions, firstly for herring, and then in the 1920s for haddock. As Ulltang (2002) recounted, the 1930s saw the development of fish population dynamics models, with Graham's yield model showing how increasing effort could reach the point of overfishing at which yield would start to decrease. Building on the earlier work of Baranov and Russell, the classic book of Beverton and Holt (1957) then provided, in particular, an age-structured differential equation model for yield in terms of recruitment, growth and mortality. Rozwadowski (2002) also described Gulland's development of Fry's concept of virtual population analysis, in which cohorts are retrospectively reconstructed by using catch-at-age data from catches in successive years. Virtual population analysis, and the approximate form known as cohort analysis, became very widely adopted in the 1970s. Derivative methods include those which are based on 'tuning', in which the virtual population analysis is calibrated to another measure of abundance such as catch per unit effort. The statistical catch-at-age models (Hilborn and Walters (1992), page 369) that came to the fore in the 1980s facilitated estimation of the abundance of cohorts that were still being fished and enabled the natural mortality rate to be estimated rather than assumed. The 1990s saw the growth of Bayesian methods, state space modelling and combinations of the two. (See Millar and Meyer (2000) and references therein.) Hilborn (2003) noted the increasing complexity of modelling, with unified frameworks able to incorporate surveys, catch per unit effort, age distributions, length distributions and tagging. He foresaw a return to simpler management procedures. Cotter *et al.* (2004) also emphasized the merits of greater simplicity and transparency.

The popularity of any methodology depends critically on the means to implement it, as the increased usage of Bayesian statistical techniques in the last 15 years shows. Increased computing power has clearly been a factor here, and, as McAllister and Kirkwood (1998) noted, it is only since the introduction of Bayesian Monte Carlo methods that such approaches have been widely applied in stock assessment. Bayesian priors have provided a means of utilizing relevant information from earlier similar studies, and Markov chain Monte Carlo methods, in particular, have enabled information about parameters of management interest to be obtained from posteriors that would previously have been intractable. Bayesian decision theory also provides a framework for evaluating policy options.

Similarly Petersen's extensive experimentation on methods of marking fish made a major contribution to the viability of mark–recapture. In 1896, he reported that, on his instructions, the plaice which were 'transplanted' in the Limfjord had various of their fins marked with holes which

> 'are cut very easily and quickly with an iron punch, and leave a scar which is almost always distinct from any accidental damage .... This way of marking the fish ... is quick, cheap, lasting, and does not hurt the fish'

(Petersen (1896), page 12). Later in the same paper (page 16), he also discussed labelling the fish with numbered bone buttons.

The inaugural meeting of the CPIEM in 1902, which was minuted in Conseil Permanent International pour l'Exploration de la Mer (1903a), established three committees; Petersen was a member of all of them. The six members of Committee B, which was charged with considering overfishing, also included Fulton, Trybom and Walter Garstang (1868–1949), who worked at the Marine Biological Laboratory in Lowestoft and the Marine Biological Association in Plymouth, before taking a chair at the University of Leeds.

By this time, Petersen's expertise on the marking of fish was certainly recognized. At Committee B in February 1903,

> 'The Convener exhibited various forms of label for flatfish based on Dr Petersen's principle, i.e. the attachment of buttons by silver wire near the middle of the dorsal edge of the body. He recommended the employment of a bone button underneath and a thin brass label of slightly concave form above. The number should be stamped on the brass label. By this method the number is not liable to obliteration and the fish is not injured .... It was generally agreed that Dr Petersen's principle should be accepted as a basis for the first experiments'

(Conseil Permanent International pour l'Exploration de la Mer (1903b), pages 131–132).

4. The concern with diminishing stocks

Smith (1994) described how, from the 1850s, concerns grew on both sides of the Atlantic about fluctuating catch levels. These were not abated by Thomas Huxley's assertion at the 1883 Fisheries Exhibition that for 'probably all the great sea fisheries ... nothing we do seriously affects the number of fish'. Garstang later noted that Huxley had been speaking only 'in relation to our present mode of fishing'. Smith (1994) also recounted how in 1896, on the basis of a decade of experimentation, Fulton published an analysis showing that, in two areas which were closed to commercial trawling, the catch per trawl haul of plaice had been higher than that in open areas. This analysis can be seen as paving the way towards the use of catch per unit effort statistics, as well as opening the long-standing debate on the efficacy of no-take zones. Fulton's conclusion was disputed by McIntosh (1899), whose view was summarized in the words 'man's operations ... are insufficient to affect the perennial abundance of sea fishes' (Garstang, 1901). In contrast, 'Garstang showed that there was clear evidence that fisheries could exhaust fish stocks. Based on the catches of British fishing vessels between 1889 and 1898, he showed that although total catch had increased by 30% the fishing power of the fleets had increased by 300%. Per unit catching power (now called catch per unit effort) had decreased from over 60 tons in 1889 to about 32 tons in 1898'

