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**MARINE BIOLOGY**

VOLUME 38



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**Preface**

**Millennium Volume of  
*Advances in Marine Biology***

This volume of *Advances in Marine Biology* is the thirty-eighth to be published since the series began in 1963. The founding editor was F. S. Russell (later Sir Frederick Russell), then Director of the Marine Biological Association's Laboratory at Plymouth.

The original idea was to publish annual volumes containing comprehensive review articles summarizing the general position of knowledge in selected individual fields of marine biology, typically those undergoing rapid development. It was hoped that this would allow biologists to keep abreast of lines of research outside their own particular field. Particular attention was to be given to fisheries since it was thought that much of the published fisheries research results appeared in journals not normally available in university biology departments. Environmental work was to be included only where relevant to the biological topic being discussed, and articles on physical and chemical oceanography were specifically excluded.

In 1968 Sir Frederick Russell was joined as editor by Sir Maurice Yonge (Professor C. M. Yonge), who had by then moved to Edinburgh. Together they took *Advances in Marine Biology* through to volume 16 in 1979. In 1980 they were joined by John Blaxter from the Dunstaffnage Marine Laboratory, Oban, who took on the role of executive editor, and attracted reviews on fisheries topics. At volume 23 in 1986 Russell and Yonge retired as editors and Alan Southward, from the Marine Biological Association, joined John Blaxter. In 1997, for volume 32, Paul Tyler, of the Southampton Oceanography Centre, became an additional editor and Alan Southward took over as executive editor. John Blaxter retired in 1998, after volume 34, and was replaced by Craig Young from Harbor Branch Oceanographic Institution, Florida. This year Lee Fuiman from Port Aransas, Texas, joins the editorial group to keep up interest in fisheries.

Since 1986 the purpose of the articles has been redefined. Those that cover aquatic fields in general, including both marine and freshwater organisms, are welcomed, as are those that include a proportion of new, previously unpublished data. The editors stress that in addition to giving comprehensive coverage of the topic, review articles in *Advances in Marine Biology* should enable a researcher to learn all that is necessary to start up work in the field. This policy, combined with the quality of contributions, has helped *Advances in Marine Biology* to achieve a high citation index. The term "comprehensive" is taken to mean inclusion of important older literature, not just those articles to be found in CD-ROM abstracts that refer mostly to the last two decades.

The editors try to commission reviews of upcoming fields that are showing increases in knowledge, but they also welcome offers from outside parties who feel they can contribute. Prospective authors are invited to contact one of the editors nearest to them, when they will be given advice and instructions on format and style. Article size is usually about 75 printed pages, but smaller or larger articles will be considered on their merits. Up to two years may elapse from commissioning an article to its publication, but the editors encourage authors to bring their articles as up to date as possible just before going to press. Contributions submitted in the correct style, ready for press, may appear in print in six months. All contributions are submitted to peer review. The series is no longer annual and now appears at least twice a year. From the early days *Advances in Marine Biology* has published longer articles by single authors and jointly authored topics that fill special volumes, as for example volumes 5 (1967, mollusc parasites), 7 (1969, euphausiids), 18 (1980, mysids and euphausiids), 27 (1990, penaeids), 32 (1997, biogeography of the oceans), 33 (1998, calanoid copepods) and 36 (1999, biochemical ecology of fish).

To celebrate the Millennium, and to give new authors an idea of the scope of the journal, a list of the reviews published in past volumes of *Advances in Marine Biology* is given here.

## VOLUME 1, 1963.

- Loosanoff, V. L. and Davis, H. C. Rearing of bivalve mollusks. pp. 1-136.  
 Bruun, A. F. The breeding of the North Atlantic Freshwater-eels. pp. 137-169.  
 Nicol, J. A. C. Some aspects of photoreception and vision in fishes. pp. 171-208.  
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 Blaxter, J. H. S. and Holliday, F. G. T. The behaviour and physiology of herring and other clupeids. pp. 261-393.

## VOLUME 2, 1964.

- Shelbourne, J. E. The artificial propagation of marine fish. pp. 1-83.  
 Cushing, J. E. The blood groups of marine animals. pp. 85-131.  
 Scholes, R. B. and Shewan, J. M. The present status of some aspects of marine microbiology. pp. 133-169.  
 Holme, N. A. Methods of sampling the benthos. pp. 171-260.

## VOLUME 3, 1965.

- Wells, M. J. Learning by marine invertebrates. pp. 1-62.  
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## VOLUME 6, 1968.

- Gulland, J. A. and Carroz, J. E. Management of fishery resources. pp. 1-71.  
 Macnae, W. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. pp. 73-270.  
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## VOLUME 7, 1969.

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## VOLUME 10, 1972.

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Cushing, D. H. and Dickson, R. R. The biological response in the sea to climatic changes. pp. 1-122.

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Stewart, L. A history of migratory salmon acclimatization experiments in the southern hemisphere and the possible effect of oceanic currents and gyres upon their outcome. pp. 397-466.

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- Horwood, J. The Bristol Channel sole (*Solea solea* (L.)): a fisheries case study. pp. 215-367.

