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Introductions and Transfers of Aquatic Species

A Symposium held in Halifax, Nova Scotia
12–13 June 1990

International Council for the Exploration of the Sea

Conseil International pour l'Exploration de la Mer

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Selected papers
from a Symposium held in Halifax, Nova Scotia
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Edited by C. Sindermann,
B. Steinmetz, and W. Hershberger

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INTRODUCTIONS AND TRANSFERS OF AQUATIC SPECIES

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Introductions and Transfers of Aquatic Species

Introduction

C. Sindermann, B. Steinmetz, and W. Hershberger

Conveners and Editors

Introductions and transfers of marine and freshwater species have occurred and are occurring on a worldwide basis, either accidentally or as a consequence of pressures from aquaculture interests. Greatest attention from aquaculturists at present is on shrimp, salmon, eel, and bivalve molluscs. Introductions of species to hydrographic provinces where they have not previously existed have been increasing, and will probably continue to do so. Thus far, the control of such movements has been variable in the extreme from country to country. Some have no restrictions; some have poorly enforced regulations; and a few have strict inspection and licensing laws. There is a growing perception that practices of one country in coastal waters or international lakes and river systems may affect adjacent countries. This perception has led, haltingly, to interest in uniform standards for importation of living aquatic plants and animals.

An important development within the past two decades has been enunciation and endorsement by countries bordering the North Atlantic of an international policy concerning introductions. Under the leadership of the International Council for the Exploration of the Sea (ICES), a "Code of Practice" has been formulated and then approved by member countries. The Code is somewhat idealistic, but it does provide an internationally uniform policy concerning introductions of marine species.

The quintessence of the Code can be given in one simple paragraph:

"The species proposed for introduction should be studied in its native habitat. The study should include known diseases, pests and predators, food habits, and biotic potential. To be included would be consideration of pathological, environmental, and genetic implications of the introduction. The study should extend over several years, and the results should be examined by a committee of specialists. If a decision is made to proceed, then a brood stock should be established in quarantine in the recipient country. Only the F_1 generation should be introduced to open waters, provided that no problems emerge."

A comparable development for freshwater living animals and plants took place in the European Inland Fisheries Advisory Commission (EIFAC) – a regional FAO body with 25 European member countries. ICES and EIFAC, through their respective working groups, have now developed codes of practice that are almost identical, and the codes have been used as background for action and regulations by some member countries as well as other nations.

Discussions within ICES and EIFAC, and subsequent ones with members of the World Aquaculture Society (WAS), led to the conclusion that an international symposium would be an effective approach to directing scientific and administrative attention to an expanding global problem. The objective of the symposium would be to focus attention on the subject of introductions and transfers of aquatic species by discussing specific case histories of recent activities – instances where introductions or transfers have had positive or negative effects, or where concern has been expressed about potential effects. Plants as well as animals would be included.

As a consequence of these discussions, a two-day international symposium on "The Effects of Introductions and Transfers of Aquatic Species on Resources and Ecosystems", sponsored jointly by ICES, EIFAC, and WAS, was held in Halifax, Nova Scotia, Canada, 12–13 June, 1990, as part of the annual meeting of WAS. Coconvener for ICES was Dr Carl Sindermann (USA); for EIFAC, Ir Bert Steinmetz (The Netherlands); and for WAS, Dr William Hershberger (USA). Six general overview papers and seventeen invited papers were presented to an audience drawn from all parts of the world, including representation from Central and South America, Asia, and Australia, as well as North America and Europe. Separate sessions were devoted to introductions and transfers of fish, molluscs, crustaceans, and aquatic plants.

The opening session of the Symposium consisted of overview papers by J. T. Carlton (USA): International transportation of aquatic organisms by man; H. Rosenthal (Germany): Introductions of aquatic species: a statistical analysis of a literature survey (1867–1989); E. M. Hallerman and A. R. Kapuscinski (USA): Ecological implications of using transgenic fishes in aquaculture; J. T. Carlton (USA): Codes of Practice; C. C.

Kohler (USA): Environmental risk management of introduced aquatic species; and W. Howarth (UK): Regulating the introductions of freshwater fish: the United Kingdom, European Community, and beyond.

The introduced fish session was chaired by R. L. Welcomme (FAO – Rome), who also presented an outstanding historical review of introductions of inland aquatic species. Other fish papers considered gene transfers in Atlantic salmon and effects of handling stress on wild and cultivated Pacific salmon.

The introduced crustacean session was chaired by D. V. Lightner (USA), who presented a detailed description of the introduction and spread of a fatal viral disease in cultured shrimp stocks in Mexico. Other crustacean papers described the invasion of North America by the European water flea (*Bythotrephes*) and the effects of introduced diseases on shrimp culture in the southern United States.

The introduced mollusc session was chaired jointly by K. Chew (USA) and H. Grizel (France). Invited papers covered a wide spectrum of major introductions, including the Pacific oyster (*Crassostrea gigas*) and the Manila clam (*Ruditapes philippinarum*) to France; the European zebra mussel (*Dreissena polymorpha*) to the North American Great Lakes; and Asiatic oyster drills to the Pacific coast of North America.

The introduced aquatic plants session was chaired by I. Wallentinus (Sweden), who also presented a review of introductions to Europe, especially *Undaria pinnatifida* to France. Other papers dealt with the impacts of introduced *Hydrilla* and *Eichhornia* in the southern United States, and the role of ship ballast water in the global distribution of coastal/estuarine phytoplankton.

The closing session of the Symposium consisted of summaries by the co-conveners and by the session chairmen. During the discussion, suggestions for statements to be transmitted to the sponsoring organizations were made (although not formally approved). They included the following:

(1) Movements of aquatic organisms beyond their normal ranges will continue to characterize aquaculture development. Scientific advice and adherence to standard protocols concerning disease control, genetics, and environmental considerations should be elements in risk assessments prior to such movements.

(2) The subject of introductions and transfers of aquatic organisms – intentional or accidental – is one of importance, and one for which WAS should establish a position, since world events and world regulatory initiatives of significance to aquaculture are moving rapidly. A study committee should be established to explore these developments and to develop a WAS position.

(3) *Transgenic species* are being developed for use in aquaculture. Procedures governing the release of genetically modified species in aquaculture should be subjects for examination by regulatory agencies and by each of the sponsoring organizations.

(4) Some introductions have been and should be considered as *biological pollution* and should be accorded research attention similar to that given to chemical pollutants. (This category would include all accidental introductions.)

(5) The differences between *introduction* of a species and *establishment* of breeding populations of a species should be clearly defined, as should the concept of "critical mass" of an introduction.

(6) Decisions about introductions should be based on *reasoned examination of all the consequences*, and not only on pressures from economically motivated sources.

(7) The majority of introductions have had no effects and have not led to establishment in the new environment; a small number have been beneficial; and an even smaller number have been disasters.

(8) Much of the recent expansion of aquaculture worldwide would probably not have occurred in the absence of international movement of species. Further introductions of species, subspecies, and races must be regarded as inevitable.

(9) As a general principle, an aquatic organism should be regarded as introduced once it has crossed a national frontier. There is a need to apply and further disseminate the Codes of Practice that have been developed to minimize the risks of international movements of aquatic organisms. The Codes should be harmonized as much as is consistent for their application in varying geographic and economic circumstances. Codes should also be drawn to the attention of other national and international organizations in order to have the special needs of aquatic introductions included in the more general protocols that are currently being developed. This includes information transfer to researchers at universities and laboratories, as well as to those experimenting with aquaculture, in both major and minor scales, and to the general public. The existence of such Codes is now often known only among governmental authorities and major aquaculture companies.

From the broad range of papers presented during the Symposium, it is apparent that introductions and transfers of aquatic species constitute an expanding worldwide problem – whether such movements are accidental or deliberate. It is interesting that in many instances the ICES/EIFAC Codes of Practice Concerning Introductions are looked to as universal constants in matters of deliberate introductions.

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A history of international introductions of inland aquatic species

R. L. Welcomme

Welcomme, R. L. 1992. A history of international introductions of inland aquatic species. – ICES mar. Sci. Symp., 194: 3–14.

A register of 1 673 000 records of introductions of 291 species into 148 countries has been analysed for trends and motives for introductions. Some introductions occurred in historical times, but the rate of movement of species between countries has accelerated since 1900. The majority of introductions have been carried out in support of aquaculture, although sport and improvement of wild fish stocks have also been significant motives. A large number of introductions have occurred through accidental escape or transmission between countries. Most introductions have proved benign in that they have had no detectable influence on native fish communities or have contributed significantly to aquaculture or capture fishery yields. A small proportion of introductions have proved ecologically undesirable, and these have arisen mainly either from species capable of producing stunted populations or from predatory species which have damaged indigenous species.

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1. Introduction

As part of its aquaculture and inland fisheries programme FAO has collected information on international introductions of inland water aquatic species. A register with a total of 1673 records of introductions of 291 species into 148 countries has been compiled with the assistance of a network of correspondents from 140 countries, working for the most part within the framework of the regional fishery bodies concerned with inland waters. This body of data provides a record of the many movements of species across national frontiers and has been analysed to shed light on past trends and motivations in introductions. This data set suffers from a number of limitations. First, where multiple introductions of any species into any one country have occurred, only the date of first transfer is recorded. Second, there has been a noted tendency in reporting data to record only those species which have either become established in the wild or are maintained either by induced breeding or by continued import for aquaculture, with the result that many of the unsuccessful transfers are probably not included in the register. Third, the register only includes records of species that have crossed national boundaries and does not include either the extensive transport of a species that frequently occurs within a country once the original introduction has taken place or the large number of introductions which have been made between different zoogeographical areas within national boundaries. This paper is an updating of the material presented by Welcomme (1988) with the incorporation of 319 additional records collected in the interim.

2. Trends in introductions

In contrast to the spread of plants and other animals of interest to man introductions of fish species have occurred very recently. Some introductions may be classified as ancient or historical (before 1800) but the major spread of exotic fish species around the world essentially dates from the middle of the 19th century. Since 1850 the number of introductions occurring in any decade has shown a steady increase, with some slight slowing during the decades 1910 and 1940 due to global conflicts (Table 1). Current records indicate that the number of introductions peaked during the early 1960s, but mean rates from 1950 through 1985 do not show any significant change, and it might be concluded that there was no reduction in the rate of international movements of fish species throughout that period.

The records indicate a sharp drop in the number of

Table 1. Number of introductions per decade for which date of introduction is known.

Date	Number		Total number	Percent
Ancient	18			1.08
1800–1849	15			0.90
1850–1859	4			0.24
1860–1869	10			0.60
1870–1879	22			1.32
1880–1889	36			2.15
1890–1899	40			2.39
1900–1909	59			3.53
1910–1919	31			1.85
1920–1929	69			4.12
1930–1939	79			4.72
1940–1949	60			3.59
1950–1954	93			
1955–1959	96	1950–1959	189	11.30
1960–1964	141			
1965–1969	84	1960–1969	225	13.45
1970–1974	124			
1975–1979	100	1970–1979	224	13.39
1980–1984	108			
1985–1989	28	1980–1989	136	8.13
Unknown			456	27.26
Total			1673	100.00

introductions from 1985 onwards, but experience has shown that this may be due to the delays with which recent data enter the records. Alternatively, there may be a real decline in the rate at which introductions are being made as legislation in many areas of the world, which has arisen from a growing awareness of the possible negative consequences of species introductions, may have slowed if not stopped the flow. There may also be a saturation effect whereby a species has been introduced to all suitable recipient areas, an effect that can be detected in Table 2, where the introduction rate of successive groups of species attains a peak and then diminishes relative to other groups. Introductions of European cyprinids (mostly common carp), poeciliids, centrarchids and salmonids, occurred relatively early and have been succeeded by cichlids, Asiatic cyprinids and crustaceans in roughly that order. In the 1980s there has been a tendency to introduce a growing number of other species in search of alternative species for tropical aquaculture.

Two-hundred-and-ninety-one species of fish have been recorded as having been introduced outside their countries of origin. Eighty-seven percent of this number have been recorded from 10 countries or less and 41% have been recorded from only one country. At the other extreme, 13 species have been introduced into more than 30 countries and four in particular, *Micropterus salmoides*, *Cyprinus carpio*, *Oreochromis mossambicus* and *Oncorhynchus mykiss*, each with over 50 host countries, may be regarded as having become pan-global within the limits set by their thermal tolerance. *Ctenopharyngodon idella* has an equally wide distribution but is maintained artificially in nearly all its host countries. Generally, the several thousand small tropical ornamental species forming part of the world's aquarium fish trade have not been registered here but some have been recorded where they have clearly become established outside their native range.

Europe, Oceania (Australia) and North America had an early history of introductions in the later decades of the 19th century and a second period of activity in the 1960s or 1970s. Introductions into Africa and the Middle East started later, reached a peak in the 1950s, and have since declined. The rate of introductions into Asia and South and Central America on the other hand have continued to increase until the present, and these regions are now the major importers of fish and crustacean species (Table 4).

This table also summarizes the different intensities of introductions in various regions as measured by the number of introductions per country. Asia, Europe, and North America are all areas where the index is high relative to the mean, whereas in Africa, the Middle East, and Oceania the index is low. In South and Central America the number of introductions has been around the average. The continental mean conceals a considerable variation between countries in any one region.

Table 2. Percentage by major species groups introduced during each decade since 1900.

Decade	Centrarchids	Cichlid	Crustacea	Cyprinids			Poeciliids	Salmonids
				Asiatic	Europe	Other		
Ancient	0.00	0.00	0.00	2.65	5.84	3.12	0.00	0.00
1800	12.06	0.31	0.00	1.59	17.52	0.00	0.00	19.46
1900	4.26	0.00	0.00	2.12	6.57	0.00	2.46	10.89
1910	2.13	0.00	0.82	2.65	5.11	0.00	1.64	2.33
1920	3.55	0.31	4.10	0.00	7.30	6.25	22.13	7.00
1930	9.93	0.31	2.46	1.06	9.49	3.12	9.02	6.23
1940	7.80	3.12	0.82	1.59	4.38	6.25	3.28	4.67
1950	18.44	26.17	0.82	2.12	5.11	12.50	4.92	12.84
1960	9.22	18.07	3.28	33.86	9.49	15.62	5.74	10.12
1970	3.55	17.13	28.69	23.28	8.76	12.50	2.46	10.12
1980	2.13	11.53	20.49	16.40	4.38	43.75	0.00	2.33
Unknown	26.95	23.05	38.52	15.34	21.90	0.00	48.36	14.01

Table 3. List of species and the number of countries into which they have been introduced, listed in numerical order.

Species	Number of countries
114	1
38	2
20	3
13	4
17	5
11	6
7	7
7	8
7	9
Carassius carassius, Labeo rohita, Salmo salar, Xiphophorus helleri	10
Catla catla, Eriocheir sinensis, Onchorhynchus tshawytscha, Osphronemus gouramy	11
Lepomis cyanellus, Trichogaster pectoralis	12
Oreochromis macrochir	13
Micropterus coosae, Salvelinus namaycush	14
Lepomis gibbosus, Cherax tenuimanus, Macrobrachium rosenbergii, Micropterus dolomieu, Oreochromis hornorum, Pacifastacus leniusculus, Tinca tinca	16
Lepomis macrochirus	18
Tilapia zillii	19
Ictalurus punctatus	20
Oreochromis aureus	22
Poecilia reticulata	24
Tilapia rendalli	28
Procambarus clarkii	31
Carassius auratus	32
Salmo trutta	33
Aristichthys nobilis	34
Gambusia affinis	40
Salvelinus fontinalis	41
Oreochromis niloticus	44
Hypophthalmichthys molitrix	47
Micropterus salmoides	56
Ctenopharyngodon idella	57
Cyprinus carpio	66
Oreochromis mossambicus	67
Oncorhynchus mykiss	87

Indeed, it is usual to find that relatively few countries within a continent have introduced an exaggeratedly large number of new fish species (Table 5).

The logic behind such high intensities of introduction is sometimes unclear. The presence of many island states (irrespective of region) and of European countries in the list of major receivers of exotic species is understandable, as both categories generally have impoverished fish faunas and introductions have been made in an attempt to increase diversity for a wide range of purposes. It is difficult to apply the same reasoning to the large number of introductions into the countries of Asia, or North, Central, and South America. Here there are numerous native species capable of fulfilling most of the functions for which fish are usually introduced, and which have themselves been exported to other regions for these purposes.

3. Motives for introductions

A broad classification of the purposes given for introductions is given in Table 6. The motives for a surprisingly large percentage of cases appear ill defined. In high percentage (19%) the reasons for which the introduction was made are now unknown and in a further 9% of the recorded introductions appearance in natural waters is attributed to accident. Furthermore, even where an objective is stated for carrying out a particular introduction there is often little information as to what precise role the species was expected to accomplish in its new home. A surprising number of introductions appear to have been performed for what today would be considered trivial motives. Among these, nostalgia of displaced peoples for familiar fauna to surround them would seem to rank fairly high. Many of the earlier movements of species following colonization may have been made on this basis, even though they were seemingly irrational in that adequate local species already

Table 4. Introductions made into different continents by decade expressed as a percentage of total per region.

Decade	Africa	Asia	Europe	Middle East	North America	Oceania	South America
Ancient	0.00	2.85	1.82	0.00	1.02	0.00	0.00
1800	1.68	4.11	22.42	0.00	6.12	7.26	2.84
1900	1.01	4.75	3.94	0.00	1.02	3.35	4.83
1910	2.68	3.48	1.82	0.00	1.02	0.00	1.42
1920	6.71	4.11	3.64	3.45	1.02	2.79	2.27
1930	7.38	4.43	4.24	3.45	1.02	5.59	4.83
1940	6.04	3.16	1.52	3.45	0.00	2.79	5.97
1950	23.49	10.13	2.73	6.90	8.16	9.50	12.50
1960	17.45	12.66	12.73	24.14	10.20	12.85	11.65
1970	11.74	13.29	16.97	6.90	4.08	4.47	20.17
1980	3.69	16.14	6.67	0.00	4.08	3.35	11.08
Repeated	0.00	0.00	0.30	6.90	0.00	0.00	0.00
Unknown	18.12	20.89	21.21	44.83	62.24	48.04	22.44
TOTAL	100.00	100.00	100.00	100.00	100.00	100.00	100.00
Intro/country	9.28	14.95	12.21	1.28	50.00	4.14	11.00
Mean				11.3			

Table 5. List of countries and the number of species they have received listed in numerical order.

Country	Species
29	1
10	2
13	3
5	4
5	5
6	6
6	7
6	8
4	9
6	10
Congo, Costa Rica, Egypt, El Salvador, Hungary, Irian Jaya (Indonesia), Korea, Sweden, Tunisia	11
Bolivia, Honduras, Ivory Coast	12
Finland, Poland	13
Argentina, Denmark, Guam, Yugoslavia	14
Czechoslovakia	16
Kenya	17
Canada, Dominican Republic, Spain	18
India, Malaysia, Peru, Zimbabwe	19
Israel, Italy, Mauritius, New Zealand, S. Africa	20
Brazil	21
Chile, Cuba, Cyprus, Indonesia, Netherlands, Thailand	22
Belgium, Madagascar, Philippines	23
France, Puerto Rico, Sri Lanka, USSR	24
USSR	27
China, Fiji, Germany	28
UK (Great Britain)	29
Australia, Panama	30
Mexico	33
China (Taiwan Province)	35
Morocco	38
Colombia	44
Hawaii (USA)	47
Japan	52
USA	79

Table 6. Purposes for which species have been introduced.

Purpose	Number of cases	Total in category	Percentage
AQUACULTURE		697	36.1
SPORT		227	11.8
IMPROVEMENT OF WILD STOCK		208	10.8
Food fishery	75		
Fill a vacant niche	44		
Forage	24		
Restoration of fishery	2		
Establish new wild stock	27		
Species conservation	2		
ACCIDENT	10	174	9.0
Escape or release from aquaria	78		
Diffusion	33		
Bait fish	9		
Introduced with other species	15		
Escape from aquaculture	20		
In ballast water	1		
Live transport for consumption	1		
Private initiative	9		
ORNAMENT (+ aquarium fish)		161	8.4
CONTROL OF UNWANTED ORGANISMS		102	5.4
Vegetation	38		
Mosquitoes	43		
Snails	6		
Phytoplankton	8		
Other fish	2		
UNKNOWN		375	18.5

existed or that the introduced species was poorly adapted to its destination. Similarly, simple dietary preferences or sporting prejudices may have motivated movements of some species such as common carp or trout. In many cases, introductions have been carried out for more than one motive and in the case of those attributed to accident in particular there was usually a primary objective for the introduction of the original captive stock.

The changing purposes for which exotic fish species have been moved from country to country are concealed to a certain extent by the large proportion of introductions taking place between the 1960s and the present day. Table 7 illustrates these trends by presenting the percentage of introductions made for each purpose by decade.

Introductions made for aquaculture have always comprised a significant proportion of the total in any decade but have grown steadily in importance. Since the beginning of the 1970s introductions made for this purpose have accounted for well over half of all introductions made. Sports fishing has provided the second major motive for introduction but has declined steadily in relative importance from the end of the last century, and since the early 1950s has ceased to be a major objective. Introductions made for the enhancement of wild stocks in lakes, reservoirs and rivers were also of great importance between 1870 and 1910 and increased in number from 1950 to 1979, when they overtook sports fishing as the second most important motive. The use of fish species for control of unwanted organisms is of more recent origin, with a peak in introductions in the 1920s and again in the decades from 1960 to 1979. Most of the introductions of fish species for ornamental purposes have been made by private individuals or have become apparent after escaping into the wild. The date at which the introduction occurred is frequently unknown and trends are difficult to identify. The date of introductions arising from various types of accident are likewise generally unknown, and no particular trend can be detected from the data. Introductions which were made for motives which are unknown tended to rise numerically until the 1960s, but as a percentage of all introductions they reached a peak in the 1930s and have since declined. The most substantial reduction in this category since 1970 indicates that introductions of exotic species have been more carefully documented in recent years.

Table 7. Changes in purpose of introductions expressed as percentage introduced by decade for each major category of use.

Decade	Aquaculture	Sport	Stock improvement	Control	Ornament	Accident	Unknown
Ancient	31.58	0.00	0.00	5.26	10.53	0.00	52.63
1800	29.41	17.65	11.76	0.00	5.88	0.00	35.29
1850	25.00	0.00	0.00	0.00	25.00	25.00	25.00
1860	18.75	43.75	6.25	6.25	12.50	6.25	6.25
1870	12.50	33.33	37.50	0.00	4.17	0.00	12.50
1880	29.27	24.39	19.51	0.00	4.88	7.32	14.63
1890	36.73	34.69	10.20	0.00	4.08	4.08	10.20
1900	26.76	28.17	22.54	2.82	5.63	1.41	12.68
1910	32.43	21.62	13.51	5.41	0.00	10.81	16.22
1920	16.46	25.32	8.86	16.46	6.33	17.72	8.86
1930	13.95	24.42	17.44	6.98	5.81	8.14	23.26
1940	21.74	24.64	13.04	7.25	4.35	7.25	21.74
1950	40.57	12.74	20.75	4.72	2.36	3.30	15.57
1960	45.39	8.49	11.07	9.59	4.80	10.33	10.33
1970	59.39	7.66	10.34	7.66	3.45	4.60	6.90
1980	67.81	4.79	7.53	3.42	3.42	6.16	6.85
Unknown	21.82	3.61	3.61	2.09	19.17	15.18	34.54

3.1. Aquaculture

One-hundred-and-seventeen species of fish have been introduced for some purpose associated with aquaculture (Table 8). Three groupings of species can be distinguished:

(i) Those species introduced into a few countries only (less than 10) which comprise over 87% of the species listed. Reasons given for these introductions are: to investigate the potential of new species; to provide material for production of hybrids; or to provide pituitary extract. In some cases, e.g. *Clarias gariepinus* and *Puntius gonionotus* (eight countries), *Colossoma* and *Rana catesbiana* (six countries), and *Clarias batrachus* (five countries), the introductions were part of a serious effort to develop new species for culture, and further spread of these species can be anticipated. In most, however, the experimental introductions met with little success and probably will not be followed by any other attempts.

(ii) An intermediate group of species (between 10 and 20) which are part of established aquaculture practice.

(iii) A group of seven species which have been introduced into 30 countries or more, which together provide a large proportion of the world's aquaculture production.

Early international movements of species (before 1900), mainly involved freshwater salmonids such as *Oncorhynchus mykiss*, *Salmo trutta*, and various species of *Salvelinus*. These were introduced into temperate regions or into high altitude waters in the tropics for aquaculture associated with the maintenance of sports fisheries as well as for limited food production. More recently (since 1970), salmonid introductions have involved anadromous forms which are being used for mariculture in cages. Common carp reached their maximum popularity in the decades between 1910 and 1940 and were successively replaced by tilapias (1950–1979) and Chinese carps (1960–1980) as preferred species (Table 9). Currently, increasing numbers of crustacean species are being transported around the world for the rapidly expanding brackish-water shrimp culture and

Table 8. List of species introduced for aquaculture and number of countries receiving them.

Species	Number of countries
47	1
16	2
8	3
8	4
8	5
6	6
4	7
4	8
1	9
Tilapia zillii	11
Oreochromis macrochir	13
Macrobrachium rosenbergii, *Micropterus salmoides*	15
Cherax tenuimanus, *Ictalurus punctatus*	16
Oreochromis urolepis hornorum	17
Oreochromis aureus	18
Oreochromis niloticus	30
Aristichthys nobilis	31
Hypophthalmichthys molitrix	33
Oreochromis mossambicus	34
Ctenopharyngodon idella	39
Oncorhynchus mykiss	48
Cyprinus carpio	50

Table 9. Percentage of major species groups introduced for aquaculture during each decade.

	Chinese carp	Common carp	Crustacea	Salmonids	Tilapia	Others
Ancient	42.86	42.86	0.00	0.00	0.00	14.29
1800	60.00	20.00	0.00	0.00	0.00	20.00
1850	0.00	0.00	0.00	0.00	0.00	100.00
1860	0.00	0.00	0.00	100.00	0.00	0.00
1870	0.00	66.67	0.00	33.33	0.00	0.00
1880	0.00	8.33	0.00	75.00	0.00	16.67
1890	0.00	16.67	5.56	66.67	0.00	11.11
1900	10.53	5.26	0.00	42.11	0.00	42.11
1910	33.33	25.00	8.33	16.67	0.00	16.67
1920	0.00	25.00	0.00	25.00	0.00	50.00
1930	0.00	28.57	0.00	14.29	7.14	50.00
1940	0.00	18.75	0.00	18.75	25.00	37.50
1950	2.17	7.61	0.00	9.78	47.83	32.61
1960	32.20	8.47	3.39	7.63	30.51	17.80
1970	20.89	6.96	11.39	6.33	28.48	25.95
1980	15.79	2.11	16.84	2.11	18.95	44.21
Unknown	9.43	5.66	27.36	5.66	12.26	39.62

the bullfrog *Rana catesbiana* is being introduced into a number of countries for frog culture.

Introduced species play a major role in the development of aquaculture across the world. The early expansion of aquaculture in Europe through the monastic tradition was based on *Cyprinus carpio*, which was exotic to most of the countries involved. Intensive commercial culture of rainbow trout in Europe, cage culture for Atlantic and Pacific salmon in Chile, culture of tilapia species in Brazil, Thailand, Cuba, Sri Lanka, Chinese carp culture throughout the world and brackish-water shrimp culture have all been based on species introduced from elsewhere. This practice has often been criticized on the basis that it has led to a failure to develop local species which may be equally desirable for culture. However, there is a well known strategy for food producers to cut risk by using technologies that are already established, which would explain the relatively narrow selection of species used in contemporary aquaculture. There is now a tendency to explore the potential of local species, which, should they prove successful for culture, may well set off a new round of movements involving such species.

3.2. Management of inland waters

Many introductions have been made with the intention of manipulating stocks of fish or crustacea in natural water bodies either for recreational fishing or for a variety of food fisheries ranging from subsistence to fully commercial. These two groups are frequently difficult to differentiate, since the same stock may be exploited by both sports and food fishermen. Introductions reported clearly as for 'angling' or 'sport' are easy to interpret, but difficulties arise in categorizing motives such as introduction of forage species for predators introduced for recreational purposes. Furthermore, catches of sports fishermen are frequently consumed and may represent a significant source of food to the angler.

3.3. Sport

Fifty-seven species have been recorded as having been introduced for sport (Table 10) and comprise two main groups of species: (i) those large species having the fighting qualities sought by sports fishermen; (ii) species in support of sports fisheries, such as forage species for large predators or species transported as bait which escaped and became established in the wild. The former account for the widespread dissemination of rainbow and brown trouts throughout the world in the earlier decades of this century (1900–1930) and the spread of *Micropterus salmoides* between 1930 and 1950. There are also those that seek diversity in their fishing and a number of minor species have been introduced to increase the variety of fish available to the recreational fisherman.

Many of the species introduced originally for sport

Table 10. List of species introduced for sport and number of countries receiving them.

Species	Number of countries
31	1
6	2
10	3
2	4
2	5
Salmo salar	6
Micropterus dolomieu	9
Salvelinus fontinalis	16
Salmo trutta	22
Micropterus salmoides	28
Oncorhynchus mykiss	44

Table 11. List of species introduced for improvement of natural fish populations and number of countries receiving them.

Species	Number of countries
43	1
15	2
5	3
8	4
Lepomis cyanellus, *Micropterus dolomieu*, *Micropterus salmoides*, *Oncorhynchus nerka*, *Oreochromis niloticus*, *Pacifastacus leniusculus*	5
Coregonus clupeaformis, *Coregonus lavaretus*, *Cyprinus carpio*, *Hypophthalmichthys molitrix*, *Lepomis macrochirus*, *Orconectes limosus*	6
Oncorhynchus tshawytscha	9

have subsequently been adopted for aquaculture or have formed the basis of stocks which are exploited by subsistence of commercial fishermen.

3.4. Improvement of wild stocks

Eighty-four species have been introduced for the improvement of wild stocks. The major motivation for such introductions is to found a new food fishery, usually by introducing some element that is perceived as lacking in the fauna of the host water body. This has been practised particularly in faunistically poor regions such as cool temperate areas affected by glaciation during the ice ages, islands east of the Wallace line or high altitude mountain lakes. Introductions have also proved necessary into new habitats such as reservoirs or regulated rivers, where the indigenous fauna lacked elements competent to establish themselves under the new regime. Allied to the above motive are those introductions made to replace faunistic elements lost through environmental change. The introduction of new salmonid species into the Great Lakes of North America was undertaken for this reason. Extensive introductions of new crayfish species into European waters have also been made in an attempt to reconstitute stocks after the native species were virtually wiped out by disease.

The introduction of one species produces the need to introduce further species. For example, when major predators are introduced into fish communities which are not adapted to heavy predation, the resulting decline in native species has made the introduction of additional food fishes necessary. Classic examples of this are the introductions of *Lepomis* species to mitigate the impacts of black bass introductions, the use of tilapias or *Cichlasoma* as forage for *Cichla ocellaris* and the introduction of *Bairdiella icistia* to provide a prey species for *Cynoscion xanthulus* in the Salton Sea. Conversely, predatory species have been introduced into many areas to control stunted populations usually of tilapias and sunfishes. A further example of serial introduction occurs where herbivorous fishes such as *Ctenopharyngodon idella* or common carp exert an eutrophicating influence on the water, changing the organisms responsible for primary production from macrophytes to phytoplankton. The resulting algal blooms can achieve nuisance proportions and *Hypophthalmichthys molitrix* has been introduced to correct this. These types of complementary introductions have been formalized in aquaculture as polyculture systems and further introductions of this type can be anticipated as knowledge of the eco-manipulation of small water bodies for extensive culture increases.

Several species have been introduced in an endeavour to conserve them in the face of possible extinction in their own habitat. Several introductions of *Hucho hucho* have been made for this purpose in Europe, as have introductions of *Gila orcutti* and *G. bicolor* within the United States and Canada. As this type of introduction tends to be made more within national boundaries, the number of cases on record is somewhat limited.

3.5. Ornament

Introductions made for ornament fall into two main groups. First, the goldfish *Carassius auratus auratus* has achieved wide distribution through its being reared in ornamental ponds, and has been introduced into 32 countries for this purpose. It has frequently escaped from these to colonize natural waters.

Second, several thousand species of small, usually tropical fishes, have been disseminated around the world by the aquarium fish trade. Movements of these species is rarely documented. It has been generally assumed that fish of this type cannot survive in temperate climates and as such have no place in a register of introductions. While this view is in part correct in temperate countries, some species have maintained populations for many years in artificial warm waters such as discharge canals from power stations and in naturally warmed waters such as hot springs. The diverse fauna recorded from the hot springs of the Banff National Park, Alberta, Canada are evidence to the persistence of such populations. In the tropics the situation is much more serious. Here, growing culture of ornamentals for export has led to the introduction of species from all over the tropical world into Brazil, Colombia, Florida (USA), Peru, Malaysia, Thailand, and Singapore, and the practice is probably more widespread than these reports indicate. Escapes from rearing installations are common and are probably responsible for the large number of small exotics reported from Colombia (26 species), continental USA (43 species), and Hawaii (12 species). However, such escapes have usually gone unreported or even unnoticed, and the penetration by small species into tropical ecosystems is probably much greater than official statistics would indicate. For instance, Brazil and Malaysia report only two species each as appearing through accidental escape from aquaria. So far, only 77 species of small tropical fish, all of which form part of the aquarium fish trade, have been recorded as having been introduced for ornamental purposes into 21 countries. Detailed analysis of the waters adjacent to rearing installations would doubtless increase this number considerably.

3.6. Control

Fish have been used for many years to control undesirable organisms in the aquatic environment, and have had much appeal in the face of the dangers to the environment of alternative, chemical control. Early attempts in the 1920s focused on the control of mosquitoes, but later (1960s and 1970s) the control of aquatic vegetation became more important.

3.7. Mosquitoes

Thirteen species of cyprinodonts and small barbs have been used for the control of mosquito larvae. Of these, by far the most important has been *Gambusia affinis*, which has been introduced into 27 countries for mosquito control and a further 13 countries for other purposes.

Gambusia is now being replaced by local species in many areas. Further dissemination of *Gambusia* is thus limited and a large number of small, native larvivorous fishes are being investigated for this role. An extensive literature exists on this topic; see for instance Gerberich and Laird (1969).

3.8. Snails

Certain fish species which are mollusc eaters in their natural habitat have been proposed for the control of the snail vectors of schistosomiasis. Some success has been claimed in the limited attempts which have been made at control in aquaculture ponds and irrigation canals by the introduction of *Astatoreochromis alluaudi* into five African countries in the 1960s. In larger bodies of water, mollusc control appears to be almost ineffective despite the presence of numerous molluscivorous species. In general this type of biological control does not appear to have been pursued much further and merits more research.

3.9. Aquatic vegetation

Numerous species of fish eat aquatic weeds and a range of specialized phytophagous habits have been described which could be used to construct complex herbivorous communities (Shireman, 1984). This potential is still largely unexploited and only a few fish have been introduced to control aquatic vegetation. Specifically, the following four species were recorded as having been introduced to control aquatic plants: *Oreochromis mossambicus* introduced into 2 countries; *Tilapia zillii* introduced into 2 countries; *Tilapia rendalli* introduced into 4 countries; *Ctenopharyngodon idella* introduced into 30 countries.

3.10. Blooms of phytoplankton

Hypophthalmichthys molitrix has been introduced into five countries to control heavy blooms of phytoplankton in natural waters.

3.11. Accident

About 9% of introductions into natural waters have been registered as unplanned, resulting from some form of accident or private initiative. This proportion is probably much higher, as many of the 18% of introductions whose motives are reported as unknown may also lie within this category. This relatively large percentage of unintentional introductions illustrates the difficulty of containing an introduced species within limited environments such as ponds or aquaria, and supports the principle that a species must be regarded as introduced into a country once a breeding pair have crossed the national boundary. Accidental introductions may arise from a number of sources including: the introduction of fry of non-target species along with those of an intentionally introduced fish, the escape or release of bait fish, and the transportation of eggs, juvenile, or adult fish in the ballast water of ships. Once established in one country some species have diffused through freshwater systems in different parts of the world. For example, carp moved naturally down the Uruguay river from Brazil to invade Uruguay and Argentina, the mitten crab diffused from an original site in West Germany to occupy much of Northern Europe, *Stolothrissa* migrated down the Zambezi River from Lake Kariba to establish itself in Lake Cahora Basa, and many of the small cyprinids introduced into one or other of the Danube countries have diffused throughout that river system. This mobility of species, once they have been introduced, illustrates the need for international agreement to limit the spread of undesirable species and to reduce risks of introduction of ones that are judged to be useful.

4. Breeding success of introductions

The reports on introductions indicate that six main patterns are common in introductions with respect to their establishment in their host environment (Table 12).

(i) The species does not establish, disappears without trace, or its fate is listed as doubtful or unknown. The 443 examples registered are probably a considerable underestimate due to failure fully to report such occurrences. Failure to establish may

Table 12. Breeding success in introduced species.

Unknown or doubtful	311	18.59
Not breeding	132	7.89
Maintained artificially	258	15.42
TOTAL NOT BREEDING	701	41.90
Breeding but disappeared	28	1.67
Local or sparse populations	504	30.13
Widespread or locally strong populations	429	25.64
Eliminated	11	0.66
TOTAL BREEDING	972	58.10
TOTAL	1673	100.00

result from the species being introduced into inappropriate climates and habitats or in insufficient numbers to ensure a breeding population being set up. There remain, however, a number of introductions where the reasons for the inability of a species to establish itself in the host waters remain obscure.

(ii) The introduced species does not breed under natural conditions and is maintained artificially or by continuous import. This is particularly common in species having commercial value for aquaculture, such as rainbow trout, the Chinese carps or eels. It is also considered desirable in species such as the grass carp, which are used for controlling undesirable organisms and whose usefulness may only be temporary. Ostensibly, species which are maintained by artificial reproduction are easier to control and to eradicate from the natural waters when their purpose has been served. However, continuous import heightens the risks of introduction of disease, and grass carp have frequently been accused of environmental degradation. Furthermore, continued failure to breed in the wild cannot be assumed, as self-breeding stocks of *Ctenopharyngodon idella* may have appeared in both the Mississippi and Danube river systems.

(iii) The introduced species become locally established in an unusual habitat. Most typically these are represented by:

(a) colonization of thermally polluted waters in the temperate zone and have been reported from Canada, Australia, Hungary, Belgium, Netherlands, and the United Kingdom. Such populations occupy areas inaccessible to native temperate fishes and persist so long as the favourable conditions are maintained, but disappear when the thermal source is removed.

(b) Colonization of cold, high altitude waters at tropical latitudes by temperate species, usually the salmonids – *Oncorhynchus mykiss*, *Salmo trutta*, and *Salvelinus fontinalis*. In these cases climatic conditions are more stable and the introductions can be regarded as permanent additions to zones whose native faunas are generally impoverished.

(iv) The introduced species establishes itself and may even increase rapidly in abundance to become a dominant element of the population. Later the species declines in abundance or disappears. The decline may occur naturally or may be the result of deliberate eradication. Most species in this category established viable but low level populations which were unable to compete on a sustained basis and died out. A few, notably *Lepomis cyanellus*, *Oreochromis mossambicus*, and *O. niloticus*, showed the typical 'boom and bust' cycle which might be expected of any species transported into waters where its preferred food is underutilized by existing species and where the resulting population explosion is later brought into equilibrium with the available resources. However, it is difficult to explain why an apparently successful introduction disappears completely, as has happened on several occasions.

(v) The introduced species establishes and maintains itself either as widespread populations at very low densities, or as isolated populations in individual water bodies or aquaculture installations. This is the most common outcome of introductions, and, although it is improbable that a new element can be inserted into a fish community without its affecting native populations to some extent, the instances in this category have had environmental, economic, and social effects that are so slight as to occasion no positive or negative comment.

(vi) The introduced species becomes a significant or dominant element of the host fauna and in these cases some impact can be anticipated from the introduction.

5. Evaluation of introductions

Many different viewpoints are brought to bear on evaluating the impacts of introductions on natural ecosystems. At one extreme is the conservationist, whose wish to preserve the existing equilibrium results in resistance to any addition to the fauna; at the other is the functional fishery manager, whose wish to increase yield motivates a wish to try any introduction that might meet his end. These opposed views tend to run parallel to the different economic groupings in the world. Northern post-industrial societies have a much stronger motivation towards the protection of the environment and thus have highly conservative attitudes to any further introductions. After a long history of haphazard introductions in the past, many now seek to approve only those species which produce minimum disturbance in the quality of the natural system. Traditionally, the more rurally oriented societies of the tropics have been tolerant of foreign species and may be prepared to support quite considerable environmental change in favour of an immediate solution to food deficiencies or to the earning of convertible currency. These attitudes are evolving, however, and tropical countries too are now showing heightened ecological awareness that is leading towards a more discerning attitude about future movements of fish species.

The many respondents to the questionnaires on which the register is based have expressed general judgements on the impact of the various introductions. Many concerns have been expressed as to the elimination of native species by competition or predation, the degradation of the aquatic environment, and the introduction of new diseases into the host fish community, but many successes have also been noted.

The introduction of the pelagic clupeid *Limnothrissa miodon* into Lakes Kivu and Kariba and its accidental diffusion downstream to Lake Cahora Basa have led to the establishment of substantial stocks of fish which form the basis for fisheries yielding 20 000 tonnes/year. Important local fisheries have been established in many countries through introductions of tilapias (principally *Oreochromis niloticus*) in lakes and reservoirs in South East Asia and Latin America, *Cichlasoma* and *Micropterus* species in Central American lakes, *Odontesthes bonariensis* and *Oncorhynchus mykiss* in Lake Titicaca, and *Puntius gonionotus* in rivers of the Philippine and Indonesian islands. Much of the world's aquaculture relies on comparatively few introduced species which, according to the most recent statistics on freshwater aquaculture production (FAO, 1989), account for some 3 763 179 tonnes or 62% of the total. Grass carp, *Ctenopharyngodon idella*, have been successfully used for control of aquatic macrophytes in many countries and probably provide the only practical method for control where the use of herbicides is overly costly or undesirable (Shireman, 1984). The control of mosquito larvae by small larvivorous fish species is also highly effective and is replacing the more costly and environmentally dangerous control with insecticides.

Replies to queries on the environmental impact of 1673 individual introductions were:

No comment	1300	77.4%
Negative	152	9.1%
Positive	210	12.5%
Equal	17	1.0%

In interpreting these replies on the basis of the number of countries which considered that any one of the 291 species had made a positive reply (with either no detectable impacts or the advantages far outweighed any nuisance the species might have caused) or negative reply (not met the objectives for which they were introduced or had shown sufficient environmental impact to be pests) indicated the following:

Table 13. Species classified as pests where introduced.

*Acanthogobius flavimanus**	*Lepomis macrochirus**
*Alburnus alburnus**	*Leuciscus leuciscus**
Ambloplites rupestris	*Macrobrachium amazonicum*
Ancistrus sp.	*Megalobrama amblycephala**
*Bairdiella icistia**	*Odontesthes bonariensis*
*Blicca bjoerkna**	*Opsariichthys uncirostris**
Cichlasoma bimaculatum	*Orconectes limosus*
Clarias batrachus	*Percottus glehni**
Eriocheir sinensis	*Phalloceros caudomaculatus**
Gambusia affinis†	*Pimephalus promelas*
Gymnocephalus cernua	*Poecilia latipinna*†
*Hemibarbus maculatus**	*Poecilia mexicana*†
*Hemiculter eigenmanni**	*Poecilia reticulata*†
*Hemiculter leucisculus**	*Pseudogobio rivulatus**
*Hypseleotris swinhonis**	*Pseudorasbora parva**
*Ictalurus melas**	*Rhinogobius similis**
*Ictalurus nebulosus**	*Rhodeus sericeus*
Ictalurus punctatus	*Rivulus harti*†
*Lepomis auritus**	*Rutilus rutilus**
*Lepomis cyanellus**	*Scardinius erythrophthalmus**
*Lepomis gibbosus**	*Serassalmus humeralis*

*Species forming dense, stunted populations.
†Poeciliid species.

Insufficient environmental impact to warrant mention by the correspondents	153	62.8%
Negative	49	16.8%
Positive	45	15.4%
Equal	14	4.8%

Species that are generally described as pests (Table 13) include mainly those which respond to their host environment by forming dense, stunted populations (*). This behaviour makes them useless for anything but forage for predatory fishes and causes a disproportionate amount of environmental nuisance. Other species in this category are burrowers, such as *Eriocheir sinensis* or *Procambarus clarkii*, which cause costly and even dangerous damage to river and pond banks. Although the numerous poeciliid species figuring in the list (†) are thought to be efficient controllers of mosquitoes, it is usually felt that local species can do this job adequately, whereas the introduced ones tend to eat the eggs of endemic fishes.

In a second set of species the negative effects of the various kinds of ecological impact are just about counterbalanced by the advantages gained from the introduction (Table 14). Their numbers include a high proportion of predatory species (†) which have been implicated in eradication of endemic fishes as well as species which form dense, stunted populations (*). The very widely introduced *Oreochromis mossambicus* and *Cyprinus carpio* may also be considered to fall within this category since, despite their value to fisheries in some areas, their poor flavour and excessive environmental impacts have led to their widespread classification as pests in others.

A wide range of species are viewed as beneficial

Table 14. Species whose introduction is viewed with mixed feelings.

*Carassius auratus**	*Esox lucius†*
Carassius carassius	*Labeo rohita*
Catla catla	*Lates niloticus†*
Cichla ocellaris†	*Micropterus dolomieu†*
Cichlasoma managuense†	*Oreochromis mossambicus**
Cirrhina mrigala	*Oreochromis urolepsis**
Clarias gariepinus	*Pacifastacus leniusculus*
Coregonus peled	*Perca fluviatilis†*
Cyprinus carpio	*Procambarus clarkii*

*Species forming dense, stunted populations.
†Predatory species.

Table 15. Species generally viewed as beneficial where introduced.

Anguilla anguilla	*Mylopharyngodon piceus*
Anguilla japonica	*Oncorhynchus keta*
Aristichthys nobilis	*Oncorhynchus kisutch*
Astacus leptodactylus	*Oncorhynchus mykiss*
Astatoreochromis alluaudi	*Oncorhynchus tshawytscha*
Carpoides cyprinus	*Oreochromis aureus**
Cirrhina molitorella	*Oreochromis esculentus*
Clarias macrocephalus	*Oreochromis macrochir*
Colossoma macropomum	*Oreochromis niloticus**
Coregonus lavaretus	*Penaeus japonicus*
Ctenopharyngodon idella	*Penaeus merguiansis*
*Dorosoma petenense**	*Puntius gonionotus*
Gymnocorymbus ternetzi	*Rana catesbiana*
Heterotis niloticus	*Salmo salar*
Hypophthalmichthys molitrix	*Salmo trutta*
Ictalurus catus	*Salvelinus fontinalis*
Limnothrissa miodon	*Stizostedion lucioperca*
Macrobrachium nipponense	*Tilapia rendalli*
Macrobrachium rosenbergii	*Tilapia zillii**
Micropterus salmoides†	*Tinca tinca*
Misgurnus anguillicaudatus	*Trichogaster pectoralis*
Mylopharyngodon aetiops	

*Species forming dense, stunted populations.
†Predatory species.

(Table 15). In many of these cases the introduction has fulfilled the primary purpose for which it was introduced, while at the same time having little impact. On the whole, the groupings contain few predators and a small number of fish which stunt. In some cases, for example the trouts, notable impacts have been detected but the advantages of the introductions far outweigh the perceived disadvantages.

6. Measures to reduce risks of transfers

Despite the general neutral or beneficient results from introductions, there are sufficient cases where the new species has been harmful, or the co-introduction of a disease organism has spread into the native fish communities as to warrant actions to minimize the risks of future movements of species. Clearly, the prohibition of further introductions would be unrealistic and would hinder development and management of fisheries and aquaculture. Unfortunately, existing legislation to control the international transfer of species, and even intranational movement between hydrological basins, is haphazard, frequently non-existent and rarely adequate for the task at hand.

It is therefore important that a code of practice be internationally agreed upon, to serve as a basis for national legislation and to lay down the minimum requirements for reasonably risk-free introductions in the future. A code which sets out the requirements for study of candidate species and for quarantining of introduced material was developed first by the International Council for the Exploration of the Sea (ICES) and later adopted by the European Inland Fisheries Advisory Commission (EIFAC). The code, slightly modified to local needs, has been adopted by the Commission for the Inland Fisheries of Latin America (COPESCAL), and considered by the Committee for Inland Fisheries of Africa (CIFA) and the Indo-Pacific Fisheries Council (IPFC) as a basis for formulation of national legislation.

7. Conclusions

The large-scale movement of fish species from one country to another has increased steadily from the middle of the last century, and has accelerated dramatically since 1950. The apparent drop in the rate at which transfers have been made since 1985 may indicate a real trend or may arise from a lag in the reporting of the more recent introductions. Historically, most introductions of fish and other freshwater aquatic organisms appear to have been made haphazardly or in response to particular local needs which have not been related to a larger scale national plan. Most have proved trivial in that the species did not become established, failed to achieve the objectives for which they were introduced, and had little or no impact on the environment or the host community.

About an equal number of introductions have resulted in a net benefit to the importing country as have proved to have been pests. Species most generally considered as pests are those which form dense stunted populations with no commercial or ecological value. Introductions of large predatory species tend to have severe consequences for the host fish community and are often considered as ecologically unsound by conservationist interests. On the other hand, the same species tend to be viewed favourably by fisheries developers for the quality and value of their flesh. They therefore fall within the intermediate category, such as the recent controversy surrounding the introduction and spread of the Nile perch in Lake Victoria (East Africa) exemplifies (Reynolds and Greboval, 1988). Comparatively few species have been responsible for significant gains in their host country, but these are sufficient to demonstrate that the well-planned introduction of new species can form a valuable tool for the development of fisheries and aquaculture throughout the world.

The risks from unplanned and haphazard introductions are sufficiently great as to warrant special legislation and vigilance by state authorities. The large number of accidental introductions and the number of cases of diffusion of species along water courses demonstrate the difficulty of containing an introduced species once it enters the waters of a host country. The risks of spread of disease organisms is even more severe. International action to contain introductions is necessary, and proper agreements should be reached between states to reduce the risks of future introductions.

8. Acknowledgements

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9. References

FAO. 1989. Aquaculture production (1984–1987). FAO Fish. Circ., (815) Rev. 1: 130 pp.

Gerberich, J. B., and Laird, M. 1969. Bibliography of papers relating to the control of mosquitoes by the use of fish. An annotated bibliography for the years 1901–1966. FAO Fish. Tech. Pap., (75): 70 pp.

Reynolds, J. E., and Greboval, D. F. 1988. Socio-economic effects of the evolution of the Nile perch fisheries of Lake Victoria: a review. CIFA Tech. Pap., (17): 148 pp.

Shireman, J. V. 1984. Control of aquatic weeds with exotic fishes. *In* Distribution, biology and management of exotic fishes, pp. 302–312. Ed. by W. R. Courtenay and J. R. Stauffer. Johns Hopkins University Press, Baltimore.

Turner, G. C. 1988. Codes of practice of manual and procedures for consideration of introductions and transfers of marine and freshwater organisms. EIFAC/CECPI Occasional Paper 23, 44 pp.

Welcomme, R. L. 1988. International introductions of inland aquatic species. FAO Fish. Tech. Pap., (294): 318 pp.

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Environmental risk management of introduced aquatic organisms in aquaculture

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Conceptual models are provided that describe the elements associated with risks of introductions of aquatic organisms and how these elements are related. The models include: Index of Colonization, which is based on escape and acclimatization potentials of the non-indigenous species; Index of Impact, which is based on the vulnerability of the receiving system(s) and the threat potential of the non-indigenous species; and a combination of the two indices, the Index of Risk. The elements of each index are assigned relative numerical values ranging from 0.0 (least risk) to 1.0 (highest risk) based on the best available scientific information. It is the relative weighting of each element that is critical rather than absolute values. Overall index values will range from 0.0 to 1.0. By separating risk into its major components and assigning relative values to each it becomes possible to identify where management steps should be implemented. The object of risk management with respect to introduced species will be to take steps to reduce the Index of Risk to the lowest value that is economically feasible.

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Introduction

Environmental risks associated with introduced aquatic organisms can be classified into five broad categories: habitat alteration, trophic alteration, spatial alteration, gene pool deterioration, and introduction of diseases (Kohler and Courtenay, 1986). Courtenay and Robins (1989) reviewed several case studies of introduced aquatic organisms in which some or all of these risks manifested themselves resulting in severe environmental impacts. It is clear from these and other case studies (e.g. see Taylor *et al.*, 1984; Herbold and Moyle, 1986; Hughes, 1986; Moyle *et al.*, 1986) that actual impacts and the degree to which they are manifested are dependent upon not only the biology of the introduced species, but also the specific characteristics of the receiving system. Accordingly, an introduction made to one area might pose a greater or lesser risk than to another. Consequently, site-specific assessments of risk are necessary even in cases where a non-native species has previously been moved and its impact, if any, recorded. Historical accounts are important to discern the level of risk a given introduced organism poses, but their existence does not eliminate the need for further evaluation.

In the sections that follow, conceptual models are provided that describe the elements associated with risks of introductions and how they are related. These models can be used to determine which aspects of a proposed introduction pose the greatest risks to aquatic communities. Armed with this information, resource managers and aquaculturists can more effectively focus management actions to reduce the risks associated with specific introductions.

Colonization potential

The first step of risk management for cultured introduced aquatic organisms is to assess the potential that the species might escape and acclimate to the natural environment. Accordingly, colonization potential, the chance that a non-native organism will become biologically established, will be a function of the likelihood that the organism will escape to the wild and its potential once there to establish a self-sustaining population. This can be numerically assessed using the following Index of Colonization (C):

$$C = (E)\,(A)$$

where E is escape potential and A is acclimatization potential.

E will be a function of the culture system, the adjacency of the culture systems to natural waters, and the consignment form of the cultured product. The more secure the culture facility and the further it is away from natural waters the lower the risk will be for escape. Likewise, organisms that are shipped live to processors or for other purposes have an additional avenue for escape not available when on-site processing is done. These elements can be given relative numerical values ranging from 0.0 (least risk) to 1.0 (highest risk) as follows:

Escape (E)
function:

1. Culture systems (e_1)
   a. closed indoor research = 0.1
   b. closed indoor commercial = 0.5
   c. outdoor culture = 1.0
2. adjacency to natural waters (e_2)
   a. near = 1.0
   b. intermediate distance = 0.2–0.9
   c. distant = 0.1
3. consignment form (e_3)
   a. live = 1.0
   b. processed = 0.0.

In following,

$$E = \frac{(e_1 + e_2 + e_3)}{3}$$

which will range from 0.1 to 1.0. (Note: E can never be zero because, short of not making the introduction, the possibility of escape can never be fully eliminated.)

The values given to the sub-elements of E (as well as values for sub-elements of subsequent indices) are subjective. The specific values assigned need not be exactly as those shown here provided they are based on the perceived relative risk. Higher values should be used when doubt exists. Because the purpose of risk management is to reduce risks, it is crucial that values assigned to each element accurately represent their relative risk so that the most critical factors can be identified and, when possible, managed. This will become clearer to the reader after all of the factors of risk have been conceptualized.

The second aspect of colonization potential is acclimatization. Similar to E, acclimatization potential can be determined using a model, the Index of Acclimatization (A):

$$A = \frac{(a_1 + a_2 + a_3)}{3}$$

where, a_1 is the niche/habitat match, a_2 is reproductive potential, and a_3 is dispersal potential. These sub-elements all deal with the ecological relationships of the non-native organism to its environment. As was done with E, relative numerical values ranging from 0.0 to 1.0 are assigned to each element. In the case of A, however, each sub-element is assigned a value and then a mean is computed to arrive at a value for each element. This is shown as follows:

Acclimatization (A)
1. niche/habitat match (a_1)
   a. temperature
   b. salinity
   c. community structure
   d. spawning/nursery suitability
   e. etc.
2. reproductive potential (a_2)
   a. fecundity
   b. single versus multiple spawns
   c. parental care
3. dispersal potential (a_3)
   a. sedentary
   b. migratory
   c. pelagic early life stages.

Values should be assigned to each sub-element based on the best available scientific information. Once again, it is the relative weighting of each element (and sub-element) that is critical rather than absolute values. The value for A will range from 0.0 to 1.0.

Impact potential

The second stage of risk management is to assess the potential impact an introduced species might have should it escape to the wild. The potential for impact will be a function of the vulnerability of various aquatic systems that might be colonized and the actual threats to each system that the introduced species poses. This relationship is shown in model form as the Index of Impact (I):

$$I = (V)\,(T)$$

where V is the vulnerability of the receiving systems and T is the threat potential of the introduced species.

