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# Linking plankton and fish production throughout the history of ICES

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The importance of plankton for the productivity of the oceans had been realized in the latter part of the 19th century, just prior to the establishment of ICES in 1902. Thus, the study of plankton was closely linked to fisheries research in the early years of ICES and remained so until the 1950s. However, a major obstacle in relating plankton and fisheries production was the lack of methods that could be used to quantify primary production, and it was usually changes in bulk properties (pH, phosphate, and oxygen) that were used to estimate production. Ironically, at about the same time as quantitative methods of determining primary production were developed, the Beverton-Holt models refocused fisheries scientists on the task of quantifying fisheries yield in relation to recruitment. Thus, there was no longer a perceived "need" for an understanding of plankton and environmental variables to predict fisheries yields, and subsequent ICES activity was dominated by a further development of the Beverton-Holt approach. Most of the major developments in the understanding of holoplankton production after the 1950s occurred outside of ICES. In the most recent decades, an understanding of the types of plankton communities likely to give rise to a net increase in organic material in marine systems emerged. This "new" production is more likely than total primary production to be directly related to fisheries production. Thus, although they lacked sensitivity, the early attempts to measure primary production were actually more appropriate in terms of estimating a basis for fisheries production than the $^{14}$C method used in recent years. Our knowledge base may finally be sufficient to accomplish the original ICES goal of quantitatively relating plankton and total fisheries production.

Keywords: fish production, fisheries yield, new production, plankton, primary production.

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## Introduction

Based on extrapolations from the agricultural sciences, there was the expectation among a number of leading northern European scientists around the time that ICES was established that there would be a direct and quantifiable relationship between the plankton production occurring in the sea and the fisheries production (measured as fisheries yield) from a given region. One of the most influential scientists at this time was physiology professor Victor Hensen from Kiel.

Today, we regard Hensen as an important, if not "the", founding father of modern biological oceanography. He was, even by modern standards, a highly productive scientist with over 100 publications to his credit. Most of these were within his field of training (human physiology), but over 30 were concerned with the "metabolism" of the ocean. His interest in the sea stemmed from a concern over the economy in his native region of Germany (Schleswig-Holstein). A contributing factor to the economic woes of the area at the time of Hensen's career was a decline in the fisheries of the region.

Hensen was convinced that the microscopic plants and animals were the "blood of the sea" (Mills, 1989) and that these organisms ultimately controlled the productivity of the sea as a whole. Hensen actually commissioned the coining of the term "plankton" by asking one of his professor colleagues at Kiel to find a name for the microscopic particles he saw in the sea. Hensen's goal was to describe the relationship between plankton and fish production. A prerequisite for being able to consider this relationship was, however, the development of methodology to quantify plankton production, and it was here that Hensen first focused his energies.

## The early years of ICES

Hensen, himself, was not actively involved in the early ICES work. However, the influence of his work is clear in the early scientific endeavors of ICES. For example, an early focus of ICES was the quantification of the relationship between plankton production and fisheries. At the time, there were, of course, no methods for direct measurement of production *per se*, so the early studies were devoted to quantifying biomasses of plankton and describing geographic and, later, seasonal differences in plankton abundance. Hensen had, in the years prior to the establishment of ICES, applied his knowledge of the physics of blood flow to the development of quantitative plankton collection techniques, which enabled comparisons to be made of plankton biomasses in different regions. Many of the early cruises carried out in the name of ICES were, thus, devoted to studies of plankton distributions in time and space.

At this time, no distinction was apparently made between phyto- and zooplankton when considering the relationship between plankton and fish production. The combined study of primary (phytoplankton) and secondary (zooplankton) producers in these early plankton studies is understandable given the dearth of knowledge concerning these microscopic organisms 100 years ago and the recognition that the plankton particles in total, regardless of their phylogeny, constitute the food that fuels the productivity of higher trophic levels. Nevertheless, the combination of the different trophic levels complicated the task of trying to unravel the relationship between plankton production and fisheries.