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- Brown, A. C. and Odendaal, F. J. The biology of oniscid Isopoda of the genus *Tylos*. pp. 89-153.
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- Ferron, A. and Leggett, W. C. An appraisal of condition measures for marine fish larvae. pp. 217-303.
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- Egloff, D. A., Fofonoff, P. W. and Onbé, T. Reproductive behaviour of marine cladocerans. pp. 79-167.
- Dower, J. F., Miller, T. J. and Leggett, W. C. The role of microscale turbulence in the feeding ecology of larval fish. pp. 169-220.
- Brown, B. E. Adaptations of reef corals to physical environmental stress. pp. 221-299.
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- Semina, H. J. An outline of the geographical distribution of oceanic phytoplankton. pp. 527-563.

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- Mauchline, J. The biology of calanoid copepods. pp. 1-660.

#### VOLUME 34, 1998.

- Davies, M. S. and Hawkins, S. J. Mucus from marine molluscs. pp. 1-71.
- Joyeux, J. C. and Ward, A. B. Constraints on coastal lagoon fisheries. pp. 73-199.
- Jennings, S. and Kaiser, M. J. The effects of fishing on marine ecosystems. pp. 201-352.
- Tunnicliffe, V., McArthur, A. G. and McHugh, D. A biogeographical perspective of the deep-sea hydrothermal vent fauna. pp. 353-442.

#### VOLUME 35, 1999.

- Creasey, S. S. and Rogers, A. D. Population genetics of bathyal and abyssal organisms. pp. 1-151.
- Brey, T. Growth performance and mortality in aquatic macrobenthic invertebrates. pp. 153-223.

#### VOLUME 36, 1999.

- Shulman, G. E. and Love, R. M. The biochemical ecology of marine fishes. pp. 1-325.

#### VOLUME 37, 1999.

- His, E., Beiras, R. and Seaman, M. N. L. The assessment of marine pollution - bioassays with bivalve embryos and larvae. pp. 1-178.
- Bailey, K. M., Quinn, T. J., Bentzen, P. and Grant, W. S. Population structure and dynamics of walleye pollock, *Theragra chalcogramma*. pp. 179-255.



# The Enhancement of Marine Fish Stocks

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Attempts to augment marine finfish stocks by releasing eggs and yolk-sac larvae were started in the 1870s, using mainly cod and plaice. Trials running over several decades in the USA, UK and Norway failed to show any statistically proven enhancement, even in coastal waters. Experiments to transplant juvenile flatfish, such as plaice and turbot, from areas of low growth to areas with spare "carrying capacity" proved effective, but only on a small scale.

Since the 1960s the release of reared, older life-history stages of plaice and cod has been tested to see whether they were more viable. The initial releases, of plaice in the UK and cod in Norway, were disappointing and probably failed as a result of inappropriate methodology before and at release with the plaice, and lack of spare carrying capacity in the inshore release areas with the cod. Later, experiments in the USA have produced more promising results for mullet, red drum, striped bass and threadfin again using older life-history stages. In Japan the release of these stages of red sea bream and flounder is now a regular practice to enhance inshore stocks.

The key to success lies in appropriate size of fish, season and area for release, and especially the availability of spare carrying capacity in the environment. In few cases, however, has the financial viability been assessed. It is considered most unlikely that successful inshore enhancements could be scaled up to help the recovery of depleted high-seas finfish stocks, in which only prudent management and good natural recruitment can be expected to alleviate the problem.

## 1. INTRODUCTION

Scientists and managers have been looking at ways of enhancing fish stocks for well over a century, enhancement being defined as "the intentional release of reared or wild fish with the aim of utilising the natural production of the sea" (Anonymous, 1994). This search may, at first sight, seem surprising since the steady rise in the world catch of finfish since World War II (Figure 1) suggests that there is no underlying problem of over-exploitation by the world's fishing fleets. The true story is entirely different. Closer analysis shows that the rise is made up of both increases

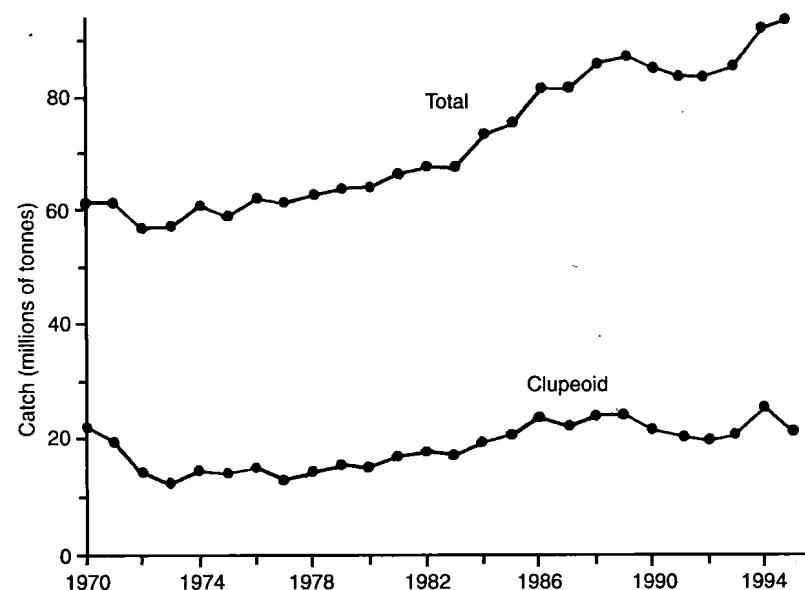


Figure 1 Worldwide finfish catch and clupeoid catch in millions of metric tonnes, 1970–1995 (FAO Yearbooks).

and decreases in the catch of traditional species and the search for, and exploitation of, new species. There has also been a fishing down of marine food webs, from long-lived, high trophic level bottom-living fish to shorter-lived, plankton-feeding pelagic fish (Pauly *et al.*, 1998). The post World War II collapse of some stocks (e.g. Japanese sardine, *Sardinops melanostictus*; California sardine, *Sardinops caeruleus*; and Atlantic herring, *Clupea harengus*) sometimes, but not always, with a partial recovery can be blamed on overfishing, followed by a fallow period when the fishery was closed or became uneconomic. Natural fluctuations may co-occur, for example those of the Peruvian anchoveta, *Engraulis ringens*, as a result of El Niño, but it is not always easy to quantify the relative effects of over-exploitation and natural causes. (Common and scientific names of species, and authorities, are given in the Appendix (pp. 53–54).)

