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A century of manipulating recruitment in coastal cod populations: the Flødevigen experience

Tim D. Smith, Jakob Gjøsæter, Nils Christian Stenseth, Marte O. Kittilsen, Didrik S. Danielssen, and Stein Tveite

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Beginning late in the 19th century and continuing throughout the 20th century, attempts have been made to augment recruitment of free-living fish populations through the release of larval and juvenile fish. Especially in Norway and the United States, such stock enhancement has been argued to be useful in the management of fisheries. This paper reviews the historical and scientific settings of four studies on the effects of manipulating recruitment of cod in southern Norway and presents new analyses of available data on young fish releases and population monitoring. Analyses suggest that the effects of the larval cod released from the Flødevigen hatchery were, in fact, detectable in beach-seine samples of 6-month-old cod. This is in contradiction to earlier analyses. Further, the behaviour of a population dynamics model fit to the beach-seine survey data is consistent with the experimental results from release of 6-month-old fish. Taken together, these results suggest that, although the release of larval cod may influence the immediate abundance of juvenile cod, the effects on the mature population are minuscule. This paper suggests that the claims of the supporters of the "Marine Fish Hatchery Movement" of the late 19th century are not supported, but points out that the Norwegian scientific dialogue, although at times heated, contributed much to our understanding of the nature of coastal cod populations and their dynamics. Although ICES did not play a major role in the "Marine Fish Hatchery Movement", many early ICES participants were involved. Scientific studies undertaken to determine the effectiveness of marine fish hatching had a direct effect on the scientific basis underlying ICES, especially the question of the variability of year classes.

Keywords: cod, hatching, Norway, recruitment.

Tim D. Smith: NOAA, National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA; tel: +1 508 495 2251; fax: +1 508 495 2066; e-mail: tim.smith@noaa.gov. Jakob Gjøsæter: Institute of Marine Research, Flødevigen Marine Research Station, 4817 His, Norway, and Division of Marine Zoology and Marine Chemistry, Department of Biology, University of Oslo, PO Box 1064 Blindern, 0316 Oslo, Norway. Nils Christian Stenseth: Institute of Marine Research, Flødevigen Marine Research Station, 4817 His, Norway, and Division of Zoology, Department of Biology, University of Oslo, PO Box 1050 Blindern, 0316 Oslo, Norway; tel: +47 22 854 584; fax: +47 22 854 605; e-mail: n.c.stenseth@bio.uio.no. Marte O. Kittilsen: Division of Zoology, Department of Biology, University of Oslo, PO Box 1050 Blindern, 0316 Oslo, Norway. Didrik S. Danielssen: Institute of Marine Research, Flødevigen Marine Research Station, 4817 His, Norway. Stein Tveite: Institute of Marine Research, Flødevigen Marine Research Station, 4817 His, Norway. Correspondence to N. C. Stenseth.

Introduction

Hatching and releasing young fish to create or supplement free-living fish populations, or more specifically to counteract the effects of too much fishing, has been a politically popular activity since the middle of the 19th century. Initial work was on freshwater and, especially in the United States, anadromous species such as Atlantic salmon. The application to marine species such as cod developed in the US and in Norway in the late 1870s. Its origin can be found in earlier reports of studies in the Lofoten Islands by the Norwegian Research Fellow in Fisheries, Georg Ossian Sars (1837–1927). After having hatched floating fish eggs to confirm the fishermen's contention that they were cod eggs, Sars (1876) suggested that by artificial hatching of fish eggs "nature might be assisted . . . so as to prevent the occurrence of unfavorable years, which exercise such a de-

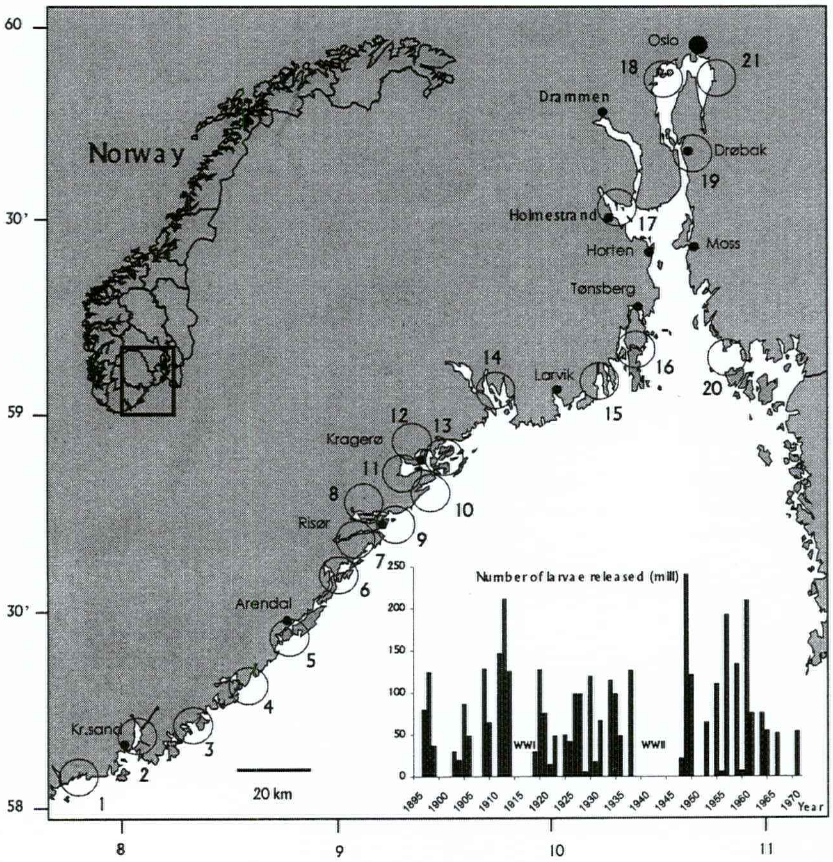
Table 1. Major events in developing and testing the possibilities of manipulating marine fish recruitment, by decade from 1870 to 1990, showing principal people and institutions involved. Four key studies shown in bold. See text for references and details.