V will be a function of the biotic and abiotic structure of the receiving system. The key factor is to determine if the integrity of particular receiving systems is especially vulnerable to impact. Such attributes, among others, as low species diversity, presence of rare or endangered species, and previous anthropogenic disturbances might predispose a given system to be more vulnerable to impacts by a non-native species. V can be assigned a value from 0.0 to 1.0 in the same manner shown for E and A:

Vulnerability (V)
function:

1. biotic (v_1)
   a. species diversity
   b. predator/prey relationships
   c. endangered or rare species
   d. etc.
2. abiotic (v_2)
   a. fertility
   b. structural complexity
   c. anthropogenic disturbance
   d. etc.

In following,

$$V = \frac{(v_1 + v_2)}{2}.$$

As many sub-elements as can be determined to be critical should be included.

Threat Potential (T) is based on the five broad categories of risk that all introductions pose, i.e.

Threat Potential (T)
function:

1. habitat alteration (t_1)
2. trophic alteration (t_2)
3. spatial alteration (t_3)
4. gene pool deterioration (t_4)
5. disease introduction (t_5)

In following,

$$T = \frac{(t_1 + t_2 + t_3 + t_4 + t_5)}{5}$$

with each element being assigned a value ranging from 0.0 to 1.0, and in accordance with the formula, T will have the same range.

Risk potential

The environmental risk that a non-native species poses can be assessed by combining the Indices of Colonization and Impact into the Index of Risk (R):

$$R = \frac{[(E)\,(A)] + [(V)\,(T)]}{2}.$$

R will range from 0.0 to 1.0.

No specific value for R is proposed as representing a critical threshold. Rather, the object of risk management will be to take steps to reduce R to the lowest value that is economically feasible.

Risk management

Kohler and Stanley (1984a) presented a protocol concerning introduced aquatic organisms that requires (1) establishment of an evaluation board or committee, (2) promulgation of a formal proposal for each proposed introduction, (3) evaluation of the proposed introduction employing a Review and Decision Model (Fig. 1, Table 1), (4) standards for research facilities conducting preliminary studies, (5) necessary permits and disease-free certifications, and (6) written reports on outcomes of introductions submitted to the evaluation board and local natural resource agency(s). However, with the exception of requiring disease-free certifications, the protocol did not cover management of risks once a decision to proceed with an introduction had been made. Most aspects of risk management must be implemented prior to introduction. Only limited control measures are available once an introduction has been made.

Pre-introduction risk management

In order to reduce risk (R) it is necessary to reduce one or more of the elements of which it is comprised, namely escape potential (E), acclimatization potential (A), receiving system vulnerability (V), and threat potential (T). The vulnerability of public waters will rarely be manageable, so efforts need to be focused on reducing index values of E, A, and T. E is perhaps the simplest risk element to reduce. Fish could be reared in indoor closed systems at sites distant from natural waters and all fish could be processed at the culture site. However, such steps would rarely be economically feasible because not all aquatic species are amenable to intensive indoor culture, the systems themselves are not proven, and it would always be more economical for aquaculturists to raise non-native species in their existing facilities, most of which are in proximity to natural waters. However, some proposed introductions might be of such high risk that only by keeping E to the absolute minimum would the species be considered safe for commercial culture. On the other hand, E will not be as important a concern if the organism has little or no chance of acclimating to the environment. For example, the giant freshwater prawn, *Macrobrachium rosenbergii*, would have little chance of acclimating to natural waters in inland temperate regions because it could not overwinter (except in heated effluents) and early life stages would not survive due to their salinity requirements.

In cases where overwintering and successful reproduction is likely, it may be possible to reduce A through programs of controlled reproduction. Induced triploidy

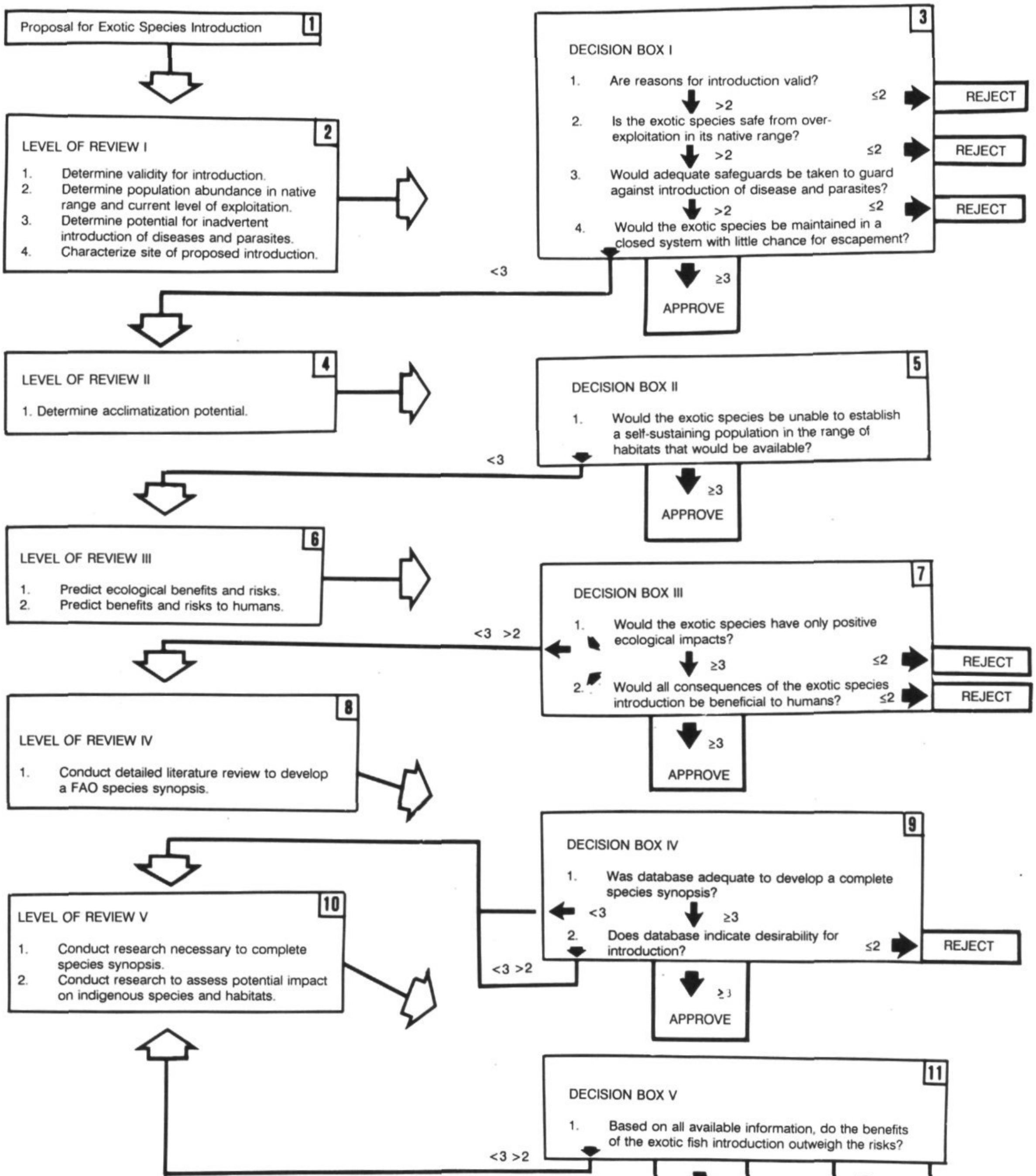

Figure 1. Review and decision model for evaluating proposed introductions of aquatic organisms. Mean opinionnaire values (see Table 1) are used at decision-making points (Kohler and Stanley, 1984a).

and chemical sterilization are already in common practice with several species (see Shelton, 1986). Accordingly, in certain cases it may be feasible to maintain breeding populations of a non-native species in secure facilities, thus reducing E, and only commercially culturing individuals incapable of successfully reproducing, thus reducing A. Such steps would also facilitate lowering T because it would allow for quarantine and therapeutic treatment of the original introduced stock, and widespread usage of only sterile offspring.

Table 1. Opinionnaire for appraisal of introductions of aquatic organisms. Each member of an evaluation board or panel of experts circles the number most nearly matching his/her opinion about the probability for the occurrence of the event. If information is unavailable or too uncertain: "don't know" is marked (Kohler and Stanley, 1984a).

Question	Response					
	No	Unlikely	Possibly	Probably	Yes	Don't know
1. Is the need valid and are no native species available that could serve the stated need?	1	2	3	4	5	X
2. Is the organism safe from over-exploitation in its native range?	1	2	3	4	5	X
3. Are safeguards adequate to guard against importation of disease/parasites?	1	2	3	4	5	X
4. Would the introduction be limited to closed system?	1	2	3	4	5	X
5. Would the organism be unable to establish a self-sustaining population in the range of habitats that would be available?	1	2	3	4	5	X
6. Would the organisms have mostly positive ecological impacts?	1	2	3	4	5	X
7. Would most consequences of the introduction be beneficial to humans?	1	2	3	4	5	X
8. Is data base adequate to develop a complete species synopsis?	1	2	3	4	5	X
9. Does data base indicate desirability for introduction?	1	2	3	4	5	X
10. Based on all available information, do the benefits of the exotic fish introduction outweigh the risks?	1	2	3	4	5	X

Post-introduction risk management

Irrespective of R, initial widespread introductions of a non-native species should be avoided. By phasing-in introductions it may be possible to circumvent unforeseen adverse impacts of an introduction through programs of eradication, selective toxicants, and possibly biological controls (see Kohler and Stanley, 1984b). Such measures are not always effective, however, particularly with those organisms that are prone to disperse and have high reproductive potential.

Conclusion

Recognizing risks before they are manifested as impacts is the most critical step in risk management. By separating risk into its major components and assigning relative values to each, it becomes possible to identify where management steps should be implemented. It is hoped that this approach will make a very complex subject easier to comprehend. No introduction can be effected without some element of risk, but the potential for adverse impact can be reduced if the risks are recognized and dealt with prior to introduction.

References

Courtenay, W. R., Jr., and Robins C. R. 1989. Fish introductions: good management, mismanagement, or no management? Crit. Rev. aquat. Sci., 1: 159–172.

Herbold, B., and Moyle, P. B. 1986. Introduced species and vacant niches. Am. Naturalist., 128: 751–760.

Hughes, N. F. 1986. Changes in the feeding biology of the Nile perch *Lates nilotica* (L.) (Pisces: Centropomidae) in Lake Victoria, East Africa since its introduction in 1960 and its impact on the native fish community of the Nyanza Gulf. J. Fish Biol., 29: 521–548.

Kohler, C. C., and Courtenay, W. R., Jr. 1986. American Fisheries Society position on introduction of aquatic species. Fisheries, 11(2): 39–42.

Kohler, C. C., and Stanley, J. G. 1984a. Implementation of a review and decision model for evaluating proposed exotic fish introductions in Europe and North America. Stock Enhancement in the Management of Freshwater Fisheries. European Inland Fish. Advisory Comm. Tech. Paper, 42(1): 541–549.

Kohler, C. C., and Stanley, J. G. 1984b. A suggested protocol for evaluating proposed exotic fish introductions in the United States. *In* Distribution, biology and management of exotic fishes, pp. 387–406. Ed. by W. R. Courtenay, Jr., and J. R. Stauffer, Jr. Johns Hopkins University Press, Baltimore. 430 pp.

Moyle, P. B., Li, H. W., and Barton, B. A. 1986. The Frankenstein effect: impact of introduced fishes on native fishes in North America. *In* Fish culture in fisheries management, pp. 415–426. Ed. by R. H. Stroud. American Fisheries Society, Bethesda. 620 pp.

Shelton, W. L. 1986. Reproductive control of exotic fishes – a primary requisite for utilization in management. *In* Role of fish culture in fisheries management, pp. 427–434. Ed. by R. Stroud. American Fisheries Society, Bethesda. 620 pp.

Taylor, J. N, Courtenay, W. R., Jr., and McCann, J. A. 1984. Known impacts of exotic fish introductions in the continental United States. *In* Distribution, biology, and management of exotic fishes, pp. 322–373. Ed. by W. R. Courtenay, Jr., and J. R. Stauffer, Jr. Johns Hopkins University Press, Baltimore. 430 pp.

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Regulating the introduction of freshwater fish: the United Kingdom, the European Community, and beyond

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This paper provides an outline of the legislation operative in the United Kingdom relating to fish introductions according to its concern with the pathological and ecological aspects of introductions. The main enactments considered are: The Diseases of Fish Acts 1937 and 1983, the Import of Live Fish Acts 1978 and 1980, the Endangered Species (Import and Export) Act 1976, the Salmon and Freshwater Fisheries Act 1975, the Salmon Act 1986, the Wildlife and Countryside Act 1981, and the Environmental Protection Act 1990. This is followed by a discussion of the difficulties surrounding the proposed European Community Directive on fish health COM. (89) 655, and the problem of securing ecological protection within the terms of the Directive. The paper concludes with some broader comparisons of legislation from other jurisdictions and an evaluation of the legislation discussed according to the requirements of Codes dealing with fish introductions.

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1. Introduction

This paper concerns the legal regulation of introductions of freshwater fish. "Introduction" is construed in a broad sense to include, first, the deliberate or accidental release, by human agency, of fish into an area of water where that species is already present (stocking), second, release where the species has been present but has ceased to be present in the waters concerned (reintroduction) and, third, the release of fish into waters where the species has not previously been present (introduction, strictly so-called) (Boitani (1976) and UK Committee for International Nature Conservation (1979) Appendix I). In ecological terms there may be profound differences between stocking, reintroduction, and introduction of fish into a water, but in law they are not clearly differentiated and broadly the same controls apply to each activity.

Within the legal jurisdictions which are to be considered in this paper, more significant functional distinctions are drawn between imports of fish into a national area and the movement of fish within a national area, since contrasting legislative provisions apply to these different kinds of translocation of fish. Of greater significance still is a distinction drawn between the different purposes underlying legislation restricting fish introductions. For example, within the law of the United Kingdom, there are two clear foci of attention: the pathology and the ecology of fish movements. Although there are some clear overlaps, the various enactments which seek to restrict fish movements tend to reflect one or the other of the distinct objectives of preventing fish disease or preventing damage to the aquatic environment including, most notably, the fish within it (Howarth, 1990a).

A general observation about the areas of law to be discussed is that they contain few absolute prohibitions. Introductions are sought for a variety of reasons, some of which are sound and justifiable, others less so, and others still where the consequences are difficult to determine in advance. This is reflected in the law, where in most instances introductions are made subject to some kind of licensing system or permission granted by an appropriate authority that is equipped to consider and deliberate upon the full implications of the proposal on the basis of the best available knowledge of the likely implications of the introduction. "Best available knowledge" is the most that can be achieved in this area, since many of the consequences of introductions are unknown and almost impossible to predict given the limited state of knowledge of certain areas relating to introductions. Nonetheless, the subjection of introductions to licensing procedures ensures that lack of knowledge can be translated into cautious decision-making on the part of the authorizing body.

Broadly, the plan of this paper is to review the state of legislation in England, Wales, and Scotland relating, first, to fish disease control and, second, to more broadly based ecological constraints upon fish movement. This is followed by an outline of imminent measures designed to secure fish health within the European Community consequent upon the removal of trade barriers between the Member States of the Community in 1992. Finally, some observations are made as to broader comparisons and objectives for legislation relating to introductions of freshwater fish.

2. Disease regulation

2.1. The Diseases of Fish Acts 1937 and 1983

The first provision concerning fish disease in Britain was the Diseases of Fish Act of 1937, which was originally passed with the object of controlling and, if possible, eradicating furunculosis in wild fisheries. Although the original objective proved to be overoptimistic, the general mechanism provided for under the Act was retained to regulate the introduction of fish disease and to minimize the spread of fish disease. Accordingly, the 1937 Act has been amended by a series of orders permitting control measures in relation to a number of other "prescribed" fish diseases. In addition, the 1937 Act has been supplemented by the Diseases of Fish Act 1983, which provides for registration of fish farms for disease prevention purposes. Hereafter "the Acts" refers to the combined effect of the Diseases of Fish Act 1937 and the Diseases of Fish Act 1983.

2.2. Restrictions upon import of live fish

A principal mechanism for control upon the spread of fish disease in Britain arises through restrictions upon the import of live fish. The Diseases of Fish Acts impose a general prohibition upon the import of live fish of the salmon family or freshwater fish, or the eggs of these fish. This allows for three kinds of restriction to operate: a prohibition upon imports of salmonids, a restriction upon the import of indigenous freshwater fish subject to import licensing and health certification, and a restriction upon the import of freshwater ornamental species subject to an import licence. Notably, the controls provided for under these Acts apply only to imports or movements of live fish, though separate legislation is capable of being employed to restrict movements of dead fish where these constitute a disease threat, and also to restrict the movement of contaminating matter present in water in which fish are transmitted (see, s. 10 (1) Animal Health Act 1981, and Salmon Viscera Order 1986, SI 1986 No. 2265).

The Acts prohibit the import into Britain of any live fish of the salmon family, unless authorized by an order of the appropriate fisheries Minister (ss. 1 (1) and (6) Diseases of Fish Acts). A Ministerial Order permitting import of salmon may specify fish by reference to the particular species concerned, the place of origin, or any other factor (s. 1 (7)). Where an order is made, the fish concerned are to be treated as if they were a freshwater species for import control purposes (s. 1 (8)). Likewise, a Ministerial Order may permit the general import of salmon of a particular specification, in which case the fish concerned are treated as if they were freshwater fish (ss. 1 (7) and (8)). The only example of an order of this kind is the Importation of Live Fish of the Salmon Family Order 1986 (SI 1986 No. 283), which applies to live fish of the salmon family which have been brought from Northern Ireland and have not been in any other country. The Acts also prohibit the import of any live freshwater fish and of live eggs of fish of the salmon family, or freshwater fish. Import of these fish is an offence unless they are consigned to a person who is licensed to receive them and who produces a licence at the time of delivery of the consignment (s. 1 (2) Diseases of Fish Act).

The overall strategy provided for under the Acts is to prohibit imports subject to a licensing scheme administered by the appropriate Minister. The import of live fish or eggs without a licence, or in contravention of any condition of a licence, is an offence. The offence is punishable to the same extent as all offences arising under the Acts: a person found guilty will, on summary conviction be liable to a fine not exceeding £1,000. In addition, the fish or eggs concerned may be seized if there is reason to believe that an offence has been committed. Seizure allows the fish or eggs to be detained by the official pending the legal proceedings or until the Minister is satisfied that no proceedings are likely to be instituted (s. 1 (4)).

2.3. Designation of waters

The Diseases of Fish Acts seek to prevent the spread of diseases through the isolation of fish and disease carrying materials connected with waters where an outbreak of disease has been identified. This facility involves the use of "standstill notices" preventing fish movements of a kind which might allow the spread of disease into otherwise uninfected areas. Isolation is provided for through the power of the Minister to designate infected waters, and land and buildings adjacent to them, for the purpose of taking a range of measures to prevent the spread of disease (s. 2 (1)). Specifically, a Ministerial Order may prohibit or regulate the taking into or out of the designated area any specified live fish, or eggs of fish and foodstuff of fish and regulate the movement within the area of any specified things (s. 2 (2)).

The Ministerial powers relating to the designation of waters apply only to those waters which in the terminology of the Acts are classified as "infected". This phrase encompasses waters in which any of a range of prescribed diseases exist among fish, or in which the causative organisms of any of those diseases are present (s. 10 (1), as amended by the Diseases of Fish Order 1973, SI 1973 No. 2093). Over the years, the definition of "infected" has been amended so that a number of damaging fish diseases have been brought within the definition. Taking the amending orders into account, the present definition of "infected" means infected with any of the diseases respectively known as bacterial kidney disease (BKD), furunculosis of salmon, gyrodactyliasis caused by *Gyrodactylus salaris*, infectious haematopoietic necrosis (IHN), infectious pancreatic necrosis (IPN), infectious salmon anaemia (ISA), spring viraemia of carp (SVC), viral haemorrhagic septicaemia (VHS), and whirling disease (*Myxosoma cerebralis*) (s. 10 (1) Diseases of Fish Act 1937, as amended by the Diseases of Fish Orders SI 1966 No. 944, SI 1973 No. 2093, SI 1978 No. 1022, SI 1984 No. 301, SI 1988 No. 195 and SI 1990 No. 616. In Scotland, only enteric redmouth disease (ERM) is also included, see SI 1986 No. 213).

2.4. Directions and authorizations for the removal of fish

After a Ministerial Order has been made for the designation of an area under the Acts, a series of additional powers arise in relation to the removal of fish from the area to prevent further spread of the disease. Accordingly, the Minister may serve a notice in writing on any occupier on inland waters situated in the designated area (s. 2A (1) Diseases of Fish Acts). A notice of this kind may direct the occupier of the waters to take practicable steps to secure the removal of dead or dying fish and regulate the manner in which fish are disposed of (s. 2A (2)). Notably, however, the Ministerial power is limited to "dead and dying fish" and falls short of a power to order the slaughter of infected fish in a fish farm; correspondingly, there is no provision for compensation to be awarded to fish farmers against whom a notice is served.

The back-up power behind a Ministerial designation order is that, in the event of non-compliance with a notice requiring the removal of dead or dying fish, the Minister may authorize an inspector to take measures to ensure that the order is complied with. In that event the expenses reasonably incurred by the inspector in carrying out the direction are recoverable from the person against whom the notice was originally served (s. 2A (5)).

2.5. Preliminary precautions

An inspector appointed by the Minister is empowered to serve a notice upon the occupiers of waters if he has reasonable grounds for suspecting they are infected (s. 4 (1), and see Reg. 4 and Sch. 2 Disease of Fish Order 1984, SI 1984 No. 455). In relation to fish farms, the effect of a notice of this kind is that no live fish, or live eggs of fish, may be taken into or out of the fish farm, and no foodstuff of fish may be taken out of the farm, without the permission of the Minister. This prohibition applies initially for a 30 day period, but the period may be extended to 60 days (ss. 4 (2) and (3) Diseases of Fish Acts). Any person who intentionally takes any fish, eggs, or foodstuff into or out of a fish farm while the taking is prohibited is guilty of an offence unless it is shown that he did not know that the taking was prohibited (s. 4 (4)).

In respect of England and Wales, if any person who is entitled to take fish from any inland waters, or employed for the purpose of having the care of any inland waters, has reasonable grounds for suspecting that the waters of a fish farm are infected, it is his duty to report the facts to the Minister. In respect of waters which are not a fish farm, the report is to be to the National Rivers Authority. Moreover, it is an offence to fail to report suspicion of this kind without reasonable excuse (s. 4 (5)). In Scotland, the same duty to report suspicion of disease applies in relation to the Secretary of State, or if the waters are situated in the area of a district board (see ss. 1, 14 and 40 Salmon Act 1986), and are not a fish farm, to the district board (s. 4 (6) Diseases of Fish Act 1937). Clearly, this places an important duty upon fish farmers and their employees, water keepers and anglers to take an active role in the reporting of fish disease since the mere omission to act in reporting suspicions, without reasonable excuse, will constitute a crime under this provision.

The offences under the Diseases of Fish Acts are supported by a collection of ancillary powers permitting inspection of waters and entry upon land for the purpose of investigation (s. 6 (1)). Inspectors authorized by the Minister are empowered to enter upon any land and inspect any inland waters in which fish or the eggs of fish or foodstuffs for fish are likely to be found, and to take samples of any fish, eggs or foodstuff, or of water, mud, vegetation, or other matter. Any person who refuses to admit or intentionally obstructs an inspector in the exercise or performance of any of these powers and duties is guilty of an offence (s. 6 (2)). Some safeguard is provided to the fish farmer against the excessive use of inspectors' powers to take samples of fish by the imposition of a duty to compensate the farmer for losses sustained in this way. Hence the Minister is bound to pay the occupier of the water an equitable sum equal to the market value of the fish taken in the sample (s. 6 (3)).

3. Ecological constraints

3.1. The Import of Live Fish Acts 1978 and 1980

The limitations of the Diseases of Fish Acts 1937 and 1983 were made apparent by an incident in 1976 when a consignment of Pacific coho salmon (*Oncorynchus* *kisutch*) was imported into Scotland (Solomon, 1979). The import of eggs of the coho salmon was permitted under a conditional licence issued by the Secretary of State for Scotland under the Diseases of Fish Act 1937 (s. 1 (3) Diseases of Fish Act 1937). Although the fish were kept in quarantine, with regular monitoring under the supervision of the Department of Agriculture and Fisheries for Scotland, it was recognized that if they matured to broodstock and spawned, without disease being identified, there were no clear powers in the existing legislation on disease control to restrict movement of the progeny of the imported fish eggs (now see s. 24 Salmon Act 1986 and s. 14 Wildlife and Countryside Act 1981). There was a clear possibility of damage to native stocks through competition, or genetic integration, and yet the law contained no clear provision to prevent the introduction of the new species (Vol. 389 House of Lords Debates (1978) Co. 1547). Primarily as a consequence of the situation resulting from the coho import, the law of Scotland was changed by the enactment of the Import of Live Fish (Scotland) Act 1978. Soon afterwards the law of England and Wales was also revised by the enactment of the Import of Live Fish (England and Wales) Act 1980.

The 1978 and 1980 Acts permit the appropriate Minister to forbid, either absolutely or except under a licence, the import into, or the keeping, or the release in any part of Great Britain of live fish or the live eggs of fish, of certain species of fish (s. 1 (1) of both Acts, definitions provided under s. 1 (6) 1978 Act and s. 4 1980 Act). The concern underlying these enactments is not merely the spread of infectious disease between fish but rather the damage to native species which may be brought about by the introduction of non-native competitors.

However, after consultation the Minister may grant a licence to any person to import, keep or release, live fish, or the live eggs of fish of a species specified in an order. Having granted a licence of this kind the Minister retains the power to revoke or vary the licence (s. 1 (5) (b) 1978 Act and s. 1 (3) 1980 Act). In the event of the Minister exercising his power either to forbid or to grant a licence for the import, keeping or release of non-native species of fish, certain powers of entry and inspection are given to persons authorized by the Minister (s. 2 (1) of both Acts). A power of seizure also arises in the event of an officer commissioned by the Commissioners of Customs and Excise, or a person authorized by the Minister, having reason to believe that an offence under the Acts has been committed in relation to any fish or eggs of fish (s. 3 (4)).

It is an offence to import, or attempt to import, keep or release any live fish of a species specified in a Ministerial Order where the order forbids absolutely the import, keeping, or release of such species. Where a Ministerial Order allows the import, keeping, or release of live fish under licence, it is an offence to do so without having a valid licence. It is an offence for the holder of a licence to contravene, or to fail to comply with, any term of the licence. It is also an offence to obstruct any person from entering or inspecting any land in pursuance of his powers of inspection. In addition to the imposition of a fine, which on summary conviction may not exceed £1,000 (s. 3 (1)), the court by whom a person is convicted may order any fish or eggs involved to be forfeited and destroyed (s. 3 (4)).

Notably the Import of Live Fish Acts 1978 and 1980 enable the appropriate Minister to introduce particular orders prohibiting the import, keeping, or release of specified species of fish. The Ministers are not placed under any obligation to make orders of this kind, and without an order in existence no legal prohibitions or criminal offences arise. This is essentially the position in England and Wales, because no orders have been introduced under the 1980 Act. In Scotland, only one order has been introduced, the Import of Live Fish (Coho Salmon) (Prohibition) (Scotland) Order 1980, SI 1980 No. 376. The reason why the powers arising under the 1978 and 1980 Acts have remained largely unused, apart from the 1980 Order, is that they have become redundant due to the creation of an overlapping provision in the offence of introducing new species of fish into the wild arising under the Wildlife and Countryside Act 1981 (s. 14 (1) Wildlife and Countryside Act 1981, discussed below).

3.2. The import and export of endangered species

Another legal mechanism regulating the import and export of fish for quite different reasons arises through the operation of the Endangered Species (Import and Export) Act 1976. This enactment gives effect to the Convention on International Trade in Endangered Species of Wild Fauna and Flora, referred to as CITES, which was signed in Washington in 1973 and came into force in the United Kingdom in 1976 (Cmnd. 5459). The basis of these measures is the recognition that international cooperation is also essential for the protection of certain threatened species.

Although CITES has been ratified by the United Kingdom, and is given effect in the UK by the 1976 Act, the European Council has also made a Regulation on the implementation of the Convention in order to ensure uniformity in the application of the Convention throughout the European Community (European Council Regulation No. 3626/82, as amended). Although both the 1976 Act and the Community Regulation serve to give effect to CITES in the United Kingdom, in some respects the Act is stricter than the Regulation in the controls which it imposes upon the international trade in endangered species.

The most significant feature of the 1976 Act is the prohibition of import or export of any live or dead animal listed under Schedule 1 to the Act to or from the United Kingdom except under licence (ss. 1 (1) and (2) Endangered Species (Import and Export) Act 1976). Notably, a range of uncommon species of fish is specifically included in Schedule 1 to the Act. The Secretary of State is to submit any application for a licence of this kind to whichever of the scientific authorities he considers is best able to advise him whether a licence should be issued before he issues or declines to issue the licence (s. 1 (3)).

In addition to the basic prohibition upon import or export of animals under the 1976 Act a number of additional prohibitions apply in relation to the sale and movement of endangered animals unless authorized by a licence issued by the Secretary of State (s. 4 (1B)). It is an offence to sell, offer or expose for sale, have in possession for sale, or transport for the purposes of sale, or display to the public any animal which has been unlawfully imported under the Act (s. 4 (1)). Also it is an offence to sell, offer or expose for sale, or have in possession for sale or transport for the purpose of sale any live or dead animal listed in Schedule 4 to the Act unless it has been imported before the passing of the Wildlife and Countryside Act 1981 (s. 4 (1A), as amended).

Separate provision arises under the Act for the Secretary of State, after consultation with the appropriate scientific authority (s. 7 (1)), to impose restrictions on the movement of live animals falling under Schedule 1 after import. Hence, when a licence has been issued or applied for, the Secretary of State may give a direction as to restrictions upon movement of the animal after import (s. 6 (1)). Where a direction of this kind has been given, the animal concerned is to be kept at the premises specified under the direction (s. 6 (2)). In such circumstances it is an offence for anyone who knows, or ought to know, that a direction has been given, knowingly to take the animal, or permit it to be taken, to premises other than those specified in the direction (s. 6 (3)).

3.3. Introduction of fish into waters in England and Wales

Section 30 of the Salmon and Freshwater Fisheries Act 1975 makes it unlawful to introduce any fish or spawn of fish into an inland water, or for a person to possess any spawn of fish with the intention of introducing it, unless he first obtains the written consent of the National Rivers Authority (Sch. 4 para. 1 (2) Salmon and Freshwater Fisheries Act 1975). The maximum penalty for the offence is a fine of £1,000. In practical terms this is a particularly important offence for fish farmers supplying coarse or game fish for restocking to keep in mind, since the restocking of a water without National Rivers Authority permission will be an offence which will be committed by the person who introduces the fish into the water.

3.4. Introduction of fish into fish farms in England and Wales

Some relaxation of the offence of introducing fish into inland waters was brought about under the Salmon Act 1986, so that the offence is not committed in relation to those fish farms which either do not discharge into another inland water, or do so by means of a specially constructed or adapted conduit (s. 34 Salmon Act 1986). Although authorization from the National Rivers Authority is no longer needed for the introduction of fish into fish farms in England and Wales, information about fish movements is required to be supplied to the Ministry of Agriculture, Fisheries, and Food under the fish farm registration scheme (s. 7 (1) Diseases of Fish Act 1983, and Registration of Fish Farming Businesses Order 1985, SI 1985 No. 1391). The National Rivers Authority have access to information about fish movements into fish farms where this is needed for disease control purposes (s. 9 (1) (d) Diseases of Fish Act 1937 and s. 38 Salmon Act 1986, as amended by s. 141 and Sch. 17 para. 3 Water Act 1989).

3.5. Introduction of salmon into waters in Scotland

A narrower counterpart to the above legislation has recently been provided for in relation to Scotland under the Salmon Act 1986. Section 24 of the Act states that a person who intentionally introduces any salmon or salmon eggs into inland waters in a salmon fishery district for which there is a salmon fishery board is guilty of an offence, for which the maximum penalty is a fine of £100. The basic prohibition upon introduction of salmon or salmon eggs is, however, made the subject of two exceptions. First, no offence is committed if the person concerned has the previous written consent of the district salmon fishery board for the salmon fishery district in which the waters are situated. Second, the offence is not committed where the waters constitute or are included in a fish farm within the meaning of the Diseases of Fish Act 1937. So far as salmon are concerned, therefore, the position in Scotland is analogous to that in England and Wales, with the fishery authority having a regulatory power to prevent the introduction of salmon where they consider such introduction undesirable.

3.6. Introduction of new species: the Wildlife and Countryside Act 1981

Section 14 of the Wildlife and Countryside Act 1981 provides that a person will be guilty of an offence if he releases, or allows to escape into the wild, any animal which is either of a kind which is not ordinarily resident in and is not a regular visitor to Great Britain in a wild state or is included in Part I of Schedule 9 to the Act (s. 14 (1) Wildlife and Countryside Act 1981). Likewise, an attempt to commit this offence, or the possession of anything capable of being used in committing the offence, is punishable to the same extent as the main offence (s. 17). In addition to a fine, which is not to exceed £2,000 on summary conviction (s. 21 (4)), the offence is accompanied by various powers of forfeiture which may be exercised by a court convicting a person of the offence. Specifically, a convicting court is bound to order the forfeiture of the animal in respect of which the offence was committed, and may also order the forfeiture of any vehicle, or boat, used to commit the offence, and any animal of the same kind found in the possession of the convicted person (s. 25 (5)).

Beyond the introduction of new species, however, there are a number of non-native species which, to some degree, have become established in Great Britain, and the release of such species is made an offence through the listing of these species in Part I of Schedule 9 to the Act. The Schedule includes the following species of fish which are already established in the wild: the large-mouthed Black Bass (*Micropterus salmonides*), the Rock Bass (*Ambloplites rupestris*), the Pumpkinseed, otherwise known as Sun-fish or Pond-perch (*Lepomis gibbosus*), the Wels, otherwise known as European catfish (*Silurus glanis*), and the Zander (*Stizostedion lucioperca*). This list may, however, be subject to variation from time to time in that the Secretary of State may add the name of any animal to, or remove it from, the Schedule (s. 22 (5)).

The offence of introducing new and "scheduled" species of fish into the wild is subject to two explicit defences. The first defence is that the provision creating the offence of releasing new species is stated not to apply to anything done under, and in accordance with, a licence granted by the Secretary of State (ss. 16 (4) and (9)). In this respect the Minister has been advised by the Nature Conservancy Council that any species that has not bred successfully in the wild should nonetheless be subject to the prohibition. Accordingly, the introduction to waters outside fish farms of species such as the Rainbow Trout (*Oncorhynchus mykiss*) is, in principle, required to be licensed but the potential difficulty constituted by the widespread introduction of these species has been avoided by the Minister making them subject to a general licence authorizing their introduction for the purposes of the 1981 Act (Newbold *et al.* 1986).

The second defence is that the accused took all reasonable steps and exercised all due diligence to avoid committing the offence (s. 14 (3) Wildlife and Countryside Act 1981). Where, however, this defence involves an allegation that the offence was due to the act or default of another person, the person charged will not be entitled to rely on the defence unless prior notice of the intention to raise this defence is given identifying or assisting in the identification of the other person concerned (s. 14 (4)).

Enforcement powers under the Act allow a person authorized by the appropriate Secretary of State to enter any land other than a dwelling for the purpose of ascertaining whether the offence of introducing new species is being, or has been, committed (s. 14 (5)). Anyone who intentionally obstructs a person acting in the exercise of this power of entry upon land is guilty of an offence (s. 14 (6)).

Despite the apparent breadth of the offence of introducing new species under s. 14 of the 1981 Act, two key difficulties surround its operation. First, it is to be noted that the offence is formulated in terms of the introduction of fish of a "kind" that are not ordinarily resident, and the listed species in the Schedule. The word "kind" is somewhat ambiguous in this context in that it could mean "species", or alternatively a particular part of a species distinguished by genetic characteristics. Although the position is somewhat unclear, the marginal note to the section indicates that it is "species" that are intended to be the measure of whether fish are of the same "kind" or not, and it follows that matters such as genetic difference between the introduced fish and the existing stock of that species are not relevant. If this interpretation is correct, then the offence would not be committed in a situation where fish of a native species are introduced even though such fish are of a significantly different genetic composition from the existing population of that species in a water. It may be a shortcoming that the provision is concerned only with the species and not with the potentially undesirable genetic character of the fish concerned. Alternatively, it could be maintained that if "species" had been intended, that word should have been used in the section rather than "kind" and, therefore, it was envisaged that genetic differences would be taken into account. The difficulty with this argument lies in the question of what constitutes a distinct genetic "kind" since, in the final analysis, it may be shown that all creatures are genetically unique.

A second difficulty inherent in the prohibition upon introduction of new species lies in the formulation of the offence as that of allowing the "release" of fish into the "wild". The meaning of this expression again presents a serious difficulty of interpretation. For example, it might be argued that the release of fish into an enclosed pond is not a release into the "wild" because of the element of containment. Similarly, the point at which "release" into the wild takes place is not without difficulty.

3.7. Release of genetically modified organisms: Part IV of the Environmental Protection Act 1990

Another problem of fish introduction which looms for the future arises from the scientific advances which have been made in recent years in the development of genetically modified organisms, and specifically the environmental harm which is capable of being caused by the release into the environment of new organisms. Aquaculture may provide a clear commercial motive for the production of genetically modified species of farmed fish, in order to increase productivity through the introduction of genetic material which enhances growth, increases hardiness and resistance to ordinary causes of mortality in farmed fish. However, well-founded anxieties exist about the potential consequences of the release or escape of genetically modified fish into the environment and the effects of transmission of new genetic material into the wild through replication or interbreeding of the introduced species. Both the advantages of genetic engineering and the general environmental concerns to which they give rise have been the subject of extensive discussion in the United Kingdom (Royal Commission on Environmental Pollution, 1989).

Legal responses to the problem of controlling the release of genetically modified organisms can be found both at European Community level and within the laws of the Member States of the Community. European Council Directive 90/220/EEC (O.J. L117, 8 May 1990, p. 15), on the deliberate release into the environment of genetically modified organisms, requires that genetically modified organisms released in the course of research and development must be pre-notified to the competent authority in each Member State, together with information specified in the Directive and a risk evaluation statement in relation to human health and the environment. The authority is then under an obligation to check the notification, carry out its own evaluation and any necessary tests, and record its decision in writing. Release of a genetically modified organism may not take place without the authority's written consent. These requirements must, as a matter of Community Law, be implemented in the national legislation of the Member States by 23 October 1991.

At a national level, within the United Kingdom the problem of controlling the release of genetically modified organisms has received the recent attention of Parliament by the enactment of Part VI of the Environmental Protection Act 1990. This Act governs genetically modified organisms of all living things, other than human beings, and necessarily therefore encompasses genetically modified fish. The general scheme of Part VI of the 1990 Act is to impose a general prohibition on importation, acquisition, release and marketing of genetically modified organisms without carrying out a risk assessment of possible damage to the environment and notifying the Secretary of State of the intention to carry out the activity (s. 108). A duty of care relating to the risk of environmental damage is placed upon persons, importing, acquiring, keeping, or proposing to release genetically modified organisms (s. 109). In specified cases, the importation, acquisition, keeping, release, or marketing of genetically modified organisms is prohibited, except in pursuance of a consent granted by the Secretary of State and in accordance with any limitations and conditions to which the consent is subject (s. 111). The substantive obligations are backed up by powers to provide for the appointment of inspectors with various powers of entry and inspection and to deal with imminent dangers (ss. 114 to 117), and various criminal offences arise in relation to the contravention of requirements (s. 118). The new provisions were planned to come into effect in October 1991 in order to ensure compliance with the obligations arising from the Community Directive by the deadline for implementation of the Directive within Member States. Hopefully, they will provide an adequate legal mechanism to prevent environmental damage being caused by the introduction of genetically modified fish, but it is apparent that this is an area in which strict precautionary measures are required.

4. Fish health and movement in the European Community

The completion of the internal European Community market by 1992 necessitates the harmonization of national trading regulations of Member States and the removal of technical barriers to trade in all kinds of goods including live animals, and specifically fish (Howarth, 1990b). The model for Community legislation in this area, provided for under the general strategy for animal health in the Community, is to maximize the permissibility of free movement of animals within the Community within the constraint of preventing the spread of serious animal diseases (8062/88 European Council Regulation concerning veterinary checks in intra-Community trade with a view to the completion of the internal market). Accordingly, Community Directives exist to prevent the spread of swine fever (85/320 to 322/EEC) and to harmonize the control measures which must be taken in relation to foot and mouth disease (85/511/EEC) and enzootic bovine leucosis (EBL) in cattle (88/406/EEC, amending Directive 64/432/EEC).

Generally, however, the policy which is evolving is to allow freedom of movement of animals for trading purposes, subject to harmonized procedures for veterinary inspection of animals at the point of dispatch (COM (88) 383 final and 8062/88). Clearly, this strategy, leading up to the removal of frontier veterinary barriers to animal trade within the Community, rests upon increased confidence that stringent and uniform health checks will be conducted upon animals at the point of dispatch. As a matter of practice this point has not yet been reached and full implementation of the Community animal health strategy is some way off, even for traditional farm livestock. In relation to live fish movements within the Community the difficulties in implementing the strategy are considerably more formidable.

Nonetheless, in accordance with the general animal health strategy, a proposed Regulation to secure standardization of the law of the Community with regard to the health conditions governing intra-Community movement of live fish is presently under discussion by the European Commission (COM (89) 655 on fish health, see also COM (89) 648 on shellfish hygiene and COM (89) 645 on fish hygiene, and Edwards (1989)). Although the details of the Regulation are not yet finalized the indications are that it is intended eventually to replace or over-ride all national provisions relating to fish disease in Member States of the Community, including the United Kingdom. Clearly, the measure will be of fundamental importance and requires the closest scrutiny from the point of view of both effective prevention of fish disease in the Community and because of the wider ecological considerations in allowing freedom of fish movements within the Community.

In relation to fish movements, however, it is apparent that the implementation of the general strategy for animal movements must take account of the presence of different contagious fish diseases in various parts of the Community. Hence, the overall objective of free movement of live fish within the Community must be modified to prevent the spread of disease by restricting the movement of fish from an area where a disease is present into an area in which it is absent.

The general mechanism for preventing the spread of fish disease, alongside the removal of trade barriers, envisages the zoning of the Community according to fish disease status. This is to be accomplished by a prohibition upon fish movements from an area of lower disease status to an area of higher status. Broadly, the framework for fish disease zoning involves the classification of diseases under three headings. First, there are infections or contagious exotic diseases of a kind not presently occurring in the Community, in relation to which Member States will be required to take immediate eradication measures in the event of an outbreak. Second, there are infectious or contagious diseases present in some parts of the Community, and having a major economic impact, in relation to which fish movements will only be permitted into areas of equivalent or lower disease status. Third, there are infectious or contagious diseases with a lesser economic impact, in relation to which a certain amount of discretion is permitted to the governments of Member States to operate disease controls at an individual fish farm level by allowing movements only between approved farms within the Community (Edwards, 1989).

In relation to imports of fish into the European Community from non-Member States, the details of the Community strategy have still to be finalized, but the indications are that imported fish will have to have come from approved sources and will have to meet standards which are at least as stringent as those applicable to movements within the Community. Regulation of Community imports will be made subject to requirements of veterinary inspection and health certification at designated points of entry into the Community before being allowed into free circulation or being placed under a customs procedure. Alternatively, importation into the Community will be prohibited if fish are found to have come from a country from which import is prohibited, or are suspected of being infected or contaminated with an infectious or contagious disease, or certification or other conditions are not complied with. Detailed provisions for these, and other matters arising under the Regulation, are to be supplied by a Community Standing Veterinary Committee.

The eventual Community Regulation which gives effect to the proposals for fish health and movements will be directly applicable in the United Kingdom, and is clearly intended as a comprehensive measure governing the movement of fishery products into and within the Community. Moreover, in the event of inconsistency, the Regulation will take precedence over current provisions operative in the United Kingdom and contained in the Diseases of Fish Acts, and other legislation previously discussed. It is vital, therefore, that the Community strategy for fish movements is accompanied by stringent operational controls to ensure that, amongst other matters, the basis upon which veterinary certification is provided at the point of dispatch of a consignment of fish is conducted in a uniformly rigorous manner throughout the Community. In addition, mechanisms will need to be devised whereby standardization of transportation procedures, water changes, and disinfection measures are achieved throughout the Community.

Beyond the operational considerations involved in securing fish health in the Community, attention will need to be given to the relationship between the proposed Community Regulation and wider ecological issues involved in relaxing constraints upon the introduction of live fish into waters (Howarth 1989). By tending to assimilate movements of fish to movements of livestock and other trading commodities the proposed Regulation appears not to address the wider ecological issues of allowing introductions. Clearly, the capacity of fish to pass from the farmed to the un-farmed aquatic environment distinguishes them from the other creatures subject to the Community's animal health strategy. For this reason it would be a dramatically retrograde step if the Regulation were to circumvent present ecological controls upon introductions. A matter which is not altogether clear in relation to the implementation of the Regulation within the Member States is the extent to which European Community Law allows derogation from the general duty to secure freedom of trade in order to safeguard the environment (Howarth, 1989, pp. 42–50). It is hoped that some legal mechanism can be found to implement the Regulation without relaxation of ecological controls.

5. Beyond

Moving on from the law of the United Kingdom and the European Community, some comparisons may be made with measures found in other jurisdictions and some evaluation provided alongside the various reports and recommendations issued by organizations concerned with introductions of freshwater fish.

The extensive comparative survey of aquaculture legislation conducted by Van Houtte *et al.* (1989) noted the widespread use of licensing powers in developing countries whereby the competent Minister is empowered to make regulations to prevent fish disease or to control fish disease through rules concerning fish import and export (ibid., pp. 72–73). More explicit examples of preventive or remedial measures in relation to fish disease are to be found in the legislation of Canada, New Zealand, and Norway. These include the vesting of a requirement to take preventive measures in the occupier of waters in the event of suspicion of fish disease; provisions allowing for different treatment and destructive actions depending on the kind of disease concerned; vaccination of freshwater fish with an approved vaccine; destruction of brood stock where genetic defects develop; sterilization of animal feeding material; and the issue of certificates indicating the presence of any harmful or harmless disease at the moment of import. Most of these provisions have been seen to have counterparts in the British legislation.

In relation to fish movements, Van Houtte's *et al.* (1989) study indicated that legislation is to be found in most countries, but varies depending upon whether controls are applied to animal health in general or to aquaculture in particular. Accordingly, Malaysia, Zambia, and the Philippines prohibit import of non-indigenous species of fish without a written permit from the competent authority and permits may incorporate conditions to avoid the spread of disease and to control the release into the environment of non-indigenous species. By contrast, more specific provisions relating to aquaculture are to be found in Venezuela, Panama, Mexico, Colombia, Spain, Canada, and France. Typically, these require application for a permit to identify the name of the species concerned; the purpose of the import; the places of origin and destination; and the provision of a sanitary certification from the export country (Van Houtte *et al.*, 1989, pp. 76–77). Although the diversity of legal provision made by different jurisdictions in relation to the movement and introduction of freshwater fish makes direct comparisons exceptionally difficult, the general impression is that the provisions to be found in Britain are as comprehensive as provisions to be found elsewhere.

The comparisons between different national legislation may not always be conclusive as an evaluation of legislation on fish transfer and introduction. Comparisons need also be made with various considered statements of principle as to the measures which are necessary to prevent the spread of disease and undesirable introductions. These appear in a number of reports of organizations that have directed attention to these issues. Notably, they have been addressed by the International Council for the Exploration of the Sea in its Code of Practice to Reduce the Risks of Adverse Effects Arising from Introduction of Non-indigenous Marine Species (revised in the 1984 ICES Co-Operative Research Report No. 130 (1984)), and the European Inland Fisheries Advisory Commission's Working Party on Introductions' Code of Practice (Annex E, Report of Fourteenth Session FAO Fisheries Report No. 364 (1987)). Both Codes stipulated that regulatory agencies of all member countries should be encouraged to use the strongest possible measures to prevent unauthorized or unapproved introductions. These Codes were conceded to need more specific instructions on their implementation and the formulation of protocols relating to procedures within countries to handle requests for introductions or transfers. These matters were addressed in the ICES and EIFAC Cooperative Research Report, Codes of Practice and Manual of Proceedings for Consideration of Introductions and Transfers of Marine and Freshwater Organisms (Co-Operative Research Report No. 159, ed. Turner (1988)). This reaffirmed that any country dealing with or contemplating introductions or transfers of aquatic organisms between countries or within national boundaries should have or should enact legislation for regulating such activity.

The need for legislation on fish introductions as advocated by the Codes is indisputable. The precise legal form of the necessary controls is not always self-evident. While some reservations have been expressed about detailed features of the British law, and outstanding difficulties noted surrounding the harmonization of provisions within the European Community, it is suggested that the general legal strategy which has been adopted is sound and comprehensive.

References

Boitani, L. 1976. Proceedings of the seminar–reintroductions, techniques and ethics. Italian National Appeal of the World Wildlife Fund.

Edwards, B. 1989. Beyond 1992: controls in the EC without internal trade barriers. A paper delivered at the Institute of Fisheries Management Workshop on the Dangers Associated with the Importation of Ornamental Fish, University of Reading, 13th April 1989.

Howarth, W. 1989. The Single Market: the case of fish disease. A paper delivered at the W. G. Hart Legal Workshop on the Single European Market and the Development of European Law, Institute of Advanced Legal Studies, London, 4th July 1989.

Howarth, W. 1990a. The law of aquaculture. Blackwell, London.

Howarth, W. 1990b. The Single European Market and the problem of fish movements. 15 European Law Review, 1: 34–50.
Newbold, C., Hambrey, J. B., and Smith, I. R. 1986. Nature conservation and freshwater fish farming. Nature Conservancy Council, Peterborough.
Royal Commission on Environmental Pollution, 13th Report. The release of genetically engineered organisms to the environment (Cm. 720 1989). HMSO, London.
Solomon, D. J. 1979. Coho salmon in north-west Europe. Lab. Leafl. no. 49. Ministry of Agriculture, Fisheries and Food, Lowestoft, UK.
UK Committee for International Nature Conservation. 1979. Report by the Working Group on Introductions, Wildlife Introductions to Great Britain.
Van Houtte, A. R., Bonucci, N., and Edeson, W. R. 1989. A preliminary review of selected legislation concerning aquaculture. Food and Agriculture Organization of the United Nations ADCP/REP/89/42.

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Pacific salmon in Atlantic waters

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A century of Pacific salmon introductions to Atlantic waters is summarized. Movements of fish were initiated in the last century, and in many countries large quantities of eggs have been introduced into rivers on both sides of the North Atlantic Ocean. The motivations for such programmes, the techniques used, and the results are analysed for most of the documented attempts to introduce these species in the Atlantic area, with special attention being given to recent introductions (since 1950). Programmes for the introduction of Pink salmon (*Oncorhynchus gorbuscha*) in Newfoundland (Canada) and the Kola Peninsula (USSR) are reviewed in detail, and the use of coho salmon (*Oncorhynchus kisutch*) for ranching (New Hampshire, USA) and farming (Europe) is described. Pacific salmon released in Atlantic oceanic areas have shown in most cases an aptitude for survival, growth, homing, and spawning, even in areas where environmental characteristics are substantially different from their home waters. Survival rates are generally lower than in the original range and straying relatively important. However, in spite of significant returns, all attempts to establish reproducing sea-going populations have failed in the northern hemisphere. Although not developing rapidly, the use of coho salmon for aquaculture in Europe has an interesting potential. The possible causes of success or failure of the different attempts are discussed; they include an analysis of the adaptive mechanisms of populations which exist in their original habitat, and the influence of the ecological characteristics of the receiving country on the biology of the species. With the exception of the limited initial transplants of the last century, one may note that most introductions were made in areas which did not satisfy the optimum environmental requirements of the species, and where temperature regimes were probably the main limiting factors. They were also made in insufficient numbers or during a period too limited to allow sufficient time for genetic adaptation to the new environment. The consequences of these introductions on native populations of Atlantic species are also discussed. It is concluded that ecological influence on native stocks has been limited in the cases described, and the existing experimental knowledge of the interactions between species is discussed. The risk of disseminating diseases, although no severe problems appear to have been created, must be considered carefully, as do all cases of live fish transfers in or out of the natural range of the species. In conclusion, the influence of the development of aquaculture practices on wild stocks is drafted.

Les introductions de saumons du Pacifique dans les eaux de l'Atlantique nord depuis un siècle sont décrites. Les transferts d'oeufs d'*Oncorhynchus* ont été initiés à la fin du siècle dernier, et des quantités importantes d'oeufs ont été introduites dans les rivières européennes ou américaines dans la plupart des pays riverains. Les motivations des différents programmes, les techniques utilisées et les résultats observés sont rappelés pour la plupart des cas, cités dans la littérature, avec une attention particulière pour les introductions récentes (depuis 1950). Les introductions de saumon pink (*Oncorhynchus gorbuscha*) à Terre-Neuve (Canada) et dans la péninsule de Kola (URSS) sont décrites de façon détaillée, ainsi que l'utilisation du saumon coho (*Oncorhynchus kisutch*) pour des programmes de pacage marin (New Hampshire, USA) ou d'aquaculture (Europe). Les saumons du pacifique libérés dans les eaux de l'Atlantique ont montré dans la plupart des cas leur aptitude à vivre, grandir, retourner au point de lâcher et se reproduire, y compris dans des zones où les conditions hydrologiques étaient très différentes de celles de leur aire de répartition originale. Les taux de survie y sont cependant généralement inférieurs et le taux d'errance supérieur aux valeurs observées dans le Pacifique. En dépit de ces retours parfois abondants, aucune introduction n'a donné lieu, dans l'hémisphére nord, à l'établissement durable de populations se reproduisant naturellement. L'utilisation du saumon coho pour l'aquaculture en Europe, bien que n'ayant pas donné de développement important à ce jour à démontré un potentiel intéressant pour l'élevage en captivité, cependant l'activité n'a pas connu de réel développement industriel. Les causes de succès et d'échec des différentes tentatives sont analysées, incluant une discussion sur les mécanismes adaptatifs réglant le cycle biologique des diverses espèces et l'influence du milieu «récepteur» sur leur biologie. Si l'on excepte certaines des premières tentatives, la plupart des introductions ont été réalisées dans des zones ne correspondant pas aux caractéristiques optimales d'environnement pour les espèces concernées et où des températures inappropriées sont probablement les principaux facteurs limitants. Les tentatives ont également concerné des nombres trop restreints d'animaux, et pendant une période trop brève pour permettre les adaptations génétiques à un nouvel environnement. Les conséquences de ces tentatives d'acclimatation sur les populations résidentes sont discutées, concluant à une incidence écologique limitée sur les stocks indigènes, dans les cas décrits. Les connaissances concernant les interactions entre espèces, acquises expérimentalement sont analysées. Le risque de favoriser la dissémination de maladies reste le principal argument d'opposition aux tentatives d'introduction de saumons du Pacifique en Europe (comme dans tout transfert de poissons vivants), même si aucune problème grave n'a été décrit dans les diverses tentatives. La conclusion fournit quelques éléments de réflexion sur l'influence du développement des techniques d'aquaculture sur les stocks de saumons sauvages.

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Introduction

Transplanting plants or animals to allow local access to a resource was probably a very early preoccupation of *Homo sapiens*, and many domesticated species are not native to the countries in which they are cultured. Among aquatic organisms, early attempts to displace or transplant have occurred for invertebrates such as oysters, which are reasonably easy to manipulate in the adult stage. The biological characteristics of fish, whose adults and juveniles are relatively difficult to transport, have made the process more difficult to realize. The history of fish displacements is associated with an increased knowledge of reproductive mechanisms, and has been stimulated by the discovery of new species in recently colonized lands.

Several reproductive characteristics of salmonids – concentration of the spawning stocks on limited spawning grounds and the large size and capability of the ova to withstand mechanical manipulation – encouraged early attempts to introduce most salmonid species beyond their natural ranges. These attempts were initiated during the last century, with periods of active transfers with varied objectives. An acceleration of movements associated with economic activities has been observed during the past 20 years. Many species once confined to temperate areas of the northern hemisphere are today represented on all the continents in either their wild or cultivated form.

In salmonids, several cases of introductions of non-migratory species can be considered to have been successful, but only a few examples of anadromous population transplants have succeeded in establishing durable self-sustaining populations. In many cases such experiments were conducted without great concern for the possible ecological consequences, and in all cases they have generated much controversy.