The new species exploited have usually been found in more inhospitable or distant waters (e.g. the Alaska pollock, *Theragra chalcogramma*), or in less accessible, deeper waters where the macrourids (grenadiers, or rattails), the blue whiting, *Micromesistius poutassou*, and the orange roughy, *Hoplostethus atlanticus*, are examples of new, and sometimes already over-exploited, resources. Some of the deep-water

species are slow-growing and show little resilience to a high rate of exploitation.

Scientific understanding of the population dynamics of many fish stocks is not always adequate to determine the underlying causes of a decline. What is indisputable is that many, if not most, stocks are being exploited beyond their maximum sustainable yield (MSY). The reasons for this include competition for fish in international waters, the reluctance of fishermen to sacrifice short-term gain for long-term stability and the inadequacy of management underpinned by a good scientific understanding of the appropriate corrective measures. These factors are such that it is probably naive to suppose that stocks can generally be exploited at a level equivalent to their MSY.

In the nineteenth century pressures on fish stocks intensified when the use of steam increased the size, range and power of fishing vessels. Subsequently corrective measures included the increase of net mesh sizes and minimum fish landing sizes, the classical signs of "growth" overfishing (Cushing, 1995) – a decrease in the numbers of large fish and in the catch per unit of effort (CPUE) – having been identified quite early by fishery scientists (Graham, 1943). The introduction of sonar, superior navigation techniques, further increases in the size and range of fishing vessels and the use of fishing fleets with mother ships by Japanese, Russian and East European fishermen pressurized near-water and distant-water stocks as well as increasing the worldwide yield.

The response of international agencies such as ICES (International Council for the Exploration of the Sea) and FAO (Food and Agriculture Organization of the United Nations) was to step up international collaboration both at a political and scientific level, albeit with limited success. A more recent corrective measure, the Total Allowable Catch (TAC), is now in wide use; it is the permitted annual catch of a stock agreed by international consensus but which has to be divided by political horse-trading between the nations involved in the fishery.

These measures are not working. An example of the parlous state of "managed" stocks is shown in Table 1, where the status of seven important commercial species in the North Sea is given. The 1994 catch was far below the 1964–1994 maximum in all except the sole, *Solea solea*. Even worse, the spawning stock biomass was below the "minimum acceptable" level in cod, *Gadus morhua*, whiting, *Merlangius merlangus*, plaice, *Pleuronectes platessa* and herring, equal to the minimum in saithe, *Pollachius virens*, and only above the minimum in haddock, *Melanogrammus aeglefinus*, and sole.

In this depressing scenario could stock enhancement increase the yield from a fishery, promote or accelerate the recovery of a depleted or collapsed stock, help the survival of a stock threatened with extinction or

Table 1 North Sea fish catches in thousands of tonnes (from Serchuk *et al.*, 1996).

Species	Maximum catch 1946–1994	1994 catch	1994 spawning stock biomass	Minimum acceptable spawning stock biomass
Cod	340	90	60	150
Haddock	930	160	150	100
Whiting	360	85	260	<260
Saithe	320	100	100	100
Plaice	170	110	250	300
Sole	35	33	80	35
Herring	1200	530	750	800

create new stocks inside or outside the natural geographical range of the species? Welcomme (1998) divides enhancement into *introductions* – intentional or accidental transport and release by man into an environment outside the species' present range – and *transfers* – where the release occurs within the present range. While the above usually take place over a limited time, *stocking* refers to the repeated injection of fish (either native or exotic) into an ecosystem from one external to it.

This review deals with the history and prospects of stock enhancement of marine finfish by transfers and stocking; it excludes the extensive work on anadromous fish like the Atlantic and Pacific salmon and sturgeon, the enhancement of which is sometimes considered to be "ranching" (Thorpe, 1980; Bannister, 1991). Nor does it deal with invertebrates, where work on species such as lobsters, prawns and many bivalve molluscs is well established.

## 2. RATIONALE FOR ENHANCEMENT

If stocks are ripe for enhancement various preconditions and problems seem to apply. The most important is whether excess carrying capacity is available to absorb releases. If a stock has declined, has it left a vacant "space" or has another species moved in to take its place? If so, could releases oust the invaders? Problems exist as to whether the releases are intrinsically viable (e.g. can start feeding or have a suitable genotype) and whether they can be released in sufficient numbers to obviate the effects of predation. We need to know the relative chances of enhancing a high-seas stock compared with a coastal stock. Germane to these problems are the mechanisms underlying recruitment.

Table 2 Examples of typical egg production of three North Sea fish species and losses by natural mortality up to recruitment (some data from Serchuk *et al.*, 1996).