Decade	Events	People and Institutions
1870s	Pelagic cod eggs identified and hatched	G. O. Sars, Research Fellow in Fisheries
1880s	First hatchery releases of larval cod in US and in Norway; efficacy argued	S. B. Baird, US Fish Commission G. M. Dannevig, Flødevigen hatchery
1890s	Efficacy assumed in US Efficacy and funding argued in Norway Negative results from hatchery experiment in Lock Fyne for plaice	US Fish Commission G. M. Dannevig versus J. Hjort, Research Fellow in Fisheries H. Dannevig assists T. W. Fulton, Fisheries Board of Scotland
1900s	**Study 1: fjord experiment** Validity of biological and oceanographic studies of fjords, "modern theory" questioned	 G. M. Dannevig versus K. Dahl (Bergen Museum) K. Dahl versus G. Swenander (Trondheim Scientific Society)
1910s	The Norwegian Parliament's 1910 Expert Committee recommends long-term beach-seine monitoring and alternate-year larvae releases Change of Flødevigen leadership	A. Landmark, H. H. Gran, T. Hansen, and O. Nordgaard *strongly advise against discontinuing*; A. Appelløf advises against continuing A. N. Dannevig replaces G. M. Dannevig at Flødevigen
1920s	**Study 2: beach-seine monitoring**	R. Løversen appointed as survey leader
1930s	Hatchery releases variable	
1940s	Hatchery releases suspended during war	
1950s	Alternate-year releases in Oslofjord	G. Dannevig replaces A. N. Dannevig at Flødevigen
1960s	Positive results from Olsofjord data Negative results from complete data Beach-Seine Monitoring leadership changed	G. Dannevig S. Tveite (Flødevigen) A. Sollie appointed survey leader
1970s	Yolk-sac cod stocking terminated 6-month-old cod raised and first releases	D. Danielssen replaces G. Dannevig at Flødevigen V. Øiestad and E. Moksness (Flødevigen)
1980s	Preliminary releasing of 1-year-old cod **Study 3: releasing 6-month-old cod** **Study 4: God's algal bloom**	E. Moksness and V. Øiestad (Flødevigen) D. Danielssen and J. Gjøsæter (Flødevigen) J. Gjøsæter (Flødevigen)
1990s	Cumulative data used for: Recruitment studies of gadoids Population dynamics modelling Effect of larvae release	 J. Gjøsæter and D. Danielssen (Flødevigen) N. C. Stenseth and colleagues (Univ. of Oslo), J. Gjøsæter and colleagues (Flødevigen), and K.-S. Chan (Iowa State Univ.)

pressing influence not only on those especially engaged in the fisheries, but on the whole country".

Following Sars' suggestion, a Norwegian and US industry developed to hatch cod eggs and release the just-hatched yolk-sac stage larvae. In the US, where the first mass hatching and release was carried out in 1878 in Gloucester, Massachusetts (Baird, 1880), the political attractiveness of this initial apparent success of making "fish so plenty by artificial means" (Goode, 1886) resulted in the quick embracing of cod hatching by the US Fish Commission as the solution to the problem of overfishing (Smith, 1994; Taylor, 1999). The efficacy of cod hatching in the US was argued solely on "unsolicited testimony" of citizens and simple (and often faulty) logic. Although no experimental testing appears to have been attempted, its utility quickly became an article of faith within the Commission. Even as late as the 1920s, senior staff of the Commission, by then renamed the Bureau of Commercial Fisheries, were apparently uncomfortable in openly questioning the agency's policy of reliance on fish hatching (Smith, 1994).

In contrast, the efficacy in Norway of the cod hatching that began in the 1880s along the southern coast at Flødevigen became highly controversial. These hatchery operations were supported by G. O. Sars until he retired in 1893. Although the testimony of citizens was



Area		Total number of larva released (mill)
1	Torvefjord	102.2
2	Topdalsfjord	151.2
3	Høvåg - Steindalsfjord	94.0
4	Bufjord - Grimstad	270.4
5	Flødevigen	392.1
6	Lyngør - Dybvåg	467.9
7	Sandnesfjord	83.4
8	Søndeledfjord	153.1
9	Risør skerries	0.0
10	Stølefjord	0.0
11	Kilsfjord	148.7
12	Hellefjord	10.0
13	Soppekilen	18.5
14	Grenlandsfjords	224.7
15	Sandefjord	383.4
16	Nøtterø - Tjøme	371.0
17	Holmestrand area	152.7
18	Vestfjord	422.4
19	Drøbak area	0.0
20	Hvaler	244.3
21	Bunnefjord	18.0

Figure 1. Map of southern coast of Norway, showing location of 21 fjords where larval cod were released, with number of larvae released in each fjord and total number of larvae released in relevant areas annually between 1897 and 1971. World War I (WWI) and World War II (WWII) are indicated.

also used in Norway, questions were raised in the 1890s by Sars' successor about the efficacy of releasing yolk-sac larvae, questions that were not asked in the US, and questions that have proven difficult to answer.

The controversies about marine fish hatching in Norway continued for decades and have been reviewed from several perspectives. Contemporaneous with the controversy, T. W. Fulton (1908) reviewed what was then known about marine fish hatching. Shelbourne (1964), in a more general review of the basis for fish farming, subsequently included the history of what he termed the "Marine Fish Hatchery Movement". More recently, several aspects of the controversy have been reviewed (Solemdal *et al.*, 1984; Smith, 1994; Solemdal, 1997; Taylor, 1999; Blaxter, 2000). In addition, Schwach (1999) has provided a useful review of the scientific and political setting, and the effect of the controversy on fisheries science.

In this paper, we re-evaluate the controversy about the efficacy of hatcheries for augmenting cod populations, drawing on data from four studies conducted from the Flødevigen facility from 1882 to the present. The first of the four studies was an experiment conducted between 1903 and 1905 comparing abundance of young cod in beach-seine hauls in two fjords before and after release of yolk-sac larvae. An independent committee of scientists in 1911 found the results to be equivocal and recommended a second study, also based on beach-seine sampling, for the systematic monitoring of young cod abundance for "at least 10 years". The uncertain time period reflected the then-already-understood fluctuations of cod populations. Although the systematic monitoring program that finally began in 1919 was continued for many decades, time ultimately proved the question to be very difficult to answer.

The issue of manipulating recruitment was reformulated in the 1980s at the Flødevigen facility, which had increasingly conducted general marine and fisheries research since the beginning of the 20th century and had become a laboratory of the Norwegian Institute of Marine Research in 1973. Rearing methodologies were developed that allowed the production of large numbers