ICES, since its inception, has never separated these trophic levels in its committee structure (although, in later years, separate working groups under the Biological Oceanography and, later, Oceanography Committee have been devoted specifically to phyto- or zooplankton).

I have been asked by the organizers of this Symposium to address the relationship between "plankton production" and fisheries. I suspect that in line with ICES tradition, a presentation dealing with both phyto- and zooplankton was anticipated. I argue, however, that it is the magnitude of phytoplankton production, where the sun's energy is converted into a form that, ultimately, can be used by fish, which will be most readily related to fish production and/or fisheries yield. The remainder of this analysis will, therefore, focus on progress through the last 100 years in relating phytoplankton (primary) production to the production of fish.

## The first measurements of primary production

The first estimates of photosynthetic activity in the sea were based on observations of pH changes (alkalinity is affected by photosynthetic removal of carbon from the surrounding medium). Moore *et al.* (1915, as cited in Mills, 1989) realized that the production of the sea could be estimated from pH changes, and he produced an estimate for annual production in a region up to a depth of 100 m off Port Erin (UK) of approximately 125 g C $m^{-2}$ $yr^{-1}$ (conversion from their original units to g made by Mills, 1989). Some few years later, pH changes were used to estimate primary production in the English Channel during the spring (Atkins, 1922, 1923, as cited in Mills, 1989). Atkins recognized, however, that pH was influenced by a number of processes in addition to photosynthesis and that there was a need for an independent method to corroborate the estimates made from changes in pH. He modified and improved the existing method of determining phosphate with the result that changes in phosphate concentration could also be used to estimate the production of phytoplankton biomass (as described in Mills, 1989).

It is interesting that most of these early attempts to estimate the magnitude of phytoplankton production were based on changes in bulk properties of seawater rather than on direct attempts to quantify the products of the photosynthetic process, especially in light of the fact that an early version of the light-dark bottle oxygen method of estimating photosynthetic activity was being used in the Oslo Fjord as early as 1916 by Gaarder and Gran (Mills, 1989). Their work was described at a meeting of ICES Delegates "from neutral nations" in 1918, but not published in English until 1927, and Mills (1989) suggested that the long delay in the routine application of the oxygen method for estimating primary production was probably a direct result of the delay in publication.

In any event, by the late 1920s, there were several different methods of estimating, albeit crudely, the magnitude of primary production occurring in the oceans. The scene would, then, appear to be set for relating the phytoplankton and fisheries production (assuming fish yield can be related to fish production at least under a small and/or relatively stable fishing intensity). In 1938, Johan Hjort, Chair of the ICES Consultative Committee, proposed a coordinated international research effort for the North Sea which, among other objectives, should deal with changes in hydrographic and plankton conditions and the fluctuations in fisheries. Instigation of the programme was delayed owing to World War II, but a programme based on the original idea was finally carried out in 1947–1948 (Smed, 1983). The phytoplankton results from this study were published by Braarud *et al.* (1953).

Thus, at the beginning of the 1950s, ICES scientists were still actively pursuing the original ICES goal of