Species (typical weight)	Minimum acceptable spawning stock biomass (tonnes)	Equivalent number of females	Fecundity (eggs per female)	Total eggs	Average recruitment number of juveniles
Cod (5 kg)	150 thousand	15 million	2 million	$3.0 \times 10^{13}$	$3.8 \times 10^8$
Plaice (0.5 kg)	300 thousand	300 million	120 thousand	$3.6 \times 10^{13}$	$4.6 \times 10^8$
Herring (0.18 kg)	800 thousand	2.4 billion	55 thousand	$1.2 \times 10^{14}$	$4.3 \times 10^{10}$

Of the two main groups of marine finfish, the elasmobranchs are K-strategists (Bone *et al.*, 1995) with few large eggs, a long incubation period, internal fertilization and, in some species, development within the female to a live-bearing stage. Most marine teleosts are r-strategists, producing thousands to millions of very small eggs per female per year. As the females grow larger their fecundity increases (Blaxter, 1988). In high latitudes the eggs may be produced in a single event or in batches over a period of several weeks; in low latitudes batch spawning is the norm, occurring over much of the year.

Since all marine enhancement studies to date have involved teleosts, we need to discuss the nature of the processes underlying survival between spawning and the recruitment of the early life stages to the fishable stocks, since extremely high mortalities must occur during the intervening period. This is illustrated in three species from the North Sea in Table 2, where typical loss rates of five orders of magnitude can be computed for cod and plaice and four orders of magnitude for herring.

Pelagic fish, such as the herring, are of great economic importance (Figure 1) and exist in huge numbers when the stock is in a "healthy" condition. They have relatively low fecundities for marine teleosts, and few year classes; they tend to fluctuate in numbers over short periods and suffer from recruitment failure as a result of natural causes or overfishing. Demersal fish, such as the cod, have more stable populations, lower overall adult numbers, more year classes and higher fecundity. They tend to suffer from growth overfishing leading to the loss of older, larger fish and therefore an excessive loss of overall egg production since the large females are more fecund.

Plots of recruits against number of spawners (the stock:recruitment relationship) give dome-shaped or asymptotic curves demonstrating density-dependence of recruit production with larger numbers of spawners (Cushing, 1995) as a result of inadequate carrying capacity (see p. 39) of the environment, excessive predation or cannibalism. These curves are computed from very "noisy" data since the recruit production or year-class strength produced by a given size of spawning stock can vary by a factor of five to ten times. These variations are a measure of big differences in the chances of survival from year to year between the egg and recruit stages. Studies at sea show mortalities in both egg and larval stages of 5–30% of the population *per day*.

There is a vast literature dealing with the factors determining mortality and survival in the early life-history stages of fish (e.g. see Bailey and Houde, 1989), the relative effects of an adequate supply of microzooplankton as food to give optimal growth and the presence or absence of predators being especially important. At the present time predation rather than starvation is thought to be the more severe source of mortality and there is an increasing awareness of the need for rapid growth, with a "race" between the larvae and their food supply and predators (so-called cohort competition) to survive (Houde, 1997). It is against this background that the more recent enhancement studies have been developed.

### 3. EARLIER WORK

Surprisingly, the first attempts to enhance marine fish stocks took place over 100 years ago at a time when the science was less well understood and when high-seas commercial stocks could hardly have been at risk. The anadromous shad, *Alosa sapidissima*, of the north-west Atlantic coast had, however, declined, as had some inshore Norwegian cod populations. Presumably enhancement of more marine stocks was considered to be advantageous if it made fishing more profitable for the predominantly inshore fishermen of that time.

The practical scientific basis for enhancement was established after Sars of Norway and others had developed techniques for egg collection, fertilization and production of yolk-sac pre-feeding larvae. All the early work involved the release into the sea of eggs and/or yolk-sac larvae (fry) and started in the USA, UK and Norway at about the same time. The early experiments, which were unsuccessful for various reasons, are reviewed by Shelbourne (1964) and Blaxter (1987) and only the more important features will be summarized here.

### 3.1. USA (several species, 1885–1930)

The first commercial hatchery, mainly for cod egg production, opened in 1885 in Woods Hole, Massachusetts on the New England coast, 1.5 million cod fry having been released in local waters in the late 1870s. Other hatcheries were soon built at Gloucester and Boothbay Harbor. The first two decades of the twentieth century were very busy and by 1917 over 3000 million fry were being produced annually from the three hatcheries. These comprised: winter flounder, *Pleuronectes americanus* (about 1800 million); pollock (saithe), *Pollachius virens* (about 1500 million); cod (over 200 million) and haddock (6 million). Spawners were caught at sea and stripped and, less successfully, captive broodstock were kept at the hatcheries from year to year. Various types of hatching box, and through-flow seawater system, were used. Mortality was often high and the surviving larvae were liberated locally, except for an unsuccessful attempt to establish a cod fishery in the Gulf of Mexico. Although experiments continued into the 1930s in the USA, no convincing evidence of enhancement was found and eventually the experiments petered out.