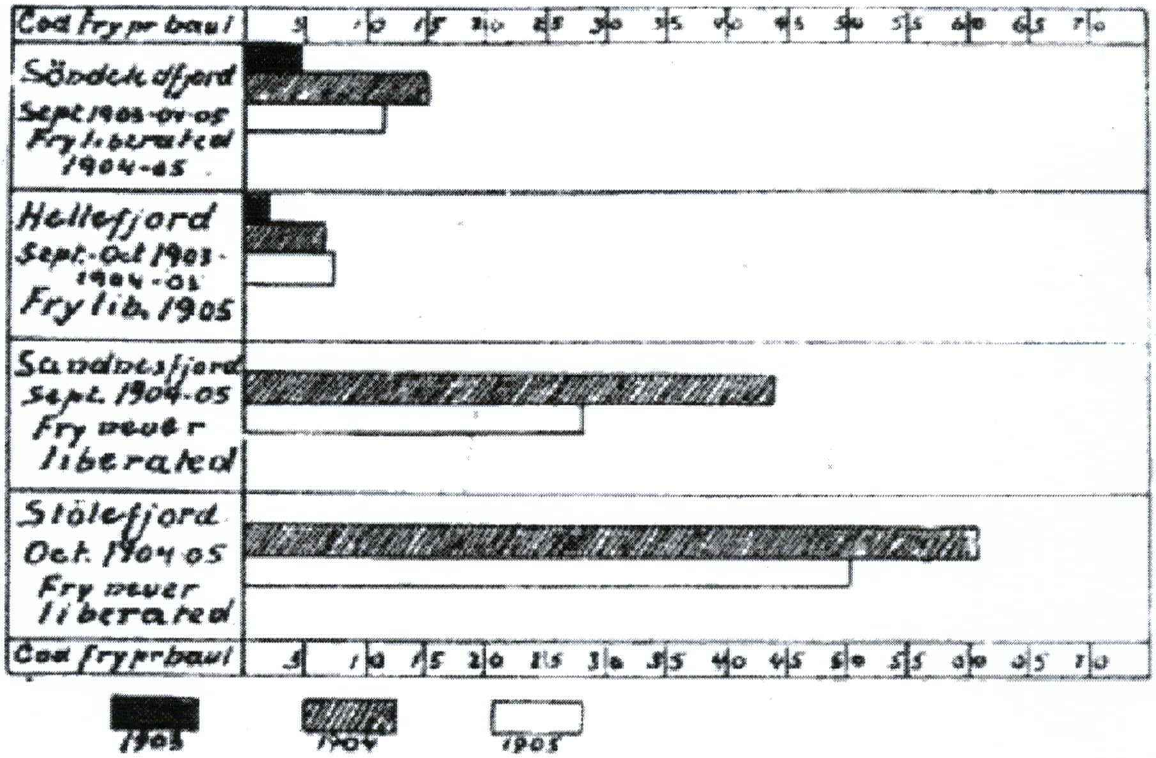


Figure 2. Juvenile cod per haul in beach seines in four southern Norwegian fjords in September/October 1903–1905, from Dahl (1909; his Figure 13).

of 6-month-old fish (Dahl *et al.*, 1984), and based on this capability, the third study was a series of recruitment enhancement manipulations using older fish reared and released between 1986 and 1989. Finally, in 1988, God, perhaps tired of waiting, conducted the fourth study by poisoning an entire year class of cod, and many other species, along the entire southern Norwegian coast (Gjøsæter *et al.*, 2000).

In this paper, we summarize the historical background and results of these four studies and present new analyses of the data sets collected during them to determine the potential effects of recruitment manipulation for cod populations. An annotated sequence of events is presented in Table 1.

The first marine hatcheries: Baird and Dannevig

In 1876, the head of the US Fish Commission, Spencer Fullerton Baird (1823–1887), published a translation of a report by Sars entitled "On spawning and development of the cod-fish" in the Reports of the US Fish Commission. Two years later, Baird succeeded in hatching cod eggs in Woods Hole, Massachusetts. In 1878, the US Fish Commission demonstrated this new capability by making its first release of several million cod larvae into Gloucester harbor and by displaying its techniques of collecting and combining eggs and milt from ready-to-spawn fish during the Great International Exhibition in London. Based on that exhibit, Gunder Mathisen Dannevig (1841–1911), a captain of sailing vessels from southern Norway, traveled to the US to review Baird's methods.

Previously, G. M. Dannevig had raised funds from local citizens and from the Norwegian legislature for a "sea-fish hatchery", and had opened his hatchery in 1882 in an old quarry in Flødevigen, near the wealthy shipping town of Arendal. Although he would advertise his hatchery as being "founded on the American model", in fact Dannevig found the US methods of culture lacking. In the end, he developed a very different approach based on holding adult cod in an enclosed basin formed

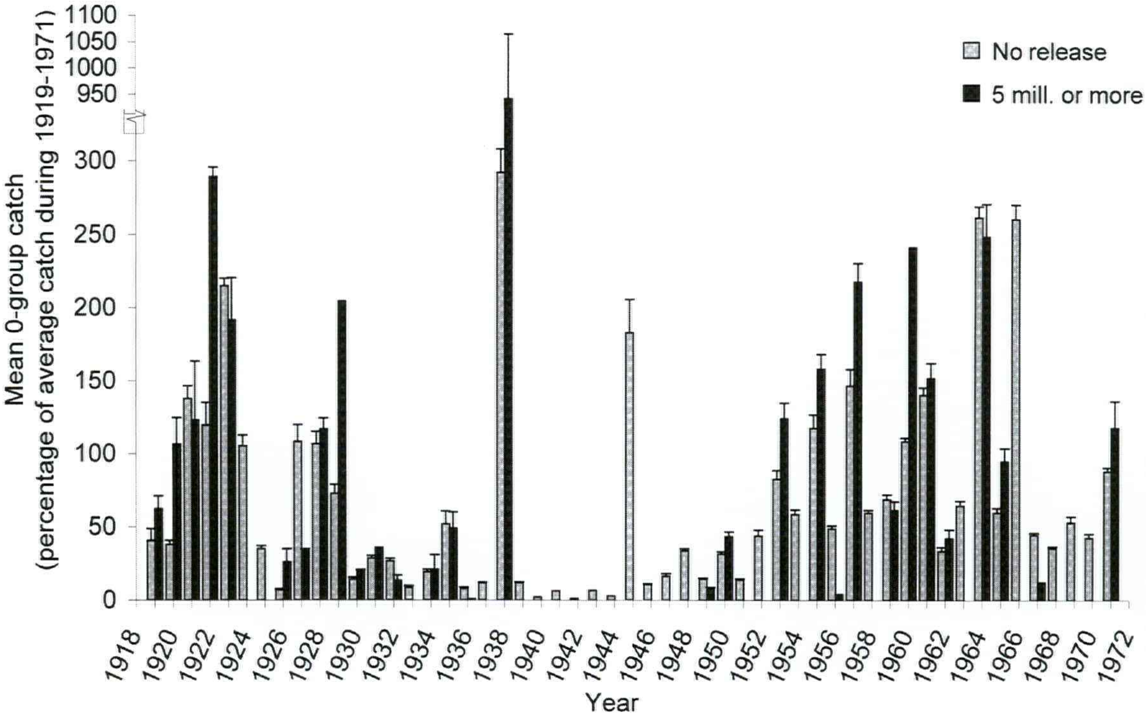


Figure 3. Mean catch of 0-group each year in areas with no larval releases and with no fewer than 5 million releases. The 0-group catch is expressed in terms of the percentage of the average catch during 1919–1971. Error bars indicate +1 SE. This figure is included for illustrational purposes and does not correspond directly to the ANOVA results, as the average catch on which these percentages are based is taken over the whole period from 1919 to 1971.

of the old quarry until they spawned, and then capturing the fertilized eggs in a filter device. Both the Woods Hole and the Flødevigen hatchery were in full production in the 1890s, annually releasing millions of cod larvae.