The aim of the present paper is to summarize more than a century of Pacific salmon (*Oncorhynchus* sp.) introductions into Atlantic waters, and to review the possible consequences and factors important to their success or failure.

1. The objectives of Pacific salmon introductions

The main reasons proposed by the initiators of introductions have always been economic ones: creating a new resource or a new sport or commercial fishery. Historically, human interventions have been made at various stages of the life history of salmon.

Transplanting a species to create a new wild population

Species which can freely reproduce

The most numerous and earliest cases of introductions followed the simplest scheme of importing eggs of the species during a limited initial period and planting them in rivers in order to create new wild populations which could establish and colonize a vacant ecological niche or displace less valuable native species. These populations might be exploited by an adequate commercial fishery in the coastal area, or a sports fishery in marine or river waters. Such motivations have probably been generated by the magnitude of salmon stocks from the North Pacific, and the apparent ease with which fisheries could be developed when stocks concentrated in the coastal or estuarine environment prior to reproductive migration.

Observations of massive returns of pink (*O. gorbuscha*) and chum (*O. keta*) salmon in Alaskan rivers and the associated net fisheries; the large sockeye (*O. nerka*) Bristol Bay net fisheries; and the manipulation of huge chinook salmon (*O. tschawytscha*) at time of spawning in American west coast hatcheries, all give some understanding of the reasons for the numerous attempts made to create a new resource in many different parts of the world, when compared to the relative scarcity of Atlantic salmon (*Salmo salar*) in most European rivers. An evolution of this phase of transplantation led to the use of frequent or continuous egg introductions to support the fragile initial runs and to reduce interannual variability in the adult returns.

Species which must be supported by "ranching" techniques

When a transplanted species could not reproduce easily (due to such adverse factors as inappropriate climatic conditions or the lack of access to suitable spawning grounds for direct deposition of eggs), "ranching" techniques were developed. The release of migrating fry, then of smolts reared in hatcheries for a longer period was practised, leading to a total disappearance of the wild freshwater phase. The run then depends exclusively upon fry and smolt releases, and the increasing cost of this phase makes continued activity even more necessary for success.

Introducing a species for total rearing in captivity

The increasing market demand for some species of fish has encouraged the development of intensive aquaculture in many countries. The objective has become to produce farmed animals, either in fresh or sea water in total captivity. As in agriculture, local species may not be the most adapted, and introduction is sometimes considered opportune. This has been the case in salmonids, and both Pacific and Atlantic salmon have been shipped to several areas of the world for this purpose. This attitude will most certainly become more and more frequent with the development of aquaculture of marine species. Though the farmer's objective is to avoid losses, substantial escapes into open waters may occur due to the failure of containment structures.

2. History and status of Pacific salmon introductions to Atlantic waters

Many attempts to establish sea-going populations of Pacific salmon species in Atlantic waters have been made on both sides of the Atlantic Ocean in the last century. More recently, "ranching" or intensive aquaculture programmes have stimulated movement of eggs. A summary of these experiments follows, attention being paid particularly to introductions for which little information is available in the international literature.

Introductions to the Northwest Atlantic

Early experiments (1872–1927)

Four of the five American species of Pacific salmon were introduced into most Atlantic states of the USA between 1877 and 1930 (Mather, 1887; Davidson and Hutchinson, 1938). The earliest and most abundant transplants were made with the "Californian" or chinook salmon, of which over 30 million eggs were received and planted into streams of the East coast, with a very active period in the decade 1870–1980. By the 1920s, only New Hampshire and Maine were continuing the introductions. In spite of these efforts, representing respectively 2 and 3.8 million eggs, natural populations generally failed to establish in rivers still not threatened by industrial development. Chinook salmon have been reported to have established a sea run population in the St John River in New Brunswick and in Ontario (Dymond *et al.*, 1929, cited in Davidson and Hutchinson, 1938). Among all other attempts made during the same period, chinook salmon acclimatized only in New Zealand (Waugh, 1980), where three million eggs were introduced between 1872 and 1910.

Everhart (1966) reported attempts to introduce silver or coho salmon (*O. kisutch*) into the rivers of Maine in 1905. Using eggs from Oregon, 1.3 million fry were planted into eleven rivers; 300 000 eggs were shipped to New Hampshire. Limited introductions of the same species and of sockeye salmon (*O. nerka*) continued during the next decade in Maine. Massive introductions of pink salmon eggs to Maine rivers were made during the period 1910–1920, when more than 27 million eggs (originating from Washington and Alaska) were planted, peaking at 6 million fry released in 1916 (Bigelow and Schroeder, 1953). While all other attempts in the area failed, fairly large numbers of adults were captured, allowing propagation of fry for a few years. All the returns were from the Washington population; none of the Alaskan fish were recaptured. The stocks declined rapidly and disappeared. More limited introductions were conducted during the 1920–1925 period, but without evidence of natural reproduction.

Recent introductions (1930–1988)

State of Maine. New attempts to introduce chinook salmon were conducted from 1934 onwards, with no success (Cooper, 1939, cited by Solomon, 1980; Huntsman and Dymond, 1940). Further attempts were made with coho salmon between 1942 and 1953 in six rivers in order to develop additional fisheries in estuaries and streams that did not support runs of Atlantic salmon. A total of 150 adults was estimated to have returned to the

Ducktrap River in 1947 and limited captures were reported in the same river estuary in 1952. In 1956 and 1957, a few jacks and adults (5.5 to 9.5 lbs) were captured in Cove Brook trap. Sporadic catches seem to have occurred for a few years in other streams, although not confirmed by fishery biologists.

More recently (1975–1980), coho salmon were imported from the west coast by two private companies as part of their marine cage rearing programme (Jaegoe *et al.*, 1981). A total of about three million eggs was received between 1975 and 1978. Escapes are thought to have been very limited. Recent attempts to establish private "ranching" of pink and chum salmon have been conducted in the area of Casco Bay (Maine). Fry from three million pink salmon eggs obtained from Alaska were released in 1981–1982. Five million eggs of chum salmon, originating from Washington state and Japan, provided 2.5 million fry which were released between 1981 and 1986. The objectives of the project were discussed by Sawyer (1983). Very little information was provided about the results. Six adult male chum salmon, all of Japanese origin, were reported in 1987, and one adult pink salmon was captured in the Miramachi River in New Brunswick, whose origin is compatible with the Maine releases.

New Hampshire and Massachusetts rivers. Considering the virtual absence of a salmonid sports fishery in the area and the restoration of Atlantic salmon populations as a long-term enterprise, several states of New England decided in the late 1960s to introduce coho and chinook salmon to develop a coastal and estuarine recreational fishery. Extreme temperature regimes (0–25°C) and inappropriate characteristics of the rivers selected, offering marginal spawning habitat, made the establishment of natural spawning populations improbable. Thus, the objective was changed to attempt to develop a sports fishery using hatchery releases of smolts.

Eggs were imported from Washington and Oregon states and the smolts released in several rivers of the northeastern United States. Solomon (1980) reported the early results of these trials, indicating an absence of recaptures in Rhode Island and Connecticut and the evidence of substantial returns in Massachusetts (North River) and New Hampshire (Great Bay, Lamprey and Exeter Rivers). In 1986, the numbers of smolts released since the beginning of the programme were respectively 3.4 and 1.1 million (established from Fawcett in Anon., 1972–1984; Martin and Dadswell, 1983 and Anon., 1987). Smolts released were usually yearlings of normal size (25–50 g), but fall planting of subyearlings in streams has been practised since 1977. Hatchery survival has generally been high, in spite of several reports of bacterial kidney disease during winter.

A total of about 20 000 adult cohos is estimated to have returned to the New Hampshire release area, of which 7 000 contributed to the marine and river sports

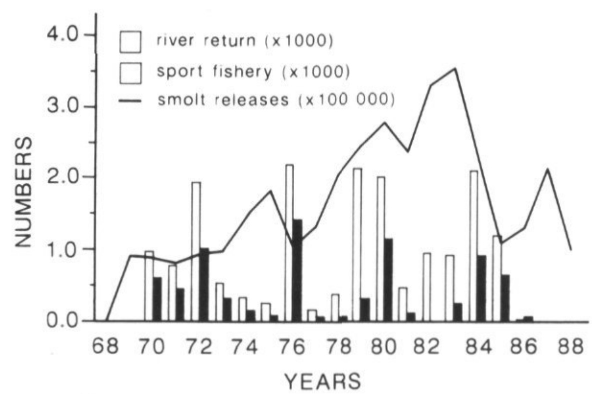


Figure 1. Introduction of coho salmon in New Hampshire.

fishery (Fig. 1). Average marine survival rate is estimated to be 0.73% (0.33–2.97%) in New Hampshire (Stolte, 1974; Anon., 1972–1988; Fawcett and Sower, 1986) and 0.11–1.45% in Massachusetts. Substantial returns have been achieved, but survival rates at sea remain low and important interannual variations are observed. No significant improvement has been obtained with "naturalized" populations, even with the F4 generation. Hatchery smolt condition cannot be overlooked as a main cause of the low returns. The original objective of using only ova produced by the returning adults to perpetuate the fishery could not be achieved easily, although F1 smolts were released as early as 1972; and frequent egg introductions from Washington state have been made to augment the local production when necessary. The composition of present releases is almost exclusively of local origin, although additional eggs continue to be introduced when the adult return is too low. Because of unavailability of coho salmon eggs in 1987 (111 000) and 1988 (431 000), chinook salmon smolts derived from Great Lakes eggs were released. Recently, low survival of collected eggs has been attributed to metal contamination in the Great Bay (NH) watershed (Anon., 1987).

Smolts have frequently been observed in July–August, concentrating close to the mouths of New England coastal rivers, from northern Massachusetts to southern Maine. Observations of immature fish were made during winter several kilometres inland from the planted watershed (Stolte, 1974). Adult fish appear in the recreational marine fishery in July of the following year near the mouth of the river planted, and normally remain through September, although disappearance of the fish in the fishery in August has been observed (Fawcett in Anon., 1982). The size of the fish is consistent with sizes observed within the original range of the species on the Pacific coast. In September, adult fish enter the river system (water temperature 15–20°C) and angler's catches in tidal or river waters continue until December (temperature 1°C). Natural spawning has been observed, but hatching survival is considered to be low.

Straying, initially considered to be limited to the tributary system of the Great Bay area, has proven to be more important. Symons and Martin (1978) reported the recapture of two tagged post smolts in Nova Scotia two months after release about 300 km north of the introduction site. Earlier, the discovery in 1976 of several underyearling parrs in a small coastal stream tributary of the Digdequash river in southern New Brunswick (Canada) indicated successful spawning of straying adults. Martin and Dadswell (1983) provided evidence of two other cases of natural spawning in the Cornwallis River (Nova Scotia), with production of viable juveniles in 1982 and 1983. Thirty verified captures of jacks and adults have been recorded in the Bay of Fundy, and frequent unverified but reliable observations have been made in the same area (Fig. 2).

The results presented in this paper suggest the possibility of establishing adult populations of coho salmon sustained by "ranching" practices in New Hampshire, and to a lesser degree in Massachusetts, and the failure of attempts further south. Returning adults have proven to be fertile but have not established durable self-reproducing populations since 1970. However, viable reproduction of returning or straying adults has been established. Captures at sea indicate a general pattern of northward migration within the coastal area, with a tendency to "investigate" the northwest oriented river mouths on their journey north.

Joyner (1973b), discussing the possibilities of developing a coastal recreational fishery for New England states, predicted such results, based upon an observation of sea surface temperatures (Fig. 3b). The oceanic conditions, which could be seasonally considered as marginal or critical, seem to maintain fish in a pocket of water close to the Maine and New Brunswick coasts, dead-ending in the Bay of Fundy. Escapes from this restricted zone could occur if post smolts migrated directly East after leaving the rivers while sea water temperatures were still favourable. They could then migrate north along the East coast of Nova Scotia, and adults would have an opportunity to colonize the gulf and estuary of the St Lawrence, although they might find an oceanic thermal barrier for their southward return migration.

The fact that no recaptures were recorded in eastern Nova Scotia seems to make this hypothesis very unlikely, as the natural (genetic) tendency of the stocks used for transplantation is to migrate northwest along the British Columbia and Alaskan coasts. Thus, captures of coho and chinook salmon within the St Lawrence systems in the Montreal area (reported later) seem more likely to have resulted from the Great Lakes introductions escaping from Lake Ontario.

Observations of the coho juveniles in streams frequented by Atlantic salmon confirm the low degree of behavioural interaction, especially in summer when the two species select very different habitats (Martin and Dadswell, 1983).

Invasion from Great Lakes transplanted stocks. Several species of *Oncorhynchus* have been introduced into the Great Lakes following a drastic disturbance of the ecological balance due to the invasion of sea lampreys (*Petromyzon* sp.). The stocking of coho and chinook salmon, carried out since 1966, was a dramatic economic success; natural spawning populations exist (Peck, 1970), but the fishery is sustained mainly by intensive release of hatchery smolts (Parsons, 1973).

Initially restricted to Lake Michigan, several populations have been introduced or have strayed to other lakes (Pearce, 1980). Pink salmon, accidentally introduced into Lake Superior, are assumed to have established in Lake Huron (Emery, 1985), and have been observed spawning in Lake Ontario tributaries (Dermott and Timmins, 1986). The invasion seems to remain restricted to the Great Lakes, since the few recaptures which have occurred on the north shore of the Gulf of St Lawrence most certainly originated from Newfoundland releases. Since the first report of coho salmon in Quebec waters upstream from Montreal (1970), 26 adults have been verified in the St Lawrence River. Chinook salmon were captured beginning in 1983, and one adult was reported from Rimouski in 1986. Spawning chinook have been observed in the area of Montreal, and one coho salmon yearling has been captured, indicating natural reproduction (Dumont *et al.*, 1988).

Compared to the important populations existing in the Great Lakes, the numbers recaptured in St Lawrence waters are minimal, but they indicate a recent tendency to spread eastwards to Atlantic waters (Fig. 2).

Introduction of pink salmon in Newfoundland. In order to establish a commercial fishery in Newfoundland, pink salmon were chosen as presenting the most interesting characteristics (adaptation to cold waters and limited competition in the river stage with local species). Five transplants involving 15 million eyed pink salmon eggs were made between southern British Columbia and North Harbour River in southwestern Newfoundland in 1959, 1962, 1964, 1965, and 1966. These introductions resulted in important adult returns and natural spawning. From 1969 returns were only by the progeny of returning adults. Results of these transplants were assessed by appropriate studies and summarized by Blair (1968), Lear (1975, 1980), and Dempson (1980). Recent and limited introductions for mariculture research led to limited escapes in New Brunswick (1977 and 1979) and Newfoundland (1979).

During the initial phase of the introduction, eggs were planted in controlled-flow spawning channels and had high survival to fry stage (82 to 91%), except for the first year when siltation reduced the survival to 38%. Results

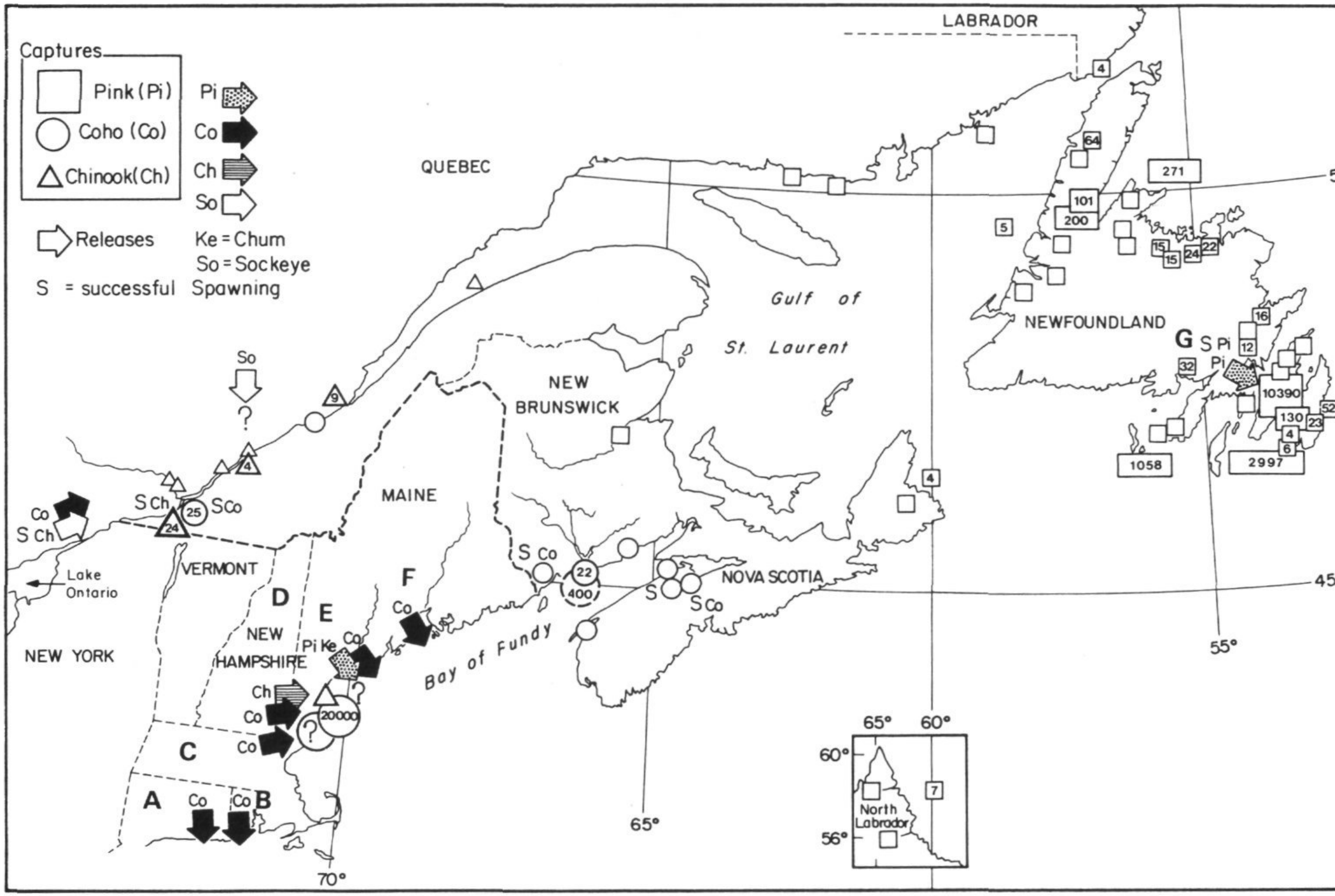


Figure 2. Recent introductions and captures of Pacific salmon in Northeast Atlantic waters (data compiled from sources cited in the text). A–B. Releases of coho in Connecticut and Rhode Island (1969–1970). C. Releases of coho in the North River, Massachusetts (1969–1988). D. Releases of coho and chinook in the Great Bay area, New Hampshire (1968–1988). E. Limited escapes of coho from cages, large release of pink and chum salmon for ranching. F. Introduction of chinook salmon (1934) and coho salmon (1942–1953) in six rivers of Maine. G. Transplantation of pink salmon to Newfoundland (1959–1966). H. Invasion by coho and chinook from Lake Ontario (1970–1988).

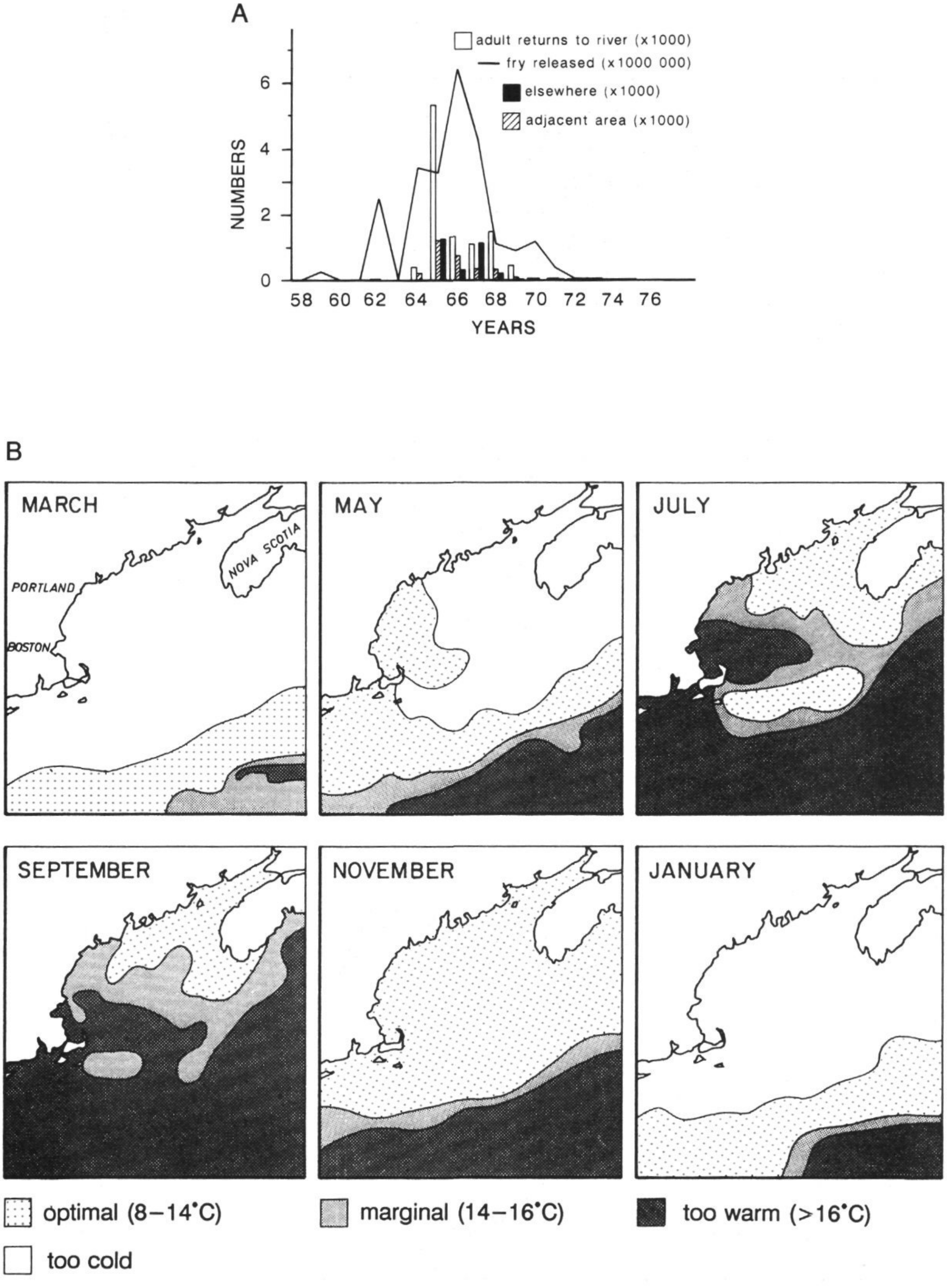


Figure 3. A. Introduction of pink salmon in Newfoundland. B. Surface temperatures of the New England Coast (redrawn from Joyner, 1973).

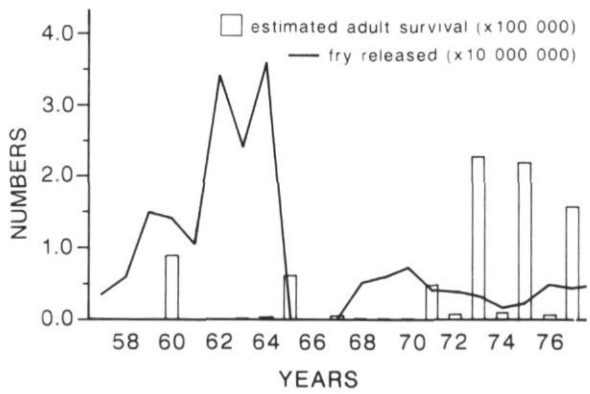


Figure 4. Introduction of pink salmon in the Kola Peninsula.

from ensuing natural spawning after 1966 were estimated at 75%. Important fry predation by brook trout (*Salvelinus fontinalis*) and to a lesser degree by brown trout (*Salmo trutta*), Atlantic salmon smolts, and eels (*Anguilla rostrata*) was observed. The number of adults returning to Newfoundland waters increased sharply over the first four plantings of eggs but declined again with the 1966 planting. Total returns fluctuated between 0.10% and 0.206% of the estimated egg deposition, without any clear trend. These numbers remain far below the survival obtained by non-profit cooperatives in Alaska, where returns of 5 to 7% to the terminal fishery are commonly observed. Only the parent strains of 1968 and 1973 gave rise to adult generations more numerous than themselves, and the absolute numbers of returning adults declined steadily (Fig. 4). Wild pink salmon populations of Alaska have been estimated by McNeil (1967) to produce 3.06 returning adults per spawner (3.4% marine survival).

Straying appeared to be relatively important. A total of 5 800 adults was caught in the coastal fishery, all round the island, and total river escapement exceeded 11 000 fish, of which 7.3% was found in rivers other than North Harbour River. A few adults were reported in streams of Quebec, Nova Scotia, and northern Labrador (Fig. 4); in Labrador, Solomon (1980) mentioned the possible existence of a self-sustaining population, with reported catches in the same fjord from 1970 to 1976. However, even if noticeable adult returns occurred in several river systems, they seem to have failed to establish durable "strayed runs".

The introduction of pink salmon eggs into Newfoundland streams resulted in high survival to the fry stage, but high predation by native species during downstream migration, in spite of very low temperatures. Oceanic adult survival was low, but many adults returned to the planted stream in spite of some wandering. However, these adult runs failed to establish a permanent population. Lear (1980) reviewed the possible causes of failure, investigating relationships with average temperatures in river and coastal areas during downstream migration, known to be controlling factors in native west coast populations, and abundance of marine predators such as herring (*Clupea harengus*). The most likely explanation remained, however, the insufficient numbers of eggs introduced during a too limited period (the original goal of 15 to 25 million eggs transplanted during two years was not achieved), and the possible poor adaptation of the selected strain.

Coming from a more northern latitude (original stock from 49–54°N was transferred to the 47°N area), and with a different preferential migration tendency, the donor stock might not have provided the best chances for rapid adaptation. In the early planning phase of the experiment, Ricker (1954) had discussed such eventualities, submitting the idea of a better adaptability of Asian Kamtchatka populations. The pink salmon transplant does not appear to have affected the Atlantic salmon population in North Harbour River, and there is no mention of the appearance of diseases.

Miscellaneous introductions. Various cases of introductions to Northwest Atlantic waters reported by Dumont *et al.* (1988) included the transplantation of cutthroat trout (*Salmo clarki*) in 1941 and sockeye salmon in its landlocked form (kokanee) to Quebec waters, in 1968, and Huchen (*Hucho hucho*) from the Danube river in 1968 and 1969.

Introduction to European waters

Early transplants

During the "boom" of the "naturalist" period, many attempts were made to introduce Pacific salmon, mainly chinook salmon, to European waters. Records of these experiments, giving the number of eggs introduced, are summarized in Table 1, as compiled from Davidson and Hutchinson (1938).

Sockeye salmon were also introduced to the Netherlands in 1990. Little information is available from these early experiments. Mazeaud (1981) reviewed the history of "Californian salmon" introductions into French rivers. Eggs first imported in 1877 from California (Sacramento River) were dispatched to many fish culture stations and reared in captivity in ponds. They showed

Table 1. Numbers of chinook salmon eggs shipped to Europe between 1872 and 1930.

Receiving country	1872–1890	1891–1910	1911–1930	Total
England	150 000			150 000
France	658 000	395 000		1 053 000
Germany	830 000	125 000		955 000
Italy	50 000	50 000		100 000
Ireland		50 000		50 000
Netherlands	500 000		400 000	900 000

high survival and rapid growth even under elevated temperatures. Artificial reproduction was commonly conducted after 1884. The first stockings of the Seine River were described in 1880 and 180 000 fry were released between 1885 and 1890.

Following the artificial reproduction of this stock by the "Aquarium du Trocadero", which perpetuated the strain in captivity for 33 years, further releases were made in several Mediterranean streams, in many Atlantic rivers (Loire, Ellé, Dordogne), and also in the Rhine River. Isolated recaptures of adults were reported in the Aude River (Mediterranean), the Creuse, and were more abundant in the Seine River drainage; the largest fish was captured in the Paris area (10 kg and 105 cm). The program was abandoned in 1913.

Introduction of Pink salmon in the Kola Peninsula (USSR)

Following an early unsuccessful attempt to introduce chum salmon in the White Sea (1933–1939), massive transplants of pink and chum salmon were initiated in 1956. Bakshtansky (1980) gave a detailed description of the results.

During a 20-year period, about 200 million pink salmon fry were released from the Kola peninsula hatcheries, using eggs mainly from Sakhalin rivers. In the early years of the programme (between 1957 and 1964), over 50 million chum fry were released, but only a few adults were recaptured.

Pink salmon returns started in 1960, with important interannual variations, from several hundred thousand to only a few individuals. These considerable fluctuations seem to be related to environmental conditions, in the river and marine habitats, which did not always meet the requirements of the fry and smolts. As in the parent population of Sakhalin Island, odd-year spawners were the more abundant. More regular migration was apparent in odd years in the 1970s, with a peak survival in 1973 (estimated catch of 226 000 adults). Adult sizes were comparable to the original Pacific stock, indicating that they found adequate food supply in their oceanic life.

Variability in the survival rate of eggs obtained from returning adults was observed in acclimated "wild" populations and in hatchery stocks; they presumably resulted from a late deposition of eggs, not allowing the embryos to reach a safe stage of development before water temperatures fell to 0°C (Azbelev and Yakovenko, 1963, cited in Bakshtansky, 1980). Due to late migration and spawning in even years, the effectiveness of natural reproduction was much lower than during odd years (Agapov, 1979).

Predation of migrating fry by native fish is probably limited in rivers (sea trout (*Salmo trutta*), Atlantic salmon, pike (*Esox* sp.)) but is greater at sea (cod (*Gadus morhua*), saithe (*Pollachius virens*), and herring (*Clupea harengus*)). Bird predation by terns (*Sterna paradisea*) is also prevalent.

In 1960, adult pink salmon appeared in northern Norway (Berg, 1961), indicating a foraging area in the Norwegian Sea (Berg, 1961). Occurrence of the species was described in Iceland in 1960 and 1961 (Gudjonson, 1961), then in Scotland (Williamson, 1975). Berg (1977) related evidence of fry migration from northern Norway rivers, following abundant adult returns and spawning in 1965 and 1973. Bjerknes and Vaag (1980, 1981) gave detailed information on the catches in the Finnmark area, and indicated frequent straying as far south as Bergen. As in the release area, the captures reached a peak in 1973 in the Finnmark fishery, then declined steadily in 1975, 1977 (12 800 captures), and 1979, with a continuing decrease in the number of spawners from one generation to the next.

Massive transplants of fry succeeded in establishing important adult returns and natural spawning, but interannual variations were large, and the general tendency was a decline in stocks when artificial propagation stopped. However, some success could be claimed, due to the large scale of the transplant (Bakshtansky, 1980), and, for some years, considerable returns, spawning, and fry migration were also observed in Finnmark and northern Norway, indicating the ability of the species to temporarily establish significant populations as a consequence of straying.

Among the various reasons proposed for explaining the inability of the transplants to perpetuate, the high dependence of fry survival on river and marine habitats seems to be predominant. Cold winter temperatures of subsurface waters, eradicating the egg deposits in some rivers almost completely, are considered to be a limiting factor (Grinyuk *et al.*, 1978). Flooding, which washed the fry down to the ocean, and insufficient suitable spawning areas were also adverse factors which made natural production unreliable. Bjerknes and Vaag (1981) considered that the introduction of eggs would be necessary for a stabilizing effect in years when conditions for natural reproduction were unfavourable, and considered that the species was economically interesting for ranching due to the low cost of egg plantings.

Competition with Atlantic salmon appeared to be minimal. Pinks generally spawned in shallow water of the lower reaches of rivers, although upstream migration of 300 km was observed. Reproduction occurred 1 to 2 months earlier than that of Atlantic salmon, and fry migrated rapidly after emergence. No disease was observed in wild pink populations, but vibriosis was diagnosed in sea-water-cultured fish in Norway. The mariculture potential of the species was assessed by Gjedrem and Gunnes (1978), who favoured producing small-sized fish (0.5 to 1.5 kg) in captivity.

In the early 1980s, the apparent tendency was to stop egg introductions from the Far East. Almost no published literature concerning the evolution of the programme since 1981 could be found. It seems that captures in Finnmark are no longer reported (Jonsson, pers. comm., 1988), but there have been rumours concerning a reactivation of the programme.

Recent introductions of coho and chinook salmon in Western Europe

France. Chinook and coho salmon eggs were introduced to assess their potential for freshwater farming by a private firm in 1971, looking for a VHS (viral hemorrhagic scepticemia) resistant species as a substitute for rainbow trout (*O. mykiss*) in contaminated areas (Bellet, 1975). Coho salmon potential for aquaculture was assessed through a NOAA-CNEXO cooperative programme from 1971 (Harache and Novotny, 1976). The rationale of culturing coho salmon in temperate waters to produce small-sized salmon with a rapid turnover was presented in Harache (1979a and b). Continuous introductions from Washington and Oregon states have occurred ever since, with a marked increase in 1976–1978, due to an increasing demand by freshwater farmers, that could not be satisfied by the establishment of a local broodstock.

Coho salmon, introduced only for cultivation in captivity, exhibited excellent performance in the freshwater phase, with survival exceeding 80% between eyed egg and smolt stage, and excellent growth using stream water in Brittany. Water temperatures, usually ranging from 6 to 18°C (with extremes of 4 and 21°C), seemed to provide almost ideal conditions for rapid growth; the fish were cultured during the major part of the year within preferred temperatures defined by Brett (1952). The marked avoidance of temperatures exceeding 15°C, cited by the same author, does not seem to present specific difficulties for coho salmon during summer months, in comparison with rainbow trout. It appeared that with eggs derived from early spawnings, and with appropriate husbandry conditions, almost all the populations provide O+ smolts either in spring or autumn, confirming the observations of Garrison (1967) obtained in Oregon. These fish undergo a true smoltification, with an acute increase in gill Na+ K+ ATPase activity (Lasserre *et al.*, 1978) and a seasonal increase in salinity tolerance (Boeuf *et al.*, 1978). These changes are associated with the possibility of salt-water rearing, with respect to dates and sizes at transfer, either in the spring or autumn (Harache *et al.*, 1980).

When kept in fresh water beyond smoltification, coho salmon present a high adaptability to rearing in captivity, with rapid growth and a good food conversion index, which allows the production of small sized salmon (0.3 to 1.5 kg) 11 to 18 months after first feeding. Survival of 75% from eyed eggs, and average weight of 150–250 g in October (10 months) are regularly obtained by a farm in Brittany. Saltwater rearing, although more sensitive to environmental factors, provides more rapid

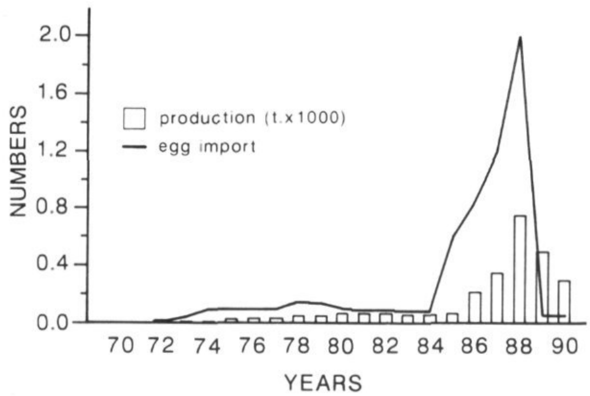


Figure 5. Introduction of coho salmon in France.

growth, reaching an average weight of 2.5 to 3.0 kg during the summer of the second year (Harache and Boeuf, 1986). Significant mortalities (30 to 50%) frequently affect post smolts during the beginning of their first summer in the sea (late June to end of July). Such mortalities, equivalent to those observed with Atlantic salmon, do not destroy the economic feasibility, due to the low price of smolts produced in five months.

Because of rapid growth, almost all of a given brood reaches sexual maturity at 2 years, but the effectiveness of reproduction remains limited (Harache, 1979b). Egg production from local broodstock was estimated at only 10% of the needs of private aquaculture companies in 1988.

The actual commercial production remains limited, especially in marine waters, but a sharp increase has been observed between 1986 and 1989, due to rapid development of freshwater farming as a substitute for rainbow trout production (Fig. 5). In 1988, more than 30 private farms were rearing coho salmon in fresh water.

Coho salmon have proved to be more resistant to furunculosis than rainbow trout and considerably more than Atlantic salmon, but they are very susceptible to *Renibacterium salmoninarum*, commonly called "bacterial kidney disease" (BKD). The disease was first recorded in fresh water in France in 1974 in coho salmon (de Kinkelin, 1975), then in marine farms in Brittany (Vigneulle *et al.*, 1977). It was observed on several occasions during the following years in fresh and sea water, usually without severe losses. However, it constitutes a threat for this species, and may appear in winter or spring following "stress periods" such as autumn transfer to sea water, cold waters, or high density rearing.

Once the possibility of transmission of BKD through the eggs was established, most of the ova imported in France after 1976 were treated with erythromycin at the time of water hardening, though the total efficiency of the treatment is still questioned.

It is obvious that aquatic farms cannot eliminate all risks of escapes following river floods or cage destruction during storms. Although limited, several cases of accidental losses have been recorded, as well as some limited intentional (though unauthorized) releases. The lack of appropriate tools for controlling oceanic captures and river returns does not permit detailed descriptions for each event. The best documented case, described by Euzenat and Fournel (1981), occurred in April, 1974, when about 50 000 one-year smolts (150 mm) escaped during a flood from a freshwater farm in the Varenne River in Normandy. A high proportion of these fish was destroyed during downstream migration, when passing through a hydroelectric turbine. A further escape of 10 000 parr (5 months) was observed in June, 1975. Thirty-two adults (weighing 0.8 to 3.5 kg) were recaptured by electrofishing between October and December, 1975, below two impassable weirs of the system. In June, 1976, 25 underyearlings were captured by comparable surveys at a time when there were no cohos reared in the hatcheries on this river, indicating a successful spawning from the first adult run in December, 1975. In 1976 and 1977, appreciable catches were made by anglers, but only 5 adults (0.9 to 4.3 kg) were captured by electrofishing. Some spawning was observed in December, 1977, but no further confirmed captures were made during the following years, in spite of intensified surveys. The run of coho is considered to have become extinct after 1978. About 90% of the adults were recaptured within the release basin (Arques River), 85% being caught in the tributary where the escape took place. Some straying occurred, however, for a distance of 100 km northward along the coast.

Other escapes from freshwater farms were reported in 1976 in southern Brittany (10 000 parr) and in 1988 (several thousand yearling pre-smolts). From the latter case, abundant catches in the estuary occurred for several weeks, and post smolts were caught by anglers at the entrance of the Bay of Brest in June of the same year. Losses from marine farms remain generally limited, but escapes have occurred on a few occasions. Four thousand large yearlings escaped from a torn net cage in the Bay of Brest in 1977; more limited losses happened in the Bay of Cherbourg, the estuary of the Jaudy River where the main farm is located, and in the Aber Wrac'h estuary in the spring of 1988 (5 000 yearling fish of 1 kg). In the last case, important catches by angling and with nets occurred during the entire summer in the vicinity of the cages, indicating an absence of migration of these fish, and an apparently normal growth (capture of one fish weighing 4.4 kg in mid-September in the vicinity of the cages). Sea-surface temperature in the area fluctuated between 14 and 16°C, with a maximum daily record of 17°C. From these escapes, no noticeable adult migration has been observed into surrounding rivers, but the absence of counting weirs does not permit definite conclusions.

Limited voluntary releases of large yearlings (636 fish) were made in the spring of 1977 in the Sienne River (west of Cotentin Peninsula) by an angling association, resulting in noticeable angler captures in the estuary in early summer, and a confirmed catch in the Channel Islands in August 1977 (Solomon, 1979). Smolts were also introduced in the Var River in southern France by an angling association in 1979, and some returns have been recorded in the Somme River following a limited release in 1980–1981. A coho, captured in Dutch waters in 1982, showed age characteristics consistent with the Somme River release. An attempt to obtain precise information about coho salmon behaviour in the sea from a "controlled" release of marked cohos, under international observation, was discussed in the "ICES Working Group on the Introduction and Transfer of Marine Species" between 1981 and 1983 (Harache and Prouzet, 1981). The final project, agreed to after considerable and productive discussion by scientific parties, was not authorized by the French Ministère de l'Environnement, in spite of generally favourable advice.

As with other prospects in salmonid aquaculture, coho salmon culture did not develop rapidly after the first results, which appeared encouraging. However, the activity finally grew significantly between 1985 and 1989, with the growing interest of some freshwater trout farmers facing stricter environmental regulations for effluent release of intensive rearing farms, and looking for a substitute species which could be reared profitably at lower densities.

Coho salmon culture represents a very competitive alternative to Atlantic salmon culture for the production of small sized fish (under 2 kg) in less than 2 years after fertilization. However, the development of the activity remains associated with the evolution of market demand for this size of fish, focusing mainly on domestic consumption, which has increased dramatically over the past several years. Different limiting factors, including maturation at two years, do not presently allow production of larger fish, as in Japan where an average size of 3 kg is reached at 18 months, in sea water of high temperature (Yoshida, 1985), or in Chile. The application of genetic sex control to this species might have considerable importance in the future, and could make coho even more competitive. However, the fact that the production remains partially dependent on egg imports will remain a severe constraint in comparison with Atlantic salmon culture, whose genetically selected populations allow a rapid progression of growth. The recent developments of the aquaculture of Atlantic salmon in northern Europe, and the drastic decline in prices which resulted reduced the interest of freshwater farmers for the species in 1990.

In view of the preceding description of attempted introductions, the establishment of permanent runs of coho in rivers of western Europe, following uncontrolled escapes from French aquaculture farms, appears very improbable. However, the potential ecological danger to native species is often stressed by opponents of coho salmon farming. A research programme designed to assess the level of competition between coho and Atlantic salmon has been initiated by IFREMER and INRA. The results lead to the conclusion of only limited interaction between the two species, due to the occupation of relatively different ecological niches.

Introduction of coho salmon in Scotland. An attempt by Unilever Research to rear coho salmon in Scotland was described by Munro *et al.* (1980). This experiment strictly applied the recommendations of the "ICES Code of Practice" concerning the introductions and transfers of marine organisms, with quarantine rearing for the whole life cycle. Eggs introduced (26 000) originated from the Capilano hatchery in British Columbia. Due to the limited water flow available, the growth was slow in fresh water, and fish reached smoltification only as yearlings. After sea water adaptation, they grew at a rate comparable to that observed on the French coast, reaching 2.2 to 2.4 kg in 18 months. Maturation was delayed due to the culture conditions, but successful spawning was achieved and a healthy F1 stock was obtained. No pathogens were detected and no fish escaped during the quarantine, confirming the initial diagnosis of a disease-free stock. Subsequent legislation was established following this experimental introduction, allowing the utilization of the F1 fish only for research purposes but prohibiting the rearing of coho in cages.

Coho salmon farming in southern Europe. Coho salmon have been introduced for farming purposes since 1975 in Spanish waters of Galicia. The annual production of a marine cage enterprise has fluctuated between 80 and 100 tonnes, with relatively good success. However, production still depends on egg importations from the US Pacific Coast and is not expanding. Cases of bacterial kidney disease have been reported. There has been a rapid development of freshwater rearing in Italy, where production reached several hundred tonnes in 1988. Relatively successful cage rearing has also been developed during winter months in a fjord on the Yugoslavian coast, where production reached about 40 tonnes in 1987. These operations remained marginal and their continuation has not been confirmed.

Miscellaneous. Sporadic and limited importations of several salmonid species to European countries have been reported in recent years. They include pink salmon releases in the Baltic Sea, between 1973 and 1976, with extremely low returns, but with records of fish in coastal waters of Sweden, Finland, Poland, and Germany (Rimsh, 1977, cited in Munro, 1979); coho salmon for cage rearing in Latvia (USSR) (Munro, 1979), coho and masu salmon (*O. masou*) in Germany for rearing in closed ponds (Welcomme, 1979), "Kokanee" in 1960 and sockeye salmon in 1972 in Sweden for lake or river release. Little information is available about the results of these introductions.

A look at the Southern Atlantic

Joyner (1980) analysed the results of transplantations to Atlantic waters of South America. Chinook, coho, and sockeye salmon were introduced in Argentina between 1905 and 1910, together with Atlantic salmon, with no success. Later experiments were conducted again with the Atlantic species. Chinook salmon were also introduced in southern Brazil in 1958. Adults were not reported but "salmon-like" fish were photographed four years later ascending falls in the Rio Uruguay. The same author analysed the world possibilities for ocean ranching of Pacific salmon, particularly in subantarctic areas (1974, 1976).

As part of the scientific programme for the Antarctic, several European or American species of fish were introduced for research purposes in the French archipelago of Kerguelen. Brown and brook trout (*Salvelinus fontinalis*) populations successfully established in fresh water, giving birth to subpopulations of resident and migratory sea trout and lake trout (*Crystivomer namaycush*). More recently, populations of coho, chinook, and Atlantic salmon were imported and released. Returns of Atlantic salmon remain exceptional, and an important fraction of the population has become landlocked in lakes. Coho salmon displayed an aptitude for migration at one year, to return and spawn at three years, with significant rates of return (0.84 to 0.55%) higher than that observed in Chile (Lindberg and Brown, 1982). However, returns fluctuated in relation to interannual climatic conditions (Davaine, 1991). Recent problems linked with the appearance of bacterial kidney disease in several species were observed. A limited population is presently in its 4th generation.

On the basis of these preliminary results, a development programme based upon ranching has continued, and a return of 350 coho (0.8% survival) was observed in 1987, following 1985 and 1986 releases. However, the economic conditions of exploitation do not appear very satisfactory in the general context of the salmon market.

3. Consequences of introductions

Though benefits are always expected from fish introductions, concern should be expressed about the possible negative effects on existing stocks. These effects include competition with native species, genetic risks, disease introduction, and overexploitation of native stocks.

Competition with native species

In the very heated debates which often occur when introductions are proposed, the potential ecological competition with native species is always raised as one of the major concerns.

Reproduction

Will the "aliens" compete for the same spawning grounds? If they spawn later will they dig out eggs from the nest, and if they spawn earlier will their larger "advanced" fry prey on emerging alevins (and vice versa)? These are the basic questions which have to be taken into consideration.

All species select similar characteristics for gravel size but may select very different habitats for water depth and current velocity, according to river size. Atlantic salmon usually select reduced depth of spawning areas, with limited current velocity, but the preferred areas overlap those of *Oncorhynchus* species. Pacific species generally spawn earlier than Atlantic salmon, with some variations among geographic races. Precise timing of upstream migration and egg deposition is regulated by river flow and temperature, and the maturation processes of an introduced population may be affected by environmental parameters, especially in delaying upstream migration.

Observations of pink salmon adult migration in the White Sea have indicated that reproduction was occurring one to two months prior to native salmon. The adults were selecting spawning grounds in very shallow waters, at sites not utilized by Atlantic salmon (Bjerknes and Vaag, 1981), generally in the lower course of the river, just above the tide mark. Spawning interaction seems to have been absent or minimal; however, in the case of large returns, which can occur with some year classes, pinks may require very wise spawning areas leading to colonization of upstream habitats, as observed in some rivers of Finnmark. Moreover, large egg deposits might have caused an avoidance effect on Atlantic salmon, due to pheromone releases (Lear, 1980).

Spawning of coho salmon, which generally occurs in autumn or early winter in New Hampshire introduced populations, was observed as late as March in 1971 (Stolte, 1974). Coho reared in fresh water in France reach maturity from late October to early December, a month before Atlantic salmon of local strains. Farming in sea water generally delays the maturation process, which may occur one or two months later than the normal date. Delayed maturation may thus result in an overlapping of spawning periods of both species.

Emergence and freshwater phase

Interspecific competition differs widely with the species considered. Pink salmon fry migrate downstream to the sea immediately after gravel emergency, at a time when Atlantic salmon alevins are still in the redds; subsequently, interaction is minimal, and to the disadvantage of the fry of Pacific species that have to pass through the habitat of fish of preceding year classes (Atlantic salmon, trout, pike), with consequent predation (Bakshtansky, 1980). Chum and fall chinook salmon feed for days, weeks or months in the river prior to migration. Coho and spring chinook, which stay in rivers for at least one year, present a higher competition potential for native salmonids. Because of earlier egg deposition, coho salmon should emerge before Atlantic salmon, in spite of a relatively longer incubation period. This fact, associated with the larger size of the fry, caused some authors to conclude that coho would be a severe potential competitor to *Salmo trutta* and *Salmo salar* (Euzenat and Fournel, 1981), with the argument that these phylogenetically closely related species did not have the opportunity to develop interspecific tolerance mechanisms because of their geographic isolation.

Gibson (1977), using an experimental approach in a stream tank, showed that "coho distributions are different when observed alone than when with either brook trout (*Salvelinus fontinalis*) or Atlantic salmon parr, but coho had little effect on the distribution of either of the two species". Interspecific displacements of coho by brook trout and Atlantic salmon were greater than displacements by coho of the other two species. Atlantic salmon parr appeared better adapted to the fast water environment than coho, and more adapted to a pool environment. Differences in preferential habitats were confirmed by Symons and Martin (1978) and Barbour *et al.* (1986) in a New Brunswick stream where juveniles of both species were discovered. Atlantic salmon were found occupying the steeper areas of fast flow, whereas brook trout occupied pools and quieter water. These experimental observations confirmed the results of Ruggles (1966) about the preferences of coho salmon for depth and current velocity. Coho were also found in pools, and less often in swampy areas where brook trout were abundant. In winter, some Atlantic salmon were found in deeper water in the brook trout/coho area. Heland *et al.* (1983), using an experimental spawning channel, monitored the downstream migration in streams containing either coho, Atlantic salmon, or an equal number of each species, all introduced as eggs. Survival, growth, and migration rates appeared identical in either isolation or competition situations. Another experiment, using three-month fingerlings, confirmed the low degree of interaction, although a density-dependent intraspecific effect was observed in coho. Laboratory tests indicated that in conditions where food abundance was reduced, coho might have a negative effect on the growth of Atlantic salmon.

The same authors, studying the chemosensory reactions to the upstream presence of fish, showed an attractant effect of Atlantic salmon parr on coho, and a repellent effect of coho on Atlantic salmon. Symons and Heland (1978) described the pursuing and predatory behaviour of yearling Atlantic salmon parr on fish from a younger class. This behaviour was later confirmed by Heland *et al.* (1983), who found that their predatory behaviour was even more active on coho fry up to 45 mm. The bottom territorial behaviour of Atlantic salmon gives them a definitive strategic advantage over the mid-water schooling behaviour of coho.

Although not abundant, the existing literature leads to the conclusion that a low level of interaction could exist between Pacific salmon juveniles and Atlantic salmon. Under a sympatric situation, coho and Atlantic salmon would have a tendency to specialize in different zones, but in the case of direct and severe confrontation, Atlantic salmon may be affected because of its slower growth. Competition between some *Oncorhynchus* species might be more significant with species such as brook or brown trout (Fausch and White, 1986).

Competition in coastal waters

The recent development of ranching techniques has resulted in important releases of fry or smolts in the North Pacific; the tremendous increase which is planned in the next twenty years has raised the question of potential overpopulation, and possible limited carrying capacity of the sea (Peterman, 1980). During their first summer at sea, juveniles of all species concentrate in a large mass which migrates continuously northwards through a relatively restricted coastal belt more than 1000 nautical miles long and continues for at least three months (Hart, 1980). This characteristic makes the juveniles more vulnerable to predation and disease. A substantial increase in numbers of juveniles may create competition for food. Such a phenomenon can only happen with large concentrations of fish, and seems unlikely to occur in the Atlantic at the present scale of introductions. Massive downstream migrations of actively feeding pinks, may, however, induce temporary perturbations in estuarine habitats; their fry may compete or be preyed upon by coastal marine species, as they cross feeding areas or migration routes of older classes of other species.

Genetic risks

The risk of natural hybridization between *Oncorhynchus* and Atlantic salmon has sometimes been raised as a possible negative consequence of Pacific salmon introductions. Within populations which are naturally interfertile, such as cutthroat and rainbow trout, the frequency of natural hybridization increases when one of them is artificially introduced in areas where the other species are in an allopatric situation. Such consequences cannot apparently occur between *Oncorhynchus* and European species, whose intergeneric hybrids are not viable in the diploïd form, at least for the cross of brown trout with coho or sockeye (Chevassus, 1979) or Atlantic salmon with coho (Blanc and Chevassus, 1979), or pinks (Loginova and Krasnoperova, 1982). The use of polyploidy techniques allows production of viable triploïd hybrids, for which the aquaculture potential has been assessed (Chevassus *et al.*, 1983).

Disease introduction

One major and real threat in the case of Pacific salmon introductions to Atlantic waters is the risk of introducing new diseases. It was shown 20 years ago that even when limiting the importations to the egg stage, viruses and bacteria could be transmitted on the surface or even inside the egg itself. Disease "profiles" of the five American species of *Oncorhynchus* have been reviewed by Wood (1974), Bell and Margolis (1976), and by Sindermann and Lightner (1988). Besides the chronic diseases of salmonids already present in European waters, such as furunculosis and vibriosis, diseases specific or characteristic of Pacific stocks must be looked at carefully.

Among the viral diseases, the major threat is Infectious Hematopoïetic Necrosis (IHN). Strictly confined to American and Pacific stocks until 1987, the virus has been found for the first time in Europe, in two French trout hatcheries, and apparently also in Italy (de Kinkelin *et al.*, 1987). This disease, which is quite close to the European Viral Hemorrhagic Septicemia (VHS), and essentially found in rainbow trout, is known to affect mainly chinook, sockeye, and chum salmon. It has also been observed recently in adult coho salmon contaminated by infected chinook broodstock (Hedrick *et al.*, 1987, cited in Hattenberger-Baudouy and de Kinkelin, 1988). Although the main vector of the disease is cultured rainbow trout, the occurrence of IHN in Japanese hatcheries seems likely to correspond with chinook and sockeye egg introductions from the United States (Sano, 1977; Kimura and Awakura, 1977). Such an eventuality should be assessed seriously when considering Pacific salmon egg transfers.

Experimental evidence for resistance to European VHS has been established in coho salmon (de Kinkelin *et al.*, 1974), chinook salmon (ORD, 1975), and experimental rainbow trout-coho salmon hybrids (Dorson and Chevassus, 1985). Infectious Pancreatic Necrosis (IPN), randomly present in all stocks of rainbow trout in Europe, is also ubiquitous in rainbow trout in North America, and has been found routinely in sockeye, chinook and, incidentally, in coho (Wainio, 1979, cited in Dumont *et al.*, 1988). It has never been found in introduced populations of coho salmon in France. Viral Erythrocytic Necrosis (VEN) has been observed in most species of salmon, but does not seem to be an acute threat to wild or cultivated stocks.

Among the bacterial diseases, furunculosis and vibriosis affect all species of *Oncorhynchus*, but the main problem may be caused by bacterial kidney disease (BKD). This gram positive rod can affect all species of salmonids, but the susceptibility of Pacific salmon seems to be very high. The pathogen may be vertically and horizontally transmitted, and can be diffused inside salmonid eggs. This disease, widespread in North America and associated with Pacific salmon and rainbow trout, is also endemic in some stocks of Atlantic salmon of the East coast (Pippy, 1969; Paterson *et al.*, 1980).

BKD was described first in Atlantic salmon stocks of the British Isles as "Dee disease" and has been found during the last ten years in cultivated populations of rainbow trout in the UK and Iceland. More recently, evidence of the disease was reported in Norway in reared Atlantic salmon. In France, the disease was first described by de Kinkelin (1975) in a coho salmon farm. Frequent reports of the disease are associated with the presence of coho salmon in hatcheries, and horizontal transmission to rainbow trout has been observed (Baudin Laurencin, pers. comm.). The disease does not usually create severe problems, but may develop following poor husbandry conditions. It has been identified as a cause of reduction in oceanic survival of Atlantic salmon, and to induce substantial mortalities in farmed coho salmon in fresh or sea water (Vigneulle *et al.*, 1977) and farmed pink salmon. Transmission through the gametes can be reduced by using erythromycin injections in broodstock and as a bath at fertilization, although the treatment is not totally reliable. Better prevention of disease transmission is obtained by using eggs from females certified free of the disease by individual inspection (using IFAT and filtration techniques or Elisa screening).