### 3.2. Scotland (plaice, 1894–1920)

In Scotland the first hatchery, for plaice eggs, was opened at Dunbar near Edinburgh in 1894. By 1898, 120 million plaice eggs and 17 million eggs of other species had been released locally off the east coast of Scotland and in Loch Fyne, an arm of the Firth of Clyde on the west coast. The hatchery was transferred to the Bay of Nigg, Aberdeen in 1899. The number of plaice larvae released on the Scottish east coast from the Bay of Nigg hatchery from 1900 to 1920 totalled 353 million. As in the USA no clear beneficial effect was established and it is instructive to look at a "balance sheet" to see why this might be so:

#### 1900–1920

Total number of plaice larvae released: 353 million	Total commercial plaice catch: 24 000 tonnes
Fecundity of a 0.5 kg female plaice: 120 000 eggs	Equivalent 0.5 kg females: 24 million
Number of females used in hatchery: 2900	

Thus over the two decades the hatchery was using only  $\frac{1}{8300}$  of the local plaice catch, demonstrating how puny the efforts were related to the potential wild stock egg production. The decline in releases from 1915

Table 3 Juvenile plaice catches in Loch Fyne (Scottish west coast) in years with and without releases of larvae. (See also Figure 4)

Years with releases	Plaice larva releases (millions)	Juvenile catch per hours fishing	Years without releases	Juvenile catch per hours fishing
1896	4.1	111.4	1903	37.3
1897	21.2	24.0	1904	8.0
1898	19.2	95.6	1905	112.0
1899	16.5	28.7	1906	16.6
1900	30.6	53.1	1907	33.3
1901	51.4	174.0	1908	30.3
	143.0 (total)	81.1 (mean)		39.6 (mean)

onwards may reflect the loss of confidence in the experiment as well as the change in priorities as a result of World War I.

A more promising effect seemed to emerge from the Loch Fyne experiments (Table 3). Between 1896 and 1901, 143 million plaice larvae were released. Monitoring the 0-group juvenile plaice by push net gave a mean yield of 81.1 fish  $h^{-1}$ . Between 1903 and 1908 when there were no releases of plaice larvae the mean push net catch of 0-group plaice was only 39.6 fish  $h^{-1}$ . These differences are not, however, statistically significant ( $t = 1.48$ , 10 df,  $p < 0.2$ ). Natural variations in brood strength are obviously considerable and can easily mask any enhancement effect unless experiments continue over many years.

### 3.3. Norway (cod and plaice, 1882–1969)

In Norway the enhancement experiments, mainly on cod, started in 1882 when G. M. Dannevig founded the commercial hatchery at Flødevigen, while a plaice hatchery was started at Trondheimsfjord in 1908. Cod were caught before full maturity and allowed to spawn naturally in ponds, giving 90% survival of eggs (Dannevig, 1963). The cod larva releases continued until 1967, mainly into the Oslofjord and adjacent coast, and aroused much controversy, mainly from other Norwegians who considered that wide differences in year-to-year conditions for larval survival and the high spawning potential of quite small numbers of "wild" fish effectively masked any beneficial effect of cod larva releases.

Some early short-term comparisons, as exemplified in Table 4, showed apparent benefits of releases. To test this further Rollefson (quoted by Dannevig, 1963) later introduced hybrid larvae by crossing plaice females

Table 4 Catches of juvenile cod in two Norwegian fjords in years with and without releases of cod larvae (data in Shelbourne, 1964).

Year	Søndelfjord			Hellefjord		
	Cod larva releases (millions)	Juvenile catch		Cod larva releases (millions)	Juvenile catch	
		Total	Per haul		Total	Per haul
1903	Nil	426	4.8	Nil	36	1.9
1904	20	1523	15.1	Nil	133	6.5
1905	28	1133	11.5	8-9	143	7.5

Table 5 Release of plaice  $\times$  flounder hybrid larvae and the percentage of hybrids in the population some months later (data in Dannevig, 1963).

Year	Hybrid larvae released (millions)	Percentage of hybrids later
1935	2	1.5
1936	13	30.0
1937	7	0.5
1938	10	96.0
1939	7	40.0

with flounder (*Platichthys flesus*) males, as shown in Table 5, in a small fjord near Trondheim. Some months later the percentage of hybrids was ascertained by shore seine sampling of the 0-group flatfish population. In some years the hybrids dominated the population of juvenile flatfish, suggesting a high survival rate, although this could not be measured.

Dannevig (1963) tested the effect of cod larva releases in the Oslofjord from 1950 to 1962 by counting the numbers of 0-group and 1-group cod using a shore seine net at appropriate intervals after release. Control counts were made after years with no larva releases. The results are persuasive (Figure 2) but Tveite (1971) examined the data over a much longer period, from 1920 to 1969, coming to a different conclusion. He recorded the numbers of 0-group cod caught by shore seine at 17 locations in the Oslofjord and adjacent coast in years when cod larvae had and had not been released (Table 6). The mean number of cod per haul was 30.2 in release years and 22.3 in non-release years, statistically a non-significant difference.