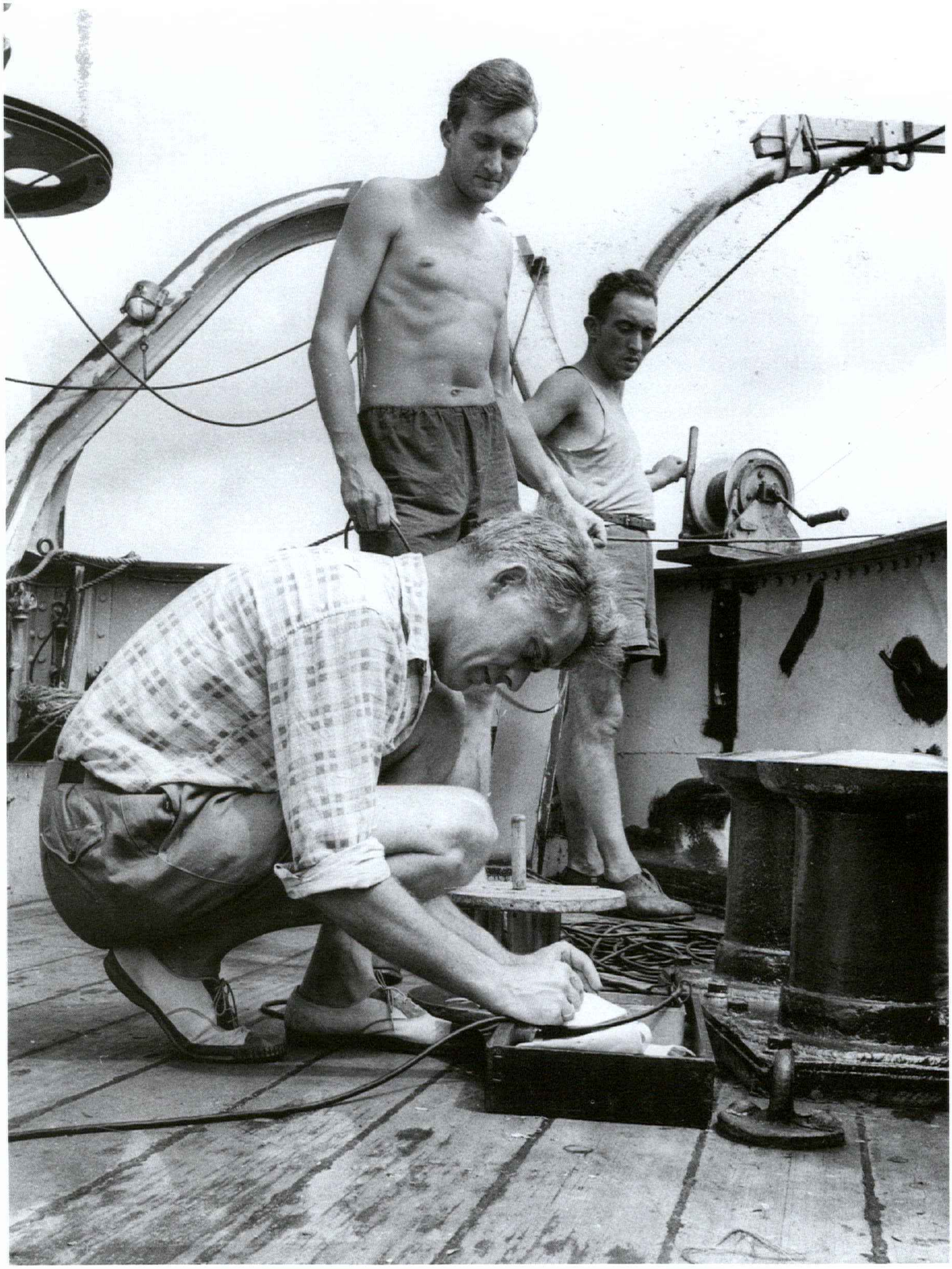

Figure 1. Einar Steemann Nielsen preparing for a light measurement on the Galathea Expedition, 21 December 1950. E. Aabye Jensen (standing) is looking on. The photograph was taken by P. Rasmussen and kindly supplied by Torben Wolff, Zoological Museum, Copenhagen.

identifying the relationship between plankton production and fisheries production.

## A change in scientific focus in the 1950s

A major scientific milestone, in terms of quantifying marine primary production, occurred in the early 1950s when the Danish pharmacology professor Einar Steemann Nielsen (Figure 1) developed the $^{14}C$ method of measuring phytoplankton photosynthesis. Man-made radioisotopes were a by-product of the war, and within months of their release on the commercial market, Steemann Nielsen had developed his now-famous method for measuring phytoplankton production. An impetus for the rapid development of the method was the upcoming Galathea Expedition, a Danish round-the-world research cruise carried out between 1950 and 1952. Use of the new method on the expedition permitted Steemann Nielsen and his assistants to collect a total of 194 measurements of primary production and yielded the first truly global estimate of marine primary production: 15 gigatonnes of carbon per year (Steemann Nielsen, 1952a; Steemann Nielsen and Aabye Jensen, 1957).