Pacific salmon species are undoubtedly the most sensitive to BKD, and the disease has been found in introduced farmed populations (Japan, Chile, France, Spain, eastern USA). However, the disease is or has been observed in other species in farmed or wild populations in the absence of Pacific salmon (eastern USA and Canada, British Isles, Iceland, Norway). The relatively recent discovery of the causative agent, and the fact that important numbers of *Oncorhynchus* eggs have been widely introduced in most countries during this century, might have facilitated an early dissemination of the disease in Atlantic waters, though this hypothesis remains quite speculative. Moreover, disease interactions between wild stocks and farmed populations may exist, as discussed by Evelyn (1987) for bacterial kidney disease.

Risks of overexploitation of native stocks

If important runs of introduced salmon develop in areas where more limited but valuable populations of Atlantic salmon exist, it is highly probable that a new fishery will develop to exploit the new resource. During high concentration periods in the coastal zone, chiefly spring or early autumn, increased and indiscriminate fishing pressure could seriously endanger a part of the run of Atlantic salmon.

4. Factors affecting success or failure in salmon introductions

The complex conditions necessary for successful introductions are inversely proportional to the degree of human intervention necessary to achieve the original objectives stated at the beginning of this paper. The path of successive questions to be answered is:

Level 1 – Can the species survive in captivity under the environmental conditions of the receiving country, either in fresh water or in the sea?

Level 2 – Can the fish thrive in marine waters if released and return to the release areas?

Level 3 – Can the population return with the precise timing required for reproduction, and produce viable sex products in sufficient numbers to perpetuate the activity?

Level 4 – Can the adults find an adequate spawning environment; and can the juveniles survive to smolt stage in the river?

Level 5 – Is the efficiency of the process sufficient to perpetuate self-sustaining populations?

All these conditions are related to the genetic adaptability of the species to the new environmental conditions encountered.

Can the species survive when reared in captivity?

Fish usually exhibit some flexibility in their environmental tolerances and Brett (1952) showed that the optimum growth temperature of Pacific salmon was slightly higher than their preferred temperatures. This fact allowed pioneer fish culturists like Donaldson in 1936 (cited in Davidson and Hutchinson, 1938) to determine an ideal temperature of 13 to 17°C for maximizing the growth of chinook juveniles; this finding applied fifty years later to coho salmon permits growth to at least equal rainbow trout in French commerical freshwater farms. Coho have shown aptitude to achieve smoltification at five months, but also to thrive when retained in fresh water beyond smoltification and to smolt again in autumn (Lasserre *et al.*, 1978).

In sea water, pink salmon have shown good adaptation to the temperature and salinity conditions of southern Norway (Gjedrem and Gunnes, 1978). After a critical period in the early summer of their first year, due to the combination of rapidly increasing temperatures and constant high salinity (Boeuf *et al.*, 1978), coho salmon show excellent growth during the following winter and summer, when they exhibit a high tolerance to oceanic salinity (35) and warm waters (Harache and Boeuf, 1986). This characteristic has been exploited in Japan, where the rearing season extends until August when temperatures exceed 21°C; at that time, coho salmon have reached an average size of 3 to 3.5 kg in 18 months from first feeding (Yoshida, 1985). Even more

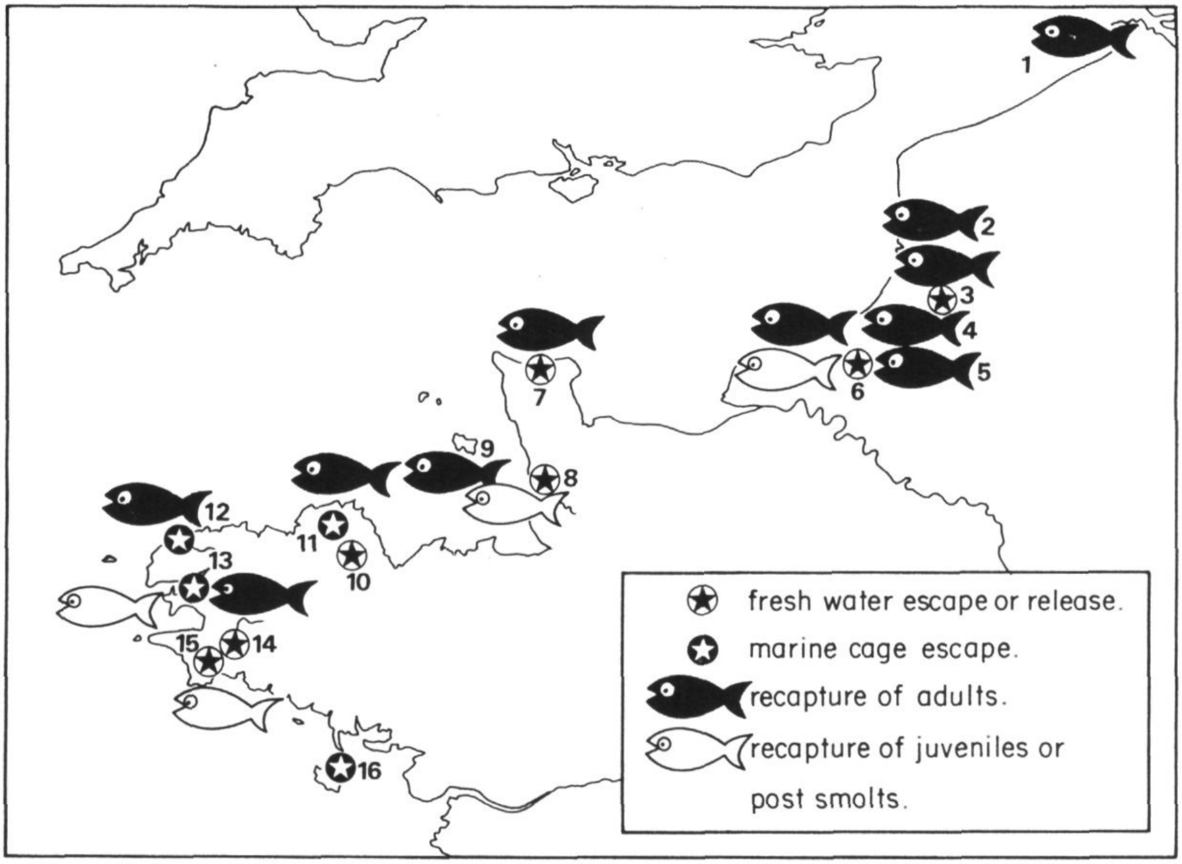


Figure 6. Escapes from aquaculture facilities and recaptures of coho salmon in Northwest France. 1 – Dutch Waters (1982). 2 – Canche (1975). 3 – Somme (1982). 4 – Bresle (1975). 5 – Eaulne (1975). 6 – Varenne (1974–1977). 7 – Bay of Cherbourg (1979–1983). 8 – Sienne (1977). 9 – Channel Islands (1977). 10 – Leff (1975–1988). 11 – Jaudy (1975–1988). 12 – Aber Wrach (1988). 13 – Bay of Brest (1977). 14 – Odet (1976). 15 – Coastal stream (1988). 16 – Belle Ile (1975).

surprising are the favourable results obtained in hypersaline waters (36–37‰) in Yugoslavia at higher salinities.

As opposed to the disappointing results of attempts to establish natural runs, the introduction of Pacific salmon for intensive aquaculture has shown several recent examples of real success in both hemispheres, leading to a total farmed production of about 30 000 tonnes in 1990 outside the natural range of the species.

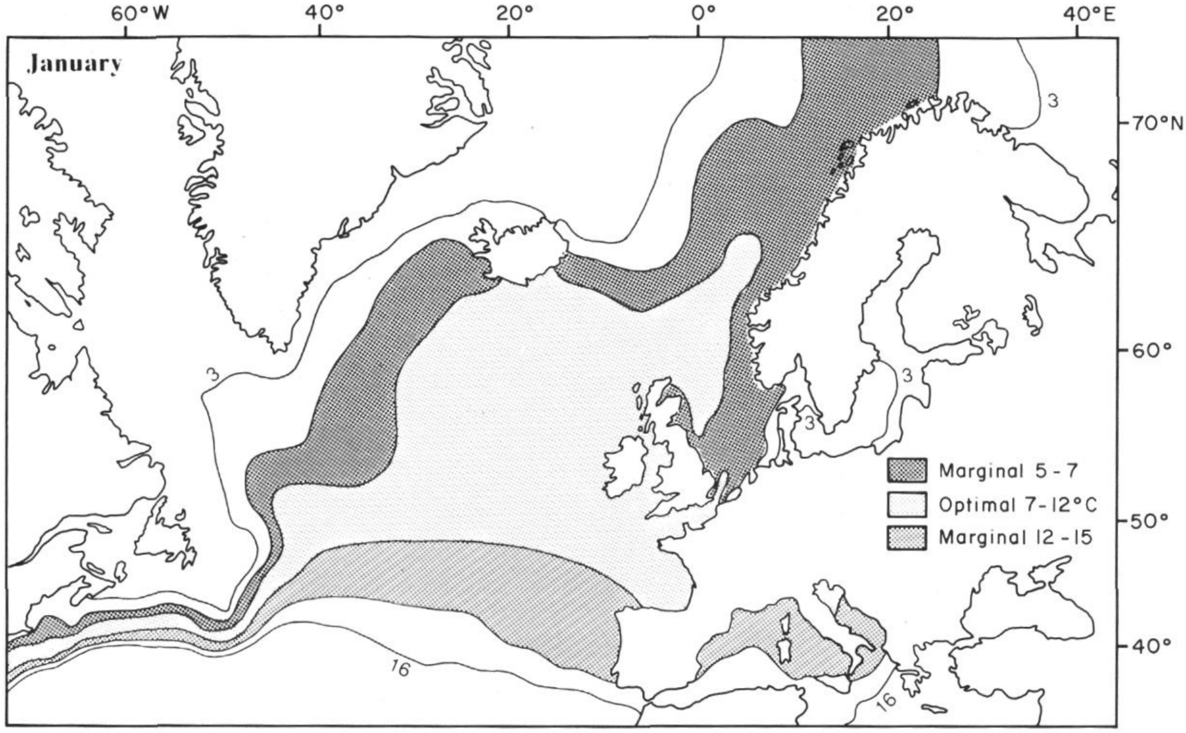
Can the fish thrive in the ocean when released and return to waters of release to reproduce?

The introduction of coho salmon in New Hampshire and the transplants of pink salmon in Newfoundland, in the White and Barents Seas, as well as the early establishment of temporary Pacific salmon runs in the Northwestern Atlantic show clearly that fry or smolts can survive and that adults can return to the release areas and reproduce, even under environmental conditions not corresponding to their native habitat. More surprising is the observation of adult returns and viable spawning of coho in streams of Normandy (France), in an oceanic area which can be considered marginal for the species. Furthermore, escapes of subadults in Brittany have shown that the fish were remaining and growing in the immediate cage area, like delayed smolts in Puget Sound (Novotny, 1980), in spite of elevated summer temperatures and salinities. All these examples show a remarkable phenotypic adaptability to new environments. However, the survival at sea is systematically lower and straying more important than that of the original donor stocks.

Can the species return in sufficient numbers to perpetuate the population?

Oceanic physical environment

The reasons for low return rates may be multiple and may vary with the species and geographic areas considered. The analysis of hydrographic conditions of the Atlantic Ocean (Robinson *et al.*, 1979) shows a completely different pattern when compared to those of Pacific waters (Figs. 7–8). Salinities are systematically



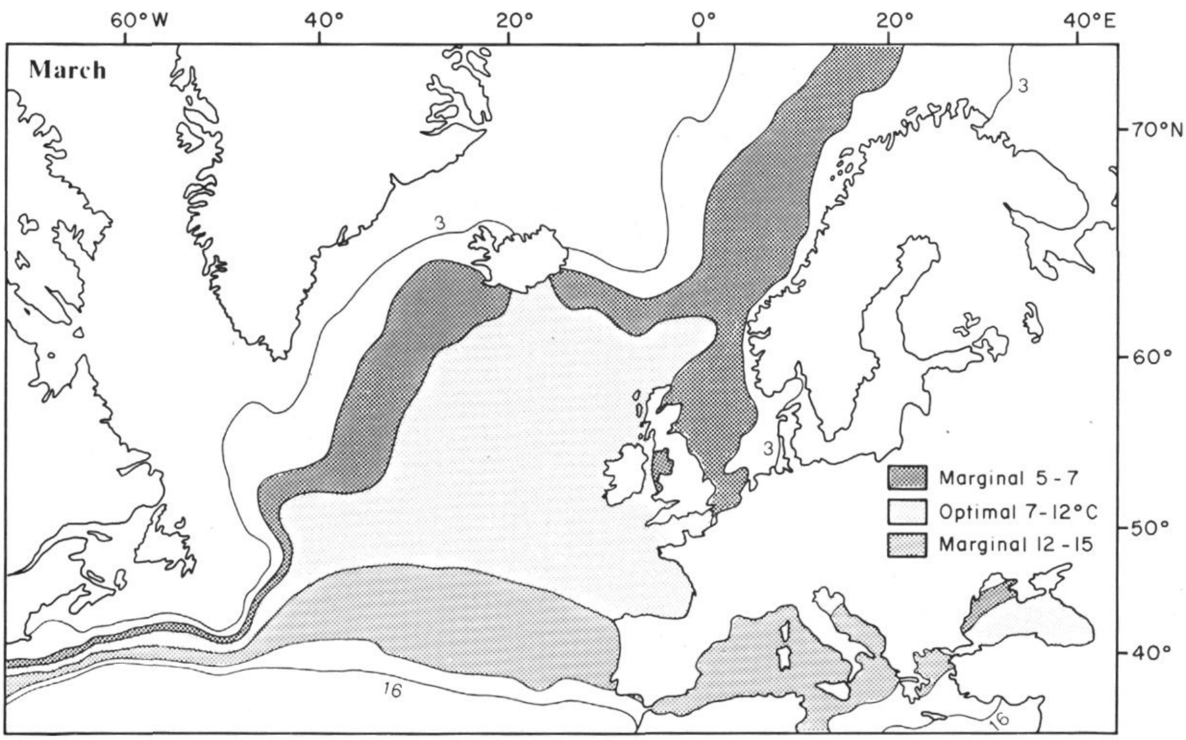
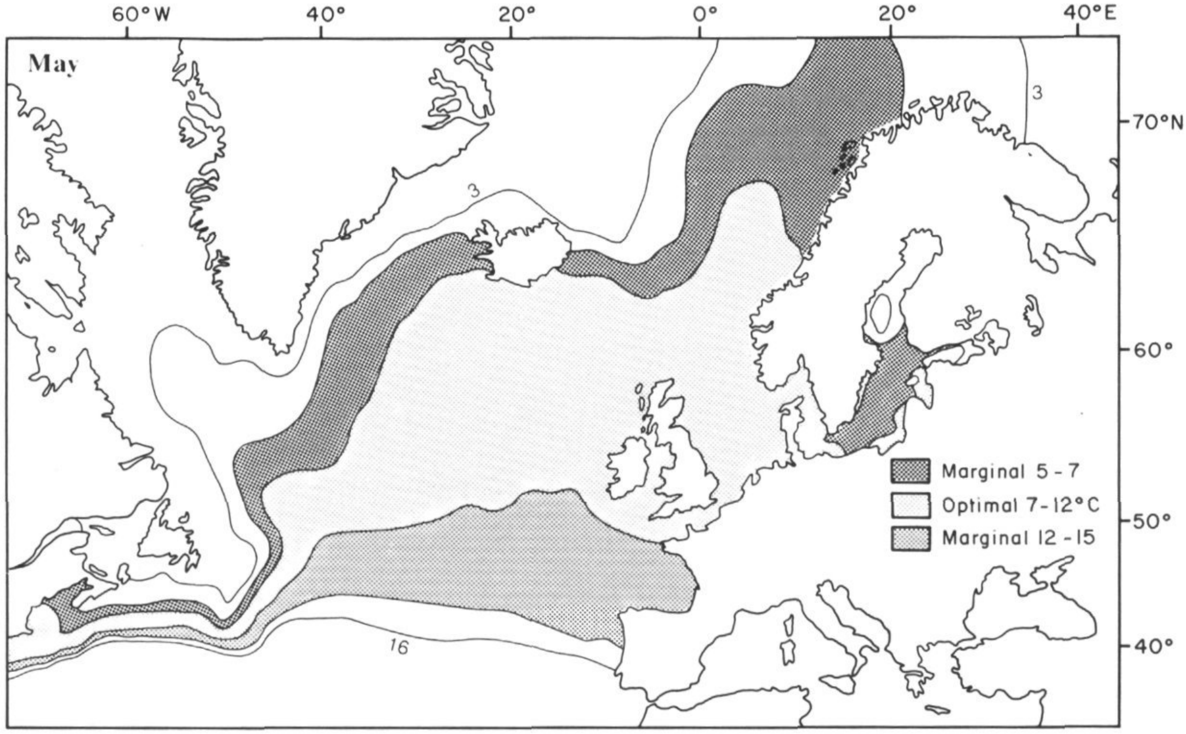


Figure 7. Average sea surface temperatures of the North Atlantic Ocean (adapted from Robinson *et al.*, 1979). Preferred and tolerable preference are given for coho salmon according to Manzer *et al.*, 1974. (*Continued overleaf.*)



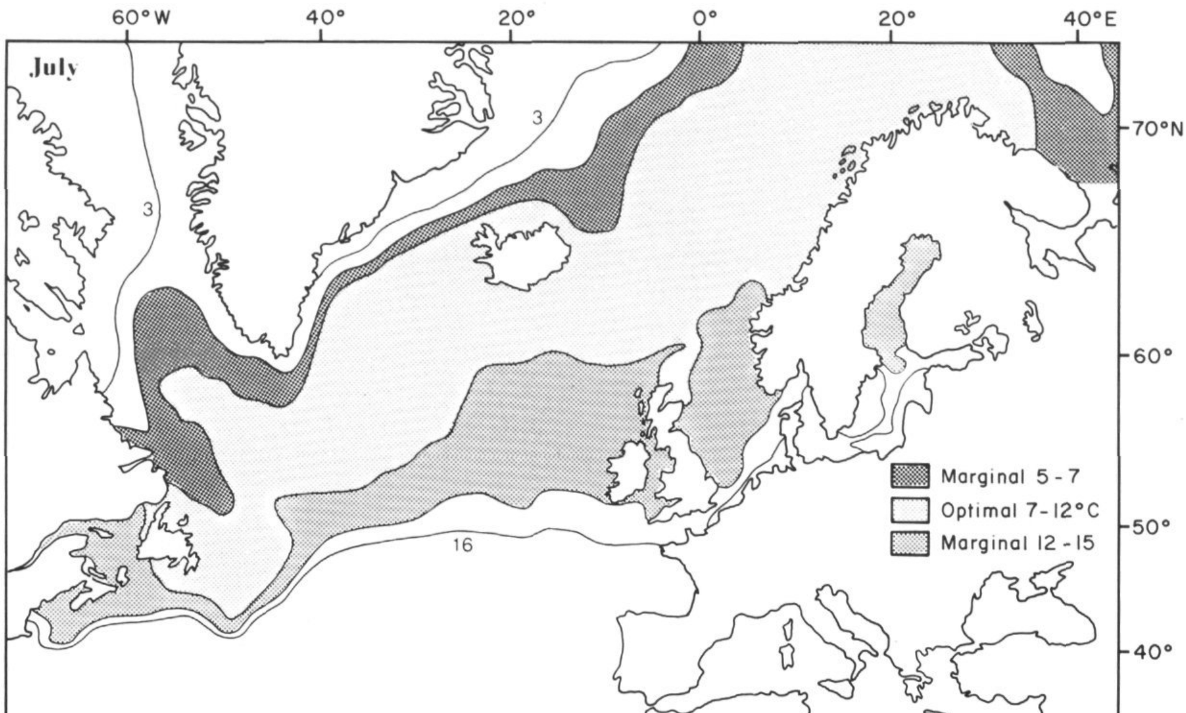
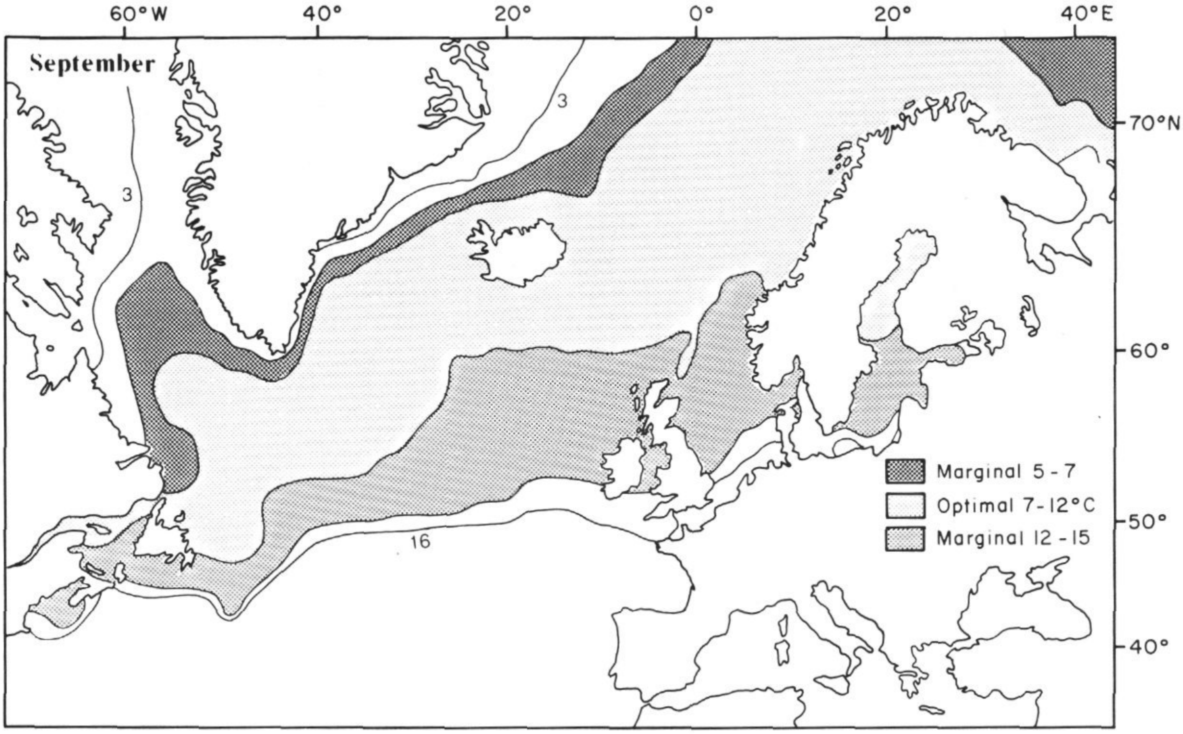


Figure 7 *continued.*



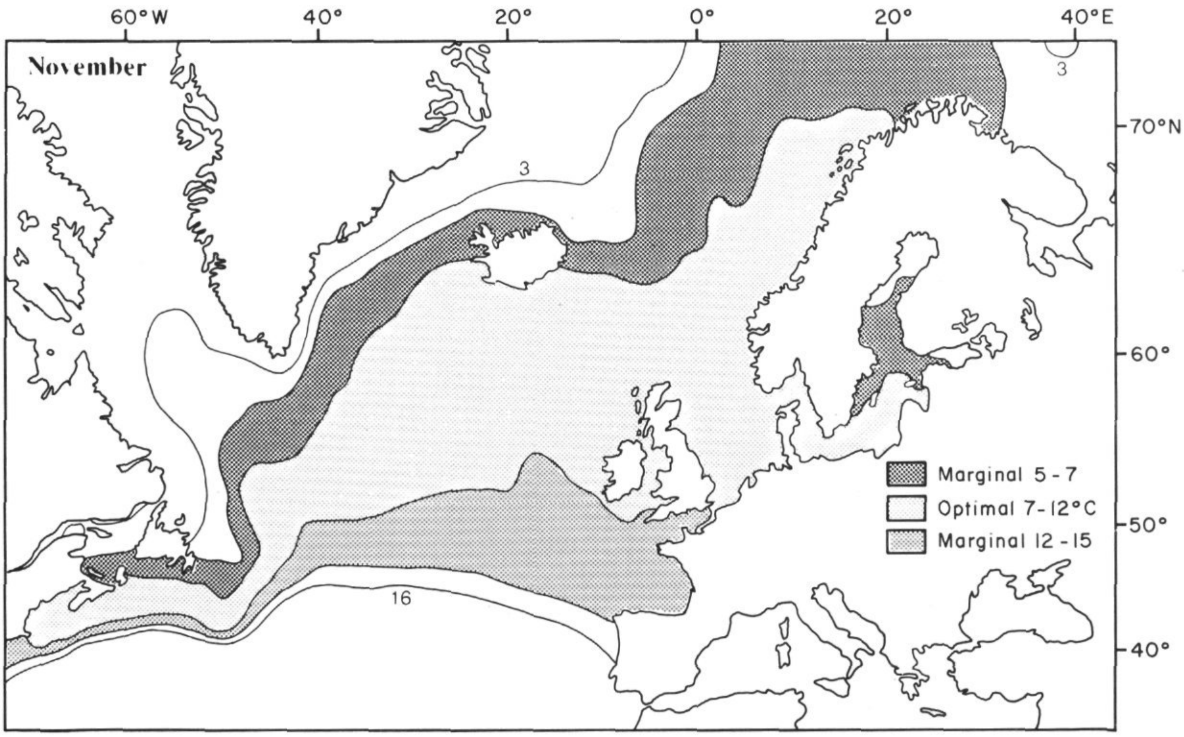


Figure 7 *continued.*

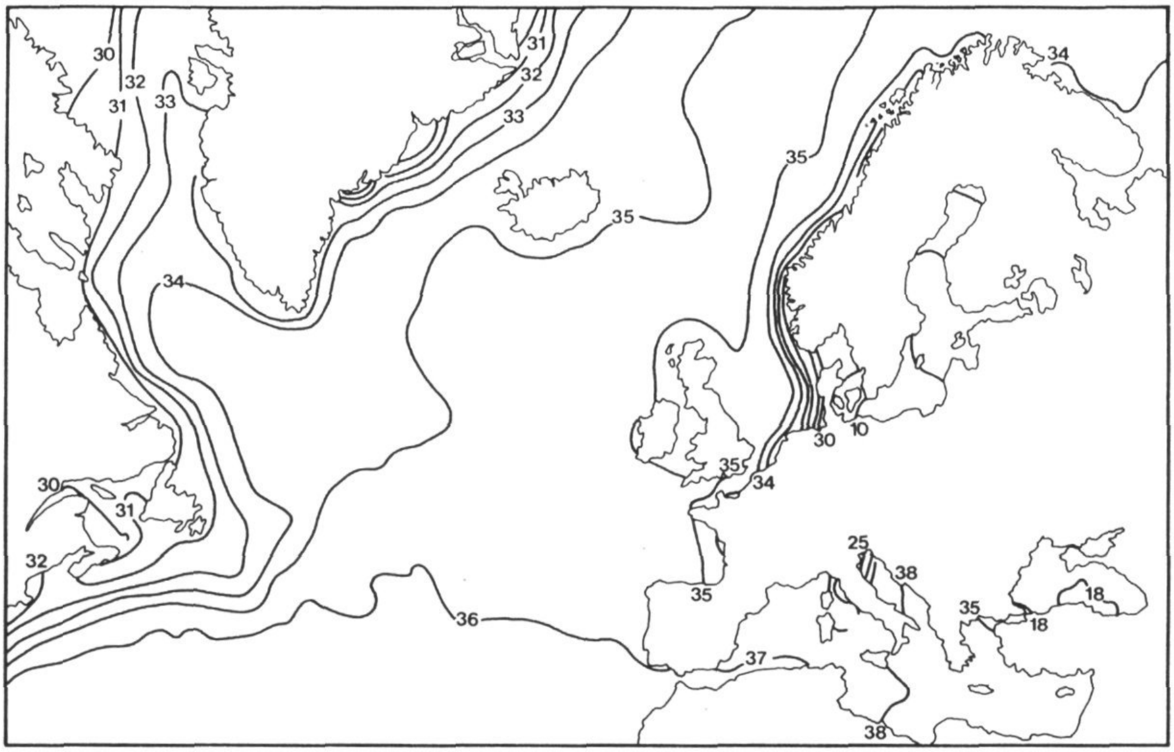


Figure 8. Mean average surface salinities of the North Atlantic.

more elevated in the open ocean and coastal zones, and temperatures present more important annual variations with very different regimes on both sides of the Atlantic. The North American coast has continental type characteristics, with a cold influence of the Labrador Current and marked thermal fronts; the European coasts present mild temperatures influenced by the Gulf Stream, and are isolated from exchange with cooler water due to the shallow waters of western Europe.

When one considers that Pacific salmon are stenothermic animals, thriving in the cool and moderate salinity waters of the North Pacific (Manzer and Ishida, 1963) and whose migrations are associated with specific current regimes, it is not surprising that survival is low and highly variable. Boeuf *et al.* (1978) have shown that coho salmon smolts exhibit a more pronounced osmotic stress when transferred to sea water of 35‰ than at lower salinities. However, if we except this critical life phase, Pacific salmon may not be so specific about this parameter (Joyner, 1973a). Within their original distribution range, they are not found south of the 33–34% surface isohalines. But this limit probably corresponds to the 15°C summer surface isotherm, since salinities of 35‰ are found only in areas where the average summer temperature exceeds 25°C. The case of successful introduction of chinook in New Zealand, in waters of high salinity and marginal temperatures in some coastal areas, shows that within certain conditions the species may adapt to a new and different environment. The use of selected geographic races was recommended by Joyner (1973b) to match particular waters of New England states. Some areas of the North Atlantic may present adequate environmental conditions for Pacific species. But how do introduced species find them and subsequently find their way back to "home" waters for spawning?

Orientation and migration patterns

Neave (1964) has discussed the features of ocean migration patterns and guidance mechanisms of Pacific salmon. Salmon use ocean currents, gyres, and eddies for their migrations, but they also migrate across oceanic areas and major current features. Balchen (1979) described the migration of fish as the consequence of a continuous process for "maximizing comfort". This involves "enviroregulation" mechanisms (McNeil, 1984) allowing the fish to select its migration routes, which may vary with species and biological stages. Celestial orientation of sockeye smolts combined with magnetic guidance has been clearly demonstrated by Brannon (1981, 1984). Quinn (1984a, b) discussed the hypothesis of magnetic field orientation in explaining the rapid (46–56 km/day) and constantly oriented approach of sockeye adults in Bristol Bay (Alaska). Harden Jones (1984) discussed the possible use of inertial clues in fish migration. Cook (1984) presented an interesting approach of orientation of Atlantic salmon with oceanic swells, and Isaksson (1980) showed the relationship of Icelandic salmon migrations with eddies situated in the Irminger, Icelandic, and Norwegian Seas.

All these mechanisms clearly rely on inherited responses to guidance stimuli (Burgner, 1980), which result in genetically determined preferential routes. Brannon (1984) described the different migration routes (north and south) of coho stocks from two tributaries of the Columbia River, concluding that adult migration appears to follow an innately directed pattern, while homing is directed by cues acquired during emigration. The role of olfactory orientation of fish, imprinted by morpholine (Hasler *et al.*, 1978), pheromones, skin mucus, or biliary salts has been discussed by Hara *et al.* (1984).

Unexpected or changing situations may affect the original scheme. Timing of the adult sockeye run of Bristol Bay (Alaska) has been shown to be strictly dependent upon oceanic spring surface temperatures (Burgner, 1980), and returns of coho or chinook in New England may be affected or delayed by a warm thermal front (Joyner, 1973b). The existence of "salmon holes" in the North Pacific, from which no tagged salmon ever return, has been established by Harden Jones (1984). The phenomenon of salmon "lost at sea", probably induced by specific hydrographic conditions, such as sinking of surface water, could account for the loss of a limited proportion of some populations, since "no species could have evolved to depend on a pattern of migratory behaviour which would allow a significant proportion of the stock to be lost for reproduction".

The adaptation of a given strain to a specific migration pattern may imply lack of adaptation to other situations. Such inadaptations have been identified as a major cause of failure when stocking sockeye and pink salmon within their own range. Pink salmon of Washington origin have established temporary populations in Maine, whereas Alaskan strains gave no returns (Ricker, 1954). General orientation of the preferred emigration and homing routes should be assessed carefully when considering a transplantation, and it is possible that the choice of Asian populations for introduction in the Northwest Atlantic, as well as North American stocks for northern Europe, would have provided better results.

Very little is known about the oceanic behaviour of Pacific salmon in Atlantic waters. Apparently, coho salmon introduced on both shores of the ocean have shown a marginal migration, and recaptures remain limited to coastal waters. They may not express the adequate migratory behaviour which could allow them to colonize more optimum areas where the bioenergetic cost would be minimal. Conversely, early pink salmon captures have indicated a wide dispersion in the North Atlantic following the first plantings in the Kola Peninsula, allowing this species to select foraging areas not too different from its temperature preference. It seems likely, however, that in both cases the proportion of fish either "lost at sea" or suffering from extreme hydrographic conditions may be high, as their adaptive mechanisms may prove to be inoperative in a very different oceanic regime.

Food source and interaction with other species

Juveniles show specific feeding behaviour at the beginning of their marine life (Healey, 1980). Chum salmon are mainly dependent upon small copepods; pink salmon concentrate on copepods and euphausid eggs; chinook and coho salmon exhibit a comparable behaviour and feed preferentially on larger invertebrates and fish (herring). Pink salmon move rapidly into the sea, whereas the other species remain for a longer time in estuarine nurseries. At later stages, Pacific species all feed on fish or cephalopods. Pink salmon transferred to the Atlantic have been shown to feed on capelin (*Mallotus villosus*), exactly like grilse of Atlantic salmon (Bakshtansky, 1980).

Unavailability of food with ideal characteristics should not be overlooked as a possible cause of low survival, especially when very large numbers of fry enter the same area at the same time (in the case of pink salmon for instance). However, the growth of introduced populations, which appears to be similar to the original stocks, shows that these opportunistic feeders have found an adequate food supply in the release areas. Competition for the same sources of food with native species of marine fish, and predation, can also represent causes of reduced survival (Lear, 1980). Bakshtansky (1980) explained that catches of pink salmon were only large when herring (*Clupea harengus*) had not been caught close to the river at the time of fry migration; he also reported heavy predation by saithe (*Pollachius virens*) and cod. The artificial rearing of fry in captivity, allowing release of larger individuals into the ocean only when the source of food has been found adequate through plankton counts, as practised in Japanese and Alaskan hatcheries for pink and chum salmon, allowed a significant improvement in the rate of survival of the "ranched" populations.

Can natural reproduction produce sufficient numbers of downstream migrants to perpetuate a self-sustaining population?

Important interannual fluctuations are observed in all anadromous populations, which depend upon both the river and the oceanic phases. Among Pacific species, pink salmon are the most vulnerable because of their simple and unvarying two-year life cycle (McNeil, 1980). Their fragility is mostly due to the importance of survival in fresh water. If the progeny of one brood year is destroyed by adverse climatic conditions, the run will disappear from the river, except if straying from neighbouring populations is sufficient to supply a new run. Other populations are protected "in time" by a complex age structure or repeated spawning. Pink salmon have developed a "protection in space", through an enormous abundance of small downstream migrants, large spawning, and feeding areas, and an imprecise homing instinct (Bakshtansky, 1980). Considering these facts, critical freshwater temperatures are most likely responsible for the relatively poor success of pink salmon transplants in the North Atlantic.

When salmon are removed from their original environment they become exposed to a new set of environmental experiences (McNeil, 1980). Salmon populations have to specialize within their own environment to maximize their survival, allowing specific adaptation to river and marine environments, migration patterns, and food selectivity. It is probable that many of these adaptations could be inoperative in the new receiving environment, and that the fish would have to specialize to face new challenges. With that prospect, salmon will need a maximum of genetic variability to succeed. Because of this, not only should a careful selection of the donor stocks, including environmental preferences and general migration patterns, be looked for, but several stocks with these characteristics should be used. Ricker (1954) stated that "relatively large plantings should be made in one or a few sites, so that there will be an adequate expandable surplus while the selection process is weeding out genes whose effects are in poor adjustment to the new situation". In the various experiments documented in this paper, one could consider that with the exception of the Russian experiment the numbers released were probably insufficient to meet these requirements.

Conclusion

Oncorhynchus introductions to Atlantic waters have neither provided "miraculous" fisheries, nor wiped out valuable native stocks. Viewed from a certain distance, one could summarize a century of transfers as follows:

Pacific salmon when released in Atlantic oceanic areas have shown in several of the cases an aptitude to survive, grow, home, and spawn, even in areas where environmental characteristics are substantially different from their home waters. Survival rates have been generally much lower than in the original range, and straying relatively important. Subsequently, the returning populations have been generally limited.

All attempts to establish durable naturally reproducing sea-going populations have failed in the northern hemisphere, and the case of New Zealand, where permanent populations of chinook established rapidly, remains unique. However, if we exclude the limited initial transplants of the last century, one may note that most of the transplants were made in areas which did not satisfy the optimum requirements of the species, and where temperature regimes were probably the main limiting factors.

In order to maintain exploitable "wild" introduced populations, the use of "ranching" techniques, either to totally "build" the runs at each generation (New Hampshire) or to support the variable natural reproduction (Kola Peninsula, northern Norway), appears necessary. However, in economic terms, some of these experiments may be beneficial because of the low cost of juveniles.

The ecological effects of introduced populations of Pacific salmon on native stocks in the Atlantic Ocean appear to have been limited in all documented cases, as shown by both direct observations and experimentation. The threat of spreading disease when displacing live fish is more serious. Even more than in terrestrial agriculture, the intensification of aquatic farming will increase the risks. Diseases will probably be as important in transfers of farmed populations within their original range (i.e. smolts of Atlantic salmon transferred to or from Norway, daily shipments of live rainbow trout, or increasing movements of turbot (*Psetta maxima*) or sea bass (*Dicentrarchus labrax*) larvae across Europe) as in the case of the importation of Pacific salmon to Atlantic waters. However, the risk of disseminating diseases such as bacterial kidney disease through Pacific salmon introductions is high and must be evaluated seriously.

The emergence of marine aquaculture less than 30 years ago permitted the transformation of a wild fish – the Atlantic salmon – into a semi-domesticated animal extensively farmed in Europe, but also in Western Canada and the United States, Chile and Tasmania. Pacific salmon culture, using mainly "wild stocks" of chinook and coho, is now flourishing in Japan and Chile, and emerging in France, Spain, and Italy in fresh and sea water. Real problems are induced by salmon farming development, but the philosophical aspects of the debate about the best choices of rearing *Oncorhynchus* in Atlantic waters or Atlantic salmon in Pacific waters may be a little futile in view of the real genetic risks to wild populations created by the development of intensive farming of Atlantic salmon within its own natural range. Unavoidable escapes will allow the dissemination of farmed animals in coastal areas, and for stocks which are interfertile a high probability of hybridization with wild stocks exists, subsequently reducing genetic variability. In this respect, the genetic risk for native populations seems real, when an important industry is being developed with the indigenous species.

Considering the time scale of evolutionary processes, the tremendous acceleration of human intervention with aquatic species over a very limited period of time could be considered as the "prehistory" of fish management. The rapid evolution of scientific knowledge and technology will most certainly generate more projects, including species transfers. The debate is only beginning, and the creation of a special working group on the subject through the ICES structure has marked a very important step towards an international understanding and management of these problems. The ICES "Code of Practice" has represented a positive approach to the problem, mainly in encouraging a more precise assessment of the possible consequences before any action takes place. Much more remains to be achieved in view of the probable increase in movements of live animals that will be associated with the development of sea farming throughout the world.

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References

Agapov, V. S. 1979. Natural reproduction in some rivers of the Kola Peninsula. *In* Problems in mariculture. Ed. by N. E. Salnikov. VNIRO, 138: 73–81.

Anon. 1972 to 1988. Annual Reports, New Hampshire Fish and Game Dept. Division of Inland and Marine Fisheries.

Anon. 1987. United States of America National Report. ICES Working Group on Introductions and Transfers of Marine Organisms. Brest (France), June 1987.

Balchen, J. G. 1979. Modeling, prediction, and control of fish behaviour. *In* Control and dynamic systems. 15, pp. 99–146. Ed. by Leondes. Academic Press, New York.

Bakshtansky, E. L. 1980. Introduction of pink salmon into the Kola Peninsula. *In* Salmon ranching, pp. 245–259. Ed. by J. Thorpe. Academic Press, London.

Barbour, S. S., Morantz, D. L., and Swinney, R. K. 1986. Habitat use by feral coho salmon and Atlantic coast salmonids in a Nova Scotia river. 116th Annual meeting AFS/IAFWA; Rhode Island, 14–18 Sept.

Bell, G. R., and Margolis, L. 1976. The Fish Health Program and the occurrence of fish diseases in the Pacific region of Canada. Fish Pathol., 10: 115–122.

Bellet, R. 1975. L'élevage du saumon de mer en eau douce. La pisciculture Française, 75.

Berg, M. 1961. Pink salmon (*O. gorbuscha*) in northern Norway in the year 1960. Acta Borealis, 17: 1–24.

Berg, M. 1977. Pink salmon (*O. gorbuscha*). Norway. Inst. Fresh. Wat. Res., Drottningholm, 56: 12–17.

Bigelow, H. B., and Schroeder, W. C. 1953. Fishes of the Gulf of Maine. US Fish. Wildl. Serv. Fish. Bull., 74: 577 pp.

Bjerknes, V., and Vaag, A. B. 1980. The status of pink salmon in north Norway. ICES CM 1980/M: 16. 11 pp.

Bjerknes, V., and Vaag, A. B. 1981. Migrations and catch statistics of the pink salmon (*O. gorbuscha*) in the Finnmark area, northern Norway. J. Ichthiol., 21(1): 48–53.

Blair, A. A. 1968. Pink salmon find new home in Newfoundland. Fish. Can., 21: 9–12.

Blanc, J. M., and Chevassus, B. 1979. Interspecific hybridization in salmonid fish. I – Hatching and survival up to the 15th day after hatching. Aquaculture, 18: 21–34.

Boeuf, G., Lasserre, P., and Harache, Y. 1978. Osmotic adaptation of *Oncorhynchus kisutch* Walbaum. II – Plasma osmotic and ionic variations and gil Na+ K+ ATPase activity in yearling coho salmon transferred to sea water. Aquaculture, 15: 35–52.

Brannon, E. L. 1981. Orientation mechanisms of homing salmonids. *In* Salmon and trout migratory behaviour symposium. Ed. by E. L. Brannon and E. O. Salo. Traduit dans Saumons, 52: 3–8 (1985).

Brannon, E. L. 1984. Influence of stock origin on salmon migratory behaviour. *In* Mechanisms of migration in fishes. NATO Conference series, IV: Marine Sciences: 103–111. Ed. by J. D. McLeave, G. P. Arnold, J. J. Dodson, and W. J. McNeil.

Brett, J. R. 1952. Temperature tolerance in young Pacific salmon genus *Oncorhynchus*. J. Fish. Res. Bd. Can., 9(6): 265–323.

Burgner, R. L. 1980. Some features of ocean migrations and timing of Pacific salmon. *In* Salmonid ecosystems of the North Pacific, pp. 153–164. Ed. by W. J. McNeil and D. C. Himsworth. Oregon State University Press.

Chevassus, B. 1979. Hybridization in aquaculture. Aquaculture, 17: 113–128.

Chevassus, B., Guyomard, R., Chourrout, D., and Quillet, E. 1983. Production of viable hybrids in salmonids by triploïdization. Genet. Sel. Evol., 15(4): 519–532.

Cook, P. H. 1984. Directional information from surface swell: some possibilities. *In* Mechanisms of migration in fishes. NATO Conference series, IV: Marine sciences: 79–101. Ed. by J. D. McLeave, G. P. Arnold, J. J. Dodson, and J. W. McNeil.

Davaine, P. 1991. Sea ranching of coho salmon in the Kerguelen islands (TAAF). ICES CM 1991/M: 20, 10 pp.

Davidson, F. A., and Hutchinson, S. J. 1938. The geographic distribution and environmental limitations of the Pacific salmon (genus *Oncorhynchus*). Bull. Bur. Fish., Wash., 48: 667–692.

Dempson, J. B. 1980. Present status of pink salmon in the Newfoundland region. ICES CM 1980/M: 27, 6 pp.

Dermott, R. M., and Timmins, C. A. 1986. Occurrence and spawning of pink salmon in Lake Ontario tributaries. Can. Field. Nat., 100: 131–133.

Dorson, M., and Chevassus, B. 1985. Etude de la receptivité d'hybrides triploïdes truite arc-en-ciel x saumon coho à la Nécrose Pancréatique Infectieuse et à la Scepticémie Hemorrhagique Virale. Bull. Fr. Pêche Pisc., 296: 29–34.

Dumont, P., Bergeron, J. F., Dulude, P., Mailhot, Y., Rouleau, A., Ouellet, G., and Lebel, J. P. 1988. Introduced salmonids: where are they going in Quebec watersheds of the Saint-Lawrence River. Fisheries, 13(3): 9–17.

Emery, L. 1985. Review of fish species introduced into the Great Lakes, 1819–1974. GLFC, Ann Arbor MI, Tech. Rep. GLFC, 31, 45 pp.

Euzenat, G., and Fournel, F. 1981. L'introduction des saumons du pacifique en France. Rapp. Conseil Supérieur de la Pêche, 111 pp.

Evelyn, T. P. 1987. BKD carriers in wild salmonid populations spreads in fish farms. Prevention and control, screening techniques. Conference on fish diseases, NORAQUA, Trondheim, Norway, 13–17 Aug.

Everhart, W. H. 1966. Fishes of Maine. Pub. Maine Dept. Inland Fish. Game. 94 pp.

Fausch, K. D., and White, R. J. 1986. Competition among juveniles of coho salmon, brook trout and brown trout in a laboratory stream, and implications for Great Lakes tributaries. Trans. Am. Fish. Soc., 115: 363–381.

Fawcett, R. S., and Sower, S. A. 1986. Introduction of coho salmon in New Hampshire. 116th Annual Meeting AFS/IAFWA; Rhode Island, 14–18 Sept.

Garrison, R. L. 1967. Coho salmon smolts in ninety days. Prog. Fish. Cult., 29(4): 219–220.

Gibson, R. J. 1977. Behavioural interactions between juvenile coho salmon, juvenile Atlantic salmon and brook trout. ICES CM 1977/M: 23.

Gjedrem, T., and Gunnes, K. 1978. Comparison of growth rate in Atlantic salmon, pink salmon, arctic char, sea trout and rainbow trout under Norwegian farming conditions. Aquaculture, 13: 135–141.

Grinyuk, I. N., Kanep, S. V., Salmov, V. Z., and Yakovenko, M. Y. 1978. Effect of ecological factors upon pink salmon populations in basins of the White and Barents Sea. ICES CM 1978/M:6, Anadromous and Catadromous Fish Committee. 6 pp.

Gudjonson, T. 1961. Occurrence of pink salmon (*O. gorbuscha*) in Iceland in 1960 and 61. ICES, Salmon and Trout Committee. 7 pp.

Hara, T. J., McDonald, S., Evans, R. E., Marui, T., and Arai, S. 1984. Morpholine, bile acids, and skin mucus as possible chemical cues in salmonid homing. *In* Mechanisms of migration in fishes. NATO Conference series, IV: Marine sciences: 363–378. Ed. by J. D. McLeave, G. P. Arnold, J. J. Dodson, and W. J. McNeil.

Harache, Y., and Novotny, A. J. 1976. Coho salmon farming in France. Mar. Fish. Rev., 38(8): 1–8.

Harache, Y. 1979a. Coho salmon farming in France. Fish Farmer, 2(1,2).

Harache, Y. 1979b. Reproduction in captivity of coho salmon. ICES CM 1979/F:51: 10 pp.

Harache, Y., Boeuf, G., and Lasserre, P. 1980. Osmotic adaptation of *Oncorhynchus kisutch* Walbaum. III – Survival and growth of juvenile coho salmon transferred to sea water at various times of the year. Aquaculture, 19: 253–273.

Harache, Y., and Prouzet, P. 1981. A proposal concerning studies of coho salmon and native salmon interactions in France, with comments from the Working Group on the Introduction of Non-Indigenous Marine Organisms. ICES CM 1980/E: 60.

Harache, Y., and Boeuf, G. 1986. L'élevage du saumon coho. *In* La salmoniculture marine, La Pisciculture, Française, 6: 57–61.

Harden-Jones, F. R. 1984. A view from the ocean. *In* Mechanisms of migration in fishes. NATO Conference series, IV: Marine sciences: 1–26. Ed. by J. D. McLeave, G. P. Arnold, J. J. Dodson, and W. J. McNeil.

Hart, A. C. 1980. Juvenile salmonids in the oceanic ecosystem – the critical first summer. *In* Salmonid ecosystems of the North Pacific, pp. 25–57. Ed by W. J. McNeil and D. C. Himsworth. Oregon State University Press.

Hasler, A. D., Scholtz, A. T., and Horral, R. M. 1978. Olfactory imprinting and homing in salmon. American Scientist, 38, May–June: 347–355.

Hattenberger-Baudouy, A. M., and de Kinkelin, P. 1988. La Nécrose Hématopoïetique des salmonidés. La pisciculture Française, 91: 7–13.

Healey, M. C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. *In* Salmonid ecosystems of the North Pacific, pp. 203–229. W. J. McNeil and D. C. Himsworth. Oregon State University Press.

Hedrick, R. P., La Patra, S. L., McDowell, T., and Wingfield, W. H. 1987. Infectious Haematopoïetic Necrosis (IHN) appearance in a new species. Third International Conference of the European Association of Fish Pathologists. Bergen, abstract no. 22.

Heland, M., Beall, E., Marty, C., and Saglio, P. 1983. Compétition interspécifique entre juvéniles de saumon coho (*O. kisutch*) et de saumon Atlantique (*Salmo salar*) en eau douce. Contrat CNEXO-INRA 86/2560. Rapport final. 37 pp.

Huntsman, A. G., and Dymond, J. R. 1940. Pacific salmon not established in Atlantic waters. Science, 91: 447–449.

Isaksson, A. 1980. Salmon ranching in Iceland. *In* Salmon ranching, pp. 131–156. Ed. by J. Thorpe. Academic Press.

Jaegoe, C. J., Small, R. L., Blake, L. M., Woodward, D. C., Smith, J. R., and Moring, J. R. 1981. Commercial aquaculture of salmon in Maine: status and future prospects. Fisheries, 6(5): 16–24.

Joyner, T. 1973a. Salmon for New England fisheries. Part 1: Historical background. Mar. Fish. Rev., 35(10): 1–3.

Joyner, T. 1973b. Salmon for New England fisheries. Part II: Effect of Ocean environment on the high seas distribution of salmon. Mar. Fish. Rev., 35(10): 4–8.

Joyner, T., Mahnken, C. V., and Clark, J. R., 1974. Salmon – future harvest from the Antarctic Ocean? Mar. Fish. Rev., 36(5): 20–28.

Joyner, T. 1976. Farming ocean ranges for salmon. J. Fish. Res. Bd Can., 33(4): 902–904.

Joyner, T. 1980. Salmon ranching in South America. *In* Salmon ranching, pp. 261–276. Ed. by J. Thorpe. Academic Press.

Kimura, T., and Awakura, T. 1977. Current status of diseases of cultured salmonids in Hokkaido, Japan. Proceedings of the International Symposium on Diseases of Cultured Salmonids, pp. 124–161. Seattle, 4–6 April, 1977. Ed. by Tavolek.

de Kinkelin, P., Le Berre, M., and Meurillon, A. 1974. Scepticémie hémorrhagique virale: démonstration de l'état réfractaire du saumon coho (*Oncorhynchus kisutch*) et de la truite fario (*Salmo trutta*). Bull. Fr. Pisc., 253: 166–175.

de Kinkelin, P. 1975. Corynebactériose des salmonidés: première observation en France. Bull. Fr. Pisc, 254: 3–8.

de Kinkelin, P., Hattenberger, A. M., Torchy, C., and Liefrig, F. 1987. Infectious Hematopoïetic Necrosis (IHN) virus: first report in Europe. Third International Conference of the European Association of Fish Pathologists. Bergen, abstract no. 57.

de Kinkelin, P. 1987. La nécrose hématopoïétique des salmonidés. La Pisciculture française, 91: 7–9.

Lasserre, P., Boeuf, G., and Harache, Y. 1978. Osmotic adaptation of *Oncorhynchus kisutch* Walbaum. *In* Seasonal variations of the gill Na+ K+ ATPase activity in coho salmon, O+ age and yearling, reared in freshwater. Aquaculture, 15: 365–382.

Lear, W. H. 1975. Evaluation of transplants of Pacific pink salmon (*O. gorbuscha*) from British Columbia to Newfoundland. J. Fish. Res. Bd Can., 32(12): 2343–2356.

Lear, W. H. 1980. The pink salmon transplant experiment in Newfoundland. *In* Salmon ranching, pp. 213–243. Ed. by J. Thorpe. Academic Press.

Lindberg, J. M., and Brown, P. 1982. Continuing experiments in salmon ocean ranching in Chile. ICES CM 1992/M: 21, 9 pp.

Loginova, G. A., and Krasnoperova, S. V. 1982. An attempt at cross-breeding Atlantic salmon and pink salmon. Aquaculture, 27: 329–337.

Manzer, J. I., and Ishida, T. 1963. Salmon of the North Pacific Ocean. Part V – Offshore distributions of salmon. Int. North. Pac. Fish. Comm., 15: 452 pp.

Martin, J. D., and Dadswell, M. J. 1983. Records of coho salmon *Oncorhynchus kisutch* (Walbaum, 1972) in the Bay of Fundy and its tributary drainage. Can. Tech. Rep. Fish. aquat. Sci. 204. Fisheries and Oceans. 6 pp.

Mather, F. 1887. Report upon the results of salmon plantings in the Hudson River. Bull. US Bur. Fish., 7: 409–424.

Mazeaud, F. 1981. La société Nationale d'Acclimatation et le saumon californien au 19ème siècle. Saumons, No. 35: 3–6.

McNeil, W. J. 1967. Survival of pink and chum salmon eggs and alevins. Symposium on salmon and trout in streams. *In* Lectures in fisheries, pp. 101–117. Ed by Northcote and McMillan. Univ. British Columbia.

McNeil, W. J. 1980. Salmon ranching in Alaska. *In* Salmon ranching, pp. 13–27. Ed by J. Thorpe. Academic Press.

McNeil, W. J. 1984. Behavioural enviroregulation's role in fish migration. *In* Mechanisms of migration in fishes. NATO Conference series, IV: Marine sciences, pp. 61–65. Ed. by J. D. McLeave, G. P. Arnold, J. J. Dodson, and W. J. McNeil.

Munro, A. L. S. 1979. Introduction of Pacific salmon to Europe. ICES CM 1979/F: 28, 6 pp.

Munro, A. L. S., Elson, K. G. R., Needham, E. A., Norris, R. J., and McGrath, E. J. 1980. The quarantine of coho salmon for a whole life cycle. ICES CM 1980/E: 51, 7 pp.

Neave, F. 1964. Ocean migrations of Pacific salmon. J. Fish. Res. Bd Can., 21(5): 1227–1244.

Novotny, A. J. 1980. Delayed release of salmon. *In* Salmon ranching, pp. 325–369. Ed. by J. Thorpe. Academic Press.

Ord, W. 1975. Resistance du saumon chinook (*Oncorhynchus tschawytscha*) fingerlings experimentally infected with Viral Hemorrhagic Septicemia Virus. Bull. Fr. Pisc., 257: 149–152.

Parsons, J. W. 1973. History of salmon in the Great Lakes, 1850, 1970. Tech. pap. Bur. Sport Fish. Wildl. US, 68. 80 pp.

Paterson, W. D., Lall, S. P., and Desautels, D. 1980. Bacterial kidney disease in Atlantic salmon (*salmo salar*) in Nova Scotia, Canada. ICES CM 1980/M: 26, 23 pp.

Pearce, W. A. 1980. Great Lakes report for New York State. Fisheries, 5(5): 9–12.

Peck, J. W. (1970). Straying and reproduction of coho salmon. *O. kisutch*, planted in a Lake Superior tributary. Trans. Am Fish. Soc., 99(3): 591–595.

Peterman, R. M. 1980. Testing for density dependent marine survival in Pacific salmonids. *In* Salmonid ecosystems of the North Pacific, pp. 1–24. Ed. by W. J. McNeil, and D. C. Himsworth. Oregon State University Press.

Pippy, J. H. C. 1969. Kidney disease in juvenile Atlantic salmon in the Margaree River. J. Fish. Res. Bd Can., 26: 2535–2537.

Quinn, T. P. 1984a. An experimental approach to fish compass and map orientation. *In* Mechanisms of migration in fishes. NATO Conference series, IV: Marine sciences, pp. 113–123. Ed. by J. D. McLeave, G. P. Arnold, J. J. Dodson, and W. J. McNeil.