It must be concluded that the release of eggs or yolk-sac larvae, at least of cod and plaice and probably similar high-fecundity/small-egg r-selected

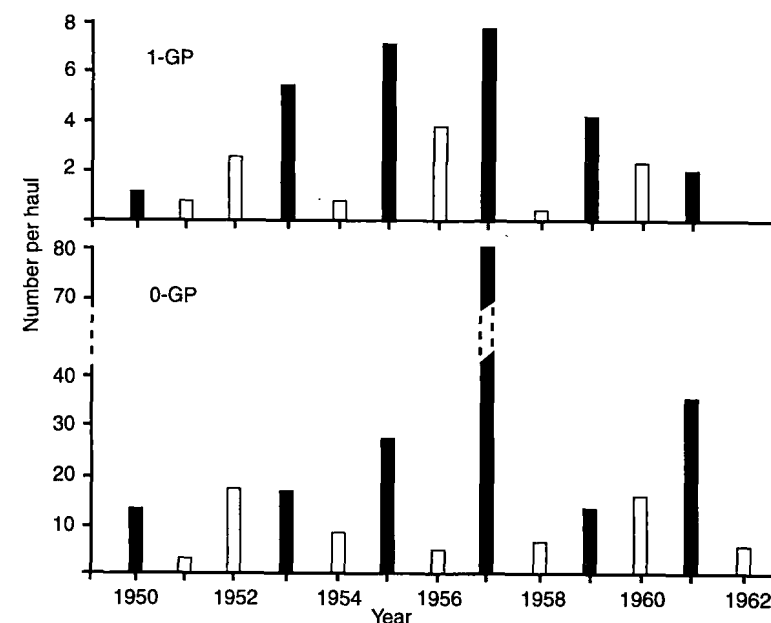


Figure 2 Mean number of 0-group and 1-group cod per haul from 1950 to 1962 in the Oslofjord. Open columns, no larvae released; black columns, year classes with larvae released. (Redrawn from Dannevig, 1963.)

species, has shown no consistently beneficial effect, owing to the masking effect of natural recruitment and year-to-year variability in the conditions for brood survival. Later in this review other areas will be discussed, as will the release of older life history stages after rearing in captivity.

### 3.4. North Sea and Baltic plaice transplants (1893-1990)

The idea of transplanting juvenile fish from nursery grounds of high density to areas of low density where the food supply would be less limiting was raised as early as 1891 using plaice. Blegvad (1933), Bagge (1970) and Hoffmann (1991) review the experiments in the Baltic and North Sea areas, and especially in the Limfjord, an almost enclosed body of water in northern Denmark.

The Danes were most active in these experiments, initially moving some 80 thousand to 200 thousand plaice annually from the outer to the inner Limfjord. The work continued to 1990 with as many as 1 million to 3



Table 6 Number of juvenile cod per haul by seine net in years with and without releases of cod larvae (from Tveite, 1971).

District	Number of years with release	Cod per haul	Number of years without release	Cod per haul
Torvefjord	8	11.3	37	12.9
Topdalsfjord	11	32.9	34	19.6
Buifjord	10	31.3	35	28.7
Arendal	28	36.3	17	40.2
Sandnesfjord	5	17.0	40	16.7
Sandelfjord	10	14.2	35	10.6
Klæsfjord	14	38.1	31	11.8
Langesund	6	34.8	11	28.3
Vrøngen-Tjøme	7	21.2	22	14.6
Hvaler	7	25.8	22	17.8
Hemestrand	7	32.3	22	28.0
Drøbak	8	67.3	21	38.7
Mean		30.2		22.3

Note: In 10 out of 12 stations average hauls are higher after release of larvae.

million fish being transplanted annually in some years. The plaice were moved at lengths of 16–19 cm (weight about 60 g). During the subsequent six months or so, they grew 8–13 cm reaching weights of nearly 400 g. From 1952 to 1957 larger fish 18–22 cm long (67–110 g) were used, and from 1984 to 1986 the fish were 17–21 cm. Marking experiments showed there was little tendency to emigrate, so the local fisheries clearly benefited. During the 60 years of experiments about 6000 mt were transplanted.

From 1928 to 1933 the Danes also transported 1 million to 2 million juvenile plaice annually (about 1000 mt) from the Esbjerg area to the Belt Sea, an arm of the western Baltic. From a length of 17–25 cm the growth increment was 10–12 cm in the first few months. About one-third of the transplants were caught commercially, with a value three times that of the cost of transplantation (Figure 3).

Other experiments in the first decades of the twentieth century included the transplantation of plaice by Norwegian, Swedish, German and British workers from Danish waters to the Oslofjord, from the Kattegat to inshore Swedish waters, and from the Danish, Dutch and English coasts to the Dogger Bank in the central North Sea. The numbers were small, on the order of hundreds to thousands, with fish 20–25 cm long. On the Dogger Bank the growth rates were high, perhaps twice that of coastal plaice, with growth increments of 10–13 cm in the first six months after transplantation. One of the most innovative experiments was by Atkinson