(Mills, 2000). Garstang did not, however, mention the marking of fish.

In September 1902, at Committee B of the CPIEM, there was a continuing effort to learn about the biology of the fish, but also a concern about possible overfishing. Of the ways of investigating it, Garstang (Conseil Permanent International pour l'Exploration de la Mer (1903c), page 99) noted that the method of counting floating fish eggs was not yet useful for all species, and that more experience was needed with using trawls of standard size. He also considered marking large numbers of fish 'to compare the number recaptured with the number set free'. Garstang (1903), page 136, noted their agreement on

'Experiments upon marked fishes, in order to determine the migrations and rate of growth of fishes, as well as to measure the percentage of fish actually caught by commercial fishing vessels'.

Many of the committee were under pressure from their Governments to focus on the practical goals that they had been set. At their meeting in December 1903,

'Dr Petersen agreed with the Convener that the general over-fishing problem was not the most essential question for practical purposes, and it was not of a character to be solved in a few years in an absolute scientific way. It would be of much more interest for the various Governments ... if they could show how to increase the stock of fishes actually existing'

(Conseil Permanent International pour l'Exploration de la Mer (1904), page 28). Accordingly they agreed to experiment with transplanting small plaice from inshore waters to deeper waters, but also to mark them.

5. Heincke and the fishing coefficient

4 years before Dahl (1917), Friedrich Heincke (1852–1929), a German delegate to the CPIEM and the first Director of the Biologische Anstalt Helgoland, had written

'*Determination of the fishing-coefficient by means of marked plaice.* The experiments with marked plaice, which have been extensively carried out in the North Sea since 1902, can be compared to experiments made with a ballot-box, containing a very large number of white balls and a very small number of black (or marked) [balls] all mixed together. If the latter are equally distributed among the white balls, and many lots of balls then taken at random from the box, the proportion between the white and black balls shown by the average of all the samples will be the same as the proportion in the total content of the box. ... The total of white balls here represents the entire plaice stock of the North Sea, the number of white balls drawn answering to the number of plaice caught each year, while the total number of black balls corresponds to the number of marked plaice set free at the beginning of the year, the black balls drawn representing those recaptured at the end of that period. The former divided into the latter gives the percentage of marked plaice recaptured in the course of a year, and this again is equal to the percentage of all those plaice in the North Sea which can be taken by the trawl, which are caught in the course of a year: this is the *fishing coefficient*'

(Heincke (1913), page 46). In the notation of Section 1, the estimate of the fishing coefficient f is $\hat{f}=m/M$, the proportion of marked fish recaptured. Dahl (1919) referred to $\hat{f}^{-1}$ as the 'coefficient of capture'.

When the total annual number of fish caught or destroyed by fishermen is known, the estimate $\hat{f}$ clearly implies a corresponding abundance estimate. Indeed, for plaice in the North Sea, Heincke (1913), page 50, estimated f at about 0.33 for those sizes of fish that are caught by the trawl. Using experimental trawling, supplemented by the market returns of the relevant countries, he estimated that 500 million plaice were caught or destroyed annually, thus implying that there were 1500 million adult plaice in the North Sea. This estimate, together with one made by Buckmann in 1932, was cited by Wimpenny (1953), who estimated that there were approximately 2000 million plaice at or near catchable size on the North Sea fishing grounds. More recently, assessments have been in terms of spawning stock biomass, which for North Sea plaice varied around 300000 t between 1957 and 1989, before declining sharply to just over 160000 t. In 1999 the European Union and Norway agreed that the spawning stock size should be maintained above 210000 t (International Council for the Exploration of the Sea (2005), page 107).