Quinn, T. P. 1984b. Homing and straying in Pacific salmon. *In* Mechanisms of migration in fishes. NATO Conference series, IV: Marine sciences, pp. 357–362. Ed. by J. D. McLeave, G. P. Arnold, J. J. Dodson, and W. J. McNeil.

Ricker, W. E. 1954. Pacific salmon for Atlantic waters. Can. Fish. Cult., 16: 6–14.

Robinson, M. K., Bauer, R. A., and Schroader, E. H. 1979. Atlas of North Atlantic–Indian Ocean monthly mean temperatures and mean salinities of the surface layer. US Naval Oceanographic Office, NSTL Station, Bay St. Louis, MS.

Ruggles, C. P. 1966. Depths and velocity as a factor in stream rearing and production of juvenile coho salmon. Can. Fish. Cult., 38: 37–53.

Sano, T. 1977. Viral diseases of cultured salmonids in Japan. Proceedings of the International Symposium on diseases of cultured salmonids, pp. 120–123. Seattle, 4–6 April, 1977. Ed. by Tavolek.

Sawyer, E. S. 1983. Sea ranching of western Pacific pink and chum salmon in the western Atlantic. Rp. National Science Foundation/OCE-83001: 19 pp.

Sindermann, C. J., and Lightner, D. V. 1988. Disease diagnosis and control in North American Marine Aquaculture. Developments in Aquaculture and Fisheries Science, 17: 352 pp. Elsevier.

Solomon, D. J. 1979. Coho salmon in north-west Europe. Possible effects on native salmonids. Lab. Leafl., MAFF Dir. Fish. Res., Lowestoft, (49), 21 pp.

Solomon, D. J. 1980. Pacific salmon in the North Atlantic; a history and assessment of current status. ICES CM 1980/M: 15.

Stolte, L. W. 1974. Introduction of coho salmon into the coastal waters of New Hampshire. Prog. Fish. Cult., 36(1): 29–32.

Symons, P. E. K., and Heland, M. 1978. Stream habitats and behavioural interactions of underyearling and yearling Atlantic salmon (*Salmo salar*). J. Fish. Res. Bd Can., 35(2): 175–183.

Symons, P. E. K., and Martin, J. D. 1978. Discovery of juvenile Pacific salmon (coho) in a small coastal stream of New Brunswick. Fish. Bull., 76(2): 487–489.

Vigneulle, M., Baudin Laurencin, F., and Mevel, M. 1977. Premières observations sur la corynebacteriose des salmonidés en Bretagne. I – Epidémiologie. Bull. Off. int. Epiz., 87(5–6): 497–498.

Waugh, G. D. 1980. Salmon in New Zealand. *In* Salmon ranching, pp. 277–303. Ed. by J. Thorpe. Academic Press.

Welcomme, R. C. 1979. Preliminary record of international transfers of fish species. FAO, Fish. Circ., 715.

Williamson, R. B. 1975. Further captures of Pacific salmon in Scottish waters. Scottish Fish. Bull., 41. 4 pp.

Wood, R. J. 1974. Diseases of Pacific salmon. State of Washington Dept. of Fisheries, Hatchery Division.

Yoshida, T. 1985. Coho salmon culture in Japan. Proceedings of the Symposium on Optimization of Smolt Production. Versailles Summit Group on Aquaculture, Tokyo, pp. 88–94.

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Ecological implications of using transgenic fishes in aquaculture

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The development of gene transfer as a means of improving cultured fish stocks is progressing rapidly, and use of transgenic fish in aquaculture seems possible within the next decade. It is likely that some transgenic individuals will escape into natural systems; the nature and extent of subsequent impacts upon native stocks and aquatic communities are presently unknown. In this review, we identify likely mechanisms of ecological impacts and key gaps in knowledge needed to predict the extent of ecological risk associated with using transgenic fishes in aquaculture. Although activity of novel proteins might give rise to novel ecological impacts, most anticipated impacts of transgenic fish would be exacerbations of those experienced with non-transgenic cultured fish. Knowledge needed for quantification of ecological risk includes quantification of phenotypic alteration and performance of transgenic lines and quantification of the viability and reproductive fitness of transgenic individuals in natural systems. Ecological concerns might be addressed by institutionalizing the execution of a risk analysis within the process of securing a permit for use of transgenic fish in an aquaculture operation.

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Introduction

In the last decade, knowledge of molecular genetics has advanced dramatically. We can now identify the structural and regulatory elements of genes and purposefully introduce into animals copies of a new gene under novel regulatory control. Gene transfer methods originally developed in the mouse (Gordon *et al.*, 1980) have been successfully applied in fish. Much effort has been devoted to development of transgenic fish, with at least 22 research groups active in 14 countries (Hallerman *et al.*, 1990a). To date, gene transfers have been reported for some 14 species of fish (Kapuscinski and Hallerman, 1990). Although some of these gene transfers have been carried out for purely scientific reasons, the majority have been aimed at producing fish with phenotypes favorably altered for aquaculture production purposes (Table 1).

As the development of transgenic fishes progresses from laboratories to secured field testing facilities and ultimately to aquaculture production facilities, the likelihood of genetically altered fishes escaping into natural systems will increase. The nature and extent of impacts of transgenic individuals on natural populations and aquatic communities are presently unknown.

Review of a range of considerations in molecular genetics, physiology, and aquatic ecology can help identify likely mechanisms of ecological impact and key gaps in knowledge. This in turn can contribute to development of a well-directed scientific research protocol and rational interim policies on use of transgenic fishes. After presenting the technical background on development of transgenic fishes, we address the ecological ramifications of introducing such fishes into aquaculture, and consider whether existing public policy regarding use of transgenic animals addresses concerns unique to transgenic fishes and adequately protects the environment.

We have previously considered the anticipated environmental impacts of transgenic fishes generally (Kapuscinski and Hallerman, 1990) and have focused upon the implications of introducing transgenic fishes into natural systems (Kapuscinski and Hallerman, 1991). In this discussion, we build upon our earlier work and focus upon the environmental impacts anticipated from use of transgenic fishes in aquaculture. Although the discussion below might to some degree be generalized to other groups, we focus upon culture of transgenic salmonids and its anticipated impacts on salmonid-dominated communities for several reasons. First, the genetic structure of salmonid populations and the ecological structure of salmonid-dominated commu-

Table 1. Gene transfers in fish aimed at phenotypic alterations of interest to aquaculture.

Gene construct[1]	Species	Reference
RAPID GROWTH		
mMT-rGH	Atlantic salmon	Rokkones *et al.*, 1989
mMT-hGH	Channel catfish	Dunham *et al.*, 1987
mMT-hGH	Common carp	Maclean *et al.*, 1987b
mMT-sGH	Common carp	Joyce *et al.*, 1988
RSV-tGH	Common carp[2]	Zhang *et al.*, 1990
mMT-hGH	Goldfish	Zhu *et al.*, 1985 Maclean *et al.*, 1987b
mMT-hGH	Loach[2]	Zhu *et al.*, 1986 Maclean *et al.*, 1987b Yenikolopov and Benyumov, 1989
mMT-hGH	Mud carp	Maclean *et al.*, 1987b
RSVbGH	Northern pike	Schneider *et al.*, 1989
SV40-hGH	Rainbow trout	Chourrout *et al.*, 1986
mMT-rGH	Rainbow trout	Maclean *et al.*, 1987a Penman *et al.*, 1990
mMT-rGH	Rainbow trout	Guyomard *et al.*, 1988
mMT-rGH	Rainbow trout	Rokkones *et al.*, 1988
mMT-hGH	Silver crucian carp[2]	Maclean *et al.*, 1987b
mMT-hGH	*Tilapia nilotica*	Brem *et al.*, 1988
mMT-hGH	Wuchang fish	Maclean *et al.*, 1987b
RESISTANCE TO FREEZING		
AFP-AFP	Atlantic salmon[3]	Fletcher *et al.*, 1988

[1] Abbreviations for elements of expression vectors: Promoters: mMT, mouse metallotheionein; RSV, avian Rous sarcoma virus; SV40, simian virus 40; AFP, flounder antifreeze protein. Structural genes: rGH, rat growth hormone; hGH, human growth hormone; sGH, salmon growth hormone; tGH, rainbow trout growth hormone; bGH, bovine growth hormone; AFP, flounder antifreeze protein.
[2] Accelerated growth observed.
[3] Antifreeze protein expressed, but not at levels protecting tissues.

nities are relatively well studied. Second, aquaculture of Atlantic salmon (*Salmo salar*) and rainbow trout (*Onchorynchus mykiss*) is well established. Third, breeding of Atlantic salmon and rainbow trout has included development of transgenic lines, suggesting the eventual use of such lines in aquaculture.

Technical background

Transgenic fish bear within their chromosomal DNA copies of a novel DNA construct introduced through gene transfer techniques. Transgenic fish include both the individuals actually manipulated in gene transfer experiments and any of their progeny which bear the introduced gene. The first generation transgenic fish are not themselves intended for use in production aquaculture, but instead as the progenitors of new genetic lines. Only after two or three generations of breeding would transgenic lines have high frequencies of individuals bearing the introduced gene in both chromosomal homologues. Breeding of some species of transgenic fishes will require outdoor confinement, implying some degree of risk of their escape.

Genetic lines of fish bearing the introduced construct will be field-tested for exhibition of improved performance in an aquaculture environment. Again, there is some risk of transgenic individuals escaping from confinement into the environment (Office of Agricultural Biotechnology, 1990).

The first transgenic lines of fish are likely to emerge from field testing within the decade, becoming potentially available for use in agriculture. In the process of developing transgenic lines, laboratory research and well confined breeding or field testing would seem to pose relatively low risk of environmental harm. As transgenic fish are ultimately distributed for final use, however, they would enter a wide range of less secure confinements. Transgenic individuals are likely to escape from confinement into natural systems, where they might survive, reproduce, and disperse to other systems, impacting conspecifics and the aquatic community at large. Consideration of possible ecological impacts at the aquaculture utilization stage is therefore important.

Phenotypic effects of transgene expression

Before approaching the issue of the ecological implications of using transgenic fish in aquaculture, we must first understand how expression of the introduced DNA construct might alter the phenotype of transgenic fish. This phenotypic alteration forms the basis for the altered performance of such fish, which in turn gives rise to the possibility of ecological impacts (Tiedje *et al.*, 1989; Kapuscinski and Hallerman, 1990).

Phenotypic effect of introduced DNA construct

Genes introduced into fish are contained in DNA constructs called expression vectors. An expression vector consists of a structural gene encoding a specific protein flanked by regulatory elements which promote or terminate DNA transcription; the regulatory elements are necessary for successful expression of the structural gene in the host. The activity of the promoter element will determine the tissue-specificity and level of expression of the structural gene in the host. The phenotypic effect of the transferred gene, and the consequent likelihood of ecological impacts should the transgenic fish enter natural systems, depend not only upon the action of the transferred structural gene, but also upon that of the regulatory elements. Activities of relatively few regulatory elements have been characterized in transgenic animals (Hallerman *et al.*, 1990b).

Few structural genes potentially altering aquaculture performance have been transferred into fish (Table 1).

Growth hormone genes have been introduced into several species of fish in the hope of increasing growth rates. High level expression of an introduced antifreeze protein gene introduced into Atlantic salmon might protect the cell contents of transgenic individuals from freezing on contact with nucleating ice crystals in supercooled sea water.

Substantial genotypic and phenotypic variation is present in first-generation populations in which gene transfer has been attempted, for a number of reasons (Kapuscinski and Hallerman, 1990). Preliminary evidence of increased phenotypic variability among first-generation transgenic fish has been observed for loach (Maclean *et al.*, 1987b) and northern pike (Schneider *et al.*, 1989) expressing introduced growth hormone genes. Because fish gaining an early size advantage through non-genetic effects can continue to grow faster than their cohorts (Hulata *et al.*, 1976), apparent growth rate enhancements of first-generation transgenic individuals in mixed groups of transgenic and non-transgenic individuals must be viewed with reservation. Further, as demonstrated in *Neurospora* (Bruce Wallace, pers. comm.), expression of a hemizygous gene (i.e. one present on only one chromosomal homologue) can lead to overdominance, with phenotypic alteration proving greater in hemizygotes than in homozygotes (i.e. individuals with copies of the gene in both chromosomal homologues). With these reservations in mind, twofold acceleration of growth rates in transgenic loach (Maclean *et al.*, 1987b) and crucian carp (Z. Zhu, Institute of Hydrobiology, Wuhan, P.R.C., pers. comm.), and 20% acceleration of growth rate in common carp (Zhang *et al.*, 1990) have been reported.

Two or three generations of breeding would produce more homogeneous lines of fish showing stable expression of introduced genes. A reliable test of the potential aquacultural utility of transgenic lines would entail comparison of growth rates of such lines with a non-transgenic line derived from the same source stock. Reproduction of original generation transgenic individuals of aquaculture species has been carried forward only one generation, and performance data are few at present. Field trials have not yet been carried out to determine the degree of phenotypic alteration in advanced generations. This gap in our knowledge impedes our ability to predict the range of changes in the performance traits of transgenic fishes.

Linkage of phenotypic change and performance

We can draw on general knowledge of physiological processes to conceptualize how several major classes of phenotypic changes (Kapuscinski and Hallerman, 1990) might affect performance and have ecological impact. We anticipate that different classes of phenotypic alteration will give rise to ecological impacts through different pathways. The most important aspects of performance at issue in the context of ecological impacts of transgenic fishes would be those affecting life history traits: for example, age and size at maturity, maximum size, longevity, reproductive effort, and offspring size.

Changes in physiological rates

The first class of phenotypic alteration in transgenic fish includes changes in physiological rates affecting one or more components of the balanced energy budget for an individual fish (Brett and Groves, 1979). Most gene transfers in fish have involved growth hormone genes (Table 1), and the intended phenotypic alteration, increased growth rate, would exemplify a change in physiological rates. Energy budgets for fish bearing introduced growth hormone genes have not been determined, and so direct comparison with those for non-transgenic individuals is unavailable.

Consideration of results from another experimental system, however, supports our hypothesis that significant reallocation of energy budget components is likely to occur. Repartitioning of energy budget components following exogenous growth hormone administration has been studied extensively in dairy cattle. Cows receiving growth hormone injections consumed 4–10% more feed than controls (Soderholm *et al.*, 1988; Chalupa and Galligan, 1989), increasing their voluntary feed intake to the extent that net energy balance did not differ between control and treated animals (Bauman *et al.*, 1989). Injected individuals exhibited a slightly higher respiration rate (Zoa-Mboe *et al.*, 1989).

These studies suggest that similar energy reallocations might occur in transgenic fish, and therefore that changes in individual growth rates would affect a number of aspects of individual performance. However, injection of growth hormones into coho salmon resulted in dose-dependent increases in growth rate, but with improved feed conversion (Gill *et al.*, 1985). The relation between energy budget components and phenotypic alteration in transgenic fishes is clearly a gap in our present knowledge.

Changes in species' environmental tolerances

A second class of phenotypic changes among transgenic fish would entail alteration of a species' tolerance of physical factors such as temperature, pH, or salinity. The transfer of an antifreeze protein gene into Atlantic salmon, aimed at improving the resistance of tissues to freezing in supercooled sea water (Fletcher *et al.*, 1988), is an attempt to realize this class of phenotypic change.

Changes in behavior

In the third class of phenotypic changes, behavioral change would occur. This might occur as a result of expression of an introduced gene for an endocrine compound, which might mediate more than one physiological process. The product of a certain introduced gene might thus alter behaviors associated with seasonal migration, territoriality, or reproductive behavior. A high frequency of precocious maturation has been observed among rainbow trout injected with growth hormone proteins (Danzmann *et al.*, 1990). Precocious maturation may prove a common occurrence among fish transgenic for growth hormone genes. Although transgenic pigs bearing introduced human or bovine growth hormone genes were lethargic (Marx, 1988), the possibility that animals bearing transgenes might prove to be aggressive must also be contemplated.

We recognize that transfers of certain genes might not fit into the categories described above. Genes conferring increased disease resistance or drug resistance, or closing a genetic 'lesion' in a key biochemical pathway might some day be transferred into fishes. The ecological implications of such gene transfers are not as clear as for those fitting within the classes described above.

Ecological implications of using transgenic fish

Escape of fish from aquaculture facilities

The number of fish escaping from a production-scale aquaculture facility can be considerable. The degree of containment in various aquaculture systems to a large degree determines the level of ecological risk associated with culture of transgenic fish (Kapuscinski and Hallerman, 1990). Attributes of a facility determining the efficacy of containment include the presence of physical or chemical barriers blocking the escape of fish via influent or effluent water, susceptibility of rearing units to flooding or storm damage, susceptibility of rearing units to bird predation, and adequacy of site security measures. Thus, minimum risk would be associated with indoor culture facilities and maximum risk with fish ranching schemes carried out in marine systems. Other possibilities between these extremes (in increasing order of risk) include tanks or raceways at contained outdoor facilities, levee or dug-out ponds, extensive aquaculture in contained bodies of water, and sea-cage aquaculture.

Estimates of the numbers or percentages of fish escaping from traditional pond or tank/raceway culture facilities prove difficult to obtain. Associations of salmon growers might argue that only minimal numbers of fish escape from sea-cage aquaculture systems. However, in 1987, a group called Restoration of Atlantic Salmon in America estimated that, on average, 15% of farmed fish escape (Mills, 1989). In 1987, fisheries scientist Peter Maitland reported one mass escape of 90 000 fish (Mills, 1989). An estimated 500 000 (Anon., 1989) to 600 000 (Richard Buck, quoted in Anon., 1990) salmon escaped from fish farms in Norway in 1988. During the past several years, a varying number of rainbow trout have ascended the River Imsa in Norway (Hansen *et al.*, 1987); these fish could only be escapees from aquaculture operations. Similarly, juvenile coho salmon observed in a coastal stream in New Brunswick (Symons and Martin, 1978) were apparent escapees fron net pen aquaculture.

After escape or release from a sea ranch operation, cultured salmon persist in the environment. A 1986 collection of fish from the open sea around the Faeroe Islands in the Norwegian Sea revealed that 3% contained canthaxanthin (a colouring added to feeds to make the flesh pink) in their tissues, indicating that at least this number had originated from fish farms (Mills, 1989). A growing number of salmon collected from Norwegian waters are escapees from sea cages. Catch statistics from the Norwegian commercial fishery showed that 15 to 20% of the fish caught had escaped from fish farms (Anon., 1989; Hansen and Bakke, 1989; Egidius *et al.*, 1990, and references therein).

Individuals from cultured stocks lack the precise homing behavior of wild fish, but do enter rivers with spawning runs (Himsworth, 1981; Hansen *et al.*, 1987; Sattaur, 1989; Hansen and Bakke, 1989). In 1987, 15 to 20% of the Atlantic salmon examined from 54 Norwegian rivers were escapees, including 42% from the River Etnelva and 80% from the River Oselva (Gausen, 1988, cited in Egidius *et al.*, 1990). In 1988, the proportion of cultured fish had increased (Moen and Gausen, cited in Egidius *et al.*, 1990). In Scotland, nearly every river in the Highlands has escaped farmed salmon (Richard Buck, quoted in Anon., 1990). Fifty per cent of the salmon caught in the Scottish Lochy River were reported as farmed (Anon., 1989).

Individuals that escape into rivers tend to return to that system when mature. Those escaping from sea cages tend to return to that locality, but ultimately are forced to enter nearby rivers by their changing physiology (Hansen and Bakke, 1989). It has been suggested (Hansen and Bakke, 1989) that because escapees from sea cages do not enter fresh water until so forced, there will be a higher proportion of escaped aquaculture fish in downstream locations than in the upper parts of a river system. Similarly, more will enter rivers near the site of culture operations than those farther away.

The observed large numbers of escapees from aquaculture operations suggest that were transgenic fish to be cultured commercially, they, too, would enter the environment in large numbers. Although improved containment might reduce the percentage of fish escaping, it is difficult to believe that such escapes could be eliminated. The ecological implications of escape of non-transgenic and transgenic fishes from aquaculture operations is considered in the following sections.

Non-genetic mechanisms for ecological impact of cultured fishes

Leaving aside for the moment the effect of the introduced genes, certain impacts on native stocks following the entry of transgenic individuals would not differ in kind from those observed following the introduction of non-transgenic, non-native stocks.

Even in cases where introduced fish do not reproduce, ecological impacts upon native stocks can be manifested through competition for resources. The stocking of hatchery-reared catchable rainbow trout into existing, self-sustaining populations of wild rainbow and brown trout in two Montana systems caused dramatic decreases in the wild populations within two years (Vincent, 1987). Cessation of stocking allowed the wild populations to recover. Repetition of stocking caused a second crash of the wild trout populations, followed by recoveries after stocking ceased. Increases in wild populations of brook (Thuemler, 1975) and rainbow and brown (McMullian, 1982, cited in Vincent, 1987) trout followed discontinuation of stocking of hatchery brook and rainbow trout, respectively. Decreases of native chum salmon populations in Soviet Asia followed introduction of another wild stock from a nearby watershed, and eventually there was a crash of the entire salmon population (P. Maitland, cited in Sattaur, 1989).

Heightened mortality rates following stocking of hatchery trout among wild trout have been attributed (Vincent, 1972, 1974) to social stresses involving space or food, stresses manifested by increased movement, decreased condition factors, and decreased growth rates relative to previous unstocked years. The behavioral bases of such impacts of hatchery trout on native trout have been described in terms of altered synchronous feeding behaviors, breakdown of social ordering and normal territoriality, and different activity patterns for the stocks (Butler, 1974; Bachman, 1984). Hatchery fish were more active than wild fish, used cover less, and exhibited greater agonistic activity (Fenderson *et al.*, 1968; Butler, 1974; Pollard, 1978; Bachman, 1984). Altered activity patterns may explain why wild brown and rainbow trout were more catchable during periods of stocking (Butler and Borgeson, 1965; Vincent, 1987).

A further potential impact of cultured fishes upon natural stocks is transmission of parasites and diseases. The most dramatic example may be the monogean fluke *Gyrodactylus salaris*, which is believed to have been introduced into Norwegian waters with the import of Atlantic salmon smolts for aquaculture in the early 1970s; it has now spread to 32 Norwegian river stocks (Egidius *et al.*, 1990). It has become one of the primary causes of excess salmon mortality in Norwegian rivers (Johnson and Jensen, 1988). For key diseases such as bacterial kidney disease, the reservoir of infection is frequently in the wild stocks, but the disease problems break out under farming conditions; such outbreaks of disease can lead to higher infection rates among wild stocks in the vicinity (Egidius *et al.*, 1990).

Non-genetic mechanisms for ecological impact of transgenic fishes

Considering now the effect of introduced genes, what ecological effects might follow from the entry of transgenic fish into a natural fish community? We anticipate that the different classes of phenotypic alterations would affect native populations through different pathways.

Growth of salmonids in stream communities tends to be limited by energy availability. Considering the case of transgenes affecting energy partitioning, the larger size of transgenic individuals bearing growth hormone genes might exacerbate the competitive problems faced by non-transgenic, native individuals, as larger individuals presumably would be favored in agonistic interactions. Should large numbers of sterile transgenic individuals enter an energy-limited community, a larger proportion of the population's production would be tied up in non-reproductive individuals. The reduction in the number of spawners and the concomitant decrease in the population's fitness could lead to a population crash.

The action of introduced genes affecting a species' environmental tolerance would increase the spatial or temporal range of habitats or times in which the species could persist. Considering the potential expansion of range, then, a transgenic fish could effectively be an introduced fish, i.e. one moved from one place to another by man, thus ending up outside its native range (Kohler and Courtenay, 1986). Impacts of introduced fishes on native fishes (Moyle *et al.*, 1986) have included extirpation of native aquatic species, reduced growth and survival rates of native species, and changes in community structure (citations in Nelson and Soule, 1987). The mechanisms for domination of native fishes by introduced fishes (Moyle *et al.*, 1986) have included competition via interference or exploitation (White, 1989), predation, inhibition of reproduction, environmental modification, transfer of new parasites or diseases, and hybridization (Busack and Gall, 1981). Through such mechanisms, major ecological impacts upon brook trout followed the introduction of brown and rainbow trout in the eastern USA, and upon cutthroat trout following introduction of rainbow trout in the western USA. It has proven difficult to predict which introductions would be ecological disasters and which relatively benign (Fausch, 1988).

Through the action of genes affecting environmental tolerances, transgenic fish might enter or persist in communities not adapted to their presence. The transfer of the antifreeze protein gene into Atlantic salmon provides an interesting case-in-point. Although expression of the gene at high levels would provide the fish protection against freezing in supercooled sea water, any transgenic individuals which had escaped into the environment would presumably behave like non-transgenic conspecifics and move to seek preferred temperatures. In most cases, they would enter systems where Atlantic salmon were already present. However, the advent of transgenic lines expressing the introduced gene, consequent expansion of sea cage aquaculture to additional ecosystems, and escape of fish from these operations would give rise to a larger influx of cultured fish into native stocks and to the range of attendant ecological impacts.

Community function in mixed-species salmonid assemblages depends upon behavior-based partitioning of food and habitat resources (White, 1989). The introduction of transgenic fish exhibiting modified behaviors would presumably exacerbate the behavior-based problems stemming from their being cultured fishes. However, the action of genes affecting behavior of transgenic fish might impact native stocks most strongly if reproduction were affected. Courtship and spawning behaviors of fishes can be complex and fine-tuned to environmental conditions (Helle, 1981). The possibility of behavioral alteration among transgenic individuals suggests that their presence at spawning sites could be disruptive, possibly decreasing the reproductive success of spawning wild individuals.

Use of sterile transgenic fish

Possible ecological impacts posed by sterile transgenic fish would be limited to those described above. The range of impacts experienced might depend on the means by which the fish were sterilized. Two mechanisms leading to ecological impacts of ploidy-manipulated fish might be envisioned. Triploid males may develop gonads, mature physiologically (Benfey and Sutterlin, 1984; Benfey *et al.*, 1989), and produce gametes, and so may be predisposed to return to rivers and attempt to mate. First, this might disturb the spawning of native fish. Second, should they succeed in spawning, the aneuploid sperm of triploid males can fertilize eggs, but the embryos will die before hatch (Thorgaard and Allen, 1987), reducing the number of viable young produced by the population. If this occurs with great frequency, it could lead to a population crash; indeed, release of sterile individuals of one set is used as a population control measure in the eradication of insects. Fish sterilized through hormone treatments, however, might not mature physiologically and might remain at sea instead of returning to spawn. Few data are available concerning the behavior of fish sterilized by these methods.

Sterilization by whatever means would obviate the potential for adaptation of populations of transgenic fish to a recipient environment. In the absence of further introductions of transgenic individuals into the system, there remains the possibility of recovery by native stocks and communities. As discussed below, the use of fertile transgenic fish in aquaculture introduces the possibility of additional ecological impacts.

Genetic mechanisms for ecological impact of cultured fishes

Escape of fertile transgenic fish from culture facilities and their entry into populations of conspecifics introduces the possibility that these individuals will reproduce. Leaving aside for the moment the action of transferred genes, reproduction of planted individuals from mismanaged hatchery stocks may threaten the genetic integrity of sympatric wild stocks. A large body of evidence (e.g. Ryman and Stahl, 1980; Helle, 1981; Cross and King, 1983) demonstrates that when hatchery programs ignore basic genetic principles, alteration of genetic variation of cultured stocks relative to their founders can result through the processes of inbreeding and genetic drift. Reproductive activity of fish released from such hatchery programs with wild stocks can give rise to genetic impacts upon the wild stocks, resulting in lowered fitness of native populations.

Unfortunately, we have relatively few data regarding the proportion of introduced fish which reproduce in natural systems. Results of studies showing little genetic effect of hatchery or transplanted fish upon native stocks (Krueger and Menzel, 1979; Wishard *et al.*, 1984) suggested low reproductive success among introduced fish. Higher levels of reproduction of introduced stocks have, however, been observed.

1. Comparison of morphological characters among rainbow trout from the Santa Ana River in California with native coast, Hot Creek hatchery trout, and introduced cutthroat trout (Gard and Seegrist, 1965) indicated that the native type had been modified, suggesting introgression of genes from introduced trout.

2. Observation of in-stream spawning of steelhead trout in the Kalama River in Washington (Leider *et al.*, 1984) showed that spatial and temporal segregation was insufficient to prevent the potential introgression of hatchery steelhead genes into the wild summer steelhead population. Although the success of hatchery-reared steelhead in producing smolt offspring was only 29% of that among wild fish, their offspring came to predominate in the population of smolts because hatchery-derived spawners outnumbered wild spawners (Chilcote *et al.*, 1986).

3. Introgressed populations of introduced and native rainbow trout have been identified among collections from the Kootenai River drainage in western Montana (Allendorf *et al.*, 1980) and the Yakima River of Washington (Campton and Johnson, 1985). These two studies indicated that introduced and native rainbow trout had interbred to panmixia wherever the two forms came into contact (Campton, 1987).

4. Observations of sea-ranched Atlantic salmon in the River Imsa in Norway (Egidius *et al.*, 1990) suggested

that their reproductive success was less than that of wild fish. They entered the river about one month after the wild fish, and many descended unspawned later in the autumn. The impact of their spawning on the native stock has not been quantified.

5. Cultured stocks planted into natural systems are not always derived from the corresponding native stocks. In situations where such cultured stocks are planted into a number of systems, gene flow from cultured to native fish caused by reproduction of cultured fish reduces the genetic variation between natural stocks. Breakdown of reproductive isolation between local populations of European brown trout was apparent after stocking of hatchery fish (Ryman, 1981).

Interbreeding of cultured and wild fish might be expected to give rise to increased heterozygosity and hybrid vigor for certain traits (Egidius *et al.*, 1990). Hybrid vigor, however, is typically observed for traits with low heritability. Survival-related traits tend to have low heritabilities (Gjerde, 1986). Interbreeding of cultured and wild fish may thus give rise to heterotic performance sufficient to impact native fish, but having done so, disappearing after one generation (Egidius *et al.*, 1990).

The genetic impacts of cultured fish upon native stocks have not, in general, been well quantified. Lack of such information implies lack of a baseline for comparison in assessing the impacts of transgenic cultured fish on native stocks. We hope that this lack of knowledge might be more adequately addressed by the time that transgenic fishes enter aquaculture production. The development of aquaculture broodstocks which are fixed for specific gene markers (e.g. Skaala *et al.*, 1988) and their use in aquaculture in association with genetic monitoring studies would provide experiments useful in developing the requisite baseline data.

Genetic mechanisms for ecological impact of transgenic fishes

Should transgenic individuals escape from culture facilities and reproduce, the expected impacts would include those possible for non-transgenic fish, plus any additional impacts due to the activity of transferred genes. The problem becomes one of determining the magnitude of the additional component of genetic impact.

Transgenic lines entering aquaculture production will probably have been subjected to at least three generations of breeding. Production of aquaculture lines from a relatively small number of transgenic founders would exacerbate the inbreeding and drift effects observed among non-transgenic cultured stocks. Transgenic fish would thus deviate even more from wild founders. The impact of their entry into natural populations would exceed that on non-transgenic cultured fishes.

Transgenic individuals could mate with each other or with non-transgenic native fish, leading to a diversity of transgenic genotypes with varying adaptive values among their descendants. It is impossible to anticipate the fitness of transgenic genotypes relative to non-transgenic genotypes. Competition among prospective breeders has been demonstrated in a wide range of species. In the general case, where males compete for access to females, size often plays an important role in determining male breeding success. Expression of an introduced growth hormone gene giving rise to large size could favorably affect mating success for transgenic males. Alternatively, should precocious maturation of growth hormone-bearing transgenic fishes prove common, it seems likely that many escapees from culture situations might reproduce as smaller, precocious males in natural systems. Recent work (van den Berghe and Gross, 1989; Fleming and Gross, 1989) has demonstrated a high degree of breeding competition among female salmon. Body size contributed to adult female fitness through positive effects on egg production, territory acquisition, and nest defense, giving rise to a 23-fold fitness advantage to the largest females in the population. Large size conferred through expression of an introduced growth hormone gene could favorably affect female reproductive success.

Given the wide range of possible transgenic genotypes to be acted upon by natural selection, adapted transgenic descendants could ultimately have minor or major impacts upon recipient genetic stocks. We cannot rule out the possibility of shifts within genetic stocks to domination by transgenic genotypes. This possibility is especially conceivable in small stocks receiving a large influx of transgenic individuals. Neither can we rule out the possibility of extinction of transgenic genotypes if their fitness values are very low in the recipient environment.

Lack of knowledge regarding reproduction-mediated impacts of transgenic fish is particularly distressing considering the potential importance of such impacts on native stocks. Because it is difficult to predict the spawning behavior of transgenic fish among native fish and the fitness of offspring so produced, measurements of reproductive success in well-isolated experimental systems is needed. For these purposes, appropriate test systems for simulating natural conditions would be a flume, artificial stream, or spawning channel (Helle, 1981) stocked with transgenic and non-transgenic individuals. Young fish might be collected at swim-up and smolt stages and screened for the presence of the introduced genetic construct. Technical details of such experimentation have yet to be worked out. Introduction of a marker gene in addition to the gene of economic value into the genome of transgenic fish would be an aid in study of reproduction of such individuals in experimental systems or for post facto assessments of impacts in natural populations.

Perspective on ecological impacts of transgenic fishes

Few phenotypic alterations, for instance those due to the activity of proteins not otherwise expressed in the species, would give rise to impacts which are truly novel in an ecological sense. More generally, the anticipated ecological impacts of transgenic fish in natural ecosystems would be exacerbations of those experienced with non-transgenic cultured fish. The degree to which such impacts would be exacerbated is impossible to quantify given present knowledge. Knowledge needed for quantification of ecological risk includes: (1) quantification of the degree of overall phenotypic alteration following transgene expression, and (2) quantification of the viability and reproductive success of transgenic fish in natural systems. Quantification of factors of ecological risk requires well-designed research in secure, dedicated facilities.

Recognizing that transgenic lines will be developed and will likely be used in the face of uncertainties regarding their ecological impacts, what policies might be adopted to minimize such impacts? Minimization of the impacts of transgenic fishes used in aquaculture has both biological and legal aspects.

Rational decisions regarding use of a particular line of transgenic fish in a particular aquaculture system should eventually entail a quantitative analysis of the risk posed to the environment within the scope of a decision-making model (e.g. Levin *et al.*, 1987; Regal, 1987; Kapuscinski and Hallerman, 1991) based upon principles of ecology. This risk analysis protocol should be institutionalized within the process of securing a permit for using transgenic fish in aquaculture.

Will public policies adequately protect the environment?

No country has in force a well-articulated set of regulations governing agricultural uses of transgenic animals. Although not yet complete, US policies are the most developed of any nation; once complete and in force, they will likely serve as the model for regulatory structures in other countries. US federal policies are aimed at regulating development of transgenic animals generally. However, cultured fishes differ from traditional agricultural livestock species because they can readily survive in natural systems. Bearing this in mind, do US policies regarding agricultural use of transgenic animals adequately protect the environment from the impacts posed specifically by transgenic fishes?

Existing regulatory framework

No single piece of US federal legislation regulates the distribution and final use of transgenic organisms. The public policy approach outlined in the Coordinated Framework for Regulation of Biotechnology (Office of Science and Technology Policy, 1984, 1986) was to apply existing legislation to the new regulatory issues raised by biotechnology. Although the policies set out in the Coordinated Framework might arguably apply well to other classes of transgenic organisms, their application to fishes leaves a number of important concerns unanswered (Hallerman and Kapuscinski, 1990). Among them:

1. Although impacts from use of transgenic cattle, pigs, sheep, or chickens would clearly be within the scope of agriculture, use of transgenic fish has implications for the environment as a whole. Still, agencies such as the Fish and Wildlife Service and the National Marine Fisheries Service will not clearly be included in policy or decision-making for use of transgenic animals.
2. Environmental release of transgenic animals within non-federally funded projects is not clearly subject to regulation.
3. Federal regulatory authorities have little authority over movement of transgenic animals within particular states.

Proposed regulatory framework

A noteworthy effort to satisfy the lack of legal authority over distribution and final use of transgenic animals was embodied in H.R. 1557 (Kastenmeier, 1989), the "Transgenic Animal Regulatory Reform Act", a bill introduced jointly to the US House Committees on Science, Space and Technology and Agriculture in Spring, 1989. The major thrust of the bill was to establish a permit requirement for use of transgenic animals in agricultural activities. Such a permit could only be granted if "the activity ... authorized ... does not constitute an unreasonable risk to human health, welfare, or the environment". Permits might thus contain restrictions that the Secretary of Agriculture deemed necessary, including designation of authorized manner and method of use, requirements for confinement of transgenic animals, and requirements for monitoring. Provisions for different kinds of permits for experimental, expanded, or commercial uses were outlined. A Transgenic Animals Advisory Committee composed of individuals with expertise in risk assessment and risk management methodologies relating to genetic engineering would review permit applications, prescribe data submission requirements and risk assessment protocols and recommend actions on specific permit applications. No action was taken on H.R. 1557, which may be reintroduced in the future.

Regulation in other countries

There are a number of Canadian federal acts which might regulate the development and use of biotechnology products (Interdepartmental Committee on Biotechnology, 1989). The National Biotechnology Advisory Committee (1989) has urged the federal government to clarify the coverage of biotechnology under such legislation. Criteria are being developed under the Canadian Environmental Protection Act for assessing permit applications for field trials and for containment during field testing. Regulations covering distribution and agricultural use of transgenic animals apparently have not yet been addressed by Agriculture Canada.

European countries vary widely in their approach to regulating development of transgenic organisms (Newmark, 1987). The possibility of a European Economic Community framework has been addressed (Commission of European Communities, 1986), and draft directives are in preparation (Ager, 1988). A recent report aimed at unifying regulatory policies among the major industrialized nations (Organization for Economic Cooperation and Development, 1986) has begun to influence development of such policies (Ager, 1988).

Efforts to regulate development of transgenic animals are apparently lacking among developing countries (e.g. China and India) where experimentation with transgenic fishes has been initiated (Hallerman *et al.*, 1989). In these societies, pressures to expand food supplies by any means may supersede any desire to protect aquatic ecosystems.

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References

Ager, B. P. 1988. Regulations and the European scene. *In* Trends in biotechnology/Trends in ecology and evolution, Special Publication, pp. 542–544. Ed. by J. Hodgson and A. M. Sugden. Elsevier, Cambridge.

Allendorf, F. W., Espeland, D. M., Scow, D. T., and Phelps, S. 1980. Coexistence of native and introduced rainbow trout in the Kootenai River drainage. Proceedings of the Montana Academy of Sciences, 39: 28–36.

Anon., 1989. Great Escape. Fish Farmer, 12: 3.

Anon., 1990. On the side of the salmon. Trout, Spring 1990: 44–59.

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society, 113: 1–32.

Bauman, D. E., Hard, D. L., Crooker, B. A., Partridge, M. S., Garrick, K., Sandles, L. D., Erb, H. N., Franson, S. E., Hartnell, G. F., and Hintz, R. L. 1989. Long-term evaluation of a prolonged-release formulation of N-methionyl bovine somatotropin in lactating dairy cows. J. Dairy Sci., 72: 642–651.

Benfey, T. J., Dye, H. M., Solar, I. I., and Donaldson, E. M. 1989. The growth and reproductive endocrinology of adult triploid Pacific salmonids. Fish Physiol. Biochem., 6: 113–120.

Benfey, T. J., and Sutterlin, A. M. 1984. Growth and gonadal development in triploid landlocked Atlantic salmon (*Salmo salar*). Aquaculture, 36: 359–367.

Brett, J. R., and Groves, T. D. D. 1979. Physiological energetics. *In* Fish physiology, vol. 8, pp. 279–352. Ed. by W. S. Hoar, D. J. Randall, and J. R. Brett. Academic Press, New York.

Brem, G., Brenig, G., Horstgen-Shwark, G., and Winnacker, E.-L. 1988. Gene transfer in tilapia (*Oreochromis niloticus*). Aquaculture, 68: 209–219.

Busack, C. A., and Gall, G. A. E. 1981. Introgressive hybridization in populations of Paiute cutthroat trout (*Salmo clarki seleniris*). Can. J. Fish. aquat. Sci., 38: 939–951.

Butler, B. 1974. Some thoughts on the effects of stocking on wild populations. *In* Proceedings of the Wild Trout Management Symposium, Yellowstone National Park, WY, Sept. 1974, pp. 83–87. Ed. by W. King.

Butler, R. L., and Borgeson, D. P. 1965. California "catchable" trout fisheries. California Department of Fish and Game Fish Bull., 127.

Campton, D. E. 1987. Natural hybridization and introgression in fishes. *In* Population genetics and fishery management, pp. 161–192. Ed. by N. Ryman and F. W. Utter. University of Washington Press, Seattle.

Campton, D. E., and Johnson, J. M. 1985. Electrophoretic evidence for a genetic admixture of native and non-native trout in the Yakima River, Washington. Trans. Am. Fish. Soc., 114: 782–793.

Chalupa, W., and Galligan, D. T. 1989. Nutritional implications of somatotropin for lactating cows. J. Dairy Sci., 72: 2510–2524.

Chilcote, M. W., Leider, S. A., and Loch, J. J. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. Trans. Am. Fish. Soc., 115: 726–735.

Chourrout, D., Guyomard, R., and Houdebine, L. M. 1986. High efficiency gene transfer in rainbow trout (*Salmo gairdneri* Rich.) by microinjection into egg cytoplasm. Aquaculture, 51: 143–150.

Commission of European Communities. 1986. Communication from the Commission to the Council: A Community framework for the regulation of biotechnology. CEC, Brussels.

Cross, T. F., and King, J. 1983. Genetic effects of hatchery rearing Atlantic salmon. Aquaculture, 33: 33–40.

Danzmann, R. G., Van Der Kraak, G. J., Chen, T. T., and Powers, D. A. 1990. Metabolic effect of bovine growth hormone and genetically engineered rainbow trout growth hormone in rainbow trout *Onchorynchus mykiss* reared at high temperature. Can. J. Fish. aquat. Sci., 47: in press.

Dunham, R. A., Eash, J., Askins, J., and Towns, T. M. 1987. Transfer of the metallotheionein-human growth hormone fusion gene into channel catfish. Trans. Am. Fish. Soc., 116: 87–91.

Egidius, E., Hansen, L. P., Jonsson, B., and Naevdal, G. 1990. Mutual impact of wild and cultured Atlantic salmon in Norway. J. Cons. int. Explor. Mer (in press).

Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams: What have we learned? Can. J. Fish. aquat. Sci., 45: 2238–2246.

Fenderson, O. C., Everhart, W. H., and Muth, K. M. 1968. Comparative agonistic and feeding behavior of hatchery-

reared and wild salmon in aquaria. J. Fish. Res. Bd Can., 25: 1–14.
Fleming, I. A., and Gross, M. R. 1989. Evolution of adult female life history and morphology in a Pacific salmon (coho, *Onchorynchus kisutch*). Evolution, 43: 141–157.
Fletcher, G. L., Shears, M. A., King, M. J., Davies, P. L., and Hew, C. L. 1988. Evidence for antifreeze protein gene transfer in Atlantic salmon (*Salmo salar*). Can. J. Fish. aquat. Sci., 45: 352–357.
Gard, R., and Seegrist, D. W. 1965. Persistence of the native rainbow trout type following introduction of hatchery trout. Copeia, 1965: 182–185.
Gausen, D. 1988. Registreringer av oppdrettslaks i vassrag. *In* Fagmote om sikringssoner for laksefisk, Stjordal, Norway, pp. 58–69. Ed. by B. Lindgren.
Gill, J. A., Sumpter, J. P., Donaldson, E. M., Dye, H. M., Souza, L., Berg, T., Wypych, J., and Langley, K. 1985. Recombinant chicken and bovine growth hormones accelerate growth in aquacultured juvenile Pacific salmon *Onchorynchus kisutch*. Biotechnology, 3: 643–646.
Gjerde, B. 1986. Growth and reproduction in fish and shellfish. Aquaculture, 57: 37–55.
Gordon, J. W., Scangos, G. A., Plotkin, D. J., Barbosa, J. A., and Ruddle, F. H. 1980. Genetic transformation of mouse embryos by microinjection of purified DNA. Proceedings of the National Academy of Sciences USA, 77: 7380–7384.
Guyomard, R., Chourrout, D., and Houdebine, L. M. 1988. Gene transfer by microinjection into fertilized trout eggs: efficient integration and germ line transmission. Third International Symposium of Genetics in Aquaculture, Trondheim, Norway, June 1988. Abstract.
Hallerman, E. M., and Kapuscinski, A. R. 1990. Transgenic fish and public policy. II. Regulatory concerns. Fisheries, 15(1): 12–20.
Hallerman, E. M., Kapuscinski, A. R., Hackett, P. B., Faras, A. J., and Guise, K. S. 1990a. Gene transfer in fish. Proceedings of the 34th Annual Atlantic Fisheries Technological Conference, St. John's, Newfoundland, August 1989. Ed. by M. N. Voight and J. R. Bota. Technomic Publ. Co. Lancaster, PA.
Hallerman, E. M., Schneider, J. F., Gross, M. L., Liu, Z., Yoon, S. J., Hackett, P. B., Faras, A. J., Kapuscinski, A. R., and Guise, K. S. 1990b. Tissue-specific, stable gene expression promoted by the RSV long terminal repeat element in transgenic goldfish. Anim. Biotechnol., 1: 79–93.
Hansen, L. P., and Bakke, T. A. 1989. Flukes, genetics, and escapees. Atl. Salmon J., 38: 26–29.
Hansen, L. P., Doving, K. B., and Jonsson, B. 1987. Migration of farmed adult Atlantic salmon with and without olfactory sense, released on the Norwegian coast. J. Fish. Biol., 30: 713–721.
Helle, J. H. 1981. Significance of the stock concept in artificial propagation of salmonids in Alaska. Can. J. Fish. aquat. Sci., 38: 1665–1671.
Himsworth, D. 1981. Impact on wild salmon runs by Oregon's ranching industry. Aqua. Mag., 7(2): 12–16.
Hulata, G., Moav, R., and Wohlfarth, G. 1976. The effects of maternal age, relative hatching time, and density of stocking on growth rate of fry in the European and Chinese races of the common carp. J. Fish. Biol., 9: 499–513.
Interdepartmental Committee on Biotechnology. 1989. Biotechnology regulations: a user's guide. Catalog no. EN40-357/1988E, Ministry of State, Ottawa.
Isaksson, A. 1988. Salmon ranching: a world review. Aquaculture, 75: 1–33.
Johnson, B. O., and Jensen, A. J. 1988. Introduction and establishment of *Gyrodactylus salaris* Malmberg 1957, on Atlantic salmon, *Salmo salar*, fry and parr in the River Vefsna, northern Norway. J. Fish Dis., 11: 35–45.
Joyce, C. M. Hayat, and Dunham, R. A. 1988. Survival of channel catfish and carp embryos microinjected with DNA at various developmental stages. Third International Conference on Genetics in Aquaculture, Trondheim, Norway, June 1988. Abstract.
Kapuscinski, A. R., and Hallerman, E. M. 1990. Transgenic fish and public policy. I. Anticipating environmental impacts of transgenic fish. Fisheries, in press.
Kapuscinski, A. R., and Hallerman, E. M. 1990b. Implications of introduction of transgenic fish into natural ecosystems. Can. J. Fish. aquat. Sci., 48 (suppl 1): 99–107.
Kapuscinski, A. R. D., and Lannan, J. E., 1986. A conceptual genetic fitness model for fisheries management. Can. J. Fish. aquat. Sci., 43: 1606–1616.
Kastenmeier, R. 1989. Transgenic Animals Regulatory Reform Act. Legislative Bill H. R. 1557, 101st Congress, first session.
Kohler, C. C., and Courtenay, W. R. Jr. 1986. American Fisheries Society position on introductions of aquatic species. Fisheries, 11: 39–42.
Krueger, C. C., and Menzel, B. W. 1979. Effects of stocking on genetics of wild brook trout populations. Trans. Am. Fish. Soc., 108: 277–287.
Leider, S. A., Chilcote, M. W., and Loch, J. J. 1984. Spawning characteristics of sympatric populations of steelhead trout (*Salmo gairdneri*): evidence for partial reproductive isolation. Can. J. Fish. aquat. Sci., 41: 1454–1462.
Levin, M. A., Seidler, R., Borquin, A. W., Fowle, J. R., and Barkey, T. 1987. EPA developing models to assess environmental release. Biotechnology, 5: 38–41.
Maclean, N., Penman, D., and Talwar, S. 1987a. Introduction of novel genes into the rainbow trout. *In* Selection, hybridization, and genetic engineering in aquaculture, pp. 323–325. Ed. by K. Tiews. Verlag, H. Heenemann GmbH, Berlin.
Maclean, N., Penman, D., and Zhu, Z. 1987b. Introduction of novel genes into fish. Biotechnology, 5: 257–261.
Marnell, L. F. 1986. Impacts of hatchery stocks on wild fish populations. *In* Fish culture in fisheries management, pp. 339–347. Ed. by R. H. Stroud. American Fisheries Society, Bethesda, MD.
Marx, J. L. 1988. Gene-watcher's feast served up in Toronto. Science, 228: 1516–1517.
Mills, S. 1989. Salmon farming's unsavoury side. New Scientist, 29 April: 58–60.
Moen, V., and Gaussen, B. 1989. Romt opprettsfisk i vassdrag 1988. Directorate for Nature Management report Number 3. 26 pp.
Moyle, P. B., Li, H. W., and Barton, B. A. 1986. The Frankenstein effect: impact of introduced fishes on native fishes in North America. *In* Fish culture in fisheries management, pp. 415–426. Ed. by R. H. Stroud. American Fisheries Society, Bethesda, MD.
National Biotechnology Advisory Committee. 1989. The regulation of biotechnology: a critical issue for Canadian research and industrial development. Catalog no. ST1-2/1988, Industry, Science and Technology Canada, Ottawa K1A OH5.
Nelson, K., and Soule, M. 1987. Genetical conservation of exploited fishes. *In* Population genetics and fishery management, pp. 345–368. Ed. by N. Ryman and F. Utter. University of Washington Press, Seattle.
Newmark, P. 1987. Discord and harmony in Europe. Biotechnology, 5: 1281–1283.
Office of Agricultural Biotechnology. 1990. Environmental assessment of research of transgenic carp in confined outdoor ponds proposed by the Alabama Agricultural Experiment Station. OAB, Office of the Secretary of Agriculture, Washington, DC.

Office of Science and Technology Policy. 1984. Proposal for a coordinated framework for the regulation of biotechnology. Federal Register 49: 50856–50907. 31 December 1984.

Office of Science and Technology Policy. 1986. Coordinated framework for the regulation of biotechnology. Federal Register 51: 23301–23350. 26 June 1986.

Organization for Economic Cooperation and Development. 1986. Recombinant DNA safety considerations: safety considerations for industrial, agricultural, and environmental application of organisms derived by recombinant DNA technologies. OECD, Paris.

Penman, D. J., Beeching, A. J., Penn, S., and Maclean, N. 1990. Factors affecting the integration of microinjected DNA into the rainbow trout genome. Aquaculture, 85: 35–50.

Pollard, H. 1978. The effects of angling and hatchery trout on juvenile steelhead trout. *In* Proceedings of the Wild Trout Catchable Trout Symposium, Eugene, OR, February 15–17, 1978, pp. 161–168. Ed. by J. R. Moring. Oregon Department of Fish and Wildlife, Corvalis, OR.

Regal, P. J. 1987. Models of genetically engineered organisms and their ecological impact. National Institutes of Health, Recombinant DNA Tech. Bull., 10(3).

Rokkones, E., Alestrom, P., Skjervold, H., and Gautvik, K. M. 1989. Microinjection and expression of a mouse metallotheionein growth hormone fusion gene in fertilized salmonid eggs. J. Comp. Physiol. B, 158: 751–758.

Ryman, N. 1981. Conservation of genetic resources: experiences from the brown trout (*Salmo trutta*). *In* Fish gene pools. Ed. by N. Ryman. Ecol. Bull. (Stockholm), 34: 61–74.

Ryman, N., and Stahl, G. 1980. Genetic changes in hatchery stocks of brown trout (*Salmo trutta*). Can. J. Fish. aquat. Sci., 37: 82–87.

Sattaur, O. 1989. The threat of the well-bred salmon. New Scientist, 29 April: 54–58.

Schneider, J. F., Hallerman, E. M., Yoon, S. J., He, L., Gross, M. L., Liu, Z., Faras, A. J., Hackett, P. B., Kapuscinski, A. R., and Guise, K. S. 1989. Transfer of the bovine growth hormone gene into northern pike, *Esox lucius*. J. Cell. Biochem. Suppl. 13B: 173.

Skaala, O., Dahle, G., Jorstad, K. E., and Naevdal, G. 1988. Interactions between wild and farmed populations: information from genetic markers. Proceedings of the Third International Symposium on Genetics in Aquaculture, Trondheim, Norway, June 1988, Abstracts: 47.

Soderholm, C. G., Otterby, D. E., Linn, J. G., Ehle, F. R., Wheaton, J. E., Hansen, W. P., and Annexstad, R. J. 1988. Effects of bovine recombinant somatotropin on milk production, body composition, and physiological parameters. J. Dairy Sci., 71: 355–365.

Symons, P. E. K., and Martin, J. D. 1978. Discovery of juvenile Pacific salmon (coho) in a small coastal stream of New Brunswick. US Nat. Mar. Fish. Serv. Fish. Bull., 76: 487–489.

Thorgaard, G. H., and Allen, S. K. Jr. 1987. Chromosome manipulation and markers in fishery management. *In* Population genetics and fishery management, pp. 319–331. Ed. by N. Ryman and F. Utter. University of Washington Press, Seattle.

Thuemler, T. 1975. Fish and the blue ribbon streams. Wisconsin Cons. Bull., 40: 16–17.

Tiedje, J. M., Colwell, R. K., Grossman, Y. L., Hodson, R. E., Lenski, R. E., Mack, R. N., and Regal, P. J. 1989. The planned introduction of genetically engineered organisms: ecological considerations and recommendations. Ecology, 70: 298–315.

van den Berghe, E. P., and Gross, M. R. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho, *Onchorynchus kisutch*). Evolution, 43: 125–140.

Vincent, R. E. 1972. Effect of stocking catchable trout on wild trout populations. Proceedings of the Annual Conference of the Western Association of State Game and Fish Commissioners, 52: 602–608.

Vincent, R. E. 1974. Effect of stocking catchable trout on wild trout populations. *In* Proceedings of the Wild Trout Management Symposium, Yellowstone National Park, WY, September 1974, pp. 88–91. Ed. by W. King.

Vincent, R. E. 1987. Effects of stocking catchable-size hatchery rainbow trout on two wild species in the Madison River and O'Dell Creek, Montana. North Am. J. Fish. Management, 7: 91–105.

White, R. 1989. We're going wild: a 30-year transition from hatcheries to habitat. Trout Summer, 1989: 14–49.

Wishard, L. N., Seeb, J. E., Utter, F. M., and Stefan, D. 1984. A genetic investigation of suspected redband trout populations. Copeia, 1984: 120–132.

Yenikolopov, G. N., and Benyumov, A. O. 1989. Enhanced growth of transgenic fish containing somatotropin genes. J. Cell. Biochem. 13B., Abstract.

Zoa-Mboe, A., Head, H. H., Bachmann, K. C., Baccari, F., and Wilcox, C. J. 1989. Effects of bovine somatotropin on milk yield and composition, dry matter intake, and some physiological functions of Holstein cows during heat stress. J. Dairy Sci., 72: 907–916.

Zhang, P., Hayat, M., Joyce, C., Gonzalez-Villasenor, L. J., Lin, C. M., Dunham, R. A., Chen, T. T., and Powers, D. A. 1990. Gene transfer, expression and inheritance of pRSV-rainbow trout-GH-cDNA in the common carp, *Cyprinus carpio* (Linnaeus). Mol. Repro. Devel., 25: 3–13.

Zhu, K. Xu., Li, G., Xie, Y., and He, L. 1986. Biological effects of human growth hormone gene injected into the fertilized eggs of loach *Misgurnus anguillacaudatus* (Cantor). Kexue Tongbao, 31: 988–990.

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The effects of stock and rearing history on the stress response in juvenile coho salmon (*Oncorhynchus kisutch*)

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Iwama, G. K., McGeer, J. C., and Bernier, N. J. 1992. The effects of stock and rearing history on the stress response in juvenile coho salmon (*Oncorhynchus kisutch*). – ICES mar. Sci. Symp., 194: 67–83.