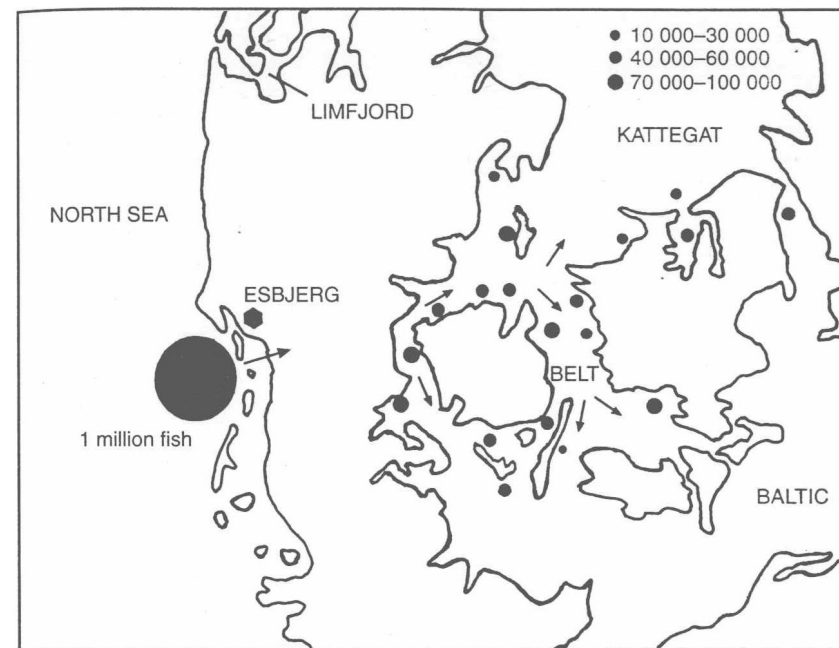


Figure 3 Danish plaice transplantation experiments 1929–1933 from the North Sea (about 1 million fish) to the Kattegat, Belt Sea and Baltic Sea. Black circles show numbers released in thousands (adapted from Blegvad, 1933).

(1910), who succeeded in transplanting a few plaice from the White Sea to the Dogger Bank. Five fish recaptured showed exceptional growth perhaps because they were adapted to grow at the lower northern temperatures.

This type of experiment never really became established as a regular technique. It is not clear why, although World War II would certainly have halted any continuing enhancement measures of this sort. Generally the weight of fish transferred, although significant for a flatfish fishery, was never going to be high, if only because of the danger of depleting the source areas when quite large juveniles are moved, as indeed appeared to be the case in the Limfjord. Another problem was who would bear the cost, and who would benefit? Many of the Danish experiments could be seen to benefit Danish fishermen (see p. 43); in the international waters of the Dogger Bank the benefit could go to non-participants in the enhancement experiments.

Table 7 Production of metamorphosed plaice and sole at Port Erin, Isle of Man, UK (from Shelbourne 1975).

Year	Target production (thousands)		Estimated production (thousands)	
	Plaice	Sole	Plaice	Sole
1964	250	Nil	161	Nil
1965	500	Nil	375	15
1966	50	50	3	5
1967	40	20	55	58

### 3.5. UK rearing and release of plaice and sole (1957–1967)

After World War II a change in the underlying philosophy driving enhancement experiments must be credited to Shelbourne. At that time the general opinion was that the release of eggs or yolk-sac larvae was unlikely to benefit recruitment, although cod releases continued in the Skaggeirak until 1962 (see p. 10). The idea of manipulating older life stages had already been developed in the successful transplantation of wild plaice in the inter-war years. Shelbourne (1964, 1975) suggested that it would be beneficial to rear fish beyond the first feeding stage and release them when they were larger and so less vulnerable to predation and starvation.

Between 1957 and 1967, Shelbourne developed a technology for rearing plaice and sole at Loughmoe and then on the Isle of Man, UK (see Table 7). The main features of the technology were the use of relatively small, shallow rearing tanks of about 0.25 m<sup>2</sup>, the use of the antibiotics penicillin and streptomycin to control bacterial levels at the early stages, and the provision of brine shrimp (*Artemia* spp.) nauplii as food in an appropriate light and temperature environment.

Rollefsen (1939) had first introduced brine shrimp as a fish food. The resting egg stage can be stored in a dry condition for many months without loss of viability and hatched within a few hours by placing in sea water. Shelbourne was the first to use brine shrimp on a large scale. Plaice larvae have the priceless advantage of a large enough mouth to take the nauplii at first-feeding, as do sole and herring, but most marine fish species of commercial importance have very small mouth gapes at first feeding, which require a smaller start-feeding organism for successful rearing. The seminal nature of Shelbourne's work with brine shrimp is exemplified by an entire symposium devoted to its use in 1979, and the existence of an *Artemia* Reference Centre in Ghent, Belgium (see Persoone and Sorgeloos, 1982).

It was not all easy going for Shelbourne; some brine shrimp nauplii were better than others. At one point those from Utah were found to contain the insecticide DDT. Those of Brazilian origin gave the best survival of plaice, and other species, but were not always available. By the time his work was completed in 1967, Shelbourne's technology yielded survivals of 30–65% between the egg stage and metamorphosis in plaice, although as in most rearing experiments, there was a very large size range ("size-hierarchy") after a few weeks. When most of the population were metamorphosing the size range was 10–25 mm. Shelbourne was also the first to realize that larvae from rearing tanks could have a number of abnormal characteristics (see p. 33) – in the case of plaice this was the presence of quite large numbers of larvae with total or partial albinism and with bitten fins. While these were probably the result of stress and/or crowding, a lack of normal behaviour also became apparent when "thumb-nail" size plaice (15–20+ mm) were released into the wild.

In 1964, 25 thousand such plaice were transported in shipboard tanks from the Isle of Man and released in Loch Ewe on the Scottish west coast 400 km to the north (Figure 4). In 1965 about 100 thousand were released in an artificial embayment of about 1 ha at Ardtoe, 300 km north of the Isle of Man (Figure 4) and others were brought up by road. In both years the transplanted plaice were lost as the result of predation or other reasons. Most of those in Loch Ewe were taken by pelagic-feeding gadoids before they could reach cover on the sea bed. Those at Ardtoe did not succeed, probably as a result of low salinities from run-off, deoxygenation of the water and lack of weaning from *Artemia* to natural food (J. Dye, personal communication).

Shelbourne's work on sole started in 1965 (Shelbourne, 1975) and continued to 1967. Using a similar technology as for the plaice he achieved survivals to metamorphosis of 50–80% of the original eggs. There was less pigment abnormality and faster growth at the high temperatures used. No releases of reared sole into the sea appear to have been made.