Proponents of marine fish hatching in both the US and Norway expressed extreme confidence in its utility for solving the problems of overfishing. In the US, there was little argument about this claim, while in Norway, the premises were challenged by Johan Hjort after he replaced Sars as "Research Fellow in Fisheries". Schwach (1999) has described several issues related to Hjort's challenge, including both scientific, political, and philosophical disagreements – all within a framework of competition for the government's funds for fisheries research.

Based on the then-current theory that cod formed spatially extensive populations that migrated over large areas, Hjort argued that Flødevigen hatchery larvae released in local fjords would not survive in the fjords, thus making them of no value to the local fisheries. Further, he argued, because of the vast numbers of cod in the sea, the comparatively minuscule releases could have little effect. Dannevig countered that the cod from the different fjords were, in fact, different, as the fishermen claimed, and hence represented local self-sustaining populations. Thus, the relative contribution of the Flødevigen larvae could not be dismissed out of hand. As Schwach (1999) has pointed out, the two views were embedded in very different visions for the future of Norwegian fisheries. Hjort's vision was for modernization of the fishing industry, while Dannevig wanted to help preserve the traditional economic structure of the coastal fisheries. Schwach has also pointed out that the budgetary commitment for the hatchery program was not insignificant, with Hjort's budget as Research Fellow in Fisheries being less than half the government's allocation to Dannevig's hatchery.

To test the efficacy of fish hatching, Dannevig had proposed an experiment to the Parliament as early as 1892. This was to compare the abundance of young cod in two or more fjords before and after release of larvae. In addition, in 1893, the legislature asked Hjort's advice

Table 2. Catches of 6-month-old cod (in numbers) in beach seines in the 1903–1905 experiment by Dannevig and Dahl for cod, whiting, pollack, and saithe. Catches after the release of cod larvae are marked in bold. Blanks indicate that data were not recorded.

Fjord	Time	No of hauls	Cod		Whiting		Pollack	Saithe
			Total	0-group	Total	0-group		
Søndeledfjord	Sep 1903	113	711	426	1 450	1309	79	84
	Aug 1904	105	**4423**		191		389	11
	Sep 1904	113	**1731**	**1523**	1 421	1306	173	61
	Aug 1905	101	**1337**		488		278	1
	Sep 1905	113	**1535**	**1133**	1 165	995	131	18
Hellefjord	Sep 1903	21	114	36	232	321	0	1
	Aug 1904	24	285		172		243	1
	Sep 1904	21	144	133	290	289	48	0
	Aug 1905	22	**56**		156		10	0
	Sep 1905	21	**180**	**143**	190	180	6	0

on a different proposed experiment, for which they had already set aside funds. This involved marking larvae being released to determine their ultimate movements. Hjort doubted that larvae could be reliably marked, and further opposed Dannevig's proposed experiment on the grounds that release of yolk-sac larvae could not have the desired effect.

The first study: fjord experiment

In an 1894 note to the Parliament, Dannevig elaborated on the value of his proposed experiment (Dahl and Dannevig, 1906):

> To obtain a fast answer I would suggest that several fjords – 4 to 6 – are studied, and that larvae are released in every second. One could not prevent that some larvae, while staying close to the surface could drift out of one fjord and into another, but it is unlikely that this would happen to such an extent that the differences between the fjords should be distorted.

Despite the Parliament's reluctance to support his experiment, Dannevig repeated his proposal throughout the 1890s and into the 1900s (Dannevig, 1910). In a similar note to the Parliament in 1903–1904, he wrote (Dahl and Dannevig, 1906):

> Our task is very practical, and can – I assume – be solved in a very simple way: We study a fjord as systematic and accurately as possible, release larvae in it, study it again, and continue like this for several years. If it turns out that the abundance of cod increase, it is justified to believe that the release of larvae is the cause. If no increase is observed, we assume that the release had no effect. As *random variation* may influence the results, we should not restrict ourselves to a single fjord or a single year, but go on till a clear-cut result is obtained (emphasis added).

It was not until 1903 that the Parliament funded Dannevig's experiment, albeit with Hjort's requirement that one of his staff oversee the field work. Although Dannevig conceded this, he insisted that the investigations be conducted under his personal leadership and expressed his disdain for the arrangements. He began beach-seine sampling of cod in September 1903 in two fjords. One was Søndeledfjord near Risør (Figure 1), with 113 locations sampled, and the other was Hellefjord near Kragerø, with 26 locations sampled. In 1904, about 33 million larvae cod larvae were released in Søndeledfjord in April and May, although owing to various hatchery problems, Dannevig estimated that not more than 20 million of those were viable. The beach-seine sampling was continued in both fjords in 1904. In April 1905, 33 million larvae were released in Søndeledfjord, of which 28 million were thought to have been viable, and in Hellefjord 10 million larvae were released. Again that year, the beach-seine sampling was repeated.

Hjort assigned the uninviting task of participating in Dannevig's fieldwork to Knut Dahl (1871–1951), who, in 1903, left a position as Fellow at the Scientific Society in Trondheim to work with Hjort. In addition to participating in Dannevig's study, Dahl conducted additional investigations in the same two fjords, as well as independent investigations in two nearby fjords, Sandnesfjord and Stølefjord. In addition to beach-seining, his studies included hydrographical studies to examine the movements of the water masses and biological examination of fish to examine growth, migration, and spawning places.

Dannevig and Dahl prepared separate reports which were published in a single volume in 1906 (Dahl and Dannevig, 1906). Dahl's report was much more extensive (more than 90 pages compared with Dannevig's 20 pages), including both his analysis of the data they collected together and his own individually collected data.

Table 3. The committee appointed by the Norwegian Parliament to evaluate the efficacy of hatching marine fish drew several conclusions, some in favour and some against. Members of the committee were the Inspector for the Freshwater Fisheries, A. Landmark from Oslo; Professor Dr. A. Appelløf from Bergen; Professor H. H. Gran from Oslo; a ship owner, T. Hansen from Lyngør; and the museum curator O. Nordgaard from Trondheim.