The effects of stock and rearing history on the physiological responses of coho salmon to a number of standardized stresses were studied in two experiments. In the first experiment, six stocks of coho salmon (*Oncorhynchus kisutch*) from various locations in British Columbia, Canada were reared in a common environment and each subjected to six standardized stressors. The challenge tests conducted were salt water (30 ppt), high pH (9.4), low pH (3.5), thermal tolerance (1°C/h), disease (Bacterial Kidney Disease), and handling (30 s dip net). Measurements included plasma ion concentrations for the salinity and pH challenges, time to dysfunction in the thermal tolerance tests, mortalities in the disease challenge, and plasma glucose concentration in the handling challenge. No differences among stocks were found in the thermal tolerance and high pH challenges. Responses to salt water, low pH, disease, and handling differed among stocks. The Chehalis River stock performed best in salt water but showed the largest plasma ion decrease in acid waters. The Eagle River stock showed the lowest increase in plasma glucose concentration, a typical indicator of stress response, in the handling challenge. The Capilano River stock had a significantly lower mortality rate during the disease challenge, while Tenderfoot Creek and Eagle River stocks had high mortality rates. These results suggest that there are genetically based differences in the stress responses among stocks of coho salmon from southern British Columbia. When performance across all challenges was compared, each stock displayed a unique response profile. The second experiment consisted of applying the same handling stress as in the first experiment to hatchery and wild coho salmon from the Quinsam and Coldwater Rivers and Robertson and Siddle Creeks in British Columbia. Hatchery and wild fish from Siddle Creek were then reared in a common environment for six months, after which the experiment was repeated. Plasma concentrations of glucose and cortisol as well as the ratio of white blood cells to red blood cells were determined before and after the handling procedure. As in the first experiment, the response of each stock was unique. Furthermore, there was not a consistent difference between hatchery and wild groups among stocks. While hatchery and wild fish showed a classical stress response to handling in some stocks, both hatchery and wild groups from Siddle Creek showed little change in plasma cortisol or glucose concentrations in response to the stressor. Identical observations were made in hatchery and wild fish from Siddle Creek after six months of rearing in a common environment. It is clear that there are significant differences among stocks of coho salmon in British Columbia in their response to standardized stressors. No generalizations can be made about one stock being more resistant to stress than another. Furthermore, our data show that those generalizations cannot be made about hatchery and wild fish. Rearing history had variable effects on the response of coho salmon to the stressors.

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Introduction

Species of Pacific salmon exist as a series of distinct subpopulations, or stocks, that are reproductively isolated from each other (Horrall, 1981). Isolation, when combined with habitat differences, has the potential to produce environmental adaptations that stocks preserve in their genotype (Ricker, 1972). It has been shown for example that fish from similar environments have more in common with each other than those from different environments (Hjort and Schreck, 1981; Wilmot and Burger, 1985; Charrett *et al.*, 1987). Genetic differences among stocks of coho salmon (*Oncorhynchus kisutch*) have been demonstrated by electrophoretic separation of isoenzymes from polymorphic loci. An isoenzyme comparison of coho by Reisenbichler and Phelps (1987) suggested that while stocks from watersheds within a given region were distinct, they shared more similarities than those from different regions. A larger isoenzyme study using coho from southern British Columbia concluded that there were genetic differences between fish from the coastal mainland, Vancouver Island and the upper Fraser River (Wehrhahn and Powell, 1987). Heritable differences among coho have also been shown by observing phenotype.

Studies showing genetic differences between stocks for meristic and behavioural traits, as well as characteristics important for intensive fish culture, have been accomplished by studying fish that have been reared in common environments. Differences in body conformation and swimming ability between coastal and inland coho have been documented (Taylor and McPhail, 1985a, b). Behavioural diversity between coho stocks was demonstrated by Roseneau and McPhail (1987). There is evidence that growth and survival vary among stocks of coho from north, central, and southern British Columbia (B. Swift, University of British Columbia, pers. comm.). Challenges with pathogens such as the causative agent of Bacterial Kidney Disease (BKD), *Renibacterium salmoninarum* (Suzumoto *et al.*, 1977) and the parasite *Ceratomyxa shasta* (Envirocon Ltd. and E.V.S. Consultants Ltd., 1983; Ching and Parker, 1989) demonstrated that stocks can react differently.

Differences among stocks can also be confounded by rearing history. Differences in resistance to stress have been demonstrated between hatchery and wild fish stressed with confinement and electroshock (Woodward and Strange, 1987). This effect may have profound implications for efforts to enhance and maintain wild stocks of fish through massive propagation by intensive fish culture. While information regarding the possible physiological differences between hatchery and wild fish is lacking one might think, on theoretical grounds that each experiences selective forces for optimum survival in their respective environments.

Challenge tests that show differences between groups of fish can be used to assess the condition of fish (or fish populations) and to show the effects of environmental stress on fish (Wedemeyer and McLeay, 1981). In this way, standardized challenge tests are potential tools in the artificial propagation of fish and in environmental impact studies. These tests compare the tolerance limits and/or performance capacities among groups. It is recognized that factors such as genetic makeup can affect the responses to challenge tests (Schreck, 1981; Wedemeyer *et al.*, 1984). This first study reported here was designed to compare the performance capacity and tolerance limits of six different stocks of coho salmon from southern British Columbia, Canada. The physiological response of each stock to salt water, low pH, high pH, thermal, disease, and handling challenges were tested. The second experiment was designed to investigate the possibility that rearing history may affect the physiological responses of coho salmon from different stocks in British Columbia to the same handling stress as in the first experiment. For each stock, fish reared in the hatchery on the particular river or creek were compared to fish caught from that water system. To study the effects of rearing environment further, the handling experiment was repeated in both hatchery and wild fish in each location after they had been reared under identical conditions for six months.

The purpose of this report is to present selected data from both studies which were conducted to test two hypotheses. The first was that there were differences among stocks of coho salmon in their response to stress. The second was that rearing history had a significant effect on the stress response within a stock of coho salmon. The presented data are representative of the entire data set and have been selected for brevity. A complete presentation of the first study was reported by McGeer *et al.* (1991). The question of stock effects was studied in both experiments, whereas the effects of rearing history on responses to handling stress of fish hatchery and wild was investigated in the second experiment involving handling stress in hatchery and wild fish.

Material and methods

Study 1: stock response to six stressors

Approximately 2000 coho salmon were obtained from each of six different Canadian Department of Fisheries and Oceans Salmonid Enhancement Project hatcheries. They were housed in the Aquaculture Unit of the Department of Animal Science at the University of British Columbia. The stocks received from the Capilano River (stock A), Chehalis River (stock B), Chilliwack River (stock C), Quinsam River (stock E), and Tenderfoot Creek (stock F) hatcheries were collected as eyed eggs in March 1988. The sixth stock (stock D) came from the Eagle River hatchery in June 1988 as 3.7 g fry. The animals collected were the offspring of late run adults native to the watershed where the hatchery was located.

Fish were reared in dechlorinated Vancouver City tap water (4 to 15°C; hardness 4 mg/l as $CaCo_3$; pH 5.8 to 6.2). All stocks were maintained with similar feeding rates, water flow and management. Fish were fed a commercial salmon feed (Ewos ST40 and ST42). Monthly samplings were used to develop growth curve projections (Iwama and Tautz, 1981; Iwama, 1982) and to maintain feeding rates. Fish from all stocks were maintained in individual 150-l oval tanks with a flow of 8 l min^{-1}. Similar densities were maintained among stocks. At various times between October 1988 and June

Table 1. Summary of challenge trials in study 1.

Challenge trial	Date	Trial length	No. fish/ stock	°C	Environment change	Fish wt (g)
Salt water	10/88	24 h	15	13	30 ppt	9.5
Disease	10/88	5 mo.	35–44	4–13	BKD	8.5
Low pH	12/88	24 h	9	7	pH 3.55	16.6
High pH	11/88	72 h	6	9	pH 9.40	12.8
Thermal	03/89	22 h	8	6	1°C/h	14.0
Handling	06/89	18 h	7*	10	30s dip	26.8

*Number of fish per stock per sample time.

1989 samples of fish from each stock were subjected to challenge tests (Table 1).

Challenge trials involved simultaneous exposure of fish from all stocks to a stressor (see Table 1 for details). The 24-h salt water challenge test was conducted using saline water at 30 ppt following procedures outlined by Blackburn and Clarke (1987). The disease challenge used the BKD disease pathogen *Renibacterium salmoninarum*. An innoculum of 0.1 ml was administered using methods described by Iwama (1980). The low pH challenge test used a concentrated drip of HCl to decrease water pH to the stated level. The high pH challenge used NaOH to increase and maintain pH levels. The thermal tolerance challenge involved increasing the temperature by 1°C per h as outlined by McLeay and Gordon (1978). The handling experiment involved 30 s dip net stress (Barton *et al.*, 1986) with sampling at 0, 1.5, 3, 6, 9, 12, and 18 h. Weight and length data collected during trials and sample weighings were used to calculate condition factors (100*(weight in g)/(length in cm)^3).

The general procedures for all trials were as follows: fish starved for 12 to 24 h prior to testing; fish non-selectively netted from rearing tanks; full anaesthesia effected; weight and length determined; and finally, transferred to a 48-l challenge box. The box was made of black perspex and was divided into compartments so that each stock could be housed and sampled separately but maintained in a common water. Normal rearing water at a flow rate of 4 l min^{-1} was supplied to the box. After a 24-h acclimation period, the fish were challenged with the appropriate environmental perturbation. At the end of a trial, blood was collected from the caudal vasculature of euthanized fish (sodium bicarbonate buffered tricaine methanesulfonate at 300 ppm and/or a blow to the head). After hematocrit values were calculated, the plasma was saved and then stored at −80°C for subsequent determinations of sodium ion concentration ([Na^+]) and chloride ion concentration ([Cl^-]). In some trials [Cl^-] was not measured. Control data were collected for each test by running a parallel trial that used all of the challenge procedures except the environmental change.

The salinity, disease, thermal tolerance, and handling challenges had modifications of the general procedures above. The salt water challenge used a water recirculation rather than a flow-through system in which the water was aerated and temperature maintained. The disease challenge used a pooled control group which included all six stocks, and each of the seven groups (six stocks, one control) was housed in separate 38-l aquaria. The acclimation period to the aquaria prior to innoculation was 45 d. Mortalities were collected daily and visually examined for presumptive signs of BKD. Beginning 90 d after innoculation and continuing for 14 d, a daily stress consisting of netting the fish in each tank was applied. In the thermal tolerance test, data collection consisted of noting the temperature at which fish either lost equilibrium or died. In that test, water was recirculated at 3 l min^{-1} and fresh water was added at a rate of 0.85 l min^{-1}. The handling experiment used a larger challenge box (150 l) and plasma was analysed for glucose concentration. The 0 h measurement served as controls. Subsamples of fish were morphologically indexed for their stage of smoltification in the handling experiment. The four level index (one for parr, four for smolt) discussed by Gorbman *et al.* (1982) was used.

Plasma ion concentrations were determined using flame photometry for [Na^+] (Model 410, Corning Instruments) and coulometric titration (Chloridometer, Haakebuchler Instruments Ltd.) for [Cl^-]. Glucose concentration was colourimetrically measured by the oxidase method (Sigma Diagnostics, kit 510).

Study 2: rearing history effects

Four stocks of coho salmon fry from hatcheries and natural streams in the watershed where the hatcheries are located were used in this study (Table 2). The names of the hatcheries are the same as in Table 2, except for the hatchery associated with the Coldwater stock, named the Spius Creek Hatchery, and the hatchery associated with the Siddle Creek stock, named the Inch Creek Hatchery. All the hatchery fish were from the 1988 broodstock returning to the hatcheries. Care was taken to select hatchery fish as randomly as possible from large production units. The production units were concrete raceways in all hatcheries except for the one on Robertson Creek, where the production units were earthen ponds. The wild fry originated from broodfish that spawned naturally in the fall of 1988. They were

Table 2. Body weight, condition factor, holding densities, and water temperatures for hatchery-reared and wild fish of study 2.

Stock	Body weight (g)		Condition factor		Density (g/l)		Temp. (°C)
	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild	
Quinsam	4.50	3.51	0.85	0.82	1.7	1.6	11.5
Robertson	5.33	4.36	0.78	0.79	2.7	2.4	14.0
Coldwater	11.01	3.25	1.03	0.96	3.3	1.9	13.0
Siddle	4.09	3.46	1.00	0.98	1.7	1.7	10.8

captured using baited minnow traps (Gee traps) which were inspected and emptied into a flow-through tank secured to the river bed. The wild fry were then transported to the hatchery within 24 h. To avoid excessive stress and physical damage to the fish, the traps were inspected as often as possible (several times a day); large rocks were added to the flow-through tanks for shelter; and transport to the hatchery was done at densities below 1 kg/m^3.

Field experiment conditions

In all facilities except Robertson Creek, both hatchery and wild fish were transferred and held in 200-l containers with a continuous flow-through supply of fresh water which was contained in large round-bottom troughs. Both groups at Robertson Creek were held in 200-l rectangular flow-through containers.

Laboratory experiment conditions

From the Siddle stock, 800 hatchery and 800 wild coho salmon were transported to the fish rearing facilities of the Animal Science Department, University of British Columbia. After an initial diet of krill, the wild fish were trained to accept the commercial fish diet on which the hatchery fish were being maintained. Both groups were moved into the same 200-l flow-through containers as in the field experiments one week prior to the experiment. The hatchery fish weighed 13.17 g with a condition factor of 1.13, and the wild fish weighed 7.09 g with a condition factor of 1.22 at the time of the experiment. The densities in those containers were 6.8 kg/m^3 and 5.6 kg/m^3, for hatchery and wild fish, respectively. During the two-day period of that study, the water temperature was 8°C.

Protocol

The following procedures were followed for both field and laboratory experiments. Fish were sampled by removing them from the 200-l containers with a hand net and immediately sacrificing them in a lethal dose of 2-phenoxyethanol. The caudal peduncle was severed and blood samples were collected in heparanized haematocrit tubes. The blood samples were then centrifuged to obtain the plasma, which was frozen at -20°C until analysis. A few μl of blood was also used to make duplicate blood smears for each fish. The smears were then air dried, stored, and later stained and counted for red and white cell numbers in the laboratory. A pretreatment control sample was taken from both hatchery and wild fish, denoted by 0 h in the data. The treatment consisted of netting the fish out of the water and holding them in air 45 s in a large dip net. In the field, samples were collected at 1, 3, 6, 9, 12, and 30 h after the treatment. Cortisol concentration was analysed for the 1, 6, and 12-h samples; glucose concentration was determined for the 3, 6, 9, 12, and 30-h samples; and blood smears were made for blood cell counts at the 6 and 30-h samples. All parameters were determined for the pretreatment control sample. In the laboratory, blood samples were collected for cortisol and glucose concentration determinations at 0, 1, 3, 6, 9, 12, and 30 h.

Assays

Plasma cortisol was determined by [^{125}I] cortisol radioimmunoassay (Baxter Healthcare Corporation, Cambridge, Massachusetts. Clinical Assay No. 529). This procedure is based on the competitive binding principles of radioimmunoassay as described by Yalow and Berson (1971). Plasma glucose was measured using a modification of Trinder's (1969) colourimetric procedure with premixed 4-aminoantipyrine (Sigma, St. Louis, Missouri. Glucose [TRINDER] Procedure No. 315). Dried blood smears were stained using Wright's and Wright-Giemsa's stains according to the procedures of the Hemacolor^R Stain Set (EM Diagnostic Systems, Inc.). Of the two smears for each fish, one was selected on the basis of an assessment of the evenness of the staining, the thickness of the smear, as well as the area covered by the smear. Using a magnification of 1000×, the total number of erythrocytes, lymphocytes, neutrophils, monocytes, and thrombocytes was counted in 15 fields for each slide. Each field counted had a minimum of 50 cells and a maximum of 200. One-third of the fields counted were from the left side, one-third from the centre, and one-third from the right side of the smear. Within these boundaries fields were chosen randomly.

Statistics

Stock means for measured parameters under control and challenge conditions were tested by ANOVA. A

Table 3. Means, by stock and treatment, for the parameters measured in each of the challenge tests. Standard errors are subscripted.

	Stock					
	A	B	C	D	E	F
Salt water challenge						
Weight change Control	−0.6	−0.7	−0.7	−0.6	−0.8	−0.8
Challenge	−0.9	−1.0	−1.3	−1.4	−1.2	−1.2
Hematocrit, Control	$49_{1.5}$	$52_{1.6}$	$53_{1.2}$	$54_{1.8}$	$54_{1.5}$	$51_{1.5}$
Challenge	$47_{1.3}$	$43^{*}_{1.1}$	$46^{*}_{1.2}$	$44^{*}_{0.9}$	$48_{1.3}$	$46_{1.1}$
Plasma [Cl$^-$], Control	$131_{1.3}$	$129_{1.5}$	$137_{4.1}$	$133_{2.4}$	$131_{2.0}$	$132_{2.5}$
Challenge	$160^{*}_{2.2}$	$166^{*}_{4.7}$	$162^{*}_{5.9}$	$180^{*}_{5.3}$	$173^{*}_{5.0}$	$169^{*}_{3.7}$
Plasma [Na$^+$], see Figure 1						
Low pH challenge						
Weight change Control	−0.1	−0.4	−0.5	−0.3	−0.9	−0.4
Challenge	−0.1	+0.9	+0.1	0.0	+0.3	+0.2
Hematocrit, Control	$44_{1.3}$	$47_{1.1}$	$48_{1.0}$	$46_{1.2}$	$50_{1.2}$	$44_{1.2}$
Challenge	$58^{*}_{1.4}$	$59^{*}_{1.4}$	$60^{*}_{2.0}$	$60^{*}_{1.3}$	$59^{*}_{0.8}$	$57^{*}_{1.2}$
Plasma [Cl$^-$], Control	$133_{1.6}$	$132_{1.7}$	$138_{3.0}$	$126_{1.3}$	$125_{2.4}$	$138_{3.0}$
Challenge	$101^{*}_{4.9}$	$82^{*}_{6.1}$	$101^{*}_{5.8}$	$105^{*}_{5.7}$	$94^{*}_{1.5}$	$90^{*}_{3.4}$
Plasma [Na$^+$], see Figure 2						
High pH challenge						
Hematocrit, Control	$45_{1.4}$	$45_{1.8}$	$40_{2.9}$	$42_{1.8}$	$46_{2.2}$	$49_{1.9}$
Challenge	$45_{2.3}$	$46_{1.1}$	$49_{1.2}$	$46_{3.0}$	$44_{0.9}$	$46_{1.8}$
Plasma [Cl$^-$], Control	$124_{1.8}$	$122_{0.9}$	$122_{1.9}$	$128_{1.8}$	$124_{2.2}$	$122_{1.5}$
Challenge	$127_{2.3}$	$130_{1.9}$	$128_{1.1}$	$126_{2.0}$	$130_{5.3}$	$132^{*}_{2.4}$
Plasma [Na$^+$], see Figure 3						
Handling challenge						
Hematocrit, 0 h	$52_{1.1}$	$48_{0.9}$	$51_{1.1}$	$46_{1.5}$	$50_{2.1}$	$52_{1.3}$
1 h	$49_{2.3}$	$50_{0.8}$	$46_{1.1}$	$47_{1.1}$	$51_{2.2}$	$49_{1.5}$
3 h	$51_{1.6}$	$49_{1.2}$	$47_{0.8}$	$48_{1.5}$	$49_{1.7}$	$51_{0.9}$
6 h	$54_{1.4}$	$50_{1.6}$	$46_{1.3}$	$48_{2.0}$	$54_{1.7}$	$50_{1.1}$
9 h	$51_{2.8}$	$54^{*}_{1.4}$	$46_{2.3}$	$47_{1.3}$	$48_{1.3}$	$53_{1.7}$
12 h	$57_{2.2}$	$49_{0.7}$	$49_{1.5}$	$49_{1.6}$	$50_{1.3}$	$52_{1.9}$
18 h	$52_{0.9}$	$54^{*}_{2.1}$	$54_{1.7}$	$50_{1.4}$	$50_{0.6}$	$54_{1.5}$
Smolt index	3.40	3.93	3.93	4.00	3.90	3.93
Plasma glucose, see Figure 5						

*Challenge mean shows significant change from control mean.
Weight in grams, hematocrit as a %, and [Na$^+$] and [Cl$^-$] as mEq/l.

factorial experiment with completely random design was used. A one-way ANOVA was used to compare stocks in the temperature and handling trials as well as the condition factor data. Where appropriate, means at particular sample times were compared using Tukey's HSD tests. Dunnett's tests were used to compare pretreatment means with means at subsequent sampling times. Disease challenge mortality to survival ratios was compared by chi-squared analysis. The error level for all statistical tests was 0.05. Data are presented as arithmetic means ± 1 SEM.

Results

Study 1: stock response to six stressors

Several parameters were measured for each test. Data for one of those parameters are shown in Figs 1 to 6 and the remaining data are summarized in Table 3. In each challenge test, unless otherwise noted, there was no significant difference among stocks for mean fish weight.

The fish used in the salt water challenge of October 1988 all experienced a weight loss during the 48 h (24 acclimation + 24 challenge) in the challenge box. Average weight loss was less in control fish than in challenged fish (Table 3). Salt water also resulted in decreased hematocrit for all stocks. Stocks B, C, and D had significantly lower hematocrits under challenge conditions (Table 3).

Plasma ion concentrations were significantly increased for all stocks when they were exposed to salt water and the magnitude of the increase differed between stocks. Under control conditions there were no differences between stocks and overall mean for plasma [Na$^+$] was 139 mEq/l and for [Cl$^-$] 132 mEq/l. In salt water, stock B showed an increase [Na$^+$]; however, this

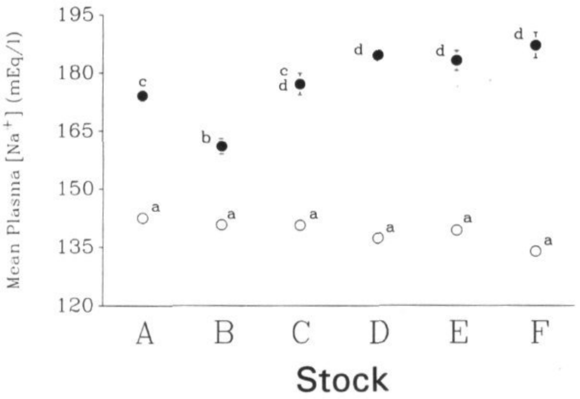

Figure 1. Plasma sodium concentration in control (open) and salt water challenge (filled) treatments for six stocks of coho salmon from southern British Columbia, Canada. Mean ± 1 s.e., n = 15. Means labelled with the same letter are not statistically different ($p < 0.05$).

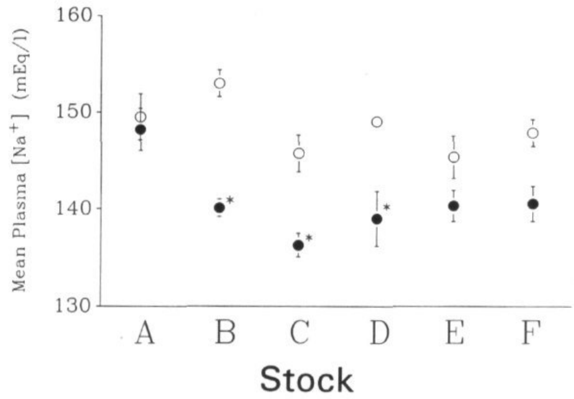

Figure 3. Plasma sodium concentration in control (open) and high pH challenge (filled) treatments for six stocks of coho salmon from southern British Columbia, Canada. Mean ± 1 s.e., n = 6. * denotes challenge means that are significantly different ($p < 0.05$) from control means for that stock.

increase was significantly less than all other stocks (Fig. 1). Stocks A and C had intermediate [Na^+] increases, while D, E, and F had the highest. Plasma [Cl^-] were also significantly increased under challenge conditions but there were fewer significant differences among stocks. The A, B, and C stocks had smaller increases in [Cl^-] than E, F, and G (Table 3).

The low pH challenge resulted in higher hematocrits and significant losses of plasma ions for all stocks (Table 3, Fig. 2). There were no significant differences in fish weight before or after, although weight loss in challenged fish was generally less than controls (Table 3). Although exposure to low pH had a significant effect on average hematocrit, there were no differences among stocks. Plasma [Na^+] was significantly decreased for all groups; especially for stock B, in which much greater declines were observed as a result of acid exposure (Fig. 2). Mean plasma [Cl^-] for all stocks was significantly reduced in acid waters and stock B suffered the largest losses (Table 3).

Exposure to high pH caused few significant differences. Hematocrits were unaffected by the challenge conditions at 72 h (Table 3). Mean plasma [Na^+] was significantly decreased from control values in stocks B, C, and D (Fig. 3). Plasma [Cl^-] was not altered significantly by exposure to high pH except for stock F in which plasma [Cl^-] was significantly lower than its control value.

The temperature tolerance challenge test did not show differences among stocks. All fish survived until 23°C and none past 25.5°C (Fig. 4). The average temperature at which death or disequilibrium occurred (the critical thermal maximum or CTM) did not differ among stocks. Stock C showed the lowest CTM and stock D the highest.

There was no consistent trend in hematocrit change from initial values for any stock in the handling chal-

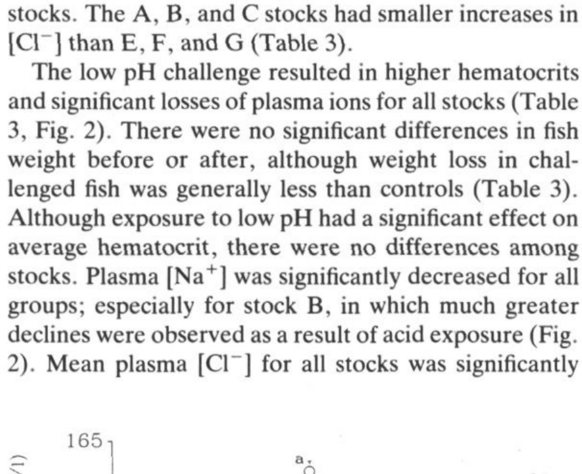

Figure 2. Plasma sodium concentration in control (open) and low pH challenge (filled) treatments for six stocks of coho salmon from southern British Columbia, Canada. Mean ± 1 s.e., n = 9. Means labelled with the same letter are not statistically different ($p < 0.05$).

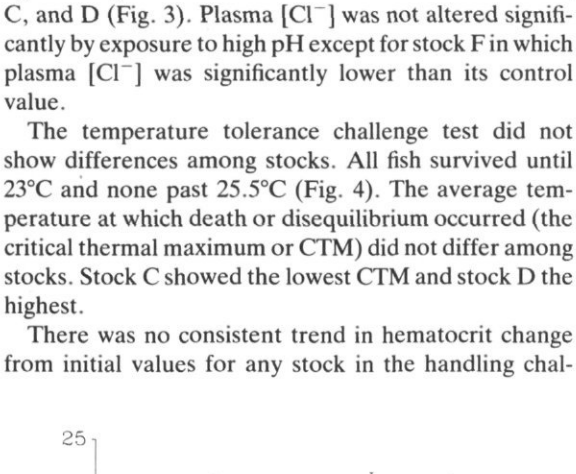

Figure 4. Critical thermal maxima of six stocks of coho salmon from southern British Columbia, Canada. Mean temperature (°C) at disequilibrium or death ± 1 s.e., n = 8. Means labelled with the same letter are not statistically different ($p < 0.05$).

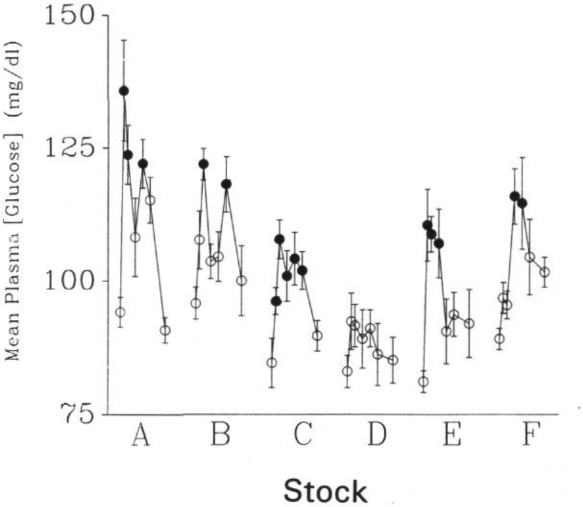

Figure 5. Plasma glucose concentration of six stocks of coho salmon from southern British Columbia, Canada, sampled at 0, 1.5, 3, 6, 9, 12, and 18 h after a dip net challenge. Mean ± 1 s.e., n = 7. Filled circles are statistically different ($p < 0.05$) from the 0 h values for that stock, while open circles are not. (From McGeer *et al.*, 1991.)

lenge. Mean resting (0 h) glucose concentrations did not vary between stocks (Fig. 5). Stock A showed the largest increase in glucose and stock D was the only group of fish that did not show a significant increase in glucose concentration at any of the sampling times. Glucose concentrations for all stocks returned to control values by the 18-h sample. The smoltification index data comparisons showed stock A to be significantly less than the others. The mean index for stock A was 3.4, while other stocks ranged from 3.90 to 4.00.

The disease challenge resulted in significant differences in survival among the stocks (Fig. 6). There were no mortalities or BKD signs in the control group. Stocks C, E, and F had intermediate levels of mortalities.

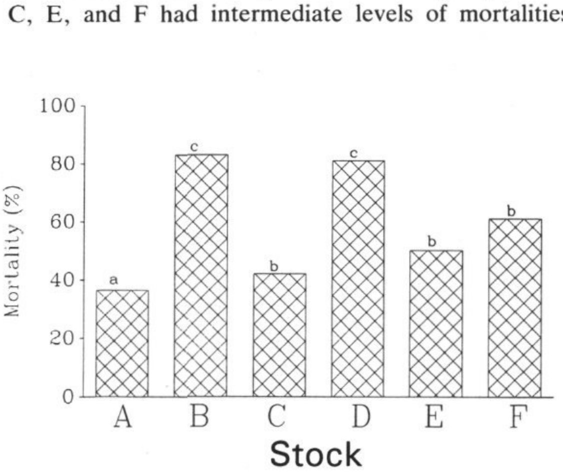

Figure 6. Percent mortality of six stocks of coho salmon from southern British Columbia, Canada, challenged with *Renibacterium salmoninarum*. Cumulative percent mortality, n = 40, and letters show statistically similar groups.

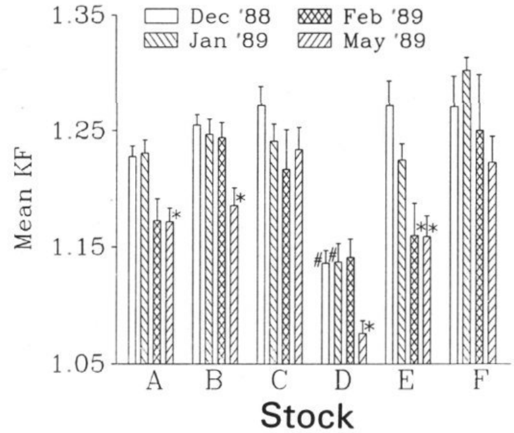

Figure 7. Condition factor of six stocks of coho salmon from southern British Columbia, Canada, at four time periods. Mean ± 1 s.e. Means labelled with # are significantly lower ($p < 0.05$) than other stocks at that sampling and * denotes means significantly lower ($p < 0.05$) than December 1988 measures for that stock. (From McGeer *et al.*, 1991.)

Mortalities in stock A were significantly lower than other groups of fish. Stocks B and D experienced mortality rates higher than other stocks. All mortalities displayed similar internal signs, which were typical of the disease.

The weight and length data, collected in December 1988, January 1989, February 1989, and May 1989, demonstrated that condition factor (KF) changed over time and that there were differences among stocks (Fig. 7). At each of the four times, stock D had significantly lower KF values. Across sampling times, all stocks except C and F showed a significant decrease in KF. The decrease in KF occurred between January and February for stocks A and E. The KF decline in stocks B and D occurred between February and May.

The sampling conducted while preparing for the handling challenge and the handling experiment itself provided information on resting plasma glucose levels. There were significant differences between resting glucose levels at different times of the day. As the day progressed, there was a decrease in plasma glucose concentration in resting fish (Fig. 8). A starvation period of 24 h did not affect the mean glucose concentration. In one sample, a 42-h starvation period produced significantly lower plasma glucose concentration. There appeared to be no relationship between resting glucose and fish weight, or glucose concentration response and fish weight.

Study 2: rearing history effects

Plasma cortisol response among the four stocks of coho salmon was varied (Fig. 9). There was no consistent trend in differences between hatchery and wild fish. The mean pretreatment cortisol concentrations were be-

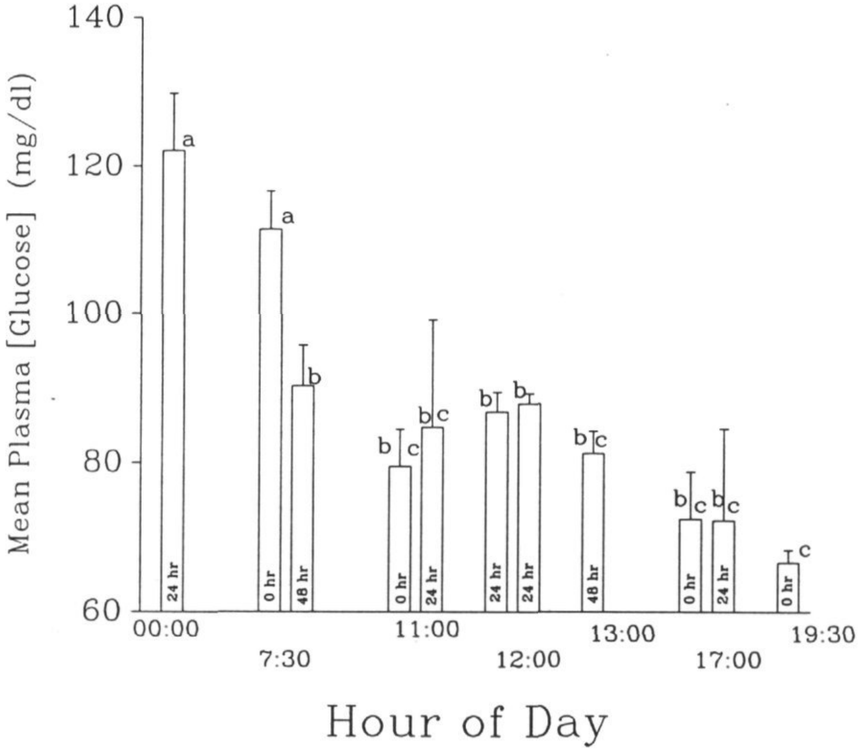

Figure 8. Plasma glucose concentration of coho salmon from southern British Columbia, Canada, sampled at various times of day. Mean ± 1 s.e., n = 16 for 00:00 h, n = 7 and n = 12 for 07:00 h, n = 12 and n = 19 for 11:00 h, n = 47 and n = 43 for 12:00 h, n = 9 for 13:00 h, n = 10 and n = 42 for 17:00 h, n = 9 for 19:30 h. Those labelled with the same letter are not significantly different ($p < 0.05$) from each other. The starvation period prior to sampling is shown at the base of each bar.

tween 13 and 15 μg/dl in hatchery fish from the Quinsam and Coldwater Rivers. Wild fish from those rivers showed consistently lower control values for plasma cortisol concentration, with means between 5 and 9 μg/dl. Both hatchery and wild fish from Robertson and Siddle Creeks showed relatively low plasma cortisol concentrations during the pretreatment control period. Hatchery fish from those two creeks and wild fish from the Siddle Creek showed mean values around 5 μg/dl. Wild fish from Robertson Creek had the lowest control values near 2 μg/dl (Fig. 9).

Changes in plasma cortisol concentration in response to the 45-s handling procedure showed an increase at the 6-h sample, followed by a gradual decline in the wild fish from Quinsam River and Robertson Creek (Fig. 9). The declining trend in plasma cortisol concentrations after the 6-h sample was also seen in the wild fish from the Coldwater River as well as the hatchery fish from the Quinsam and Coldwater Rivers; the increase from pretreatment control levels was not seen in these groups. Hatchery fish from Robertson Creek showed little change in plasma cortisol concentration in response to the handling procedure (Fig. 9). Similarly, both wild and hatchery fish from the Siddle Creek showed no response to handling with respect to changes in plasma cortisol concentrations; mean values for hatchery and wild fish remained between 3 and 8 μg/dl. After about six months of rearing in a common environment, both wild and hatchery fish from the Siddle Creek showed nearly an identical response to the same handling procedure (Fig. 12a).

Plasma glucose concentrations in both hatchery and wild fish during the pretreatment period were similar and means were between about 50 and 100 mg/dl (Fig. 10). Wild fish had lower glucose concentrations relative to hatchery fish during the control period in the Quinsam River, Coldwater River, and Siddle Creek stocks. In the Robertson Creek stock, wild fish showed glucose concentrations which were higher than the hatchery fish.

Plasma glucose concentrations increased in response to the handling procedure in both hatchery and wild fish from the Quinsam River and Robertson Creek and in the hatchery fish from the Coldwater River (Fig. 10). There was a general trend for a return toward control levels in all those groups with time. Plasma glucose concentrations in the wild fish from the Coldwater River showed a very consistent decline with time in response to the handling procedure (Fig. 10). As in the results for plasma cortisol concentrations, both hatchery and wild fish from the Siddle Creek showed little response to the handling procedure, with significant differences occurring sporadically (Fig. 10). Furthermore, the same result

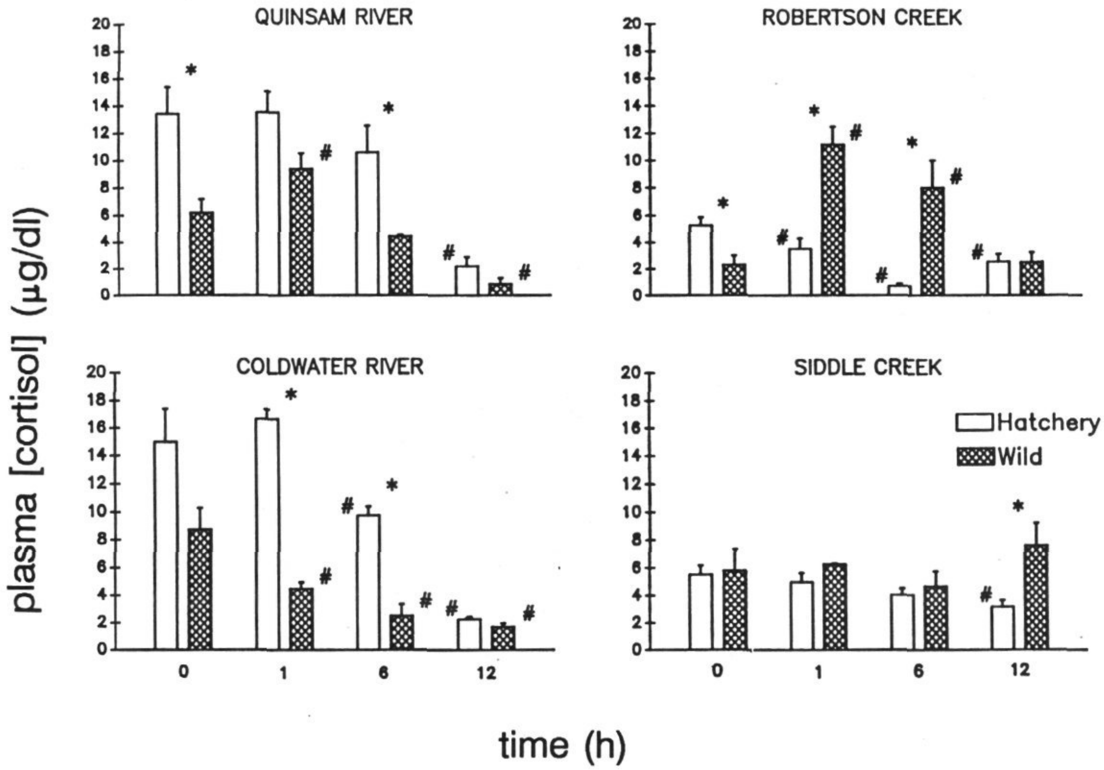

Figure 9. Plasma cortisol concentration in hatchery (open) and wild (crosshatched) coho salmon from four stocks in British Columbia, Canada, sampled at 0, 1, 6, and 12 h after a dip net challenge. Mean ± 1 s.e., n = 8. # denotes statistical significance from 0 h measurements, while * denotes significant difference between hatchery and wild for that sampling time ($p < 0.05$).

with even less variability was obtained from Siddle Creek fish after six months of rearing in a common environment and on the same feed (Fig. 12b).

The ratio of white blood cells to red blood cells (WBC/RBC) did not differ significantly between hatchery and wild fish from all stocks during the pretreatment control period; mean values (×100) were in the range of 2 to 4 (Fig. 11). The acute handling procedure did not elicit a response with respect to WBC/RBC in either hatchery or wild fish from the Quinsam River nor in hatchery fish from Robertson Creek. There was a reduction in WBC/RBC in response to handling in both wild and hatchery fish from Siddle Creek and in the wild fish from Robertson Creek; a trend which continued to the last sample at 30 h after handling (Fig. 11). The mean values at 30 h had declined to about 0.5 to 1.5. Both hatchery and wild fish from the Coldwater River showed a similar decline in WBC/RBC to those levels in 6 h after the handling procedure, but also showed a recovery to control values by the 30 h sample.

Discussion

Stock response to six stressors

Challenge tests have a wide variety of applications and purposes (reviewed by Wedemeyer *et al.*, 1990). In the context of our experiments, the challenges not only uncovered a few unique traits but also served as comparative indicators in assessing the performance capacities of stocks of coho salmon. As discussed by Schreck (1981), challenges can be useful in selecting genotypes that are physiologically best suited to tolerate stress. The screening of fish stocks for useful characteristics is one aspect of challenge testing. Another use of challenge tests is to build a response profile that can be compared with other profiles. While the individual challenge test results illustrate some interesting and potentially important differences among the six stocks, the challenges should also be viewed in combination.

Life history information on each of the six stocks showed that all are thought to migrate to sea water at one year of age. Therefore, no group was expected to perform very well in the salt water challenges. Fish in stock B were best able to regulate blood ions. Plasma [Na^+] of 170 mEq/l or less after 24 h is indicative of a functional smolt (Clarke and Blackburn, 1977; Johnson and Heifetz, 1988). Although fish with higher levels may survive the 24-h challenge and some may survive in the longer term, growth is impaired (Clarke, 1982). The combined [Na^+] and [Cl^-] results suggest that while stock B fish were most competent in regulating plasma ion concentrations, stocks A and C may also have been competent in ion regulation.

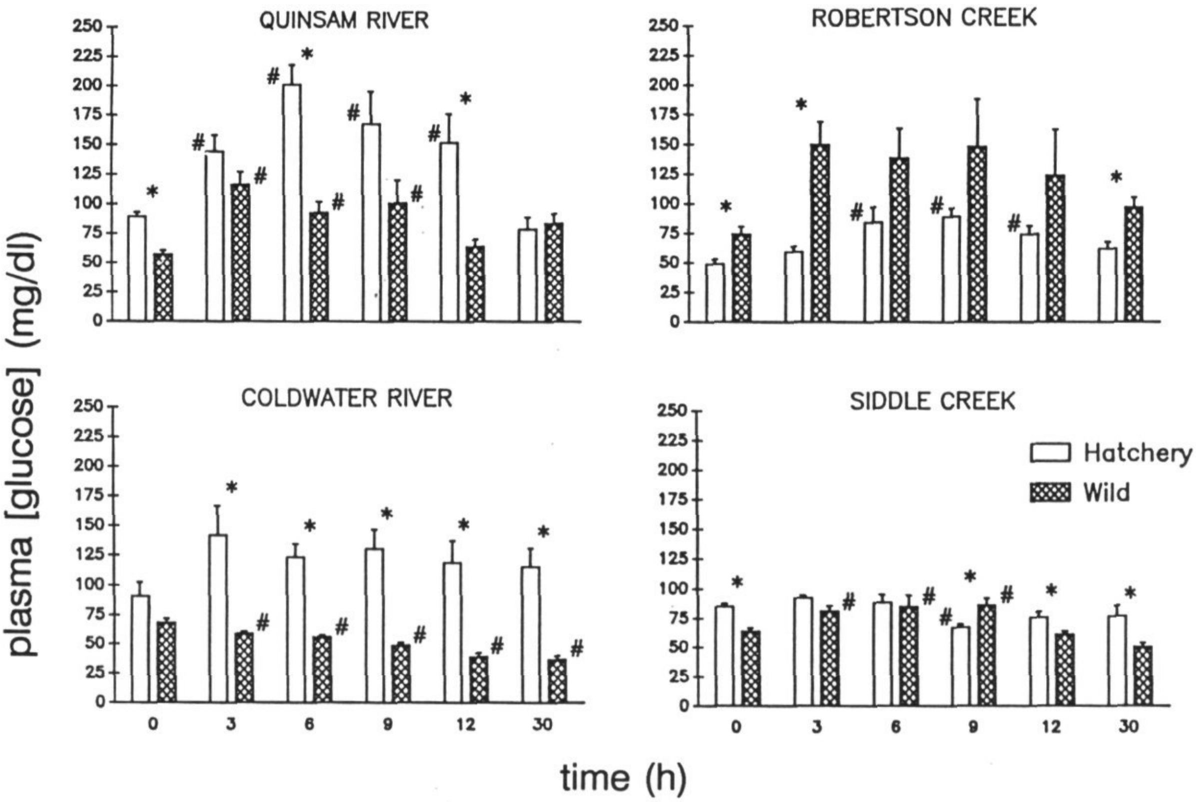

Figure 10. Plasma glucose concentration in hatchery (open) and wild (crosshatched) coho salmon from four stocks in British Columbia, Canada, sampled at 0, 3, 6, 9, 12, and 30 h after a dip net challenge. Mean ± 1 s.e., n = 8. # denotes statistical significance from 0 h measurements, while * denotes significant difference between hatchery and wild for that sampling time ($p < 0.05$).

There was also a differential response among stocks exposed to acidic conditions. While fish in stock B were most competent in salt water, they showed the largest disturbance in response to acidic conditions. Plasma $[Na^+]$ in stock B was consistently lower than in other challenged stocks. The works of Schom (1986) with Atlantic salmon and Swarts *et al.* (1978) with brook trout suggest that the ability of fish to survive low pH exposures is better in fish from native waters with a low pH. Variable effects have also been observed in trout exposed to low pH in waters of different alkalinity (McDonald, 1983b; Booth *et al.*, 1988). Another brook trout study (Robinson *et al.*, 1976) also concluded that acid tolerance has a genetic component. Peterson *et al.* (1989), furthermore, have shown species differences in sensitivity to low pH conditions. The available records do not indicate anything unique in the watersheds or hatcheries where stock B originates.

In fish exposed to acid, ion, and hematocrit changes occur through a number of mechanisms which have been reviewed by Fromm (1980) and McDonald (1983a). The reduction in plasma $[Cl^-]$ and the increase in hematocrit which were observed in fish from all stocks in response to acid exposure concur with published reports. The reduction in $[Na^+]$ and $[Cl^-]$ occurs as a result of both a decrease in active ion uptake by gill tissue and an increase in the passive efflux of ions from the fish (Booth *et al.*, 1988; Wright and Wood, 1985). Increases in hematocrit have been documented in rainbow trout exposed to pH 4.0 (Audet and Wood, 1988; Milligan and Wood, 1982). The latter study showed that increases in packed cell volume were due to increased recruitment from the spleen, lower plasma volume, and a swelling of red blood cells as a result of the extracellular acidosis.

Fish exposed to high pH experience an inhibition of ammonia efflux, resulting in large increases in plasma ammonia concentration, and, under some conditions, death (see Randall and Wright, 1988). There is recent evidence that rainbow trout can acclimate and reestablish ammonia excretion rates in water of pH 9.5 (Wilkie, 1989) and water quality, particularly water hardness, has large effects on the physiological effects of exposure to water of pH near 10 (Yesaki, 1990). A likely explanation for the lack of change in $[Na^+]$, $[Cl^-]$, and hematocit in fish from all stocks exposed to pH 9.4 is a combination of short exposure time, pH value, water quality. At pH values less than 9.6, the length of time for ion losses to occur is greatly extended. Another rainbow

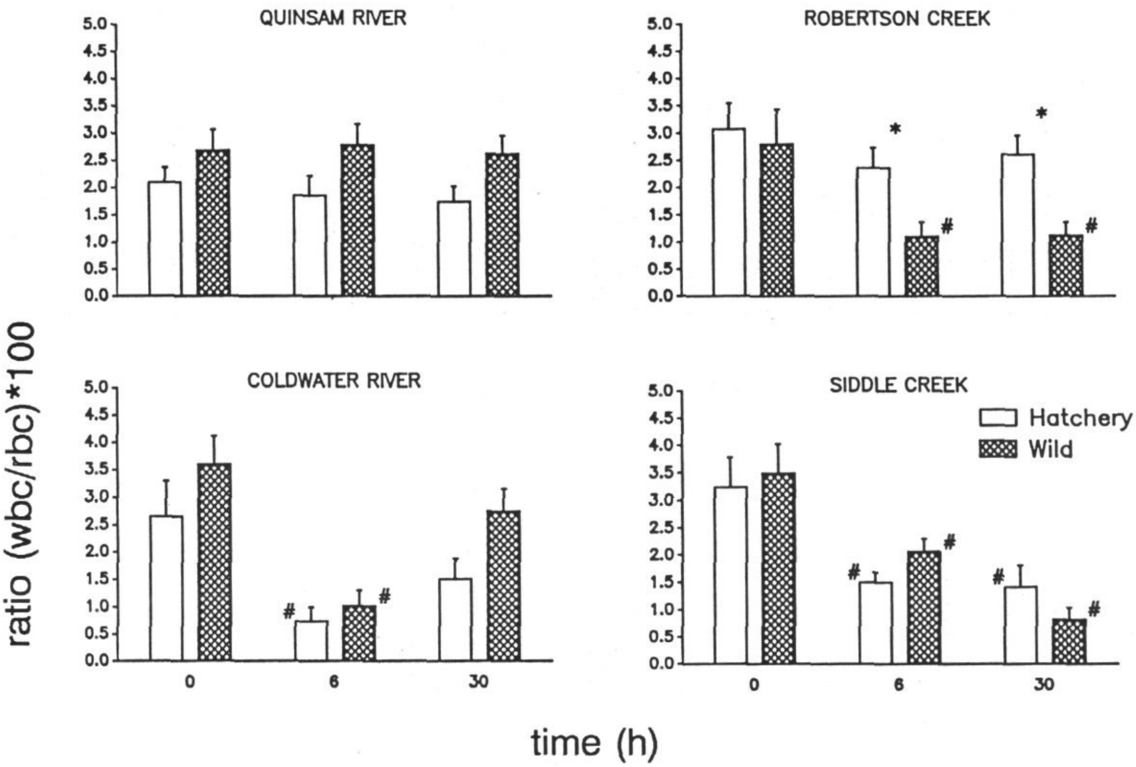

Figure 11. Ratio of white blood cells to red blood cells in hatchery (open) and wild (crosshatched) coho salmon from four stocks in British Columbia, Canada, sampled at 0, 6, and 30 h after a dip net challenge. Mean ratio (100*WBC/RBC) ± 1 s.e., $n = 8$. # denotes statistical significance from 0 h measurements, while * denotes significant difference between hatchery and wild for that sampling time ($p < 0.05$).

trout study (Heming and Blumhagen, 1988) observed a progressive decline of plasma ion concentrations over the course of a 96-h experiment at pH 8.7 and a 20% mortality in a 24-h challenge at pH 9.7. Yesaki (1990) found that rainbow trout showed significant $[Na^+]$ decreases after approximately 24 h at pH 10.

The handling experiment provided interesting results concerning the effects of stock and time of day. Glucose is frequently used as an indicator of stress (Mazeaud *et al.*, 1977; Wedemeyer *et al.*, 1990; Wedemeyer and McLeay, 1981). The resting levels of glucose, excluding diurnal effects, did not differ among stocks. In all trials, stock D showed the lowest increase in plasma glucose concentration. All other stocks showed significant increases in glucose concentration with stock A having the largest increase. Factors which can alter glucose response include rearing temperature (Barton and Schreck, 1987), nutritional status (Barton *et al.*, 1988), and stocking density (Congelton *et al.*, 1984). Refstie (1986) found that there was a genetic component to stress-induced glucose changes among different groups of Atlantic salmon. The index of smoltification suggested that fish in stock A were at a lower level of smoltification. Plasma cortisol concentrations, which change with smoltification (Specker and Schreck, 1982; Barton *et al.*, 1985), may have been different in those fish compared to fish of other stocks; thereby affecting plasma glucose concentrations. Diurnal variation in resting glucose concentrations has been shown by Congelton *et al.* (1984). In that study, levels were low at night and elevated during the day. Our studies are contradictory to this pattern, but are in agreement with the study of Barton *et al.* (1986), which showed decreasing levels as the day progressed. The lack of hematocrit changes observed in the handling challenge reflects the sampling times used. The hematocrit changes observed by Casilla and Smith (1977) were most dramatic in the first 20 min after stress. Our first sample was not taken until 1.5 h after handling.

The thermal challenge did not show differences between stocks. The CTM for all stocks was within a narrow range. The upper limit of the CTM range was close to the lethal temperature that Piper *et al.* (1982) reported for coho salmon. It is also 0.7°C less than a CTM previously reported (Becker and Genoway, 1979) for coho salmon acclimated to a similar rearing temperature (5°C). There is evidence of stock and genetic differences in CTM for other species of fish. Fields *et al.* (1987) found that a Wisconsin stock of largemouth bass had a significantly lower CTM than a Florida stock. A selection experiment with rainbow trout (Ihssen, 1986)

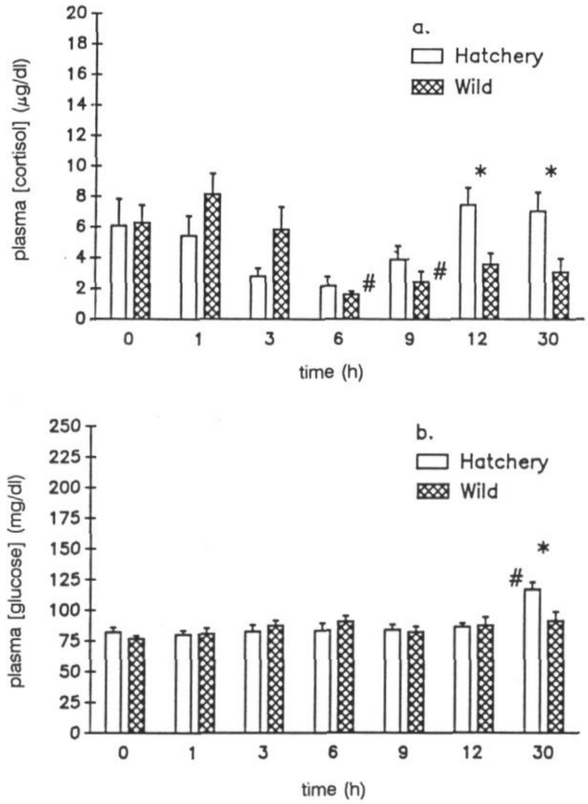

Figure 12. Plasma cortisol concentration (a) and glucose concentration (b) in hatchery (open) and wild (crosshatched) coho salmon from Siddle Creek stock, British Columbia, Canada, sampled at 0, 1, 3, 6, 9, 12, and 30 h after a dip net challenge. Mean ± 1 s.e., n = 8. # denotes statistical significance from 0 h measurements, while * denotes significant difference between hatchery and wild for that sampling time ($p < 0.05$).

observed an upward shift in CTM in the first generation and concluded that temperature tolerance is heritable. The CTM similarities among stocks in our experiments may reflect the small geographic and latitudinal differences as well as the similar habitat temperatures associated with each stock. The good agreement in the CTM values with those in the literature suggests that rearing conditions were not unduly stressful.

The disease challenge resulted in significant differences in survival among the stocks. Studies with rainbow trout in sea water (Refstie, 1982) and Atlantic salmon in fresh water (Gjedrem and Aulstad, 1974) have shown that resistance to *Vibrio anguillarum* can vary among stocks. Experiments with coho salmon (Ching and Parker, 1989) and chinook salmon (Envirocon Ltd. and E.V.S. Consultants, 1983) using *Ceratomyxa shasta* demonstrated that the ability to survive parasitic infection varied among stocks. They also found that fish from stocks that are exposed to the pathogen in their natural migration routes exhibited higher survival rates when challenged. A study by Suzumoto *et al.* (1977) linked the differences in BKD resistance among three groups of coho salmon to different transferrin genotypes.