With hindsight these experiments were naive for the following reasons:

1. No estimate was made of the potential "carrying capacity" of the new environments.
2. No census was made of potential predators.
3. The optimal conditions for release were not established. For example would it have been better to release the fish at night to reduce losses by "visual" predators?
4. The problem of the fitness of reared fish for release in the wild was not considered (see p. 33). No experiments were done to test the bottom-seeking or burrowing behaviour of reared plaice, nor to test the ability

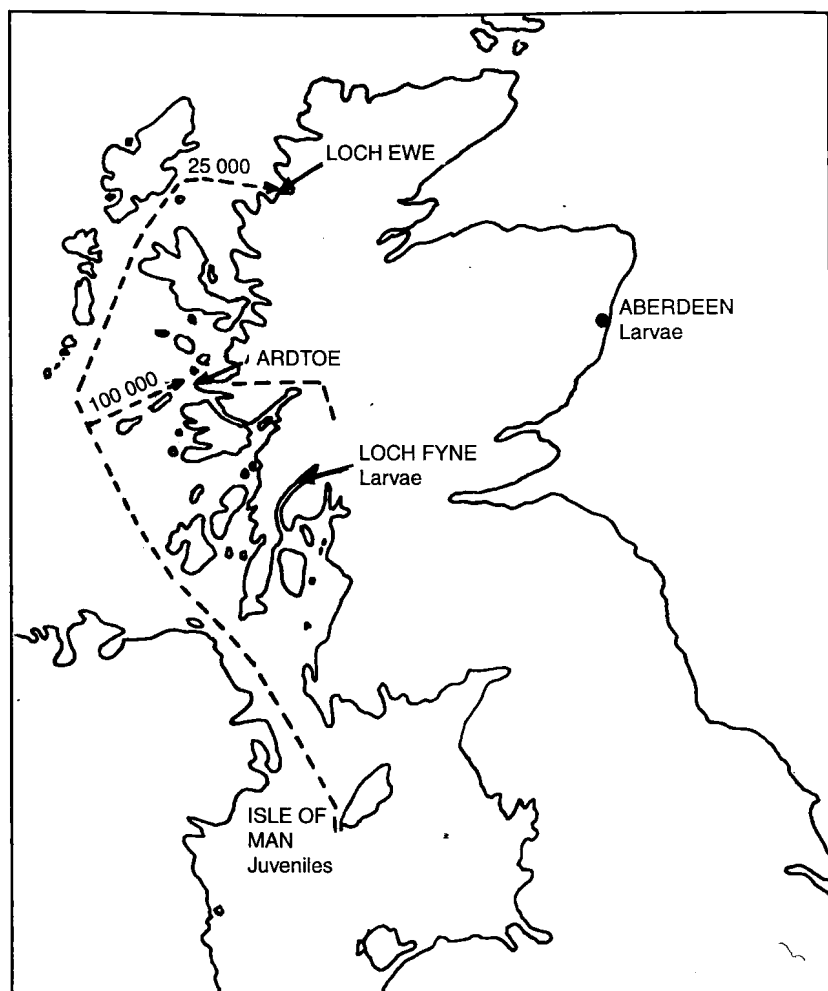


Figure 4 Transfer of newly metamorphosed plaice from the hatchery at Port Erin, Isle of Man, to Scottish west coast sites (Loch Ewe and Ardtoe) 1964-1965. Loch Fyne and Aberdeen, the sites of earlier newly hatched larval releases, are also shown.

of abnormally coloured individuals to match the substratum on which they settled.

5. Apart from abnormally coloured individuals there was no way of checking whether plaice recaptured later were indigenous or transplanted.

Table 8 Results of intentional introductions (see p. 5) of marine species.

Species	Introduction		Result	References
	From	To		
Herring (eggs)	Scotland	New Zealand	Eggs died en route	Anon, 1914
Herring (eggs)	Baltic Sea	Aral Sea	Established but stock remained small	Bibov, 1960
Mullet, <i>Mugil so-uy</i> (juveniles)	Sea of Japan	Black Sea	New fishery established	Starushenko and Kazansky, 1996
Whitefish, <i>Coregonus lavaretus</i> (fry and juveniles)	Hatchery	Puck Bay, southern Baltic	Partial success	Pelczarski, 1998

### 3.6. Introduction of new species

The introduction of new species into non-indigenous habitats has been widely practised in the fresh waters of Europe, Asia and Africa (see papers in Cowx, 1998) but is outside the scope of this review. There is also a huge literature on the introduction of salmonids into new areas and their enhancement by ranching. The reader may refer, for example, to Stewart (1980), Thorpe (1980) and Cowx (1998) for more information.

Some examples of attempts to introduce or reintroduce species into sea areas are shown in Table 8. The efforts have been sporadic, no doubt because of the risks involved, which include cost-benefit aspects and chances of success.

### 3.7. Fertilization by nutrients

Many lagoons are highly eutrophic, although the balance of nutrients may not be optimal for high productivity; often there is adequate nitrogen but inadequate phosphate (D'Ancona, 1954). Input from rivers and run-off of fertilizers from agriculture in the hinterland may often make it unnecessary to take such measures as "ploughing" the sea bed. Addition of appropriate nutrients may be advantageous if it leads to an increase in fish production. High algal production may be beneficial if the fish are