For	Against
1. A given number of eggs hatched in the hatchery give a far higher number of viable larvae than a similar number hatched in nature.	1. The number of cod spawning along the coast and in the fjords is so great that some hundred million larvae released from the hatcheries have no influence.
2. When the hatching started in 1983, it was very difficult to obtain enough parent fish for the work, but after some years of releasing larvae, the stock grew and plenty of mature fish were available in the area.	2. The larvae will be carried away with the currents and will be far away from the place they are released before they settle to the bottom.
3. From the many fjords where larvae were released, there were many statements from fishermen who gave assurance that the cod stock had increased some time after the larvae were released there.	3. During the official investigations in the Risør and Kragerø areas in 1903, 1904, and 1905, no increase in the number of *pelagic* larvae could be observed after the release of several million larvae.
4. During the official investigations in the Risør and Kragerø areas in 1903, 1904, and 1905, it was found that many more 6-month-old cod larvae were released in those years than in other years. Whiting, which were not released, were caught in lower numbers.	4. The increase in juvenile cod mentioned in point 3 (For) was also observed in neighbouring fjords where no larvae were released.
5. Studies conducted by Dannevig in Stendalsfjorden near Lillesand and paid for by Nedenes County in 1904, 1905, and 1906 gave similar results.	
6. A number of competent people in Norway and abroad, in particular in the United States, have declared that they believe that hatching is useful.	
7. The results of releasing plaice larvae in Loch Fyne have, according to systematic investigations, shown that the plaice population there increased.	

The data they collected together appeared in one appendix, and the data from Dahl's independent investigations appeared in another. The core of the common data is given in Table 2, which shows the number of 0-group cod, whiting, pollack, and saithe from the beach-seining in two fjords.

Dannevig compared the beach-seine catch rates (Table 2) and argued that the catch rate increased 212% and 68% in the two fjords, respectively, after the release of cod larvae. From these results, he concluded "on behalf of Arendal Fiskeriselskab and generally all those who believe in the hatching" that there was no need to continue these experiments, since these studies "have given a new proof…that artificial hatching is not only the best, but the only way of upholding and enhancing the fisheries in our fjords. Further studies would therefore be a waste of money that should rather be used to hatch more larvae" (Dahl and Dannevig, 1906).

Dahl, on the other hand, did not find Dannevig's analysis convincing. His own summary included the details of the jointly collected data, as well as his additional data from the two nearby fjords where Flødevigen larvae were not released (Figure 2). The top two panels of Dahl's figure corresponded to Dannevig's analysis for Søndeledfjord and Hellefjord. Dahl agreed that the 0-group cod were undoubtedly more abundant in Søndeledfjord after larvae were released in 1904 and 1905, but also noted that they were more abundant in Hellefjord in those years even though larvae were only released in the latter year. Further, Dahl's data showed substantial fluctuations in larval abundance between 1904 and 1907 in the other two fjords, and other data suggested that the fluctuations tended to be consistent all along the Skagerrak coast. Dahl (Dahl and Dannevig, 1906) would draw not only on the fluctuations, but also on this possible coast-wide regularity to argue against hatching:

> This regularity shows that we are confronted with such a great phenomenon of nature that it is not to be expected that we are able to prove any impact of the meagre intervention that human beings with their hatchery of relatively small amounts of drifting fry, can be able to execute.

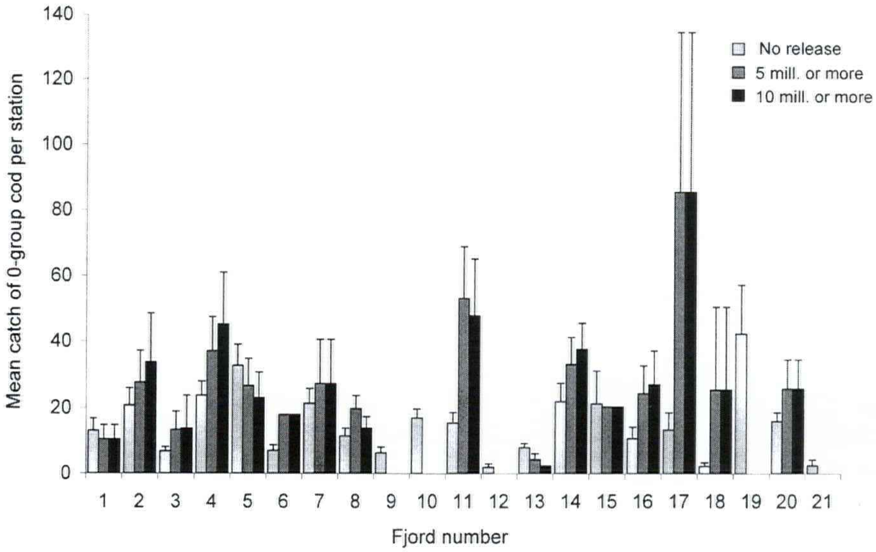


Figure 4. Mean catch rate (C) of 0-group (6-month-old) cod in each fjord (see Figure 1 for key) for those years with no larval releases, with no fewer than 5 million released, and with 10 million or more released between 1919 and 1971. Error bars indicate +1 SE. This figure is included for illustrational purposes and does not correspond to the results of the permutation test, as this is a test for independence between larval release and 0-group catch.

The case was not as clear, Dahl argued, as Dannevig had suggested. In addition to the variability from year to year, Dahl had concerns about Dannevig's conduct of the experiment. Dahl would later express strong frustration with his collaboration with Dannevig, suggesting that Dannevig was motivated by the need to maintain a subsidy for his hatchery from the Parliament and for selling his hatching equipment to other North Sea countries (Schwach, 1999). At some point, Dahl wrote in pencil "*Fordømt løgn*, Knut Dahl", which means "Damned lie", on the first page of the copy of a hectographed report that was labeled as being authored by "Dannevig, controlled by Dahl". This document is held at the library of the Institute of Marine Research in Bergen (Solemdal *et al.*, 1984), and the signature has been authenticated by handwriting experts. An expression as strong as this must hide more than disagreement about the scientific results, and suggests that there may have been unscientific methods involved, which Dahl did not have the strength to correct, and possibly could not tell Hjort. For Dahl, therefore, the only way to show his disagreement may have been his writing "damned lie".

Dahl concluded from his hydrographical and biological studies that three key questions remained to be answered:

1. Will the cod eggs spawned in a fjord stay in the fjord as pelagic eggs and larvae, through the later development and till they reach the stage of harvestable fish?
2. Will the released larvae stay in the fjords, and will they grow up till they become harvestable fish there?
3. If the answers to the first two questions are yes, will the increased catch of fish be large enough to pay the costs of raising and releasing the larvae?

Although Hjort and Dahl did not believe that cod in fjords were separate populations, other evidence was accumulating against the hypothesis that all cod belonged to one large, oceanic population. Dahl had been succeeded in Trondheim by Gustaf Swenander (1874–1953), a scientist educated in Uppsala. Swenander sharply criticized some earlier investigations Dahl had done in Trondheimfjord, suggesting that they did not disprove the hypothesis of local populations (Swenander, 1906). By the end of the century, the German zoologist Friedrich Heincke (1852–1929) had convincingly shown that herring consisted of several populations (Heincke, 1898). Another assistant of Hjort's, Hjalmar Broch (1882–1969), showed that this was the case in Norwegian waters (Broch, 1906, 1908).