The results of the disease challenge do not necessarily indicate a difference among stocks to BKD alone, as the challenge was really a combination of disease and chronic mild stress. The differences in mortalities could have resulted from differences in BKD susceptibility or the ability to deal with the stress, or a combination of both. The stress response results in a readjustment of metabolic processes and, if the stress is chronic, the fish will be less immune to disease (Wedemeyer and Goodyear, 1984). Work by Maule *et al.* (1989) using chinook salmon and by Ellsaesser and Clem (1986) using channel catfish showed that immune system function and disease resistance is compromised under conditions of acute stress. It is, however, likely that the differences observed in the challenge are related to the BKD rather than the stress. Stock A, which showed the largest increases in glucose concentrations in response to the handling stress, also had the lowest mortality rate in response to the disease challenge. Stock D showed the lowest glucose response to handling and a high mortality rate in the disease challenge. The netting procedure in the disease challenge, furthermore, was initiated about three months after the initial innoculation of the pathogen. It is very probable that the disease challenge results arose from differences between stocks in BKD resistance and the stress served to enhance the progression of the disease.

The weight and length data confirmed reported differences between coastal and inland stocks of fish in body conformation. At each of the four times that weight and length data were collected, fish of stock D were significantly longer than fish of equal weight from other stocks. In our groups of fish, the only one from an inland source was stock D. These condition factor results confirm those of Taylor and McPhail (1985a), who demonstrated that inland stocks tend to be long and thin, while coastal stocks tend to be short and deep bodied; and that these distinctions had a genetic basis. A more recent study (Swain and Holtby, 1989) using two groups of coho salmon from within a close geographic range, but from different habitats, demonstrated that body morphology depended on habitat. Stream type fish had thinner bodies than the lake type. The methods used leave open the possibility of differences being environmentally induced, but only if they are fixed after an induction in early life.

Our data also show that the changes in body conformation occur over time. This was associated with the smoltification process, as there are a series of morphological changes that occur, including a decrease in condition factor, as salmon undergo the transition from parr to smolt (Gorbman *et al.*, 1982; Winans and Nishioka, 1987). Barton *et al.* (1985), using coho salmon, documented condition factor decreases similar to the changes we observed in the coastal stocks.

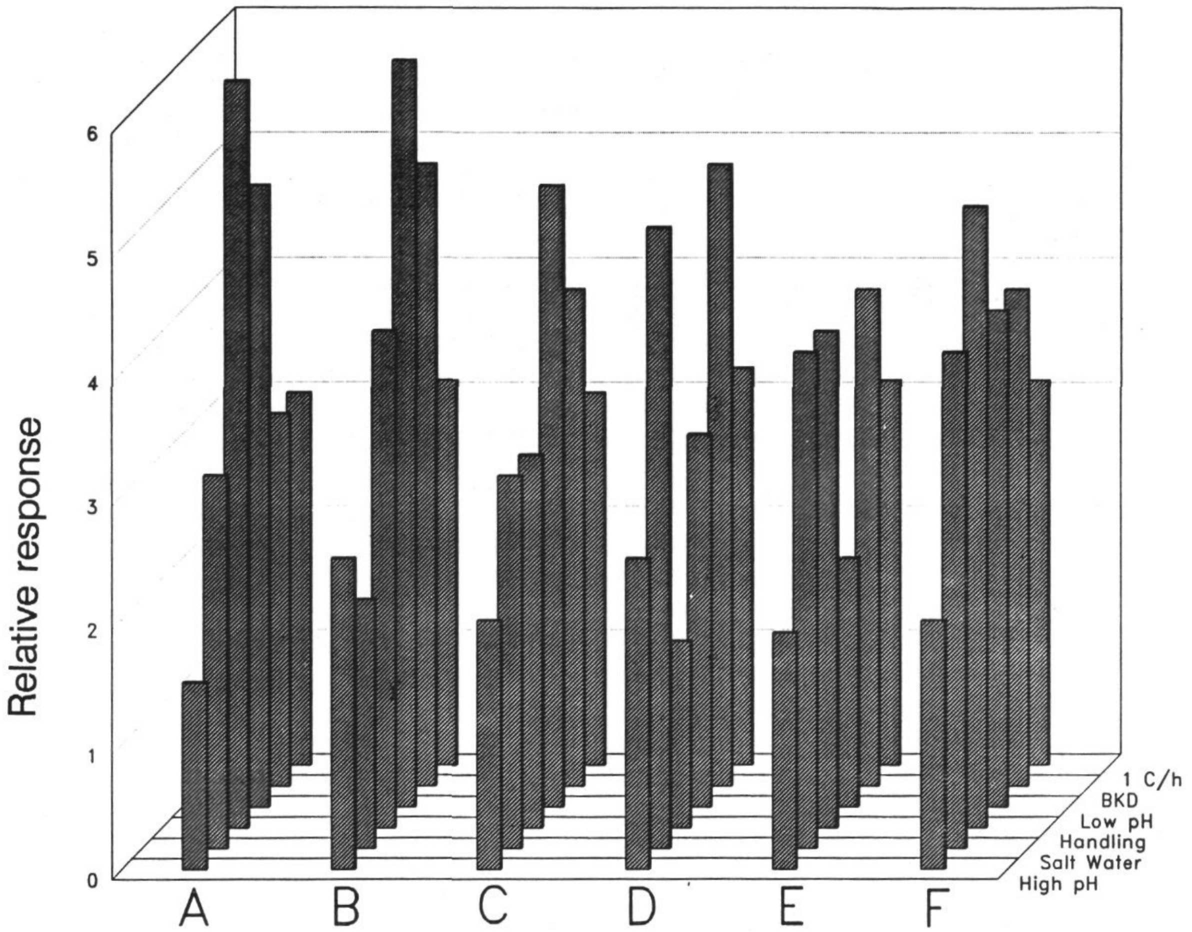

Figure 13. Relative response profile of six stocks of coho salmon from southern British Columbia, Canada. The mean disturbance experienced by each stock (relative to other stocks) in a selection of challenges was given a numeric value ranging from 1 (no effect) to 5 (large or life threatening reaction). (From McGeer *et al.*, 1991.)

When the challenges are viewed in combination for each stock, the stocks differed from each other in their physiological response to the challenge tests. A performance profile for each stock was constructed by assigning a relative numerical value to responses of a selected group of challenges (Fig. 13). The performance profile is taken from McGeer *et al.* (1991), where the complete data set of this study is reported. The concept of a profile of various stress measurements was used by Buckley *et al.* (1985) to assess the effects of environmental degradation by comparing stocks of largemouth bass. They demonstrated the benefits of a multidiscipline approach in studying fish stocks. The use of a number of short duration challenge tests to develop performance profiles of stocks of fish should contribute to the existing base of knowledge about stocks.

Information on stocks and performance profile results of this type are potentially useful for: improving rearing and enhancement management; selecting stocks for transplantation or commercial aquaculture; monitoring environmental degradation; and for demonstrating the importance of maintaining the integrity of stocks. The test procedures used, and measurements collected, are all relatively simple and experiments of this nature are easy to conduct. To improve the performance profile, efforts might best be used in conducting salinity, pH, and handling challenges. Other tests might include the use of reference toxicants and either swim stamina or hypoxia-tolerance tests. These challenges should be repeated over time to gain an understanding of the changes over time or seasons. A better understanding of the influences of maturity and rearing environment is needed to gain full benefit from test results.

Rearing history effects

It is difficult to give a sample explanation for the variability in the responses of hatchery and wild coho salmon across all the four stocks to the acute handling procedure. The variability cannot be assigned to the fish or experimental conditions (Table 2). The plasma cortisol and glucose concentrations in both hatchery and wild fish during the pretreatment control period are in general agreement with resting values reported in the literature (see Barton *et al.* 1986), suggesting that those fish were not in a stressed state. Those values, however, for other groups studied here were significantly higher.

While the range of pretreatment control values for plasma glucose concentration was similar between hatchery and wild fish, it was lower in wild fish from the Quinsam River, Coldwater River and Siddle Creek, but higher than hatchery fish from Robertson Creek. Differences between wild and hatchery fish for blood glucose have been shown in previous studies using rainbow trout (Wydoski *et al.*, 1976; Casilla and Smith, 1977; Woodward and Strange, 1987), largemouth bass (Williamson and Carmichael, 1986), and chinook salmon (Barton *et al.*, 1986).

The plasma concentrations of cortisol were as high as the peak levels after the acute handling procedure was carried out in both the hatchery and wild fish from the Coldwater River as well as the hatchery fish from the Quinsam River and probably obscured increases in this parameter in response to the handling procedure in those groups. This suggests that, in some hatchery and wild groups, fish were in a stressed state before the experiment. If this is taken into account, the changes in plasma concentrations of cortisol and glucose in response to the handling procedure are in general agreement with the established trends for these parameters; that is, an initial increase followed by a consistent decline with time back to control values. An exception to this trend was observed in both hatchery and wild fish from Siddle Creek, where there was no response to handling.

The WBC/RBC values of both hatchery and wild fish from all stocks during the pretreatment control period were in the normal range for resting fish (McLeay, 1975). When there was a response in WBC/RBC to the handling procedure, it was a decline with time. Lymphocytopenia, or the reduction in total white blood cell numbers, has been reported for fish in response to stress (see review by Barton and Iwami, 1990). This trend was observed in some groups of fish, but as in the cortisol and glucose data it did not occur consistently in all groups. Hatchery and wild fish showed very similar responses, whether there was no response to the treatment (Quinsam River) or whether, as in the case of the Coldwater River stock, there was an initial decline in WBC/RBC and a recovery to control values by the 30-h sample. It is now known why this recovery did not occur in both hatchery and wild fish from Siddle Creek where WBC/RBC continued to decline with time. Hatchery and wild fish from the Robertson Creek, in contrast, differed in their response to handling; hatchery fish showed little change, while WBC/RBC in wild fish showed a declining trend as in the fish from Siddle Creek.

It is interesting to note that while hatchery and wild fish from Siddle Creek showed little response to the handling procedure with respect to changes in the plasma cortisol and glucose concentrations, both showed a decline in WBC/RBC that did not recover with time. One cannot conclude with the present data whether this stock of fish was resistant to the stress of handling or if both groups experienced stress, which was reflected in the WBC/RBC ratio, but lacked the mechanisms to elicit the increased cortisol and glucose concentrations characteristic of the normal stress response in fish. The data for the hatchery fish from Robertson Creek, on the other hand, showed little change in cortisol concentration and in WBC/RBC ratio in response to handling but showed the well documented pattern of an initial increase in glucose concentration in response to handling followed by a decline toward control values with time. While further work is needed to clarify whether these results represent stocks of fish that are relatively resistant to handling stress, with explanations for the WBC/RBC ratio changes in the Siddle Creek fish and glucose concentration changes in the hatchery Robertson Creek fish other than the handling procedure, these stocks represent potentially interesting groups of fish for studies on stress in fish.

The possibility that the observed effects in response to the acute handling challenge were based on genetic differences among stocks more than on the rearing environment is strongly supported by the remarkable repetition of the plasma cortisol and glucose concentration results in both the hatchery and wild fish from Siddle Creek after about six months of rearing in a common environment, water supply, and on the same feed. Not only were there similarities in the range of values between the two experiments, but the relationship between hatchery and wild fish was also maintained.

Conclusions/Summary

The results of our experiments demonstrate that while stocks had similar reactions to a number of the imposed challenges, others showed significant differences in their responses. For example, fish from Chehalis River appeared to be most competent in ionic regulation in hypersaline waters, and fish from Eagle River displayed minimal metabolic response (as measured by glucose) to handling. The field and associated laboratory experiments suggested that fish from Siddle Creek were most resistant to the stress of handling, compared to fish of three other stocks. It is reasonable to speculate that the differences in these challenge test results have some genetic basis. However, as the unique response profiles show, generalizations cannot be made about the stress resistance of a particular stock. While fish in Eagle River showed little response to handling stress, they were particularly susceptible to bacterial kidney disease infection.

These data show no consistent effects of rearing history on the stress response in coho salmon. Other than a few exceptions, such as the consistently higher cortisol and glucose concentrations in hatchery fish over wild fish in the Quinsam and Coldwater River stocks and the consistently higher WBC/RBC ratios in wild fish over hatchery reared fish in the Quinsam stock, the effects of rearing in a hatchery or in the wild on the measured parameters were very variable.

While these data do not show whether intensive fish culture produces a more robust or compromised animal, compared to the wild counterpart, they do show that there are physiological differences in response to stress among different stocks of coho salmon. This should serve as a caution to managers of government enhancement programmes that employ the techniques of intensive culture, and especially the movement of fish stocks among enhancement facilities, that stocks demonstrate a unique response profile to stress that suggests that transplantation of stocks to foreign environments can result in unpredictable results.

The functional significance of these results to the survival of the animal and to its success in contributing to the population in the wild environment has not been demonstrated. Physiological studies, such as these reported here, should be considered in conjunction with investigations of a behavioural and ecological nature to understand how the performance of a stock to a particular stress might affect its fitness in nature.

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References

Audet, C., and Wood, C. M. 1988. Do rainbow trout (*Salmo gairdneri*) acclimate to low pH? Can. J. Fish. aquat. Sci., 45: 1399–1405.

Barton, B. A., and Iwama, G. K. 1991. Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. Ann. Rev. Fish Dis., 1: 3–26.

Barton, B. A., and Schreck, C. B. 1987. Influence of acclimation temperature on interrenal and carbohydrate stress responses in juvenile chinook salmon (*Oncorhynchus tshawytscha*). Aquaculture, 62: 299–310.

Barton, B. A., Schreck, C. B., Ewing, R. D., Hemmingsen, A. R., and Patino, R. 1985. Changes in plasma cortisol during stress and smoltification in coho salmon, *Oncorhynchus kisutch*. Gen. Comp. Endocrinol., 59: 468–471.

Barton, B. A., Schreck, C. B., and Fowler, L. G. 1988. Fasting and diet content affect stress-induced changes in plasma glucose and cortisol in juvenile chinook salmon. Prog. Fish. Cult., 50: 16–22.

Barton, B. A., Schreck, C. B., and Sigismondi, L. A. 1986. Multiple acute disturbances evoke cumulative physiological stress responses in juvenile chinook salmon. Trans. Am. Fish. Soc., 115: 245–251.

Becker, C. D., and Genoway, R. G. 1979. Evaluation of the critical thermal maximum for determining thermal tolerance of freshwater fish. Env. Biol. Fish., 4(3): 245–256.

Blackburn, J., and Clarke, W. C. 1987. Revised procedures for the 24 hour seawater challenge test to measure seawater adaptability of juvenile salmonids. Can. Tech. Rep. Fish. aquat. Sci., 1515: 35 pp.

Booth, C. E., McDonald, D. C., Simons, B. P., and Wood, C. M. 1988. Effects of aluminium and low pH on net ion fluxes and ion balance in the brook trout (*Salvelinus fontinalis*). Can. J. Fish. aquat. Sci., 45: 1563–1574.

Buckley, L. J., Halavik, T. A., Laurence, G. C., Hamilton, S. J., and Yevich, P. 1985. Comparative swimming stamina, biochemical composition, backbone mechanical properties, and histopathology of juvenile striped base from rivers and hatcheries of the eastern United States. Trans. Am. Fish. Soc., 114: 114–124.

Casilla, E., and Smith, L. S. 1977. Effects of stress on blood coagulation and haematology in rainbow trout (*Salmo gairdneri*). J. Fish. Biol., 10: 481–491.

Ching, H. L., and Parker, L. 1989. Experimental exposure of trout and salmon from 12 British Columbian stocks to the myxozoan parasite *Ceratomyxa shasta*. J. aquat. Anim. Health, 1: 205–208.

Clarke, W. C. 1982. Evaluation of the seawater challenge test as an index of marine survival. Aquaculture, 28: 177–183.

Clarke, W. C., and Blackburn, J. 1977. A seawater challenge test to measure smolting of juvenile salmon. Fish. Mar. Serv. Res. Dev. Tech. Rep., 705: 11 pp.

Congelton, J. L., Bjornn, T. C., Burton, B. H., Watson, B. D., Irving, J. I., and Ringe, R. R. 1984. Effects of handling and crowding on the stress response and viability of chinook salmon parr and smolts. Bonneville Power Administration, Portland OR. 151 pp.

Ellsaesser, C. F., and Clem, L. W. 1986. Haematological and immunological changes in channel catfish stressed by handling and transport. J. Fish. Biol., 28: 511–521.

Envirocon Ltd. and E.V.S. Consultants Ltd. 1983. Studies on the fish pathogen *Ceratomyxa shasta*: its effects on chinook salmon of the Fraser system. Report to the Department of Supply and Services Canada, Richmond, BC. 48 pp.

Fields, R., Lowe, S. S., Kaminski, C., Whitt, G. S., and Philipp, D. P. 1987. Critical and chronic thermal maxima of northern and Florida largemouth bass and their reciprocal F_1 and F_2 hybrids. Trans. Am. Fish. Soc., 116: 856–863.

Folmar, L. C., and Dickhoff, W. W. 1981. Evaluation of some physiological parameters as predictive indices of smoltification. Aquaculture, 23: 309–324.

Fromm, P. O. 1980. A review of some physiological and toxicological responses of freshwater fish to acid stress. Env. Bio. Fish., 5: 79–93.

Gharrett, A. J., Shirley, S. M., and Tromble, G. R. 1987. Genetic relationships among populations of Alaskan chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. aquat. Sci., 44: 765–774.

Gjedrem, R., and Aulstad, D. 1974. Selection experiments with salmon I. Differences in resistance to vibrio disease of salmon parr (*Salmo salar*). Aquaculture, 3: 51–59.

Gorbman, A., Dickhoff, W. W., Mighell, J. L., Prentice, E. F., and Waknitz, F. W. 1982. Morphological indices of developmental progress in the parr-smolt coho salmon, *Oncorhynchus kisutch*. Aquaculture, 28: 1–19.

Heming, T. A., and Blumhagen, K. A. 1988. Plasma acid-base and electrolyte states of rainbow trout exposed to alum (aluminum sulphate) in acidic and alkaline environments. Aquat. Toxicol., 12: 125–140.

Hjort, R. C., and Schreck, C. B. 1981. Phenotypic differences among stocks of hatchery and wild coho salmon. *Oncorhynchus kisutch*, in Oregon, Washington, and California. Fish. Bull., 80(1): 105–119.

Horrall, R. M. 1981. Behavioral stock-isolating mechanisms in Great Lakes fishes with special reference to homing and site imprinting. Can. J. Fish. aquat. Sci., 38: 1481–1496.

Ihssen, P. E. 1986. Selection of fingerling rainbow trout for high and low tolerance to high temperature. Aquaculture, 57: 370.

Iwama, G. K. 1980. Incubation time resulting from experimental injections of kidney disease bacterial into juvenile coho salmon. Prog. Fish Cult., 42: 182–183.

Iwama, G. K. 1982. Comment on “Simple growth model for salmonids in hatcheries”. Can. J. Fish. aquat. Sci., 39: 1220–1221.

Iwama, G. K., and Tautz, A. F. 1981. A simple growth model for salmonids in hatcheries. Can. J. Fish. aquat. Sci., 38: 649–656.

Johnson, S. W., and Heifetz, J. 1988. Osmoregulatory ability of wild coho salmon (*Oncorhynchus kisutch*) and dolly varden char (*Salvelinus malma*) smolts. Can. J. Fish. aquat. Sci., 45: 1487–1490.

Madsen, S. S., and Naamansen, E. T. 1989. Plasma ionic regulation and gill Na^+/K^+-ATPase changes during rapid transfer to sea water of yearling rainbow trout, *Salmo gairdneri*: time course and seasonal variation. J. Fish. Biol., 34: 829–840.

Maule, A. G., Tripp, R. A., Kaattari, S. L., and Schreck, C. B. 1989. Stress alters immune function and disease resistance in chinook salmon (*Oncorhynchus tshawytscha*). J. Endocrinol., 120: 135–142.

Mazeaud, M. M., Mazeaud, F., and Donaldson, E. M. 1977. Stress resulting from handling in fish: primary and secondary effects. Trans. Am. Fish. Soc., 106: 201–212.

McDonald, D. G. 1983a. The effects of H^+ upon the gills of freshwater fish. Can. J. Zool., 61: 691–703.

McDonald, D. G. 1983b. The interaction of environmental calcium and low pH on the physiology of the rainbow trout (*Salmo gairdneri*) I. Branchial and renal net ion and H^+ fluxes. J. Exp. Biol., 102: 123–140.

McGeer, J. C., Baranyi, L., and Iwama, G. K. 1991. Physiological responses to challenge tests in six stocks of coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. aquat. Sci., 48: 1161–1171.

McLeay, D. J. 1975. Variations in the pituitary-interrenal axis and the abundance of circulating blood-cell types in juvenile coho salmon, *Oncorhynchus kisutch*, during stream residence. Can. J. Zool., 53, 1882–1891.

McLeay, D. J., and Gordon, M. R. 1978. Effect of seasonal photoperiod on acute toxic responses of juvenile rainbow trout (*Salmo gairdneri*) to pulpmill effluent. J. Fish. Res. Bd Can., 35: 1388–1392.

Milligan, C. L., and Wood, C. M. 1982. Disturbances in haematology, fluid volume distribution and circulatory function associated with low environmental pH in the rainbow trout (*Salmo gairdneri*). J. Exp. Biol., 99: 397–415.

Peterson, R. H., Coombs, K., Power, J., and Paim, U. 1989. Responses of several fish species to pH gradients. Can. J. Zool., 67: 1566–1572.

Piper, R. G., McElwain, I. B., Orme, L. E., McCraren, J. P., Fowler, L. G., and Leonard, J. R. 1982. Fish hatchery management. US Dept. Int. Fish and Wildlife Ser., Washington DC. pp. 134–135.

Randall, D. J., and Wright, P. A. 1989. The interaction between carbon dioxide and ammonia excretion and water pH in fish. Can. J. Zool., 67: 2936–2942.

Refstie, T. 1982. Preliminary results: differences between rainbow trout families in resistance against vibriosis and stress. Develop. Comp. Immun. Suppl. 2: 205–209.

Refstie, T. 1986. Genetic differences in stress response in Atlantic salmon and rainbow trout. Aquaculture, 57: 374.

Reisenbichler, R. R., and Phelps, S. R. 1987. Genetic variation in chinook, *Oncorhynchus tshawytscha*, and coho, *O. kisutch*, from the north coast of Washington. Fish. Bull., 85(4): 681–701.

Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. *In* The stock concept in Pacific salmon, pp. 19–160. Ed. by R. E. Simon and P. A. Larkin.

Robinson, D. G., Dunson, W. A., Wright, J. E., and Mamolito, G. E. 1976. Differences in low pH tolerance among strains of brook trout (*Salvelinus fontinalis*). J. Fish. Biol., 8: 5–17.

Rosenau, M. L., and McPhail, J. D. 1987. Inherited differences in agonistic behaviour between two populations of coho salmon. Trans. Am. Fish. Soc., 116: 646–654.

Schom, C. B. 1986. Genetic, environmental, and maturational effects on Atlantic salmon (*Salmo salar*) survival in acute low pH trails. Can. J. Fish. aquat. Sci., 43: 1547–1555.

Schreck, C. B. 1981. Stress and compensation in teleostean fishes: response to social and physical factors. *In* Stress and fish, pp. 295–321. Ed. by A. D. Pickering. Academic Press, London.

Specker, J. L., and Schreck, C. B. 1982. Changes in plasma corticosteroids during smoltification of coho salmon, *Oncorhynchus kisutch*. Gen. Comp. Endocrin., 46: 53–58.

Suzumoto, B. K., Schreck, C. B., and McIntyre, J. D. 1977. Relative resistances of three transferrin genotypes of coho salmon (*Oncorhynchus kisutch*) and their hematological responses to bacterial kidney disease. J. Fish. Res. Bd Can., 34: 1–8.

Swain, D. P., and Holtby, L. B. 1989. Differences in morphology and behaviour between juvenile coho salmon (*Oncorhynchus kisutch*) rearing in a lake and in its tributary stream. Can. J. Fish. aquat. Sci., 46: 1406–1414.

Swarts, F. A., Dunson, W. A., and Wright, J. E. 1978. Genetic and environmental factors involved in increased resistance of brook trout to sulfuric acid solutions and mine acid polluted waters. Trans. Am. Fish. Soc., 107: 651–677.

Taylor, E. B., and McPhail, J. D. 1985a. Variation in body morphology among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Can. J. Fish. aquat. Sci., 42: 2020–2033.

Taylor, E. B., and McPhail, J. D. 1985b. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Can. J. Fish. aquat. Sci., 42: 2029–2033.

Toews, D. P., and Hickman, C. P. 1969. The effect of cycling temperatures on electrolyte balance in skeletal muscle and plasma of rainbow trout *Salmo gairdneri*. Comp. Biochem. Physiol., 29: 905–918.

Trinder, P. 1969. Determination of glucose in blood using glucose oxidase with an alternative oxygen acceptor. Ann. Clin. Biochem., 6: 24.

Wedemeyer, G. A., Barton, B. A., and McLeay, D. J. 1990. Stress and acclimation. *In* Methods in fish biology, pp. 451–490. Ed. by C. B. Schreck and P. B. Moyle. American Fisheries Society, Bethesda MD.

Wedemeyer, G. A., and McLeay, D. J. 1981. Methods for determining the tolerance of fishes to environmental stressors. *In* Stress and fish, pp. 247–275. Ed. by A. D. Pickering. Academic Press, London.

Wehrhahn, C. F., and Powell, R. 1987. Electrophoretic variation, regional differences, and gene flow in the coho salmon (*Oncorhynchus kisutch*) of southern British Columbia. Can. J. Fish. aquat. Sci., 44: 822–831.

Wilkie, M. 1989. The effects of a highly alkaline environment on the acid-base balance and excretion of nitrogenous waste in the rainbow trout (*Salmo gairdneri*). ms.

Wilmot, R. L., and Burger, C. V. 1985. Genetic differences among populations of Alaskan sockeye salmon. Trans. Am. Fish. Soc., 114: 236–243.

Winans, G. A., and Nishioka, R. S. 1987. A multivariate description of change in body shape of coho salmon (*Oncorhynchus kisutch*) during smoltification. Aquaculture, 66: 235–245.

Woodward, C. C., and Strange, R. J. 1987. Physiological stress responses in wild and hatchery-reared rainbow trout. Trans. Am. Fish. Soc., 116: 574–579.

Wright, P. A., and Wood, C. M. 1985. An analysis of branchial ammonia excretion in the freshwater rainbow trout: effects of environmental pH change and sodium uptake blockade. J. Exp. Biol., 114: 329–353.

Wydoski, R. S., Wedemeyer, G. A., and Nelson, N. C. 1976. Physiological response of hooking stress in hatchery and wild rainbow trout (*Salmo gairdneri*). Trans. Am. Fish. Soc., 5: 601–606.

Yalow, R. S., and Berson, S. A. 1971. *In* Principles of competitive protein binding assays, ch. 1. Ed. by Odell and Daughaday. J. B. Lippincott, Philadelphia.

Yesaki, T. Y. 1990. The survival and physiology of rainbow trout (*Oncorhynchus mykiss*) in alkaline hard water. MSc Thesis, University of British Columbia.

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Introductions of marine bivalve molluscs into the United Kingdom for commercial culture – case histories

S. D. Utting and B. E. Spencer

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Most introductions of non-indigenous bivalves into UK coastal waters have been deliberate and all have involved species of commercial value. The introduction of *Mercenaria mercenaria*, whether deliberate or accidental, remains subject to speculation. Imports of live oysters from Europe and the USA, which probably began in the 1870s, continued until 1962 when trade in live oysters had declined. *Ostrea edulis* seed for relaying was imported from France and Holland in quantities that ranged from less than 100 t $year^{-1}$ to 1100 t $year^{-1}$. *Crassostrea virginica* seed was imported from America and Canada until 1939, to be replaced by *Crassostrea angulata* from Portugal which had been imported since 1926. Imports of seed *Crassostrea* spp. never exceeded 300 t $year^{-1}$. Before the 1960s the deposit of imported species was not controlled to prevent the introduction of pests, parasites, and diseases. Legislation, codes of practice, and guidelines have since controlled the introduction, deposit, and release into the wild of non-indigenous bivalves in UK territorial waters. As a result of this, and the availability of seed from UK hatcheries since the 1960s, no new pests, etc., have been introduced with seed of non-indigenous species. The Ministry of Agriculture, Fisheries and Food, Conwy, UK, has introduced seven species of non-indigenous bivalves under strict quarantine to assess their commercial viability. *Crassostrea gigas* and *Tapes philippinarum* have considerable potential since they grow faster and survive better than the native equivalents. *Tiostrea lutaria* may be of some value, and *C. virginica*, reintroduced in 1984, is currently being assessed. The three other species were unsuitable for commercial culture or no better than indigenous species and were destroyed. Further introductions are not planned at present. The UK bivalve industry has a range of temperate water species with which to trade in home and overseas markets.

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Introduction

Probably more species of bivalve molluscs have been introduced into the coastal waters of the United Kingdom (UK) than of any other group of marine animals. Most of these introductions were made deliberately and all of the latter involved species of commercial value. This paper catalogues the bivalves which have been introduced, explains the rationale for the introductions, describes the fate of the various species, and summarizes the legislation which was enacted to control the movement and spread of molluscan shellfish pests which were co-introduced with the earlier imports of bivalves.

Case histories of introductions

1. Introductions of non-native species before 1960

Before 1960 the ecological implications of importing and depositing non-native bivalves were disregarded. Imported species received no quarantine treatments and as a result a number of other unwanted marine invertebrates were introduced and successfully colonized some areas of the UK.

1.1. Oysters

The expansion of the railway network in the mid-19th century, with the potential for the rapid transit of perishable products to the main centres of population, led to a great increase in the rate of exploitation of what were considered to be the richest natural oyster beds in Europe. These were located in the Thames estuary and in the rivers of Essex. In 1864 almost 500 million oysters, equivalent to 30 000 t, were sold on Billingsgate Market, London (Yonge, 1960).

By 1876 the native flat oyster (*Ostrea edulis*) had dramatically decreased in abundance owing to the continuous over-dredging for it in open waters without allowing sufficient closed time. In response to the scarcity of the flat oyster a trade in live American oysters (*Crassostrea virginica*) from the United States and Canada had already started. These were being shipped across the Atlantic, as deck cargo, during winter and early spring to be relaid for fattening in coastal waters or to be sold direct for consumption. The American oysters fattened in the summer months but failed to breed.

This trade probably started in the early 1870s with the formation of two companies, the Conway Oyster Company Ltd. and the Anglo-American Oyster Company. The latter, which had relaying sites at Shoreham, in the Salcombe estuary, and in the Menai Strait was short lived and went into liquidation in 1876 following disastrous losses of oysters in transit from America. The Conway Oyster Company experienced poor fattening of the imported oysters in the Conwy estuary and subsequently gained the lease to ongrowing ground off Cleethorpes and at Brightlingsea, Essex.

From 1876 to 1902 records of the numbers of oysters (not differentiated by species) landed in the UK were kept by the Sea Fisheries Inspectorate of the Board of Trade. Quantities of oysters imported for consumption or for relaying in coastal waters appeared as a statistical record in 1901. Data were collated by the Board of Agriculture and Fisheries from 1902 and from 1919 by the Ministry of Agriculture, Fisheries and Food (MAFF). Figure 1, drawn from the published statistics, shows the decline of the industry from its peak in the mid-19th century. It also shows that demand from 1900 until 1940 was met largely by importations.

The practice of importing half-grown oysters of about 35 g mean weight for relaying was well established in the latter part of the 19th century and undoubtedly contributed significantly to British landings during that period. For example, the Conway Oyster Company was importing 1 million seed American oysters per week in the early 1870s, of which an unknown proportion were for relaying (Report of the Commons Select Committee, 1876). In 1879, 90 663 barrels at a little over 1000 oysters per barrel were imported from New York (Philpots, 1890).

Quantities imported for relaying from 1901 to 1962, when the practice had diminished, are shown in Fig. 2. Importations, which were mainly of *O. edulis* from Holland and France, reached a peak, at 40 million individuals, in 1937. This was towards the end of a period of restocking beds that were severely depleted by

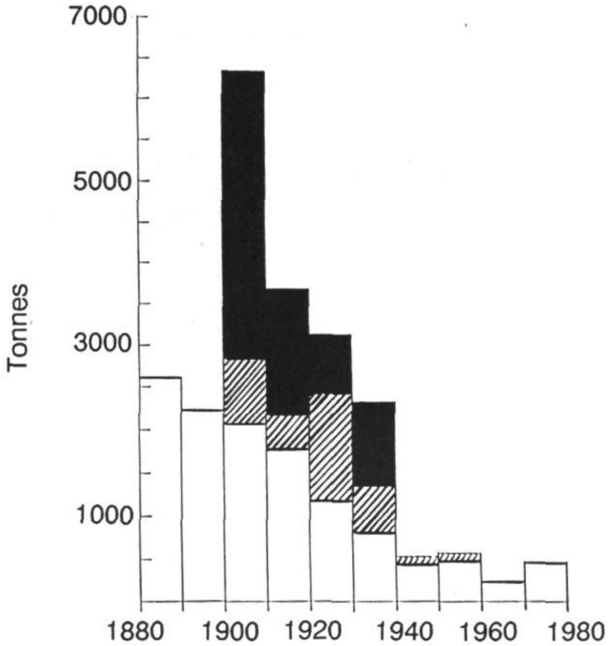

Figure 1. Landings of oysters of mixed species in the UK (open histograms) and imports, for direct consumption, of European flat oysters (hatched histograms) and American oysters (closed histograms). Values are 10-year means extracted from official statistics for 1880 to 1980. Before 1901 no data were collected of quantities of oysters imported for consumption. Tonnages are calculated using the official convention of 800 oysters per cwt., equivalent to 15 748 oysters tonne^{-1}.

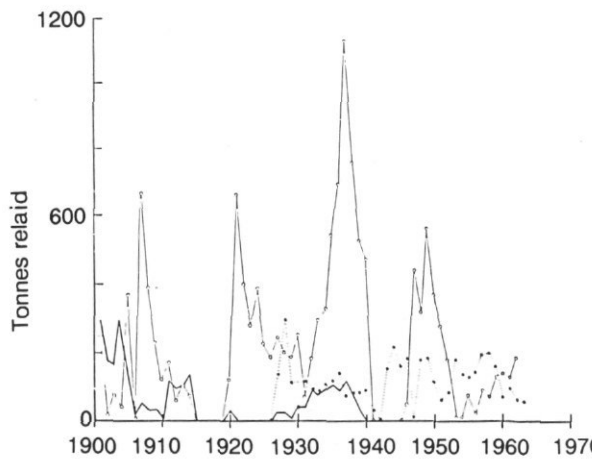

Figure 2. Tonnages, for relaying, of imported *Ostrea edulis* from Holland and France (○—○), *Crassostrea virginica* from the USA (——) and *Crassostrea angulata* from Portugal (●--●) from 1901 (when records began) to 1962 (when imports ceased).

an unknown disease in the 1920s. American oysters were imported for relaying until 1939. After World War II trade in this species was not re-established and it was replaced by the Portuguese oyster (*Crassostrea angulata*), which had been imported since 1926. Importations of the latter species ceased in the 1960s as a consequence of a disease in its native habitat.

Importations for relaying were successful in maintaining a reasonable level of supply of consumable oysters, although the scale was never sufficient to restore production to levels achieved in the late 19th century.

Importations were not controlled in such a way as to avoid the introduction of pests. As a result, the slipper limpet (*Crepidula fornicata*) and the American tingle (*Urosalpinx cinerea*), which are both native to the USA, became established in Britain. *Urosalpinx*, a shell-boring gastropod preying especially on flat oyster spat, became a serious pest to oyster fisheries in some parts of England (in Essex and Kent). Its distribution never extended beyond these areas and it has declined in abundance since the 1960s due to the collapse of oyster fisheries in these areas and, more recently, by the effect of tri-butyl tin (TBT) on its reproductive capability. *Crepidula* is more widely distributed, especially around the south coast of England and Wales. It competes with other filter-feeding invertebrates for food and space, and in waters with high concentrations of suspended particulate material it encourages the deposition of mud.

During the earlier part of this century another pest had been introduced, the crustacean gut parasite of mussels (*Mytilicola intestinalis*). It is generally considered to have been introduced from the Mediterranean (where it is endemic in *Mytilus galloprovincialis*), probably with mussels fouling the hulls of ships. It was first found in 1937 in Southampton Water. Although heavy mortalities of mussels in Europe in 1949–1950 were attributed to heavy infestations with *Mytilicola* it is now considered not to be a serious pest. It can live in a number of bivalve hosts including *Mytilus edulis*, *O. edulis*, *C. gigas*, and some clam species.

1.2. Clams

The American hard shell clam (*Mercenaria mercenaria*) was introduced at the same time as the American oyster but, unlike the American oyster, became established as a self-sustaining population on the south coast of England, in Southampton Water. Its introduction, whether deliberate or accidental, is subject to speculation. It may have been brought by American servicemen during World War I, or as ballast in sailing ships from New York, or it may have been discarded from transatlantic liners returning from New York.

The first major survey in 1979 of the extent of the fishery revealed a total population of around 15 000 t. Clams were harvested by hand before 1970 for marketing on the Continent but by the mid-1970s a dredge fishery had started and this increased landings until the mid to late 1980s, when the stock declined. Irregular recruitment and the lack of any significant spatfall after the closure in the early 1970s of the Marchwood Power Station at the head of Southampton Water probably accounted for this decline.

2. Introductions of non-native species after 1960

The era of massive commercial importations of oyster seed for relaying ended in the 1960s with a growing awareness of the risks involved in introducing alien pests, parasites, and diseases and of the possible ecological consequences for native communities.

The 1960s were notable for two reasons, the implementation of the Molluscan Shellfish (Control of Deposit) Order 1965 and the development of hatchery culture techniques.

2.1. Legislation

The Molluscan Shellfish (Control of Deposit) Order 1965, revoked and strengthened as the Molluscan Shellfish (Control of Deposit) Order 1974 and further amended in 1983 under the Sea Fisheries (Shellfish) Act 1967, prohibits the deposit in tidal waters, within the seaward limits of the territorial waters adjacent to England and Wales, of any part of any kind of molluscan shellfish, whether live or dead, taken from outside these waters, unless a licence to deposit has been granted by the Minister of Agriculture, Fisheries and Food (in England) or the Secretary of State (in Wales), and the conditions of that licence have been complied with. A similar order, The Molluscan Shellfish (Control of Deposit) (Scotland) Order 1978, applies to Scotland.

These Orders enable the control of movements for deposit of molluscan shellfish around the coastline and the control of the deposit of molluscan shellfish from outside territorial waters. Deposit refers to the immersion of the animals in coastal waters, in other tidal areas, or on adjacent land where there is the risk that effluent from tanks, pits, ponds, or hatcheries may be discharged into designated waters. As far as the Order relating to deposits in England and Wales is concerned the transfer and deposit of molluscan shellfish between areas around the coast needs to be administered flexibly to avoid undue constraint to trade, but with care to avoid the spread of pests and disease. To this end the coastline of England and Wales is divided into 27 designated areas which are related to the prevalence and intensity of major pests and disease (Fig. 3). This map shows the distribution of the principal pests, *Mytilicola*, *Crepidula*, and *Urosalpinx*, and of the microcell sporozoan parasite (*Bonamia ostreae*), which has been responsible for severe mortalities of the European flat oyster throughout the Atlantic coast of Europe. This parasite became

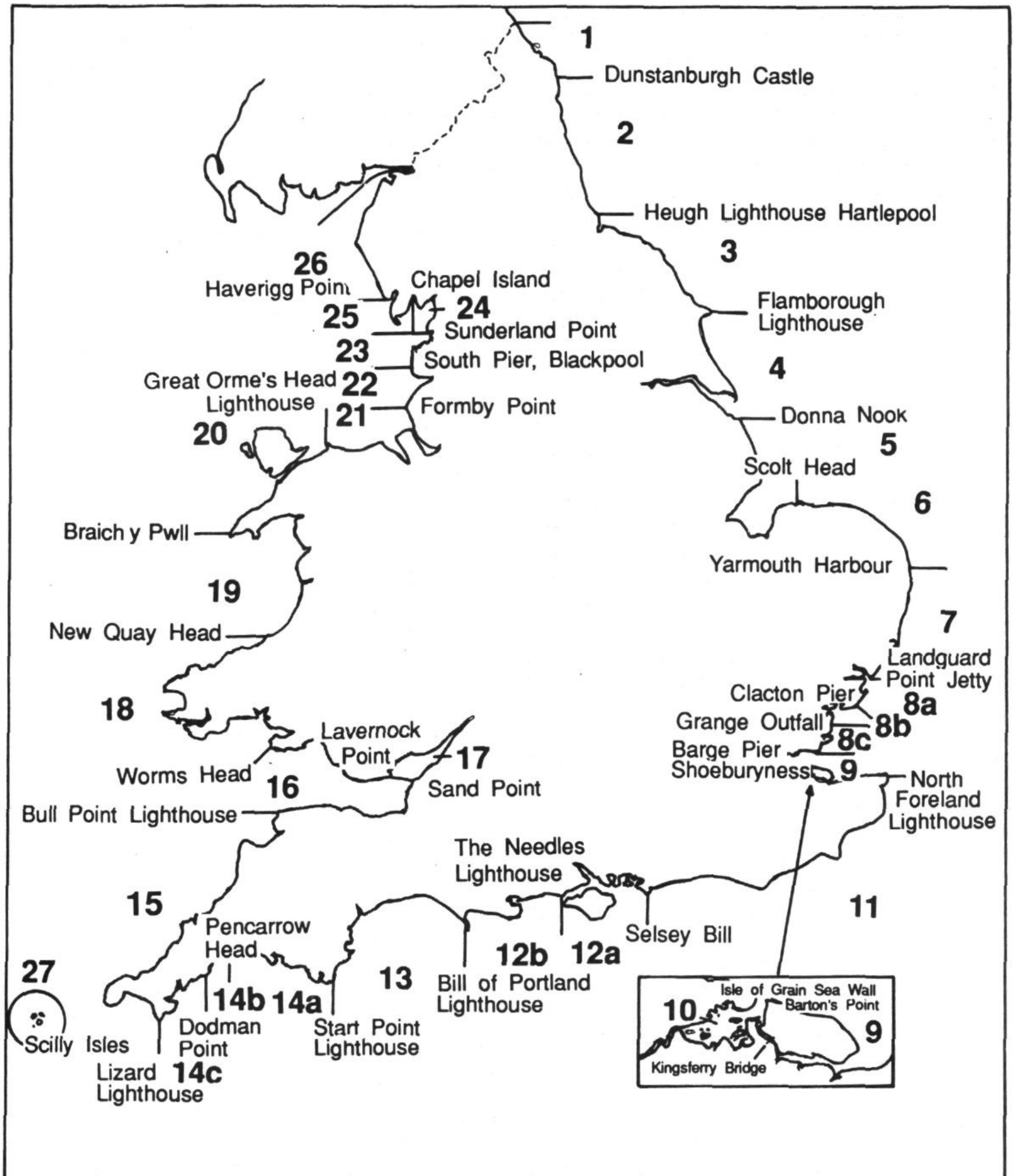

Figure 3. A map of England and Wales showing coastal areas designated in the Molluscan Shellfish (Control of Deposit) Order 1974, as varied in 1983, and the incidence of shellfish pests and diseases. Key: Areas 1, 3, 5, 6, 19, 20, 21, 22, 23, 26, and 27 = no pests or diseases recorded; Areas 24 and 25 = *Mytilicola* only; Area 4 = *Crepidula* only; Areas 2, 7, 10, 11, 13, 14(a) (b), 15, 16, 17, and 18 = *Mytilicola* and *Crepidula*; Area 9 = *Mytilicola*, *Crepidula*, and American tingle; Areas 12(a) (b) and 14(c) = *Bonamia*, *Mytilicola*, and *Crepidula*; Areas 8(a) (b) (c) = *Bonamia*, *Mytilicola*, *Crepidula*, and American tingle.

evident in the River Fal in 1982 and before effective control measures could be introduced had been transferred with licensed and unlicensed oyster deposits to the Helford River, to north and mid-Essex, and to some parts of the south coast. Since that time, with variation of the Control of Deposit Order in 1983, the further spread of this parasite has largely been prevented.

Movements of bivalves for deposit between coastal

Table 1. Species of bivalves introduced to the UK since 1960 by the MAFF Fisheries Laboratory, Conwy.

Species	Year	Fate
1. Chilean oyster, *Tiostrea chilensis*	1962	Stock intentionally destroyed
2. Chilean mussel, *Choromytilus* (syn. *Mytilus*) *choros* (syn. *chilensis*)	1965	Stock intentionally destroyed
3. New Zealand oyster, *Tiostrea lutaria*	1963, 1966	Self-sustaining population in Menai Strait
4. Pacific oyster, *Crassostrea gigas*, Canada	1965, 1972	Commercially grown
5. Pacific oyster, *Crassostrea gigas*, USA	1978	Commercially grown
6. Manila clam, *Tapes* (syn. *Venerupis*) *philippinarum* (syn. *semidecussata*), USA	1980	Commercially grown
7. Mangrove oyster, *Crassostrea rhizophorae*, Brazil	1980	Research. Stock intentionally destroyed
8. American oyster, *Crassostrea virginica*, USA	1984	Evaluation of culture potential

areas of England and Wales are controlled by a system of licensing. There are two forms of licence (a) a General licence which permits deposits anywhere within the designated area from which they were taken and between areas with similar types and/or levels of infestation, and (b) a Special licence which permits the deposit of molluscs from an infested area to areas which are free from infestation or have a lower level of infestation than the area of origin.

Importations from overseas of molluscs for deposit require special licences and these may only be granted subject to certification, by the authorities in the country of origin, that the shellfish are pest and disease free. At present, few countries can provide adequate information on the health status of their stocks or have the ability to establish a satisfactory certification scheme. Consequently the importation of molluscan shellfish species for deposit in the form of direct relaying in the sea from outside of the UK, except for the Channel Island of Guernsey and some parts of Eire, is prohibited. If sufficient justification can be shown and if suitable and well-managed quarantine facilities are available, it may be permissible to introduce and deposit non-indigenous species for research purposes or with the intention to breed them and subsequently release their progeny in tidal waters. The issue of a special licence in these cases is assessed on individual merit. Also, conditions are attached to the licence which define water sterilization and handling treatments and the method of disposal of the stock when experiments are completed, to ensure that the risk of escape of non-indigenous organisms is reduced to an acceptable level.

Introduction of non-indigenous species to evaluate their culture potential is only permitted through the quarantine facilities of the MAFF Fisheries Laboratory, Conwy. The decision to import a new species is reached after careful evaluation of the need for the introduction and of the status of the species in its native habitat. This is dealt with in more detail later.

Since 1981 the introduction of non-indigenous species for deposit and cultivation in the sea has been more strictly controlled under the Wildlife and Countryside Act (1981). Under Section 14 of the Act it is an offence to permit, except under licence, the release of non-indigenous species into the wild. Cultivation of non-native bivalve species, for example the Manila clam (*Tapes philippinarum*), in well-secured trays or beneath secure and well-maintained mesh covers on the ground of the foreshore may be allowed under special licence of the Control of Deposit Order. Fisheries Departments are responsible for issuing licences and may consult with the Nature Conservancy Council to obtain an opinion of the consequences of the deposit on the local ecology.

2.2. The role of bivalve hatcheries with introductions

Techniques for the hatchery production of marine bivalves were sufficiently reliable in the 1960s to be applied on a commercial scale (Walne, 1974). Since then, seven species of non-indigenous commercially valuable bivalves have been introduced into the UK (Table 1). Imported broodstock, after thorough cleansing to free them of epifauna and flora, were deposited in quarantine tanks within the laboratory at Conwy. Effluent sea water discharged from these tanks was collected in large-volume, outdoor, concrete tanks, where it was sterilized by adding powdered, or a solution of, sodium hypochlorite at a rate to give 100 ppm free-chlorine. The treated water was held for a minimum of 24 h before discharge into the sea (Dare *et al.*, 1977).

Once induced to spawn, the parent stock was destroyed by boiling and buried on land. Up until 1979 the progeny were reared without quarantine to a size suitable for planting in trays in the sea to assess their culture characteristics in home waters. This was done by MAFF in controlled experiments to establish that the new species had advantageous characteristics and presented little or no risk to the environment. Then small quantities of animals were given to commercial hatcheries as broodstock.

Over the years the way in which introductions have been made has gradually been improved to further minimize any risk. Quarantine has been strengthened to include the rearing of the larval and juvenile stages in

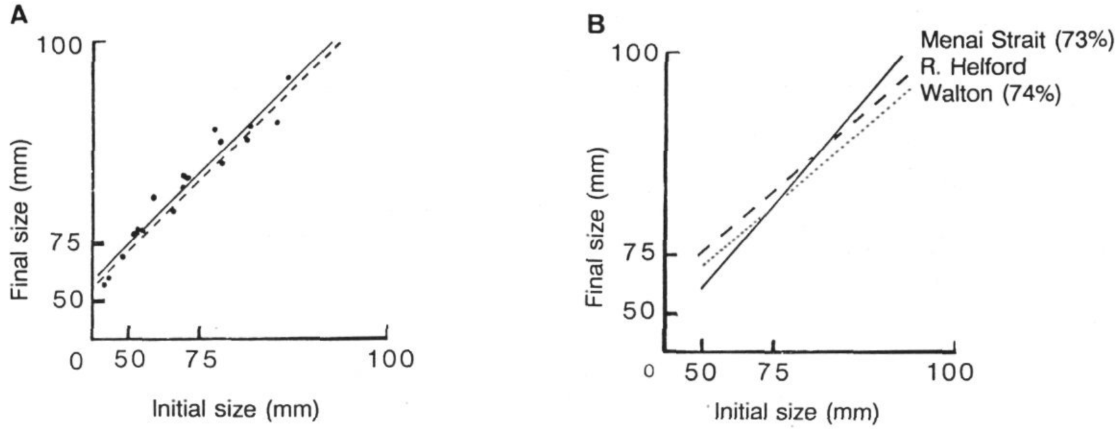

Figure 4. A. The growth in one year in North Wales of the flat oyster (*Ostrea edulis*) and the New Zealand oyster (*Tiostrea lutaria*). —— New Zealand oyster; – – – European oyster (Walne and Mann, 1975). B. The growth and survival of the New Zealand oyster at three sites in the UK. Percentage survival in parentheses for two sites.

line with the code of practice and guidelines produced by the ICES "Working Group on Introductions and Transfer of Marine Organisms" and the EIFAC "Working Party on Introductions" (1988).

For introductions made in the 1980s (Table 1) MAFF has held F1 juveniles in quarantine at Conwy for eight months, during which time 200 individuals were removed at two-monthly intervals for histopathological examination by the MAFF Fish Diseases Laboratory, Weymouth. Once it was established that the animals were free of disease, progeny were permitted to be transferred to the sea in suitable containment, so as to comply with the Wildlife and Countryside Act, for performance assessment. A further sample was taken for examination four months later as a final check on the health of the progeny.

Since the adoption of quarantine procedures no new pests or disease organisms have been introduced into coastal waters in association with hatchery produced seed of exotic species.

Six of the seven species introduced through Conwy (Table 1) were assessed for their suitability for aquaculture. The seventh, the mangrove oyster (*Crassostrea rhizophorae*) from Brazil was required for physiology experiments undertaken in a quarantine facility at the University of Southampton. In all cases broodstock were brought in under MAFF control and deposited at the Conwy Laboratory. F1 progeny from the mangrove oyster were subsequently released to the University of Southampton for research.

Three species unsuitable for commercial culture, either because of poor survival in our climatic conditions (Chilean oyster and mangrove oyster) or because they offered no cultural advantages over related native species (Chilean mussel), were destroyed. One species, the New Zealand flat oyster (*Tiostrea lutaria*), kept at MAFF's experimental site in the Menai Strait is now resident there as a self-sustaining population. This oyster broods its larvae to the stage of metamorphosis, so that upon liberation from the parent the larvae settle within a few hours in the vicinity of the parent. Consequently the stock is contained within a small area. *T. lutaria* is superficially similar to *O. edulis* and grows at a similar rate (Fig. 4A). It is not cold tolerant and survives poorly in the intertidal zone in cold winters. It is also susceptible to the pathogen *Bonamia ostreae*. At present there are no plans to transfer the species to other parts of the UK, although MAFF trials have shown that it grows well in other areas (Fig. 4B).

Two species have considerable potential for commercial culture, the Pacific oyster (*C. gigas*) and the Manila clam (*T. philippinarum*). The Pacific oyster was first introduced in 1965 (Table 1). Summaries of its introduction and the results of culture assessments are given by Walne and Spencer (1971) and Walne and Helm (1979). UK production is currently around 600 t year^{-1} but production in some areas of the UK has been severely constrained by TBT, from anti-foulant paints, which has been present in the sea water. Since 1987 the use of TBT-based anti-foulant paints has been restricted and growth of Pacific oysters in areas which were previously affected by TBT has improved significantly; production is expected to increase by 30% per year.

The Pacific oyster is an extremely robust, fast-growing animal which requires temperatures well in excess of those prevailing in British waters for successful recruitment. There have been reports of small numbers of naturally recruited spat in exceptionally warm summers in shallow, enclosed bodies of water, for example, Emsworth Harbour, but widespread and substantial recruitment such as occurs along the southern Atlantic coast of France is considered most unlikely. Commercial production is sustained by supplies of hatchery produced seed.

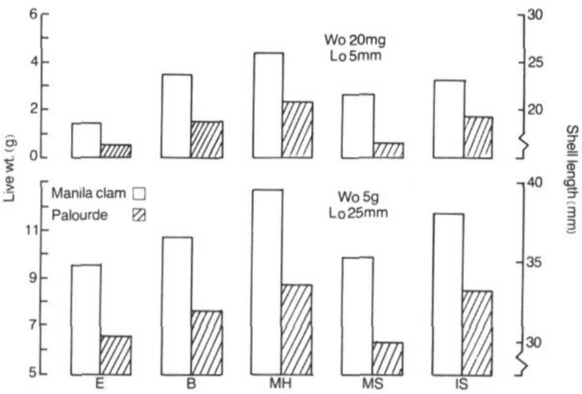

Figure 5. The growth, measured as live weight (g) and shell length (mm) of the Manila clam (*Tapes philippinarum*) and the native palourde (*Tapes decussatus*) at five sites in the UK. The initial sizes of clams were 20 mg (5 mm) and 5 g (25 mm). Sites: E = Essex – dammed creek; B = R. Beaulieu – raft; MH = Milford Haven – nursery; MS = Menai Strait – intertidal; IS = Inland Sea – intertidal.

The Manila clam is a more recent introduction. Broodstock were imported from the State of Washington, USA, in 1980 and, like the New Zealand and Pacific oysters, pre-dates the Wildlife and Countryside Act of 1981. It has proved to be another hardy, fast-growing species with substantial potential for commercial production (Utting, 1987a, b; Spencer, 1990). The rationale for its introduction was to prevent the UK industry from being severely disadvantaged in the lucrative European market for clams, where first sale value exceeds £5000 per tonne. The species was introduced into France in 1973 and is now being cultured from hatchery seed in many European countries.

Manila clams are well suited to the UK environment and grow faster than the native palourde, *Tapes decussatus* (Fig. 5). Production in the UK, which currently stands at less than 5 t year^{-1}, is sustained from a supply of hatchery produced seed because, like the Pacific oyster, it is most unlikely to recruit in UK waters.

To further reduce the remote chance of recruitment, methods of producing triploid seed of Manila clams are being investigated at Conwy. To date 67–77% of fertilized embryos treated with the chemical cytochalasin-B (Allen *et al.*, 1989) have been found to be triploid. Survival of treated embryos ranged from 60 to 80% of control diploid batches and was probably related to seasonal changes in water quality which occur at the laboratory (Utting and Helm, 1985).

The recent reintroduction of the American oyster was made in 1984 (Utting, 1987a) from a stock in the James River, Chesapeake Bay. This particular stock has been under the close health scrutiny of the American National Marine Fisheries Service and was free of known oyster pathogens, coming from an area with a mean salinity of 8 ppt. Culture evaluation with F1 progeny reared in the Conwy hatchery has shown that this species grows more slowly than the Pacific oyster in most areas tested (Fig. 6). The American oyster appeared more suited to conditions in the Essex river systems and Poole Harbour than elsewhere.

It is too early to assess the commercial potential of the species in UK waters, but since it has previously had an impact in UK oyster production without any sign of successful natural recruitment over a long period, the outlook is hopeful. Its future will probably depend on how the Pacific oyster industry develops now that the problem over TBT has been alleviated.

Conclusion

With the more recent introductions the UK shellfish industry now has a wide range of the world's more valuable temperate water bivalve species with which to compete in European and worldwide trade. There are no plans, nor does there appear to be the need, for further introductions in the foreseeable future.