Thousands of marine primary production measurements have been made in subsequent years from the development of the $^{14}C$ method (a superficial search in *Aquatic Sciences and Fisheries Abstracts* yields about 4000 hits on "marine primary production" for the period covering the last 20 years). Nevertheless, "modern" estimates (about 20–53 gigatonnes per year ) of global marine primary production are of the same order of magnitude as Steemann Nielsen's original estimate. At the time he presented his estimate, however, it clashed with current thinking in that it had been argued (Rabinowitch, 1945) that primary production in the oceans was about an order of magnitude higher than Steemann Nielsen found it to be. Rabinowitch's estimate was made by extrapolating results from light-dark bottle oxygen determinations made over several days on samples taken in the Sargasso Sea (Riley, 1939). Thus, the Galathea Expedition and, especially, the primary production estimate for the sea that it provided was truly a milestone in the history of plankton research.

Given that ICES has its base in Denmark and the Galathea Expedition was Danish, one might have expected an ICES role in the planning and/or execution of the cruise and this milestone of obtaining a global estimate of primary production. However, this was not the case. The Galathea Expedition was led by Anton Frederik Bruun from the University of Copenhagen's Zoological Museum. Before moving to the Museum, Bruun had been employed at the Marine Biological Laboratory which, at the time of the Expedition, was housed together with the Danish Biological Station and ICES in Charlottenlund Castle. Å. Vedel Tåning was the Director of the Marine Biological Laboratory which was housed on the floor below ICES at the Castle. He and Bruun had not parted on good terms. It is unclear exactly what caused their differences, although their personalities were apparently quite different, and I have heard it suggested that Vedel Tåning may have been jealous of Bruun as he felt that their common leader, Johannes Schmidt, preferred Bruun to himself.

In any event, Vedel Tåning was opposed to the Galathea Expedition. Through his brother, Tage Tåning, a newspaper editor, Vedel Tåning launched a public attack on Bruun and the Galathea Expedition in the form of a very acrimonious exchange of views on the Expedition and the people involved, published in *Berlingske Aftenavis* in the period 12–15 June 1950. Thus, although the geographic distance between the Zoological Museum and Charlottenlund Castle where ICES was housed was only a few kilometers, the possibilities for cooperation between ICES and the Galathea initiative were not good.

Although the Galathea Expedition was not credited as a Danish contribution to ICES, Steemann Nielsen, after publishing a short version of his results in *Nature* (Steemann Nielsen, 1952b) did choose the *Journal du Conseil* as the outlet for the more detailed Expedition primary production measurements (Steemann Nielsen, 1952a). The same year, he became a paid "consultant" at the Plankton Laboratory of the Danish Commission for Fisheries and Marine Research. It was probably in this capacity that he so actively participated in ICES activities in the mid-to-late 1950s. He was Chair of the Plankton Committee for much of this period, and it was under his leadership of the Committee that ICES held a meeting on "Measurements of Primary Production in the Sea" just prior to the 1957 Council Meeting in Bergen.

The report from the meeting (ICES, 1958) indicated that, by this time, the use of the new $^{14}C$ method of estimating primary production was widespread in the ICES community. Thus, the ICES scientific community, in the late 1950s, was well armed to continue the search for the relationship between plankton and fisheries production – although Steele (1958) did warn at the Bergen meeting that the new $^{14}C$ method (as well as the other older methods) of measuring primary production might "lead to a dead-end" in the pursuit of the original ICES goal as:

> the abstract nature of the units used in these production studies makes it difficult to imagine the detailed steps to the higher tropical [sic, read *trophic*] levels where the study of the species involved can no longer be neglected.