But the argument between Hjort and Dannevig was not to be resolved by science, and in the end, an independent committee was established by the Parliament to settle it. On 1 July 1911, the Norwegian Parliament, with 77 votes for and 42 votes against, decided (Anon., 1911):

to submit the question of hatching of saltwater fish, its usefulness and justification, for an expert committee of five members. It is assumed that the Director of

Fisheries and the Arendal Fiskeriselskap [a local branch of the 'The Society for Development of the Norwegian Fishing Industry'] may suggest members for the committee.

In November 1911, the committee members were appointed and asked to evaluate the hatching of fish based on existing data and on "available literature from home and abroad". If they found that they could not draw final conclusions based on the material available, they should suggest new investigations (Anon., 1911).

The committee met several times, in both Oslo and Flødevigen, using material supplied by the Director of Fisheries and the Arendal Fiskeriselskap as well as from other sources. They developed a series of seven arguments thought to support and four to refute the value of hatching of marine fish (Table 3). The committee failed to resolve the issue and concluded that "it is impossible, based on the available facts to arrive at a firm conclusion on the question, whether a sufficient number of released larvae grow to harvestable fish in areas where they can be utilized by Norwegian fisherman, so that a hatchery with the technique now applied gives a positive yield". Further, they agreed that it "is not likely that a final conclusion will be reached in the near future", and that "a special investigation on the question of hatching will take a long time, probably at least 10 years, to have a hope of reaching a firm result". They found it "very regrettable that the important investigations [conducted by Dahl and Dannevig during 1903–1905] were not continued for more years".

Based on this, the majority agreed that they would not have recommended that a sea fish hatchery be established. However, because the hatchery was there already, they would "strongly advise against discontinuing the work even if it is possible or likely that the methods now used can be replaced by better methods in the future". In the minority, however, Professor Appelløf concluded that the hatchery should be closed, as its positive effects had not been proven. The whole committee, however, praised the work of Dannevig and wrote, "the work was initiated after best advice from practical and scientific authorities…and started with great inventiveness and technical skill, so that it has become a model for similar institutions in other countries...." Even if it should turn out that hatching sea fish with the methods then used could not be recommended, "one will always have to recognize the present director's skill, and the great work he has done to the honour and benefit for the country".

Although not in complete agreement, the committee did recommend reinstituting the beach-seine surveys begun during the 1903–1905 experiment in conjunction with alternate year releases of cod larvae. They also thought it could be wise to do such studies in the inner Oslofjord "where they could expect help from scientists and students at the University of Christiana [now Oslo], who surely would participate in the work without pay out of interest for the cause...." Even if such investigations could not answer the question, the committee thought that they would "bring scientific results of the greatest importance, and results that hardly can be obtained in other ways".

The second study: beach-seine monitoring

The Flødevigen hatchery operations continued after the reports of Dahl and Dannevig (1906), reaching a peak by 1913 of over 200 million larvae. The release of yolk-sac larvae continued until 1971, with fluctuations in output and gaps during World War II (Figure 1). Complete records were maintained, including, for example, the number and weight of both the male and female brood stock. Eventually, however, the 1911 recommendation for beach-seine surveys was adopted, and a standardized program of surveys began in 1919 [Gjøsæter *et al.*, In press (a)]. This program of surveys has been supervised by only two team leaders since 1919. Ragnvald Løversen was in charge from 1919 until 1968, and Aadne Sollie, who began working on the project in 1957, has been in charge since 1969. During 1919 and 1920, 87 stations were sampled along the south coast, with 33 still sampled today. The 1911 committee's recommendation that Oslofjord be included in the study was not taken up until 1936 when it and fjords on the southeastern coast towards the Norwegian-Swedish border were added to the survey.

Dannevig had two sons, both of whom were involved in fish hatching. Harald Christian Dannevig (1871–1914) went to Scotland in the early 1890s to lead the construction and first activity of a fish hatchery at Dunbar, a copy of the Flødevigen hatchery. The main focus was plaice because the species "appears to be declining very considerably on the fishing grounds" (Fulton, 1908). One of the first activities was to conduct an experimental test of the efficacy of releasing plaice fry, an experiment that failed to convince and contributed to the eventual closure of the hatchery (Smith, 1994; Blaxter, 2000). H. C. Dannevig also brought the hatching technique to Newfoundland and later to New South Wales. There, he became the Director of Fisheries for the Commonwealth of New South Wales in 1908, but apparently did not pursue fish hatching (Mawson *et al.*, 1988). He was lost at sea when the RV "Endeavour" sank with all hands during exploratory fishing operations in the South Pacific.

G. M. Dannevig's second son, Alf Nicolay (1886–1960) was trained at the University of Oslo, starting his career as Director of Flødevigen in 1911, even before he had finished his education in 1913. He remained in that position until 1957. Focusing throughout his career on the early life history of fish and on determining ages of fish through otolith and scale readings, he published remarkably little on releasing cod larvae. A. N.

Dannevig did conduct his own study of the effects, however, conducting the alternate-year release experiment that the 1911 committee had recommended. A. N. Dannevig's son Gunnar (1914–1971) was also trained at the University of Oslo, doing his thesis on freshwater fish. His first position was at the Institute of Marine Research in Bergen, where he worked on cod and sprat. In 1957, he became Director of Flødevigen. In addition to his administrative duties, he continued work on sprat in the Skagerrak area and was a pioneer in studies of the effects of acid rain on trout and salmon.

G. Dannevig later published some results from A. N. Dannevig's alternate-year Oslofjord experiment that suggested the release of larvae did, in fact, make a difference (Dannevig, 1963). He also discussed results obtained by Rollefsen in the 1930s that demonstrated high but variable recovery rates of an identifiable plaice-flounder hybrid released as larvae. Later, Stein Tveite (1971) thought G. Dannevig's results looked so promising that he assembled the cumulative data from all the fjords and used analysis of variance to test for a positive effect of cod larvae release. However, when all fjords were included, G. Dannevig's conclusion from the Oslofjord data could not be supported. Later, when G. Dannevig learned of Tveite's analysis, he realized that effects of hatching were doubtful, but still suggested that the issue should be pursued with more years using a systematic program (G. Dannevig personal communication to Tveite), echoing again the 1910 committee's recommendation. A systematic program was not initiated, however, and large-scale hatching and release of larval cod ceased at Flødevigen in 1971 immediately following G. Dannevig's death.