Herdman (1920), page 30, indicated clearly his familiarity with the work of Heincke. It is therefore of note that he nevertheless attributed the essentials of the method to Petersen. He wrote

> 'Petersen's method, of setting free marked plaice and then assuming that the proportion of these recaught is to the total number marked as the fishermen's catch in the same district is to the total population, will only hold good in circumscribed areas where there is practically no migration and where the fish are fairly evenly distributed'.

In fact, far from being the first advocate of the approach, Heincke had been one of the most sceptical. Heincke and Henking (1907) reported that they had released about 600 plaice in a restricted area of the North Sea and then trawled to recapture them. Johnstone (1908), page 175, said that they found that

> 'the results were inconclusive. Marking experiments of this nature ... seem to indicate that from 10 to 25 per cent of the marketable plaice present ... throughout an entire year are caught by the fishermen. But so many uncontrollable factors affect experiments of this kind that their results are problematical ones.'

Hermann Bolau also had criticisms of the protocol (Bolau, 1906). These were discussed by George Philip Farran from Dublin, who was Assistant Naturalist in the Fisheries Branch of the Government service. Farran (1909), page 10, wrote

> 'It is generally admitted that the proportion of marked fish returned can in some degree indicate the "intensity of fishing" on the ground in question, but Bolau has given very strong reasons why the figures thus arrived at should be received with the greatest caution. The figure ... will be too high if it happens that the plaice when marked are liberated in a spot where fishing is pursued with vigour and are captured before they have had time to disperse. It will, on the other hand, be too low if allowance is not made for fish which may have perished as the result of capture or marking or may have migrated to other fishing grounds. The conditions which, according to Bolau, must be fulfilled before any reliance can be placed on the returns are:- The marked fish must spread over the area in question in the same proportion as the rest of the fish; where fish are plentiful more must be marked than where they are scarce; the number of marked fish must be very large; only perfectly healthy vigorous fish should be liberated. The first of these conditions seems unnecessary in view of the second, and in any case we can have no guarantee of its fulfilment.'

Johnstone (1908), page 199, however, was not persuaded by '... those whose genius confines itself to the task of criticism'. He said

> 'It is contended that the marked plaice segregate themselves and that the percentage caught is more or less accidental and depends on the distribution of the fishing boats. But the advocates of the method claim that the number of marked fishes recaught is a measure of the intensity of fishing; and the results of such experiments made in England and on the continental side of the North Sea indicate that about 25 per cent, on the average, of all the marked plaice liberated are caught again within the year after the date of liberation. Perhaps it would be straining the results of these experiments to maintain that man annually catches one quarter of all the marketable plaice in the sea, but it is not really improbable that such may be the case.'

Heincke's eventual acceptance of the recapture approach seems to have resulted from his acknowledgement (Heincke (1913), page 46) that although Hensen's egg counting method appeared theoretically feasible, it had failed to yield any worthwhile results owing to a range of practical problems. Smith (1994), page 152, noted that Hensen's goal of the 1890s was eventually realized in 1923 when Buchanan-Wollaston reported to the International Council for the Exploration of the Sea estimates of numbers of plaice based on egg production. More recently, egg production methods (Quinn and Deriso (1999), page 206) have been widely used to estimate spawning biomass for a range of marine pelagic species. Applications to various demersal species have also been advanced lately (e.g. International Council for the Exploration of the Sea (2006)).

As we have noted, one concern of the September 1902 meeting of Committee B of the CPIEM was the percentage of fish being caught. The results that were subsequently reported by the Danes caused considerable surprise. Hjort and Petersen (1905), page 17, noted that 'the number of marked fish returned is extraordinarily great'. They had found that, of 1099 marked plaice that had been released in the North Sea, 43.4% were returned in 14 months and, of 121 plaice that had been marked and released in the Skagerrak, 58.5% were caught in 14 months, and 80% of those that had been released in the Kattegat were caught in 4 months. They observed (page 17) that

> 'Through these high percentages, one gains a good notion of the intensity of the plaice fishery in the North Sea and Danish waters'.

Contradicting McIntosh (1899), they concluded (page 25), 'The Danish investigations have shown ... that it is above all man who is weakening the stock'.