The development of the $^{14}C$ method for measuring primary production was truly a scientific milestone. However, scientific milestones in the 1950s were not restricted to the plankton community. In 1957, Beverton and Holt presented their classic model relating fisheries yield to recruitment. This approach obviated the "need"

Table 1. Estimated primary and fish production in three ocean provinces (from Ryther, 1969).

| Province | Primary production (t organic carbon) | Trophic levels | Efficiency (%) | Fish production (t fresh weight) |
|---|---|---|---|---|
| Oceanic | $16.3 \times 10^9$ | 5 | 10 | $16 \times 10^5$ |
| Coastal | $3.6 \times 10^9$ | 3 | 15 | $12 \times 10^7$ |
| Upwelling | $0.1 \times 10^9$ | 1.5 | 20 | $12 \times 10^7$ |
| Total | – | – | – | $24 \times 10^7$ |

to invoke plankton production or ecology in order to estimate potential fisheries yields. The Beverton-Holt approach forms the very basis of modern fisheries assessment work in the ICES Area. Thus, since the late 1950s, the major thrust of ICES activity has been through the further development and application of the Beverton-Holt models. Thus, ironically, just as sensitive, quantitative methods became available for measuring primary production in the sea and with the scene apparently set for relating plankton and fisheries production, the interest in establishing the relationship between fisheries and plankton production waned within ICES.

## Advances in relating plankton and fisheries production occur outside ICES

Although the major focus within ICES was now directed towards assessment based on the approach presented by Beverton and Holt (1957), plankton work continued within ICES under first the Plankton Committee followed by the Biological Oceanography Committee and, since the late 1990s, the Oceanography Committee. The focus and interest in plankton work within ICES has, however, largely drifted away from the original ICES goal of quantifying the relationship between plankton and fisheries production. Measurement of primary production has remained a focus for the various working groups dealing with phytoplankton, and a major international symposium, "Measurement of Primary Production from the Molecular to the Global Scale" was organized by ICES in 1992 in La Rochelle (Li and Maestrini, 1993). However, rather than linking phytoplankton production to fisheries, the primary foci of phytoplankton activities within ICES since the mid-1980s have been harmful algal blooms (especially the interaction of these with aquaculture activities; e.g., Parker and Tett, 1987) and identifying changes over time in phytoplankton biomass or activity. This latter interest is, of course, an attempt on the part of ICES scientists to contribute to the knowledge base relating to coastal marine eutrophication and to such activities as the North Sea Task Force and preparation of the 1993 Quality Status Report for the North Sea (North Sea Task Force, 1993).

Although ICES scientists were following a somewhat different track with respect to plankton research after the 1950s, scientists outside ICES continued directly or indirectly to try to quantify the relationship between plankton and fisheries production. In the period following the development of the $^{14}C$ method for measuring primary production, large numbers of primary production estimates from various types of marine environments began accumulating. By the mid-to-late 1960s, the number of estimates was sufficient to allow estimates of total annual primary production for various ocean regions (Ryther, 1969 and references therein). Using these estimates and assuming simple ecological efficiency factors, Ryther (1969) predicted the potential fish production possible for oceanic, coastal, and upwelling regions of the world's oceans (Table 1).

In this seminal paper, Ryther pointed out that total production of fish was not the same as the potential yield to fisheries both because human beings are competing with other carnivores for the fish produced and because it is necessary for some stock to remain in order to ensure the future survival of the stock. Nevertheless, he identified the possibility for using the approach of relating primary production to potential fish production to identify maximum potential fisheries yields. He used his analysis to argue (somewhat prophetically, it now seems)

> it seems unlikely that the potential sustained yield of fish to man is appreciably greater than 100 million tons. The total world landings for 1967 were just over 60 million tons, and this figure has been increasing at an average rate of about 8 percent per year for the past 25 years… At the present rate, the industry can continue to expand for no more than a decade.