Tveite's analysis was followed up in the present paper using the same methods where the response variable was the percentage of the mean catch in the periods 1920–1935 and 1936–1965, but applying it to a more extensive data set. In contrast to Tveite's results, the present analysis showed a significant effect from larval release on the average 6-month-old cod abundance by fjord even when peripheral areas and releases below 5 million larvae were excluded (Figure 3). Further, fjord-specific permutation tests (testing for independence between larvae release and the amount of 0-group catch, using a model-free approach (see Chan *et al.*, 2002), supports the apparent tendency for beach seine catch rates of cod to be higher when there are more yolk-sac larvae released (significant for 6 out of 16 fjords when releases above 5 million are considered, significant for 4 out of 16 fjords when releases above 10 million are considered; Figure 4).

This finding of significantly higher beach-seine catches in many fjords where yolk-sac larvae were introduced is consistent with G. Dannevig's conclusions from his father's alternate-year releases in Oslofjord. Further, the data suggest that the increase in the 6-month-old cod population may have been substantially greater than 1% in many cases (Chan *et al.*, 2002). This conclusion should, however, be treated with great care, since there may be undetected biases in the comparisons being made. One concern is that the basis for decisions on where to release larvae is generally not documented (except in A. N. Dannevig's alternate-year experiment), and fjords may have been selected in response to requests from residents. Another possibility is that there may have been more larvae released in years and in fjords where the mature stock population was high. If such selection took place, perhaps in the expectation that only in such fjords were there hopes for an effect, then the results could be as the data suggest. Furthermore, this would mean that one assumption, which needs to be made prior to the permutation test would be invalid. The permutation approach does cope with the fact that the 0-group abundance series is serially correlated and non-stationary, but requires that, for each fjord, the amount of larvae released is independent and identically distributed over the test period. Moreover, the release of larvae may only have an effect on the 0-group in exceptionally good years, as suggested by Giske and Salvanes (1999).

To explore this conclusion further, additional statistical analyses were conducted (Chan *et al.*, 2002). Those analyses suggested percentage increases of 6-month-old fish from release of one million larvae of 2–13% for four of the fjords. This potential percentage increase was evaluated by examining the population dynamics implications of the data from the beach-seine monitoring study. The population model developed from these data by Chan *et al.* (In press) was used to predict the theoretical effects of augmenting recruitment of 6-month-old cod. That age-structured population dynamics model was based on the fjord as the ecological unit, and the parameters were estimated using the data from 54 time-series of 6-month-old cod from 15 fjords covering the period 1919 to the present. The model assumed that 6-month-old and 1-year-old individuals remain more or less within the local coastal site where they settled as larvae, and that older and mature cod spawn in deeper waters of each fjord. The model was expressed in delay coordinates of 6-month-old cod abundance, the component of the cod population for which the better data are available, and fit as a time-series using the data from coexisting species and other covariates (e.g., temperature and the North Atlantic Oscillation index). This resulted in an ARMAX (2,2) statistical model that provided an appropriate fit to the data (see Chan *et al.*, 2002).

Using this fitted model, the implications of a range of percentage augmentations of 6-month-old cod abundance were considered. For example, 1% and 10% increases of 6-month-old cod would increase the mature population by only 0.16% and 1.54%, respectively. Thus, although increases are possible from larval releases, at best they would have essentially negligible effects in comparison with the high stochasticity in the dynamics of cod population and marine systems more generally.

The third study: releasing 6-month-old cod

By the turn of the century, Hjort and Dahl (1900) had suggested that releasing cod at an older age could be better than releasing yolk-sac larvae:

> The vital question is, without doubt, to discover methods by which one can cause the myriads of tiny larvae, which can at present be produced without any great difficulty in millions, to attain a reasonable size at a comparatively small cost.

G. M. Dannevig had managed to grow some cod beyond the larval stage in the Flødevigen Station's outdoor basin using natural plankton production, demonstrating that the artificially hatched larvae were viable (Rognerud, 1887). However, it proved impossible to keep large numbers of fish beyond the larval stage. This problem proved to be very difficult to resolve (Dannevig and Dannevig, 1950; Dannevig and Hansen, 1952), and although progress was made in rearing juvenile flatfish in England (Shelbourne, 1964), it was not until the 1970s that the first successful mass rearing of juvenile cod was accomplished. This was done in the outdoor basin at Flødevigen, opening new possibilities for G. M. Dannevig's vision (Øiestad *et al.*, 1976; Ellertsen *et al.*, 1981; Kvenseth and Øiestad, 1984). Tagged juvenile cod released in 1970 and 1971 suggested that coastal cod were stationary, and high recovery rates were obtained (Danielssen and Gjøsæter, 1994). The implications of this new technology for G. M. Dannevig's old dream was discussed in 1982 during an international symposium on propagation of cod in Flødevigen at the Station's 100-year anniversary (Anon., 1984).

The first large-scale experiment involved releasing nearly 1100 artificially reared, marked juvenile cod in Flødevigen in 1976–1977 (Moksness and Øiestad, 1984). The results were promising as the released cod had good survival and did not migrate far from the place where they were released, answering two of the questions raised by Dahl in 1906. In 1986–1989, Danielssen and Gjøsæter (1994) released nearly 40 000 6-month-old cod along with 2400 older cod, all marked with Floy tags, in the Risør Fjord, one of the fjords studied by Dahl in 1903–1905. For fish released at 6 months old during the years 1986–1989, the total recapture rates were 2%, 4%, 16%, and 10%, respectively. For the older cod, the recapture rates were substantially higher: 25% and 50% for 1988 and 1989, respectively. This experiment confirmed earlier studies (Moksness, 1990), suggesting that survival was good and migration limited, but the augmentation rates were so low that the costs of juvenile cod would have to be reduced considerably for G. M. Dannevig's dream to be economically viable. Analyses using the model of Chan *et al.* (2002) confirmed the conclusions of Moksness (1990), as did subsequent experiments at still larger scales conducted in various parts of Norway and Denmark.

The fourth study: God's algal bloom experiment

During the spring of 1988, a bloom of toxic algae (*Chrysochromulina polylepis*) occurred along the Norwegian Skagerrak coast. Dead fish could be seen lying on the bottom, and a picture of a dying goldsinny wrasse was spread all over the world through the cover of *Newsweek* magazine (August 1988, No. 31). Fish farmers in Norway and Sweden lost 800 t of fish. Expressions such as "catastrophe" and "disaster" were commonly used in newspapers, television, and radio – and many scientists supplied the media with rather worrying descriptions of what seemed to happen. The beach seine monitoring program initiated to study cod recruitment, and other Norwegian sampling efforts, documented the effects of this bloom which killed a major part of the coastal biota, including most of the 0-group cod [Gjøsæter *et al.*, In press (b)]. Older cod had a higher survival because they could go deeper and avoid the most serious effect of the algae, but they too suffered increased mortality. Subsequent observations and analyses of the time series available revealed that the effect was very short lived, with no detectable long-term effects. The cod populations recovered quickly, although most of the 1988 year class was killed. In fact, the effect on the survival of cod seemed to be restricted to only a few summer months (see also Julliard *et al.*, 2001).