Dahl, however, was more optimistic about the cod fishery. He reported that, in spring 1905,

> '433 cod from traps were marked ... in the Sndeled fjord .... Of these marked fish, 71 were recaptured in the first year after liberation viz. 16 - 17%.... The results of this experiment cannot of course be regarded as a definite answer to the question in what degree the fish stock is affected by fishery. ... But so much is evident, that at least a very considerable proportion of the stock of cod is not affected by fishing'

(Dahl (1909), page 17).

6. Estimates made by Johansen and Garstang

Heincke (1913) appears to imply that the methodology represented by his ballot-box analogy (see Section 5) had been used since 1902. Seeking supporting evidence, we found that Johansen (1928b) certainly claimed to have estimated abundance via the fishing coefficient before 1913. He wrote

> 'In 1906 I propounded that the size of the stock of a given species ... can be calculated by means of the marking experiments, introduced a long time ago, in connection with statistics of the weight of all the fish of this species landed from the area in question in the course of a year and by means of an investigation as to how many of these fish are included in that part of the stock for which the marking experiments can give information regarding the intensity of the fishing'.

Referring indirectly to Johansen (1906), he said,

> 'I attempted to employ this method ... to calculate the number of plaice in the Kattegat over three years of age .... Marking experiments carried out on plaice in the Kattegat showed that on an average about 50 per cent of the fish over three years of age were recaptured in ... one year, and by means of an age analysis of samples of captured fish it was calculated that approximately 15 million fish of the III-group and older fish were caught annually. ... The stock of the III-group and older fish was thus decreased by fishing in the course of a year from 30 to 15 million approximately'

(Johansen (1928b), pages 89–90).

In fact, such calculations were performed before 1906. There was some disagreement at Committee B in July 1905 (Conseil Permanent International pour l'Exploration de la Mer, 1905) on

Table 1. Garstang's (1905) marked plaice recovery data

Country	*Marked*	*Recovered*	*Annual %*
Sweden	1178	101	8
Denmark	1220	387	29
Germany	1919	157	8
Holland	459	12	3
England	1463	286	17
Totals	6239	943	14

how to estimate abundance. Heincke proposed more work on the 'floating eggs' method, but the British (page 70) were not willing to pay for this. Heincke, for his part, was unconvinced (page 64) by a report by Garstang. This report (Garstang (1905), page 4) included the data in Table 1 showing how many of the marked plaice that had been released up to the end of 1903 had been recovered by the end of June 1904. Note that the percentages shown are not based on the first two columns, but specify the proportions that were recovered within 12 months of liberation.

Garstang interpreted the data with some caution, excluding, for instance, small fish which were more easily damaged by marking. He noted that the low level of recaptures by the Dutch could be ascribed to their trawling methods but was more wary of the German data. Although four of the countries had used a modified form of Petersen's method of marking, the Germans had adopted labels which were easier to put on but which had a greater tendency to fall off. More crucially from our perspective, he produced an abundance estimate by the method that Heincke described 8 years later. Acknowledging that the actual quantity of fish that had been landed was unknown, Garstang wrote (page 25)

> '... if we assume that three or four million of plaice represent the maximum total catch of plaice on the south part of the Dogger Bank, in the course of a year, we shall obtain a figure which ... will probably serve for our present purpose. The intensity of fishing on the Dogger Bank as shown by the Dutch marking experiments was 13.9 per cent per annum .... Taking 1/5th as probably more closely approximating to the real intensity we may conclude that the total population of plaice on the south part of the Dogger Bank is not more than 15 or 20 millions.'

7. Meek's evidence and Fulton's contribution

Did anyone calculate abundance by using the fishing coefficient before Garstang in 1905? The report of the Committee on Ichthyological Research (1902), recording their meeting in 1901, makes this appear unlikely. The witnesses to the Committee included Fulton and Garstang, and, although it was agreed that a 'census of the sea' was needed, no witness appears to have mentioned either Petersen or the possibility of a mark–recapture approach.

We thus read with surprise the following comments by Alexander Meek (1865–1948), a lecturer in zoology at Newcastle College, who was in charge of the scientific experiments of the Northumberland Local Fisheries Committee. Meek (1904a), page 79, said

> '... a calculation may be offered to give an indication of the number of the resident population of plaice of from 2 to 4 years old. We marked 471, and we recovered from the catches of fishermen in the district 54. This is, allowing slightly for loss, one-eighth part, and may be taken therefore to represent approximately the catching power of the inshore fishermen. As near as we can gather the fishermen

caught in the inshore waters for the year ending June 30th, 1904, 440 cwts. of plaice. The population of plaice of the inshore waters from about 7 to 14-in. long may be said to be therefore 3,520 cwts. If the average weight of the fish be, say 1/2 lb., the population in numbers is about 800,000.'