Ryther's simple 1969 model, as well as essentially all of the more sophisticated ecological models that followed his and from which fisheries yields can be estimated, use primary production estimates determined using the $^{14}C$ method developed by Steemann Nielsen as input data. Nixon (1992) collated $^{14}C$ primary production determinations from a number of different regions and related them to fisheries yields from the same regions. Later, Nielsen and Richardson (1996) extended the Nixon data set to include two points from the Kattegat, one from the 1950s and one after nutrient enrichment of the Kattegat from the period 1984–1992 (Figure 2). A relationship between these primary production and fisheries yield data does emerge both between the different sites studied and within the Kattegat site under changing nutrient availability. It is, however, not a clean relationship, and it is necessary to log transform both axes in

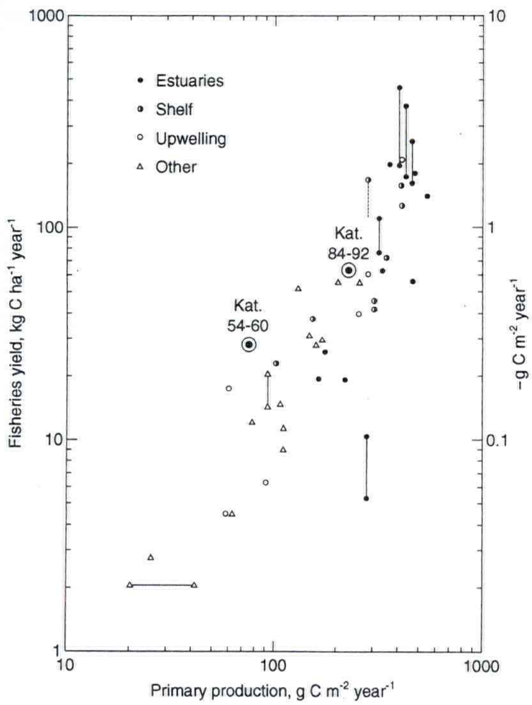


Figure 2. Fisheries yield as a function of primary production (from Nixon, 1992). Values for total yield and primary production in the Kattegat 1954–1992 (Richardson and Heilmann, 1995) are superimposed (from Nielsen and Richardson, 1996).

order to bring it out. One of the reasons why the relationship is not more easily quantified is, of course, that fisheries yield is not a constant function of fish production. However, we must also consider whether the $^{14}C$ method really provides the most suitable primary production data for relating plankton activity to fish production.

Here again, Ryther (1969) provided interesting insight in his discussion of ecological efficiency where he pointed out that the "size of an organism is an essential criterion of its potential usefulness to man...the larger the plant cells at the beginning of the food chain, the fewer the trophic levels that are required to convert the organic matter to a useful form." Just prior to Ryther's contribution, Dugdale and Goering (1967) had identified two forms of primary production – "new" and "regenerated" based on the nitrogen nutrient giving rise to the production. New production is that which gives rise to an increase in organic material in the system and is fueled by the introduction of new nitrogen in the form of nitrate to the system (for example, through upwelling). Regenerated production, on the other hand, is based on the reuse of nitrogen already within the system (ammonium) and cannot lead to an increase in organic material in the system as a whole.

In practice, the primary production occurring in every marine system will be composed of a mixture of both new and regenerated production. However, the percentage of the production which can lead to an increase in organic material will vary from about 10 to 90% of the total. The $^{14}C$ method of measuring primary production determines total primary production and, thus, does not differentiate between new and regenerated production.

By the end of the 1980s, it became clear that small phytoplankton cells are generally associated with regenerated production and large cells with new production (e.g., Cushing, 1989; Kiørboe, 1993). New production will give rise to the classically depicted short food chain, with primary producers (phytoplankton) being directly consumed by mesozooplankton (Cushing, 1989). The phytoplankton community under such conditions is characterized by a high percentage of large phytoplankton cells and an efficient transfer of energy to the higher trophic levels (see Ryther, 1969). Thus, Kiørboe *et al.* (1990) suggested that it is new production and not the total primary production measured with the $^{14}C$ method that should relate most directly to fish production. Ironically, of course, this means that the bulk parameter methods (changes in pH or nutrient concentrations) used to determine primary production prior to the development of the $^{14}C$ method were actually more appropriate for providing estimates of the basis for fish production than the primary production determinations obtained using the $^{14}C$ method. The method that appeared to provide such tremendous potential for quantifying primary production and its relationship to fish production when it appeared in the early 1950s may then, actually, have introduced unnecessary error in the quantification of the relationship between primary production and fish production.