In effect, this algal bloom can be regarded as a large-scale experiment where, instead of adding juvenile cod, most juveniles of the 1988 year class were removed. Analyses of data from the beach-seine monitoring program demonstrated that this experiment, although dramatic in its immediate effect, had no long-term effect on the cod stock (Gjøsæter *et al.*, 2000). This is – with opposite sign – consistent with the earlier conclusion drawn based on the Chan *et al.* (2002) model. Whereas adding larvae annually had a small effect, at least on the 6-month-old cod abundance, adding larvae in any single year would have an even lesser long-term effect on the mature cod population. Although continuing to kill off the young fish would obviously have the dramatic effect of killing off the cod population, this experiment confirmed that single incidents of adding or removing juvenile cod would have only a limited and transitional effect.

Discussion

By the beginning of the 20th century, the "Marine Fish Hatchery Movement" had successfully claimed that recruitment of marine fish, especially cod, could be increased by release of larval or yolk-sac stage fish. The goal as posed in the United States was "to make fish so plenty by artificial means, that every fisherman may take all he can catch" (Goode, 1886). Although this goal was adopted without proof by the US Fish Commission as a primary basis for fisheries management, substantial controversy over its feasibility developed in Europe. That controversy, although at times acrimonious, especially in Norway, stimulated research over the 20th century that not only addressed the claims of the "Marine Fish Hatchery Movement", but also contributed substantially to our understanding of the population structure and dynamics, life history, and ecology of cod.

The four studies described in this paper answered several questions even while raising others. The early-century fjord experiment did not resolve the controversy over the claims of the "Marine Fish Hatchery Movement", but did focus attention on two questions posed by Dahl (Dahl and Dannevig, 1906), namely the potential contributions of naturally spawned eggs and of released larvae to the mature cod in each fjord. These questions arose in the midst of, and influenced, the then-evolving understanding of what Heincke termed "*localform*", and what we now know as fish populations and stocks. Hjort's initial challenge to Dannevig was based in large part on the assumption that cod formed a single, large oceanic population, in contrast to our present-day understanding of the existence of population structures both at the fjord and larger spatial scales.

The fjord experiment also contributed to our understanding of the variability of what has come to be known as year-class strength. The glimpse into the variability in the abundance of 6-month-old cod in the fjord experiment in 1903–1905 hinted at much higher variability than Hjort and his colleagues had expected. This hint would focus the attention of Hjort and his colleagues for nearly a decade and would set the stage for one of the major breakthroughs in fisheries science (Solemdal *et al.*, 1984; Solemdal, 1997). By 1914, they had painstakingly demonstrated that much of the fluctuation in cod and herring catches that had stimulated the application of science to fisheries in the middle of the 19th century was, in fact, due to seemingly random variability in the abundance of young fish each year. In the early 1900s, however, the nature of this variability was not clear. For example, Dahl (Dahl and Dannevig, 1906), starting from the thoroughly imbedded migration-thinking point of view, explained the coast-wide regularity in the fluctuating beach-seine catches as being due to:

> the ability of the volume of water to transport the eggs as well as the drifting fry, and through their movements to influence their distribution.... As the mass of water in the Skagerrak in various seasons as well as in various years is moving differently, it will thus be a matter of course that on the Skagerrak Coast there will be good and poor spawning years; even if the number of spawned eggs or pelagic larvae in one year has been just as abundant as in another year....

The fjord experiment also set the stage for the remarkable Norwegian beach-seine monitoring program, the second study described in this paper. Although recent analyses of those data have revealed much about the dynamics of fjord populations of cod and other species of fish (Chan *et al.*, In press), earlier analyses served to keep alive the vision of the "Marine Fish Hatchery Movement". G. Dannevig's (1963) analysis of the beach-seine data and the alternate-year larval releases that the 1910 committee had recommended gave a tantalizing glimpse of the effect that release of larvae might have on 6-month-old cod abundance. However, despite Tveite's (1971) contrary conclusions from examination of a longer time-series, it now appears that the full time-series answered affirmatively Dahl's two questions about the possibility of augmenting recruitment. Only the question of the cost and the benefit remain unaddressed.

Although the Norwegian larval release program ended in the early 1970s, the possibility of rearing and releasing not larval but 6-month-old cod became a focus at Flødevigen. The juvenile cod study drew on new technology for identifying released fish (e.g., Kristiansen *et al.*, 1997) and clearly demonstrated the potential for augmenting fjord cod populations to at least an age of 1 year. The question of cost and benefit was then addressed, albeit with a negative answer. Although the rearing of juvenile cod proved too expensive for their release in fjords, the animals themselves became experimental tools to address these and other questions about, for example, the specific effect of augmenting recruitment and the general ecology of fjord cod populations. For example, Blaxter (2000) questioned the capacity of a fjord to support a substantially increased juvenile cod population, and the genetic and behavioural fitness of artificially reared young fish. Howell and Ellis (2002) describe studies of several aspects of fitness of juvenile fish, identifying both labile and non-labile characteristics that are important for the survival and growth of young fish. Although such questions arise from the practical viewpoint of the "Marine Fish Hatchery Movement", they also address fundamental ecological issues.

The beach-seine monitoring study that was established to evaluate the claims of the "Marine Fish Hatchery Movement" also allowed evaluation of the effects of God's algal bloom experiment. Contrary to the concerns that arose about the fragility of nature because of the vivid news photographs of the die-off of marine life, these monitoring data showed rapid recovery and stability of fjord ecosystems. This demonstration provided valuable insight into the effects of environmental degradation even though the conclusions never drew the world's attention, as did the initial die-off.

Taken together, these four studies of the possibility of augmenting recruitment of marine fish did more than meet the expectations of the 1910 committee. In addition to resolving the claims of the "Marine Fish Hatchery Movement", these four studies did "bring scientific results of the greatest importance, and results that hardly can be obtained in other ways".

Along with that committee, we must acknowledge that the "great inventiveness and technical skill", as well as vision and persistence, of G. M. Dannevig and his son and grandson contributed greatly to our understanding of the ecology of cod.

This is not to say, however, that the "Marine Fish Hatchery Movement" is dead; it still arises regularly, especially in conjunction with the increasing commercial fish farming operations (Howell and Ellis, 2002). But the promises of hatchery augmentation of recruitment still attract the imagination of legislatures and fishermen with its vow to "make fish so plenty". The problems that plagued the movement more than 100 years ago still arise, with the enthusiasm of the hatchery folks rapidly outstripping both the scientists' ability and willingness to address the hard questions of ecological and physiological feasibility, and managers' balancing of costs and benefits. These are questions that Norway finally answered in the 1980s. The lessons of this century of study should stand as a cautionary tale about the importance of testing the claims of the "Marine Fish Hatchery Movement" rather than just blindly assuming that marine fish hatching will solve fishery management needs.

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