Far from claiming novelty, Meek called this 'a method which has been adopted before', suggesting that he regarded this approach as well established by 1904. The impression is reinforced by his well-considered critique of his estimate of 800000 plaice. He continued (page 79),

'Considering the large proportion obtained from some of the districts this number will probably be found to err by being too large .... On the other hand, however, many more plaice are caught than are sent to market or used for crab bait; and as a matter of fact our labelled fish were sometimes caught by others than professed fishermen.'

The records of the Committee on Ichthyological Research (1902), paragraph 2700, give a further indication of the work going on in Northumberland. Meek told the Committee

'there is a very exceptional fisherman at Beadnell, Mr Douglas, who is carrying on experiments in the marking of crabs and lobsters'.

Meek (1899), pages 52–53, indicated that Douglas had been marking crabs at least since 1895, albeit with the initial goal of determining their spawning season and habits. Meek (1904b), page 58, reported that

'The average annual catch of lobsters on the coast of Northumberland ... is 39,555, say 40,000. In 1902, Mr Douglas, Beadnell, labelled and liberated 100 lobsters and 12 were recovered. But this percentage is more than likely too small, for of one group of 10, 8 were recaptured, and we have reason for believing that some of the labels were destroyed through ignorance. The fishing strength of the fishermen may be estimated to be about 20 per cent, and any other losses so far as nature is concerned must be so small as to be negligible. The population of adult lobsters on the Northumberland coast may therefore be said to be about 200,000.'

Similar calculations for crabs were also given.

Despite Johansen's claim, which was noted in Section 2, it appears that Petersen in 1889 was not alone in conducting large scale tagging experiments in the sea. In 1886 the Fisheries Board for Scotland had also acquired a research vessel, and Fulton (1890), page 14, reported that

'A series of experiments, designed to ascertain the migrations of the food-fishes and their rate of growth was carried on last year on board the "Garland" .... Such experiments are also being carried out in Denmark.'

This indicates that the work in Scotland and in Denmark was essentially contemporaneous. Fulton (1904) strengthened the impression by referring to

'the experiments on the marking of fishes to ascertain their migrations which I carried on in the years 1889 - 1892'.

The scale of the Scottish studies was reported by Fulton (1890), pages 353–354, when he wrote

'... last year ... numbered brass labels were attached to about 1000 fishes .... The experiments were chiefly conducted in the Firth of Forth and St Andrews Bay.... As the cost of these experiments is very small, they will be continued on a large scale.'

Petersen (1893), page 24, footnote, acknowledged that

'Dr Wemyss Fulton has ... given the first contribution to a more rational investigation into the biology of the plaice ...'.

More significantly, Fulton (1890), part III, section D, gave the earliest indication that we have found of interest in what became known as the fishing coefficient. In reviewing international fisheries work, Fulton (1890), page 374, wrote

'Dr Petersen continues his scientific investigations into the fishing grounds .... The marked plaice, as a rule, did not wander far; thirty per cent of the large mature fishes were recovered in the course of a year, which shows that about a third of the fish on the fishing grounds are caught annually.'

8. Some conclusions on the distribution of marks

Our original goal was to attempt to establish to whom the credit for the concept of the Petersen estimator should be correctly attributed. For, although the Petersen estimator is just a ratio estimator, it appears to have been developed independently. The above evidence suggests, however, that some other questions should be considered. To what extent is the concept of the Petersen estimator merely an extension of that of the fishing coefficient? To whom should the credit for the latter be given? Who created the conditions in which it was possible to gather the data to calculate a Petersen estimator? Why historically was Petersen given the credit for the estimator that bears his name?