## Linking primary production and fisheries yield anno 2000

Marine science today is very much focused in different disciplines. This is in contrast to the climate in marine science 100 years ago when ICES was established. A holistic rather than disciplinary approach to ocean science dominated within ICES and the scientific community at large for the first half of the century (Parsons and Seki, 1995) and it was during this period that the most serious attempts to relate primary and fish production took place. Today, ICES fisheries biologists traditionally focus on assessments using methods based on the Beverton-Holt models developed in the late 1950s and, generally, have little use for plankton or primary production data. Likewise, plankton biologists and ecologists have a tendency to focus alone on processes occurring within the plankton. We plankton ecologists often justify our work in the expectation that it somehow will be relevant for understanding processes affecting the ultimate yield of fish (e.g., Bartsch *et al.*, 1989; Heath *et al.*, 1999; Richardson *et al.*, 1998; Richardson *et al.*, 2000). However, it is very seldom, if ever, that the link between plankton studies and fish production or yield is unequivocally established.

Perhaps the only way to develop hypotheses that can be tested concerning these assumed links is through ecosystem modelling. However, there has not, in recent decades, been a strong tradition for cooperation between fisheries scientists, plankton ecologists, and ecosystem modellers. This has resulted in ecosystem models that do not incorporate the newest understanding of plankton or fish biology. For example, many of the ecosystem models currently in existence still base their energy input to the system on total primary production measurements using the $^{14}C$ method even though we now realize that this method is not the most appropriate for identifying the energy available for fish production within a system.

## Challenges for the 21st century

At the end of the 20th century, public and political interest returned to a more holistic concern for the oceans. Scientists, in reaction to this holistic interest in the sea, were also beginning to move from their discipline camps into an arena where holistic discussions could be brought forward. One of the best examples of this was the ICES Symposium on "Ecosystem Effects of Fisheries" held in Montpellier in 1999 (Hollingworth, 2000). In one sense, "history repeats itself" here as one of the concerns voiced at the time of the establishment of ICES was that the development of the steamship might have ecosystem effects on the fish stocks themselves.

Especially in light of this public concern over the ocean as an ecosystem and not just a fishing ground, it may be time to revert to the original goal of linking primary and fish production. Understanding and quantifying plankton production processes will never lead to prediction of the production within individual commercial stocks, as some of the early ICES scientists had hoped. However, an understanding of the energy going into a system is critical in order to predict the limits for energy to be taken out of the system. I believe that the next chapter in the history of relating plankton and fish production will belong to the ecosystem modeller. Ryther (1969) demonstrated, using a simple approach and with what we now know was a naive understanding of plankton processes, the potential for using estimated primary production to calculate limits to the theoretical potential fisheries yield from different regions. Such ecosystem considerations would seem to have a promising role for use in association with traditional stock assessments in order to set fisheries in an ecological context. Ecosystem modelling has come a long way since the days of Ryther. While both the modelling and our understanding of the interacting processes within the ecosystem can still be improved, the major challenge in the decades to come will be to develop the dialogue necessary between fisheries biologists, plankton ecologists, and ecosystem modellers to complete the job of establishing the link between plankton and fish production started by the ICES founding fathers a century ago.

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While preparing this paper, I had the privilege of interviewing Jørgen Møller Christensen, Torben Wolff, Ole Bagge, David Cushing, John Steele, and Keith Brander, all of whom provided me with useful personal insights on meetings and events that occurred "before my time". It is a privilege to know these scientists well enough to impose my questions upon them, and I fancy that future "historians" will look with envy upon my opportunity to consult these experts.

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