It can indeed be argued that the Petersen estimator is simply a corollary of the notion of the fishing coefficient f. The key principle of the two concepts is that

> 'the number of marked fish recaptured bears the same proportion to the number released as does the total number of fish captured by the fishermen in the same time to the total stock of fish on the ground'

(Farran, 1909). We therefore expected that highlighting the role of f would lead to some sharing of the credit for the Petersen estimator. The quotation from Fulton (1890) in Section 7 shows this expectation to be ill founded. It seems likely that Fulton was attributing to Petersen not only the data but also the inference that an annual recovery of 30% of the marked fish implied that annually about a third of the population was caught. If so, then not only was Petersen recording the proportions of marked animals recaptured, as Bailey (1952) noted, but also, in some of his early work, he is using the estimated fishing coefficient to make inferences about the population as a whole.

We have substantiated above the assertion of Buckland *et al.* (2000) that recapture data were used to estimate abundance at least as early as 1913. We have seen here, however, that there is no strong reason for regarding as novel the methodology of Heincke (1913), nor indeed that of Johansen (1906). Abundance calculations were made by Garstang (1905), and before that by Meek (1904a, b). Indeed Meek's are the earliest *explicit* estimates of the total population size derived via the fishing coefficient that we have been able to trace.

Yet Le Cren's attribution of the Petersen estimator to Dahl is by no means entirely undermined. Before 1914, the scientists were working on large scale problems, where the available statistic was often the weight w of the total catch of the species for an extensive area over a whole season. Using the estimated fishing coefficient $\hat{f}=m/M$, they first estimated the total weight of the adult population of the species by $\hat{W}=w/\hat{f}$ and then the size of the population by using $\hat{N}=\hat{W}/\mu$, where μ is the average adult fish weight for the species. Dahl (1919) covered both approaches, envisaging his coefficient of capture, M/m, being multiplied either by the weight w to estimate the total weight or by the number n that are caught to estimate the population size N. From today's standpoint the distinctive feature of Dahl's experiments in the tarns near Bergen is their relatively small scale in both duration and geographical area. It may thus be that he was the first to be working in a context in which the count n was available, allowing direct estimation of the size of the population.

Petersen's contribution to marking technology provides much of the explanation for the association of his name with mark–recapture before 1914. Successful marking requires a reliable tag that remains securely attached to the fish without damaging it, and gradually a general recognition grew that Petersen's was the best available. We noted in Section 3 that in 1903 Committee B adopted Petersen's label for flatfish, and in Section 6 that in 1905 a modified form of Petersen's label was being widely used. Also Meek (1904b), page 71, reported that the label which was used in the Northumberland experiments of the previous year was the modified form of the Petersen label that had been adopted in the international investigations.

Our evidence suggests a need to qualify the assertion of Le Cren (1965) that 'Dahl may have been the first to calculate an estimate of total population'. It would, however, seem churlish to query Le Cren's hope that ' the method will continue to be known ... as the "Petersen Method"' or his belief that Petersen was 'one of the main founders ... of population ecology itself'. Indeed our evidence indicates that Petersen's early use of the fishing coefficient should be added to his recognized contributions, namely the principle and protocol for the Petersen estimator, and the development of the Petersen label.

However admirable the level of international co-operation in fisheries research before 1914, the scientists who were involved were not entirely free of national pride, nor of the need to secure governmental funding. Our investigation suggests a need to be wary of some of their claims, including the assertion, which was recorded in Section 2, that it was chiefly the Danish biological station which brought into use marking of fish to investigate their growth and migration. Similarly, we noted in Section 7 the apparent overstating of Petersen's role by Johansen. Both of these claims fail to do justice to the work of Fulton. Furthermore, if Johansen was claiming to have initiated abundance calculations in 1906, he was overlooking earlier work by Meek and Garstang, and possibly others.

If Dahl was indeed the first to estimate total population size by using recapture data and a direct count of the total catch, then arguably the lack of the appropriate data was the main reason that the estimate had not previously been calculated in this way. We have seen that between 1890 and 1913 the notion of the fishing coefficient, and the 'Petersen principle' that underlay it, was, at differing time points, understood and accepted by a wide group of scientists. It looks likely that Petersen himself was the first in this group, followed closely by Fulton, and then others including Meek, Garstang, Johansen and Heincke. It seems entirely plausible that any one of this group, and indeed many of the others who were immersed in the work of the International Council for the Exploration of the Sea, would have considered trivial the direct calculation of the Petersen estimate $\hat{N} = nM/m$, if it had been possible in the problems that they were addressing to count the total number n of fish caught. In their circumstances, however, the preliminary estimation of the total population weight was simply a matter of necessity.

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