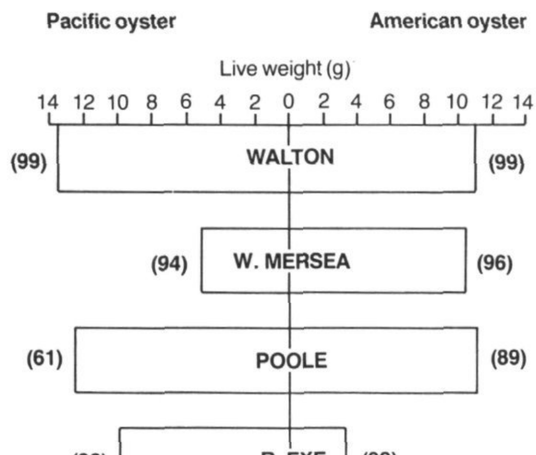

Figure 6. The growth, measured as live weight (g), and survival (%) of American oysters (*Crassostrea virginica*) and Pacific oysters (*Crassostrea gigas*) in trays at six sites in the UK during 1986. Percentage survival in parentheses. Note TBT affected growth of Pacific oyster at West Mersea.

References

Allen, Jr., S. K., Downing, S. L., and Chew, K. K. 1989. Hatchery manual for producing triploid oysters. University of Washington Press, Seattle, Washington. 27 pp.

Anon., 1988. Codes of practice and manual of procedures for consideration of introductions and transfers of marine and freshwater organisms. ICES Cooperative Report, No. 159. Ed. by G. E. Turner. 44 pp.

Philpots, J. R. 1890. Oysters and all about them. John Richardson, London. 1370 pp.

Spencer, B. E. 1990. Clam trials are encouraging. Fishing News.

Spencer, B. E., Helm, M. M., and Dare, P. J. 1977. Recommended quarantine measures for marine molluscs. Tech. Rep. MAFF Direct. Fish. Res. Lowestoft, (32), 7 pp.

Utting, S. D. 1987a. Fresh prospects for bivalve farming. Fish Farmer, 10: 17–18.

Utting, S. D. 1987b. The potential of clams. Aquaculture Ireland, 31: 16–17.

Utting, S. D., and Helm, M. M., 1985. Improvement of sea water quality by physical and chemical pre-treatment in a bivalve hatchery. Aquaculture, 44: 133–144.

Walne, P. R. 1974. Culture of bivalve molluscs. 50 years' experience at Conwy. Fishing News (Books), West Byefleet. 173 pp.

Walne, P. R., and Helm, M. M. 1979. Introduction of *Crassostrea gigas* into the United Kingdom, pp. 83–105. *In* Exotic species in mariculture. Ed. by R. Mann. MIT Press, Cambridge, Massachusetts. 363 pp.

Walne, P. R., and Mann, R. 1975. Growth and biochemical composition in *Ostrea edulis* and *Crassostrea gigas*, pp. 584–607. *In*: Proceedings 9th European mar. biol. Symp. Ed. by Harold Barnes. Aberdeen University Press. 760 pp.

Walne, P. R., and Spencer, B. E. 1971. The introduction of the Pacific oyster (*Crassostrea gigas*) into the United Kingdom. Shellfish Information Leaflet No. 2. 14 pp.

Yonge, C. M., 1960. Oysters. Collins New Naturalist Series, London. 209 pp.

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Introduction in Europe, from 1972 to 1980, of the Japanese Manila clam (*Tapes philippinarum*) and the effects on aquaculture production and natural settlement

J. P. Flassch and Y. Leborgne

Flassch, J. P., and Leborgne, Y. 1992. Introduction in Europe, from 1972 to 1980, of the Japanese Manila clam (*Tapes philippinarum*) and the effects on aquaculture production and natural settlement. – ICES mar. Sci. Symp., 194: 92–96.

La palourde du Pacifique (*Tapes philippinarum*) a été introduite en France entre 1972 et 1975 par la Société SATMAR et en Angleterre en 1980 par le laboratoire de Conwy. Les introductions ont porté en premier lieu sur du naissain et par la suite sur des adultes, dans chaque cas en provenance de la côte ouest des Etats-Unis. La production aquacole a été lancée à partir d'adultes. Les organismes scientifiques ont développé les recherches de base à partir du naissain produit par la SATMAR à l'échelle semi-industrielle, recherches qui aboutirent à la mise en oeuvre de programmes de transfert. L'aquaculture de la palourde commença en premier lieu sur la côte atlantique, dans la frange intertidale et en claires ostréicoles. Les caractéristiques de cette nouvelle culture sont données. Les maladies rencontrées sont citées. Il est observé des développements naturels dans les bassins de production.

The Pacific Manila clam (*Tapes philippinarum*) was introduced in France between 1972 and 1975 by the SATMAR Corporation, and in England through the Conwy Laboratory in 1980. Initially, spat were introduced and later adults, both from the west coast of North America (Puget Sound area). Aquaculture production in France started from adults. Until 1975, experiments with the spat were conducted at half-industrial scale, and research activities and plans to transfer the knowledge were set up. The breeding began at first on the French Atlantic coast in intertidal areas and at the same time in oyster ponds. Characteristics of the new culture are presented in this paper. The diseases met with in larval production and growout are also discussed. Natural developments of the species are observed.

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Introduction

Following the work of Loosanoff and Davis (1963) in the United States, Walne (1966) in England and Lucas (1970) and Flassch *et al.* (1975) in France, techniques concerned with controlled production of molluscs developed rapidly. Several hatcheries (the Madec hatchery in Brest Harbour, 1966, then the SATMAR hatchery on the Cotentin Peninsula in 1972) were set up using American techniques to produce flat oysters (*Ostrea edulis*) (phytoplankton production and larval production in large tanks of several cubic metres). Following the outbreak of epizootic disease in 1965 in Portuguese oysters (*Crassostrea angulata*), a large demand for seed oysters arose. For this, SATMAR, the only remaining hatchery at the time, actively developed the techniques of controlled production of the species.

Since 1972, knowledge of hatchery techniques has increased, and in an effort to diversify the controlled production of bivalves, steps have been taken concerning imports of Manila clam (*Tapes philippinarum*) from the Pacific coast of North America. This species was accidentally introduced into North America in 1936 (Quayle, 1964). It was imported with Pacific oysters (*Crassostrea gigas*) from Japan, which were placed overboard in Ladysmith Harbour. Since 1941, Manila clams have colonized the coastal zone from Vancouver southward, spreading as far as California. The natural distribution of the Manila clam extends between the latitudes of 25° and 45° North. Prior to the introduction into France of the Pacific oyster (Gruet *et al.*, 1976; Grizel and Héral, 1990), the hard clam (*Mercenaria mercenaria*) was repeatedly imported (Ruckebusch, 1949) in 1861 (Arcachon Basin), in 1910 (Seudre Basin), and

Table 1. Schedule of Manila clam introductions into France.

Date of request	Date of receipt	Origin	Number	Weight kg	Size
08.11.1972	15.05.1973	Puget Sound (Southwestern Canada)	500 000	1.6	Spat (3–4 mm)
03.01.1974	21.06.1974	Puget Sound	300	15.4	Adult (60 mm)
04.02.1974	08.08.1974	Puget Sound	300		Adult
		Puget Sound	400	25	Adult (64 mm)

from 1936 to 1939 in Southern Brittany. Natural beds, whose size has varied over the years, have developed in the Seudre Basin and in the Gulf of Morbihan.

The development of new techniques, on the one hand, and examples of the successful introduction of other non-native species (hard clams and Pacific oysters) on the other, have thus paved the way for importing the Manila clam. Several stages in the process occurred: the elaboration of introduction procedures, the development of hatchery techniques, the improvement of breeding through research, the refinement of transfer and development operations, the establishment of a profession and, unfortunately, the occurrence of problems such as epizootic diseases and commercial competition.

Formation of the European stock

Introduction of the Manila clam into France was carried out under the supervision of the Institut Scientifique des Pêches Maritimes (Scientific Institute of Marine Fishing). Details of these operations are listed in Table 1. As regards importation into England, it was not until 1980 that 50 clams from Puget Sound were received by the Conwy Laboratory (B. Spencer, pers. comm.) of the MAFF (Ministry of Agriculture, Fisheries, and Food). Manila clams which were subsequently introduced into Spain and Italy (Breber, 1985) came from this introduced stock. All the imports mentioned above were carried out in accordance with the health controls in force in the United States, France, and England (histological examinations, quarantine periods, etc.). This import was made in accordance with 1972 ICES Code of Practice for the introduction of non-indigenous species.

Biological data

Initial research focused on the biological reaction of the species to the temperate ecosystem of the Atlantic coast, and production control techniques for spat were improved in hatcheries.

The potential of first season growth (Fig. 1; Lucas, 1977; IFREMER, 1988), of subsequent growth (a general reference growth curve was described for the use of

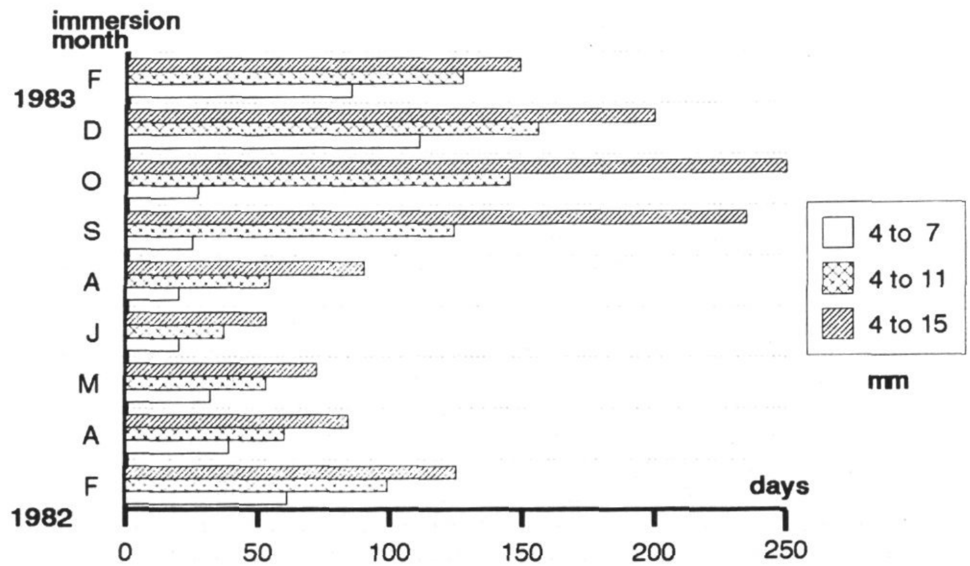

Figure 1. First-season growth of *Tapes philippinarum*, Ile-Tudy, Brittany, 1982/1983. Number of days required to develop seed spat bred in plastic mesh bags (10 000 spat m^2).

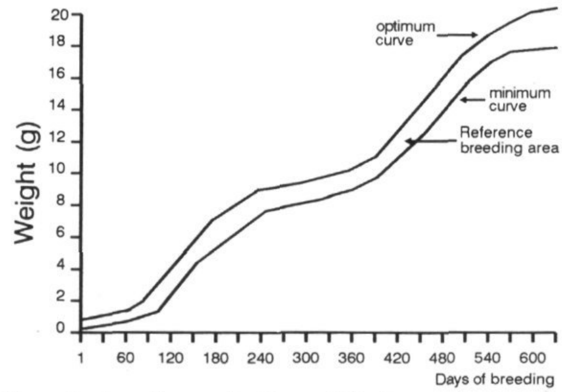

Figure 2. Growth curve for *Tapes philippinarum*, beginning in mid-March.

farmers, based on five years' data; Fig. 2; Flassch, 1978, 1987; de Kergariou *et al.*, 1982; Menesguen *et al.*, 1984; IFREMER, 1988), and the natural reproductive cycle (Goulletquer, 1983; Beninger and Lucas, 1984) were studied. Problems to be resolved quickly were identified as optimum immersion size and impact of predators. Breeding strategy was directed according to the behaviour patterns of the principal predator, the green crab (*Carcinus maenas*) (IFREMER, 1988).

Production development

In France, growers concerned with molluscs have been established for decades, i.e. oyster and mussel farmers. Since the introduction of production trials with Manila clams, few shellfish breeders have become involved, and so new experts from agriculture, universities, and institutes of technology have appeared. This new type of breeding was introduced with the aim of diversifying mollusc breeding (oysters, mussels, cockles). Once the scientific basis was established, national and regional programmes were developed – programmes aimed at testing the proposed techniques and the different sites in which the production experiments were carried out (IFREMER, 1988; Flassch, 1989).

Problems encountered

Epizootic diseases

The Manila clam, which is generally fairly resistant, has been subject to two outbreaks of bacterial disease which have altered the rate of production growth (Table 2). This has affected production procedures during the period in which all of the necessary ingredients for the long-term establishment of production were being set up (hatcheries, creation of new firms, mechanization).

The first outbreak, developed in a hatchery (Anon., 1987), was caused by a *Vibrio* strain not previously described, and was given the name of VRP (*Vibrio* of *Tapes philippinarum*). This strain has new distinguishing characteristics, in particular:

- it attacks larvae and spat
- it is specific to the Manila clam (Pacific oyster larvae (*Crassostrea gigas*) and the scallop (*Pecten maximus*) are not affected)
- larvae begin to die on the fifth day
- a very small dose is enough to trigger the disease
- it cannot be detected by direct inoculation of water samples on a Petri dish
- it does not develop in an environment which is specific to *Vibrio* (TCBS)
- a strain of the pathogen isolated at Brest from contaminated stocks is resistant to chloramphenicol, but is sensitive to streptomycin and very sensitive to furan.

Sanitary measures and the use of appropriate antibiotics have reduced the effect of this disease on hatchery production.

The second disease occurred in the natural environment for the first time in spat, at the end of 1986. Then, in 1987, it occurred in both spat and juvenile clams. It was first recognized, on the breeding grounds in the region of Landeda and in the Aber Benoît River (Finistère, France), by a brownish deposit on the inside of the shell. The infected spat died quickly. The juveniles rose partly from bottom sediments before dying. Infected clams grew very slowly. The pathogenic origin of this "Brown Ring Syndrome" was discovered in late 1988 (Paillard *et al.*, 1989). The cause of the disease is an unidentified bacterium very similar to the *Vibrio* type called "P_1" (not dangerous to human health). The formation of the brown matter correlates with the proliferation of this organism in the cellular zone which forms the periostracum of the shell.

Research findings about the pathogen (Paillard and Maes, 1990) help to explain some of the epidemiological characteristics observed:

Table 2. Evolution of French production in tonnes of the Manila clam (*Tapes philippinarum*).

Year	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
Aquaculture production	2	4	10	100	200	400	460	550	550	450*

*Effect of the brown ring disease.

- the organism is sensitive to temperatures above 27°C
- the disease can only be reproduced with high doses of the pathogen ($10^5 - 10^6$ ml^{-1})
- the higher the number of Manila clams in the breeding ground, the higher the risk of infection
- the brown ring appears at the earliest on spat of between 8 and 10 mm
- growth of spat of this size which appear healthy will proceed normally if carried out under the correct technological conditions (IFREMER, 1988)
- *Vibrio* P_1 is sensitive to Furazolidone; standard protocol for the use of this product has been suggested to breeders in order to provide 2 mm spat with the best chance of survival.

The spread of the P_1 disease has hindered the development of Manila clam culture, but the field strategy adopted in close cooperation with the breeders has enabled the process of infection to be controlled (Table 2).

Natural production and markets

French producers are facing commercial problems which are directly linked to the ability of the species to reproduce naturally in controlled breeding grounds. French production is almost entirely exported to Spain. The ex-producer price rose from 50 to 55 FF/KG (8.3 to 9 US $) between 1984 and 1988 and fell in 1989 to between 35 and 45 FF/KG. Over the past two years, there has been severe competition from Italian producers exporting *Tapes philippinarum* to Spain. It was only in 1983 that the first Manila clams were imported into Italy from Great Britain (Breber, 1985). In 1983, 200 000 spat were sown in the Venice Lagoon (Chioggia Basin); in 1984, 1 250 000 spat were sown in the Venice Lagoon (Pessestrina), and the same amount at Rosalina. In the space of six years, stocks have increased naturally to such an extent that Italian production in 1989 amounted to more than 6000 t.

So the French breeders face increased competition from other areas with natural production. The latter is becoming particularly widespread in southern Brittany. In that area, natural production is considerably larger than that of the breeders. In 1990, natural production reached 1500 t as compared with 500 t from aquaculture production.

Discussion

Apart from the initial import of Manila clams (500 000 spat) (Table 1), the batches that have been introduced into France and later into England were small and therefore easy to control, at least as regards epibionts. The imports of Pacific oysters (*Crassostrea gigas*) (Grizel and Héral, 1990), which included as much as 562 t of adults and 10 000 t of seed on collectors, were not so easily controlled. Batches of tens or hundreds of adults can be processed individually, but it will always be very difficult to assess in advance the influence of a species on the marine environment and, conversely, the effect of the receiving ecosystem on the species introduced. Therefore, ICES and EIFAC developed a Code of Practice for introductions – designed to prevent disasters.

As regards the Manila clam, the number imported into Europe is very small, especially if one considers the fact that the 500 000 spat imported by SATMAR in 1972 disappeared very quickly, falling victim to predators. In all, 1050 adults generated a combined European breeding and natural stock of over 20 000 t in 1989. A genetic survey carried out on the French stocks (Moraga, 1986) shows that the species is still highly heterozygotic, which aided its adaptation and enabled a large stock to be formed from only a few individuals.

Natural production of *Tapes philippinarum* is very high compared with that from controlled breeding. The quality of the aquaculture product has been improved and in most cases the taste is much better. Research to produce clams of a different quality emphasizes genetics – for example, the development of batches of polyploids. These products will be easily distinguished from the natural product, since their energy, which will no longer be used for gametogenesis, should be more evenly distributed and thus should improve the quality of the product, as in the case with oysters.

Conclusions

The European population of Pacific Manila clams (*Tapes philippinarum*) has grown from four batches of between 50 and 400 clams to form a stock which yielded 20 000 t in 1990 – the amount of natural stock being much larger than the amount from controlled breeding. The two production methods (natural production and aquaculture) have to cohabit. But controlled breeding will only continue if it is able to produce clams of a different quality, such as *Tapes philippinarum/Tapes decussatus* polyploids, or to produce clams that are disease-resistant, or that have a colour more acceptable to consumers – to maximize the value of the crop.

References

Anon. 1987. Mise en évidence d'une maladie spécifique des élevages larvaires de la palourde. Equinoxe, 15: 32–35.

Beninger, P. G., and Lucas, A. 1984. Seasonal variations in condition, reproductive activity, and gross biochemical composition of two species of adult clam reared in a common habitat, *Tapes decussatus* and *Tapes philippinarum*. J. exp. mar. Biol. Ecol., 79(1): 19–37.

Breber, P. 1985. L'introduzione e l'allevamento in Italia dell'arsella del pacifico, *Tapes semidecussatus*, Reeve (Bivalvia, Veneridae). Oebalia, XI (2), N-S: 675–680.

Flassch, J. P. 1978. Culture de palourdes sur sable en étang marin menée à l'Ile Tudy. Résultats et perspectives. Bull. CNEXO, 119: 7–8.

Flassch, J. P. 1987. L'élevage des palourdes en France en 1987. Aqua Rev., 15: 13–16.

Flassch, J. P. 1989. Les filières de production, la palourde. Deuxième rencontre interrégionale, Aqua Cultures. Actes des journées des 12 et 13 juin 1989 – La Baule: pp. 38–48.

Flassch, J. P., L'Herroux, M., Laubier, L., and Aveline, C. 1975. Continuous spat production of flat oyster *Ostrea edulis* in running water. Proc. 6th Annl. Meeting, World Maricult. Soc., pp. 193–201.

Goulletquer, P. 1983. Croissance et reproduction de *Ruditapes philippinarum* (Adam Reeves 1850) en fonction des conditions d'élevage (milieu lagunaire et claire) DEA. Poitiers Univ., 21 pp.

Grizel, H., and Héral, M. 1990. Introduction into France of the Japanese oyster *Crassostrea gigas*. J. Cons. int. Explor. Mer, 47: 399–403.

Gruet, Y., Héral, M., and Robert, J. R. 1976. Premières observations sur l'introduction de la faune associée au naissain d'huîtres japonaises *Crassostrea gigas* (Thunberg), importé sur la côte française. Cah. Biol. Mar., XVII: 173–184.

IFREMER 1988. La palourde, dossier d'élevage. IFREMER Publ., 106 pp.

de Kergariou, G., Pérodou, D., and Claude, S. 1982. Bilan des essais de prégrossissement et d'élevage de la palourde sur le littoral morbihanais. ISTPM, 20 pp.

Loosanoff, V. L., and Davis, H. C. 1963. Rearing of bivalve molluscs. Adv. Mar. Biol., 1: 1–136.

Lucas, A. 1970. Conchyliculture expérimentale. Publ. CNEXO, 1, 74 pp.

Lucas, A. 1977. Culture of the Manila clam (*Venerupis semidecussata,* Reeve) from hatchery reared spat. Publ CNEXO, 4: 317–330.

Menesguen, A., Flassch, J. P., and Nedelec, J. 1984. Utilisation de l'analyse mathématique de la croissance dans la comparaison de diverses techniques d'élevage de la palourde. Oceanol. Acta, 7(4): 499–507.

Moraga, D. 1986. Polymorphisme génétique de populations cultivées de la palourde du pacifique *Tapes philippinarum*. C.R. Acad. Sci. Paris, t. 302, Série III, n° 17.

Paillard, C., Percelay, L., le Pennec, M., and le Picard, D. 1989. Origine pathogène de l'"anneau brun" chez *Tapes philippinarum* (mollusque, bivalve). C.R. Acad. Sci. Paris, t. 309, Série III: 235–241.

Paillard, C., and Maes, P. 1990. Etiologie de la maladie de l'anneau brun chez *Tapes philippinarum*: pathogénicité d'un *Vibrio* sp. C.R. Acad. Sci. Paris, t. 310, Série III: 15–20

Quayle, D. B. 1964. Distribution of introduced marine Mollusca in British Columbia waters. J. Fish Res. Bd Can., 21(5): 1155–1181.

Ruckebusch, H. 1949. Le clam. Note sur *Venus mercenaria* son introduction et son élevage dans le bassin de la seudre. Rev. Trav. Pêches Marit., 15(4): 99–122.

Walne, P. R. 1966. Experiments in the large scale culture of the larvae of *Ostrea edulis*. Fish. Inv. Ser. 2, 25(4): 1–53.

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A collection of case histories documenting the introduction and spread of the virus disease IHHN in penaeid shrimp culture facilities in Northwestern Mexico

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Lightner, D. V., Williams, R. R., Bell, T. A., Redman, R. M., and Perez A., L. A. 1992. A collection of case histories documenting the introduction and spread of the virus disease IHHN in penaeid shrimp culture facilities in Northwestern Mexico. – ICES mar. Sci. Symp., 194: 97–105.

Prior to 1989, IHHN (infectious hypodermal and hematopoietic necrosis) had not been detected in either cultured shrimp at facilities bordering the Gulf of California or in stocks derived from that region of Mexico. However, IHHN disease was diagnosed in samples of cultured shrimp in 1989 and 1990 from sites previously negative for the disease. Significantly, the University of Sonora and University of Arizona shrimp culture research station at Puerto Penasco, Sonora, Mexico, which reared almost exclusively the highly IHHN susceptible blue shrimp *Penaeus stylirostris* in super-intensive raceway culture, had no cases of IHHN from its inception in 1973 until mid-1990. Imported shrimp are implicated as the source of IHHN virus that led to the 1989–1990 IHHN epizootic. Supporting this contention was the diagnosis of IHHN in late 1987 in a sample of postlarval *P. vannamei* which had been imported (from one of several commercial hatcheries in the United States and Central America that were supplying Mexico at that time) and distributed to several shrimp culture facilities bordering the Gulf of California. The case histories summarized in this report document the introduction, establishment, and rapid spread of IHHN in the developing shrimp culture industry of Northwestern Mexico.

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Introduction

IHHN (infectious hypodermal and hematopoietic necrosis) was first recognized in 1981 in Hawaii in imported stocks (from culture facilities in South and Central America, but not from Mexico) of *Penaeus stylirostris* (Lightner, 1983; Lightner *et al.*, 1983a). By 1982, IHHN was also diagnosed in imported *P. vannamei* (Brock *et al.* 1983; Lightner *et al.*, 1983b). Studies run in 1981–1983 in Hawaii on these and other imported penaeid shrimp stocks, and diagnostic examinations of preserved specimens submitted to our laboratory from numerous culture sites in North, South, and Central America, and from the Central Pacific and IndoPacific region, showed clearly that IHHN was present in cultured penaeid shrimp in many facilities in those regions, but absent in shrimp from Mexico (Lightner *et al.*, 1983b). Subsequent studies have shown IHHN to be very widely distributed in the North, South, and Central American, Caribbean, and Central Pacific Culture facilities that rear *P. vannamei* alone or with *P. stylirostris*, and in some IndoPacific facilities in which *P. monodon* is reared (Brock and Lightner, 1990; Lightner and Redman, 1991).

Demonstration of a virus as the cause of IHHN was documented in 1983 (Lightner *et al.*, 1983a). IHHN virus (IHHNV) was characterized in 1990 and determined to be related to the parvoviruses (Bonami *et al.*, 1990; Bonami and Lightner, 1991). Age and species differences in susceptibility to IHHN virus were later reported (Bell and Lightner, 1984, 1987). In the 1984 study, IHHNV virus-infected *P. vannamei* and *P. stylirostris* were found to differ histologically in incidence of diagnostic Cowdry type A intranuclear inclusion bodies (CAIs) in most tissues, with the more IHHN resistant *P. vannamei* displaying significantly fewer CAIs than did the highly susceptible *P. stylirostris*.

Despite its apparent resistance to IHHN, RDS (= "runt deformity syndrome") in *P. vannamei* was recently linked to IHHN virus infection (Kalagayan *et al.*, 1991). In their study, histologically IHHN positive and negative postlarvae were compared in nursery growouts. While no difference was found in survival between IHHN-positive and -negative populations, significantly lower growth rates and a higher rate of deformities characterized the IHHN-positive juveniles. However, despite the recent findings that the growth of juvenile *P. vannamei* in semi-intensive and intensive culture is impeded somewhat by IHHNV infection, the species is highly resistant to IHHNV relative to Mexican *P. stylirostris* (Brock *et al.*, 1983; Bell and Lightner, 1984; Lightner, 1988), and consequently, *P. vannamei* is the principal species reared by most of the shrimp culture industry in the Americas.

IHHN has a widespread distribution in culture facilities in the Americas, but its distribution in wild shrimp populations has remained virtually unknown (Lightner and Redman, 1991). Based largely on epizootiological data and on a number of examples in which IHHN has been diagnosed in cultured penaeid stocks derived directly from single spawn wild broodstock, IHHN had been presumed to be enzootic in wild populations of *P. monodon* in the IndoPacific (Lightner and Redman, 1991; Brock and Lightner, 1990). Recently, however, IHHN was diagnosed in postlarval *P. vannamei* reared from single spawn wild broodstock in several Ecuadorian hatcheries, indicating that IHHN virus is also enzootic in wild penaeids in Ecuador (Lightner and Bell, unpublished data).

Reported in the present paper are the findings from a collection of case histories made by the University of Arizona from 1973 to June 1990 that document the probable absence of IHHN virus in Gulf of California penaeids prior to 1987, and the introduction and spread of the virus in penaeid shrimp culture facilities in Western Mexico that border the Gulf of California in the subsequent three years.

Materials and methods

Diagnostic methods

Diagnostic methods used for IHHN have been described previously (Lightner, 1988; Lightner and Redman, 1991; Brock and Lightner, 1990). Specifically, in the cases reported here of IHHN in *P. stylirostris*, diagnosis of the disease was accomplished by direct histological demonstration of pathognomonic eosinophilic Cowdry type A intranuclear inclusion (CAI) bodies in samples taken directly from cultured populations. Diagnoses of IHHN infections in *P. vannamei* were accomplished by both direct histopathology and by bioassay of suspect populations with IHHN virus-free Mexico derived juvenile *P. stylirostris*. In all cases Davidson's AFA fixative was used as the preservative, and routine paraffin histological methods employing hematoxylin and eosin staining were used (Bell and Lightner, 1988).

Results

Case histories

Because operators of many of the facilities which cooperated in this study wished not to be identified, a code number is used to identify most of the facilities referred to in the following text, in Fig. 1, and in Table 2. This report consists of a collection of case histories, and, hence, the order in which the case findings are given is roughly in chronological order.

Puerto Penasco, 1973 to 1980

The first experiments with super-intensive culture of penaeid shrimp began in 1973 in the Northern Gulf of California town of Puerto Penasco, Sonora, Mexico. Initial studies were carried out with *P. californiensis*, and later with *P. stylirostris* and *P. vannamei* (Mahler *et al.* 1974; Salser *et al.*, 1978; Lightner, *et al.* 1984). Broodstock from which all IHHN virus-free stocks reared at Penasco (and later by MCE/HI discussed below) were obtained from Mexican shrimp trawlers at the approximate sites indicated by "X's" on the map shown in Fig. 1. During the period 1973 to 1986, several thousand broodstock animals were obtained from the Gulf of California regions shown.

In terms of growth, survival, final harvest size, and ease of culture, *P. stylirostris* easily outperformed the other two species tested at Penasco, and in so doing set the highest production records (50 000 kg/Ha per crop, or with 2.2 harvests per year over 100 000 kg/ha/year) reported for penaeid shrimp up to that time (Lightner *et al.*, 1984), production levels that would not have been possible if IHHN had been present in those Gulf of California-derived stocks of *P. stylirostris*.

During the period 1973 to 1980 a total of 1603 case samples ($n = 1$ to >1000, averaging about 10 individuals per sample) of *P. stylirostris*, *P. vannamei*, and *P. californiensis* were processed in disease diagnostic studies relating to the operation of the University of Arizona/University of Sonora research facility and MCE commercial prototype (MCE/PP) at Puerto Penasco, Sonora, Mexico. None of these 1603 samples was positive for IHHN (Table 1). Furthermore, we have recently selectively retrieved and examined histological slides made from samples of shrimp with various diseases from these 1603 cases, and in none of these retrospective studies have signs of IHHN infection been found.

Marine culture enterprises (MCE/HI) 1980 to 1987

Commercial development of the super-intensive raceway shrimp culture technology developed in Puerto Penasco was begun on the island of Oahu in Hawaii by MCE in 1980. At the same time MCE and the University

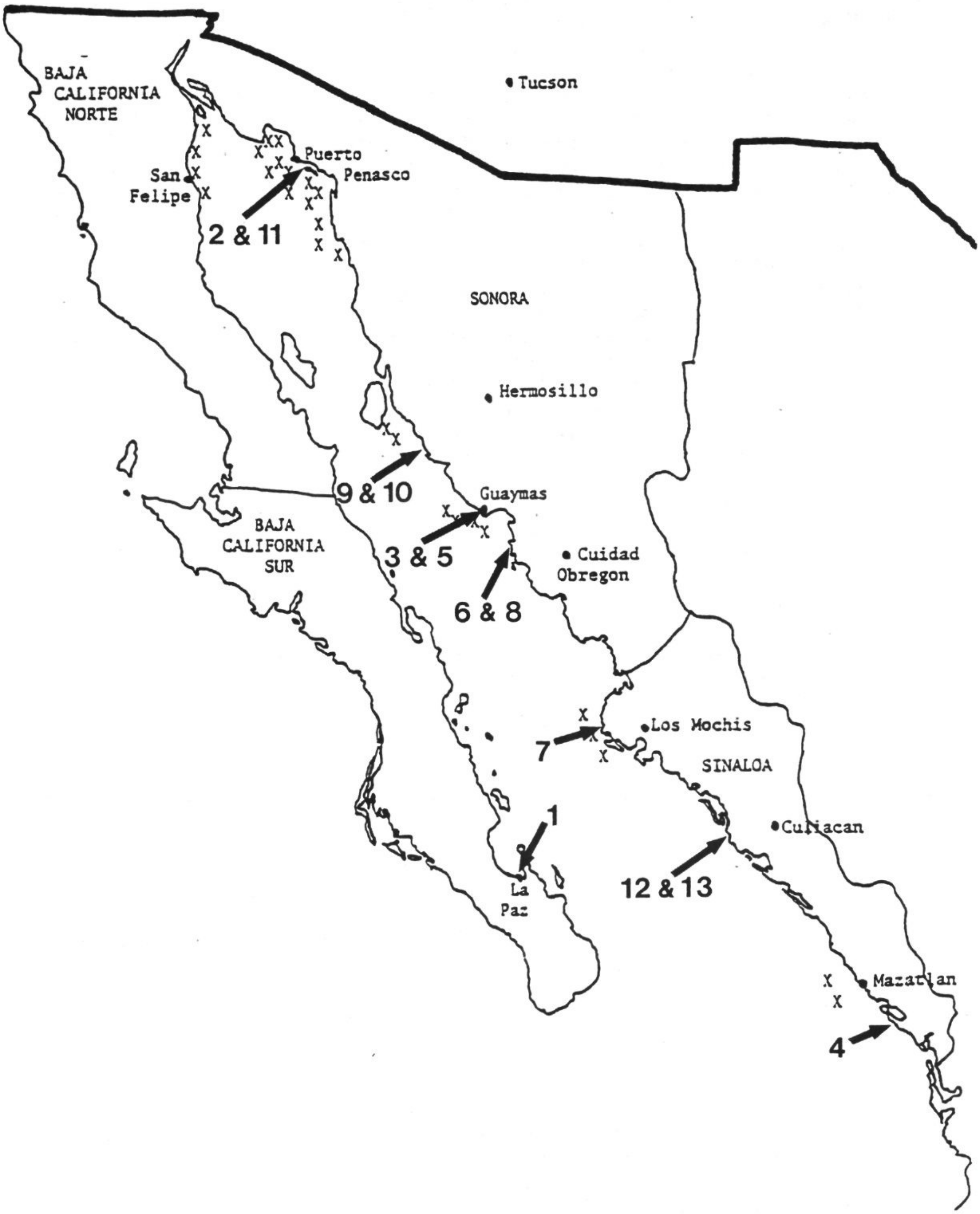

Figure 1. Map of the Gulf of California in Northwestern Mexico showing the approximate locations in the Gulf (marked by X's) from which wild adult penaeid shrimp were obtained during the period 1973 to 1986 by the cooperative shrimp culture program of the Universities of Arizona and Sonora at Puerto Penasco, and later by Marine Culture Enterprises of Puerto Penasco and Honolulu, Hawaii. Also shown are the approximate locations of commercial and research shrimp culture facilities that submitted the diagnostic samples used in this study. The facility numbers shown correspond to those listed in Table 2.

Table 1. Summary of diagnostic case results as they relate to penaeid shrimp derived from the Gulf of California in Mexico prior to 1987.

Year	Species	Number of Cases	IHHN status
1973 to 1980 (in Penasco)	*P. stylirostris*	1603*	negative
	P. californiensis		negative
	P. vannamei		negative
1980 to 1985	*P. stylirostris*	22**	negative
	P. vannamei	2**	negative
1980 to 1986	*P. stylirostris*	~1500***	negative

* Routine cases from the Universities of Arizona and Sonora research station and the MCE prototype in Puerto Penasco.
** Broodstock populations from Gulf of California.
*** Routine cases from SPF (IHHNV-free) Mexico-derived stock reared at MCE in Hawaii.

of Arizona terminated its joint research program with the University of Sonora at Puerto Penasco.

Twenty-two shipments of adult wild and cultured postlarval *P. stylirostris* and *P. vannamei* from the Gulf of California were imported into Hawaii from 1980 to 1986 by MCE/HI. Following the discovery of IHHN in other imported stocks at the facility (Lightner *et al.*, 1983a), all subsequent populations were held in quarantine in Hawaii and tested for IHHN. All 24 of these Gulf of California derived stocks of *P. stylirostris* and *P. vannamei* were found to be IHHN virus-free (Table 1).

The Mexico derived IHHNV-free *P. stylirostris* stocks were developed and cultured by MCE/HI in super-intensive "raceways". Approximately 1500 samples (n = 1 to >1000, averaging about 10 individuals per sample) from Gulf of California-derived populations of *P. stylirostris* were processed in support of the research and development of culture methods and shrimp populations for MCE/HI during the period June 1980 to October 1986 (Table 1). As was the case at MCE/PP in Puerto Penasco, Mexico, harvest densities of these IHHNV-free *P. stylirostris* at MCE ranged from 3 to 6 kg/m^2/crop (or 30 000 to 60 000 kg per Ha per crop with 2.5 crops per year, representing the highest production levels ever achieved in penaeid shrimp culture), and reached 7.9 kg/m^2 of 17 g average whole weight shrimp in one experimental growout (MCE/HI, unpublished data). As was the situation in Penasco, the record production levels achieved by MCE/HI would not have been possible had IHHNV been present in the cultured stocks, a fact that was vividly demonstrated in mid-1987, when a massive epizootic of IHHN ended the commercial culture of *P. stylirostris* at MCE/HI (Rosenberry, 1987, 1988, 1990). While the exact source of IHHNV which caused the 1987 MCE/HI epizootic was not determined, other shrimp culture facilities in Hawaii had shrimp stocks which were IHHNV-positive within a few months prior to the MCE tragedy. In hindsight, it appears likely that the contamination and spread of IHHNV in the MCE/HI facility was via MCE's relaxation and eventual disregard for its own facility quarantine and broodstock isolation policies – management practices which had worked very well from 1983 through 1986.

Samples from facilities in Mexico, 1987 to 1990

A number of research and commercial shrimp culture facilities (approximate locations shown in Fig. 1) in Mexico submitted samples for diagnostic purposes to our laboratory (Table 2), especially after 1987 when commercial shrimp culture began to develop in that country (Garmendia Nunez and Garcia-Sanchez, 1990; Rosenberry, 1990).

Facility no. 1. The first IHHN-positive case from Mexico was submitted by this research facility in November, 1987. The sample was from a shipment of postlarval (PL) *P. vannamei* which had been imported from a commercial hatchery in the United States. The shipment was shared among three facilities, all in the Mexican states of Sinaloa and Baja California del Sur. Following notification of the IHHN-positive status of the imported postlarval *P. vannamei*, Facility no. 1 was depopulated, disinfected, and restocked with Gulf of California derived *P. californiensis*. IHHN was not detected in a subsequent sample of juvenile *P. californiensis* from Facility no. 1 that was submitted in June, 1988 (Table 2).

Facility no. 2 (University of Sonora, Puerto Penasco). A research facility for all of its 17-year history, this facility produced primarily *P. stylirostris* for others or cultured them for its own use. Samples from the facility of *P. stylirostris* of various ages during (and prior to – see "Puerto Penasco, 1973–1980" above) the period April, 1988 to September, 1989, were all negative for IHHN. Some stocks provided by this facility were, in fact, used as IHHNV-free indicator shrimp in bioassay tests for IHHNV run in Tucson, AZ; Honolulu, HI; or in Ocean Springs, MS during the same time period. However,

Table 2. Summary of University of Arizona cases from Western Mexico dating from 1987, the year in which the first case of IHHN was diagnosed in the region.

Sample date	Facility	Region of Gulf	Species	Life stage[1]	Source	IHHN Status
11–18–87	1	Southern	*P. vannamei*	PL	Imported	+
6–8–88			*P. californiensis*	J	Hatchery	neg
4–19–88	2	Northern	*P. stylirostris*	A	Hatchery	neg
4–19–88			*P. stylirostris*	PL	Hatchery	neg
3–4–89			*P. stylirostris*	PL	Hatchery	neg
9–29–89			*P. stylirostris*	J	Hatchery	neg
5–8–90			*P. stylirostris*	J	Hatchery	+
6–8–90			*P. stylirostris*	PL,J,A	Hatchery	+
6–5–89	3	Central	*P. stylirostris*	PL	Hatchery	+
6–23–89			*P. stylirostris*	PL	Hatchery	+
10–23–89			*P. stylirostris*	J	Farm	+
12–20–89			*P. stylirostris*	J,A	Farm/Hatch	+
6–9–89	4	Southern	*P. vannamei*	PL	Hatchery	neg
2–8–90			*P. stylirostris*	PL	Hatchery	neg
5–8–90			*P. vannamei*	PL	Hatchery	+
5–8–90			*P. stylirostris*	PL	Hatchery	+
5–8–90			*P. stylirostris*	J	Farm	+
6–13–89	5	Central	*P. stylirostris*	J	Hatchery	+
4–27–87	6	Central	*P. stylirostris*	PL,J,A	Hatchery	neg
7–12–89			*P. stylirostris*	J	Hatchery	+
12–1–89			*P. stylirostris*	J	Hatchery	+
2–2–90			*P. stylirostris*	J	Hatchery	+
4–11–89	7	Southern	*P. vannamei*	A	Farm[2]	+
10–23–89	8	Central	*P. stylirostris*	J	Farm	neg
11–13–89			*P. stylirostris*	J	Farm	neg
5–29–90			*P. stylirostris*	J	Hatchery	+
12–20–89	9	Northern	*P. stylirostris*	J	Farm	+
2–9–90			*P. stylirostris*	J	Farm	neg
5–18–90	10	Northern	*P. stylirostris*	J	Farm	+
5–8–90	11	Northern	*P. stylirostris*	PL,J	Hatchery	+
5–19–90			*P. stylirostris*	PL,J	Hatchery	+
5–24–90			*P. stylirostris*	J	Hatchery	neg
5–25–90			*P. stylirostris*	J	Hatchery	+
6–2–90			*P. stylirostris*	PL,J	Hatchery	+
1–30–90	12	Central	*P. stylirostris*	J	Farm	+
6–11–90	13	Central	*P. stylirostris*	J,A	Farm	+

[1] Abbreviations: PL = postlarvae; J = juvenile; and A = subadult or adult.
[2] Farm imported IHHN + PL *P. vannamei* in 1987, and it has been selling IHHN + PLs and pond-reared broodstock since early 1989.

samples of postlarvae, juveniles, and broodstock taken from the facility in May and in June of 1990 were positive for IHHN (Table 2).

Facility no. 3. Located in the central region of the Gulf of California, this commercial hatchery and super-intensive farm first began production in 1988. During its three-year history, the facility produced only *P. stylirostris*. Samples submitted to our laboratory for diagnostic purposes in June, 1989 were positive for IHHN. Likewise, all subsequent samples submitted in 1989 from the facility were positive for IHHN (Table 2). Discussion of the facility's history with its owners revealed that it (and Facility no. 5) had received stock from Facility no. 6 after it had become IHHN contaminated. In addition this facility frequently obtained new stocks of wild broodstock from the commercial fishery in the region.

Facility no. 4. The first construction phase of this commercial hatchery was completed in early 1989, and its first hatches were produced from adult wild *P. vannamei* collected from the Southern region of the Gulf of California. Fifty thousand postlarvae from one of these hatches were acquired in June, 1989. The population was divided into two separate populations that were reared under quarantine conditions in Tucson and Hawaii. The IHHNV status of the population was tested by direct histology and by bioassay with juvenile *P. stylirostris*, and it was found to be negative for IHHNV by both tests. Likewise, a sample of 25 postlarval *P. stylirostris* taken from the hatchery in February, 1990, was negative for IHHN.

Construction of the hatchery was completed in 1990, as was the first phase of construction of its associated semi-intensive farm. Samples of postlarval *P. vannamei* and postlarval and juvenile *P. stylirostris* taken in May, 1990 from the facility's hatchery and its farm all gave IHHN positive results (Table 2). The most probable source of IHHNV contamination was the hatchery's use of adult pond-reared *P. vannamei* that were purchased by the facility in early 1990 for use as broodstock. These pond-reared broodstock were purchased because, at the time the broodstock was required for use in the company's hatchery, no sexually mature wild broodstock were available in the offshore fishery (although some were collected and introduced into the facility). The pond-reared broodstock were purchased from Facility no. 7, which had been tested positive for IHHN in April, 1987.

Facility no. 5. This research facility, located in the central region of the Gulf of California, has reared *P. californiensis* and *P. stylirostris* experimentally for approximately the past 12 years. IHHN was not diagnosed in the earliest samples from the facility processed by our laboratory; these samples were juvenile and subadult *P. californiensis* taken from the facility's super-intensive raceway culture systems in 1980. However, a more recent sample of juvenile *P. stylirostris* taken in June, 1989, from that facility was IHHN positive (Table 2). The population from which the sample was taken had been obtained from a commercial hatchery (Facility no. 6), which was found also to be IHHN positive in July, 1989.

Facility no. 6. This commercial hatchery, the first in Mexico, became operational in 1986. It has reared only *P. stylirostris* since its inception. Its broodstock requirements were obtained primarily from the commercial shrimp in the region. Exhaustive samples of postlarvae, juveniles, and broodstock from the facility, taken for another purpose in April of 1987, were negative for IHHN. Complaints of poor survival of stock purchased from this facility by various growout farms in the Mexican states of Sonora and Sinaloa resulted in samples being submitted to our laboratory for diagnosis in July, 1989. Those samples, and subsequent samples from the facility taken in December, 1989 and February, 1990, were positive for IHHN (Table 2). As was the case with Facility no. 4, Facility no. 6 also had in its history direct contacts with Facility no. 7, as well as recent introductions of wild broodstock from the local commercial fishery.

Facility no. 7. According to the operators of this facility (a growout farm using semi-intensive ponds), they have imported postlarval *P. vannamei* (from a number of commercial hatcheries in the US and Central America) and subsequently resold quantities of the imported postlarvae to other shrimp farms for growout. In addition, personnel at Facility no. 1 identified Facility no. 7 as one of two importing shrimp farming cooperatives that imported the postlarval *P. vannamei* population which was later found to be IHHN positive (sample submitted by Facility no. 1 to this laboratory on November 11, 1987; Table 2). Two years later (April, 1989), a sample of live subadult pond-reared *P. vannamei* from Facility no. 7 was submitted to our laboratory for determination of potential SPF (specific pathogen free) status. IHHNV infection was detected in samples taken from these shrimp by direct histology and by bioassay with juvenile *P. stylirostris* (Table 2).

Facility no. 8. This super-intensive growout farm, located in the Central region of the Gulf of California, submitted samples to this laboratory for diagnosis of disease problems several times, beginning with its first growout crops in 1989. The farm has reared only *P. stylirostris* since its inception early in 1989. Samples submitted in October and November of 1989 were negative for IHHN, but samples submitted in May of 1990, because of very high mortality rates, were IHHN positive. Postlarvae from which the IHHN positive stocks were reared had been purchased from Facility no. 11 (IHHN positive in 1990; Table 2).

Facility no. 9. This facility, located in the Central region of the Gulf of California, consists of low density experimental growout ponds. According to information provided with the two samples submitted to our laboratory for diagnosis, all the shrimp grown out at this facility since its construction more than a decade ago have been *P. stylirostris* produced by Facility no. 2. IHHN was diagnosed by direct histology in the first of the two samples, which was taken in October, 1989; IHHN was not detected in the November, 1989 sample from the same site (Table 2). Nothing in the available history of Facility no. 9 provided any insight as to the source of IHHN virus contamination.

Facility no. 10. This facility, located in the Central region of the Gulf of California, is a large (160 Ha) newly constructed farm that uses semi-intensive ponds for growout. The farm has its own hatchery. In early 1990, the completed section of the farm (100 Ha of ponds) was stocked with postlarval *P. stylirostris* that were produced from the farm's on-site hatchery from spawns obtained from wild broodstock obtained from the nearby commercial fishery. Within 45 days of stocking, a mass mortality of juveniles was noted in some ponds. Subsequent samples and draining of several other ponds revealed that mortality rates of up to 95% had occurred prior to day 60 of the crop in all of the farm's growout ponds. Samples of moribund shrimp from several growout ponds taken in May, 1990 showed that acute IHHN infections had caused the epizootic (Table 2).

Although the postlarval *P. stylirostris* used to stock the farm were produced by the facility's on-site hatchery using only captive wild adult *P. stylirostris* for broodstock, a review of the facility's history (during its construction) revealed that it had obtained postlarval *P. stylirostris* from Facility no. 3 (which was IHHN positive in mid and late 1989) in 1989 in order to bioassay its seawater source. These postlarvae were grown out at the facility to subadults and later transferred to the broodstock holding area of the farm for possible future use as broodstock. Although this potentially IHHNV contaminated stock was removed prior to the time wild adult *P. stylirostris* (collected by shrimp trawlers from the Gulf of California) were introduced to the facility, this stock may have been the source of IHHNV contamination at the facility.

Facility no. 11. Construction of this Northern Gulf of California commercial hatchery was completed in early 1990. The facility produces only *P. stylirostris*. A series of samples submitted for determination of SPF status from the facility in May, 1990, showed that postlarvae produced from the oldest broodstock in use at the facility were negative for IHHN, but that those PLs produced from newly acquired wild broodstock were positive for IHHN (Table 2).

Facility no. 12. This facility is a low density pond farm located on the Southern Gulf of California in the State of Sinaloa (Fig. 1). A sample of juvenile *P. stylirostris* reared at the farm from postlarvae purchased from Facility no. 6 was submitted to this laboratory in January, 1990 for diagnosis, and the sample was IHHN-positive (Table 2).

Facility no. 13. This farm has a similar history and location as does Facility no. 12. Samples of *P. stylirostris* from the three different crops in ponds at the farm were submitted in June, 1990 for diagnosis. Two of the three samples were positive for IHHN (Table 2). One source of postlarvae used by the farm in 1990 was Facility no. 2.

Discussion

Review of the case histories given above for the University of Arizona–University of Sonora project and the MCE (Marine Culture Enterprises) commercial prototype at Puerto Penasco from 1973 to 1980; for the MCE/HI (on Oahu, Hawaii) case histories from 1980 to 1987, in which Mexico derived shrimp stocks were reared in Hawaii; and for the 13 Mexican facility case histories from 1987 to June 1990, illustrate that penaeid shrimp collected from the Gulf of California and/or reared in culture facilities in the region were negative for IHHN until 1987. However, this changed in 1987 with the introduction and spread of IHHNV with imported stocks of penaeid shrimp.

Importation of postlarvae of a species native to Western Mexico occurred as a result of the rapid growth of the growout portion of the shrimp culture industry in Mexico. By 1987 the developing Mexican shrimp culture industry had grown to dozens of farms with a total culture area of 1600 Ha. The sources of "seed" (postlarvae and juveniles of *P. vannamei* and *P. stylirostris*) used to stock the farms were wild postlarvae captured seasonally in estuaries in the region, or postlarvae from the three hatcheries then present in the region. Because demand far exceeded the available seed supply, postlarval *P. vannamei* were imported by commercial shrimp farming cooperatives from commercial sources in the United States, Panama, and Ecuador. Facility no. 7 (Table 2) was among those cooperatives which imported postlarvae to meet their own farm's "seed" requirements and to sell excess postlarvae to other cooperatives. Our case histories show that at least one (and probably many more than one) of the imported populations of postlarvae was IHHN positive.

Further inspection of the case histories that are summarized in Table 2, and given in more detail in the Results section, indicate that some of the IHHN-positive cases can be traced directly or indirectly to contact with Facility no. 7, which was an importer of IHHN positive postlarval *P. vannamei* as early as 1987, and which provided pond-reared subadult *P. vannamei* and *P. stylirostris* for use as broodstock to several Mexican hatcheries. However, in other cases, the history provided by the facility operators provided no indication of the source of IHHNV contamination, and contamination presumably occurred as a result of normal shrimp culture practices in the region. While initially considered to be remote, the possibility that IHHNV became enzootic in wild shrimp populations in the Gulf of California by 1989 cannot be ignored, and such a scenario would readily explain the very rapid spread of the virus even into facilities with no history of direct contact with imported IHHNV-infected postlarvae. Subsequent studies done on wild penaeid shrimp in 1990–1991 have confirmed that IHHNV is indeed enzootic in a number of wild populations of penaeid shrimp in the Gulf of California (Pantoja-Morales and Lightner 1991).

Finally, a common practice by hatchery managers in Mexico has been to release excess postlarvae (those which were produced but not sold or required for stocking in their own facilities) into the Gulf of California in an effort to enhance the commercial fishery. Released postlarvae sometimes numbered in the millions. Inevitably, this practice resulted in the release of IHHNV-infected postlarvae into the wild. This practice may have contributed to the extraordinarily rapid spread of IHHNV in Mexico.

Summary

Evidence for IHHN introduction in the region of Mexico bordering the Gulf of California may be listed as follows:

1. Wild broodstock obtained from all regions of the Gulf of California and shrimp cultured in Western Mexico were IHHN-negative for 15 years (1973 to 1987).
2. Imported postlarval *P. vannamei* in late 1987 were IHHN-positive.
3. A facility which imported postlarvae became and remained IHHN-positive.
4. All facilities tested which received pond-reared broodstock or postlarvae (or had other contact) from this importing facility became IHHN-positive in 1989 or 1990.
5. Until 1990 facilities using exclusively wild broodstock and with no history of contact with postlarval importers remained IHHN-negative, but became IHHN-positive during 1990.

The inadvertent introduction of IHHNV with imported shrimp and its spread by normal shrimp cultural practices in Mexico has had catastrophic consequences for the developing shrimp culture industry of Northwestern Mexico, especially for those companies and cooperatives that reared *P. stylirostris*. Due to the lack of adequate regulatory infrastructure in Mexico, the ignorance or indifference of components of the shrimp culture industry to the IHHN problem, the lack of sensitivity of our current detection methods for IHHNV, the paucity of diagnostic lab capabilities in Mexico, and most importantly the presence of large highly susceptible populations of *P. stylirostris* in the region, it seems doubtful that the introduction and spread of IHHNV in the region could have been prevented. Consequently, the commercial culture of *P. stylirostris* in many areas of the Gulf of California region has been abandoned in favor of culturing more IHHN-resistant species like *P. vannamei* or *P. californiensis*. However, neither of these species is as easily cultured as *P. stylirostris* nor does either grow to as large a size in the same growout period. Thus they bring lower profits to the farmers.

While those companies in Mexico that rear exclusively *P. vannamei* show little concern about the consequences of IHHN in their stocks, recent papers linking IHHNV to RDS in the species (Kalagayan *et al.*, 1991; and Holloway *et al.*, 1990), and the recent diagnosis of RDS in *P. vannamei* reared in Mexico (at Facility no. 7), suggest that even these companies will ultimately have to deal with the disease.

Long-term solutions to the IHHN problem in Mexico and in other areas of the Americas may ultimately take one of three forms: (1) the rearing of specific pathogen-free (SPF) shrimp stocks in regions protected from importation of the virus by vigorously enforced regulations that control regional movements of shrimp stocks, and that require the inspection (using adequate and approved diagnostic procedures) and quarantine of imported stock; (2) the development of IHHN-resistant stocks of *P. stylirostris*, and development of stocks of *P. vannamei* which are even more resistant to IHHN than those now being cultured; or (3) the rearing of penaeid species which are more IHHN-resistant than either of the former species.

Acknowledgments

The numerous shrimp farmers and researchers in Mexico are thankfully acknowledged for freely providing information (along with diagnostic samples) in the hope that their experiences with IHHN might lead to a greater collective understanding of the IHHN epizootic in Northwestern Mexico and to the eventual control of the disease. This study developed as part of cooperative efforts with US and Mexican institutions to develop SPF shrimp stocks. The work was supported in part by the USDA, Cooperative State Research Service, under Grant 88–38808–3320 to the US Marine Shrimp Farming Consortium.

References

Bell, T. A., and Lightner, D. V. 1984. IHHN virus: infectivity and pathogenecity studies in *Penaeus stylirostris* and *Penaeus vannamei*. Aquaculture, 38: 185–194.

Bell, T. A., and Lightner, D. V. 1987. IHHN disease of *Penaeus stylirostris*: effects of shrimp size on disease expression. J. Fish Dis., 10: 165–170.

Bell, T. A., and Lightner, D. V. 1988. A handbook of normal shrimp histology. Special Publication No. 1, World Aquaculture Society, Baton Rouge, LA.

Bonami, J. R., and Lightner, D. V. 1991. Unclassified viruses of crustacea. *In* Atlas of invertebrate viruses, pp. 597–622. Ed. by J. R. Adams and J. R. Bonami. CRC Press, Boca Raton, FL.

Bonami, J. R., Brehelin, M., Mari, J., Trumper, B., and Lightner, D. V. 1990. Purification and characterization of IHHN virus of penaeid shrimps. J. Gen. Virol., 71: 2657–2664.

Brock, J. A., Lightner, D. V., and Bell, T. A. 1983. A review of four virus (BP, MBV, BMN, and IHHNV) diseases of penaeid shrimp with particular reference to clinical significance, diagnosis and control in shrimp aquaculture. Proc. 71st Mtg., Intl. ICES CM 1989/Gen: 10, 18 pp.

Brock, J. A., and Lightner, D. V. 1990. Diseases of Crustacea. Diseases caused by microorganisms. *In* Diseases of marine animals, vol. 3, pp. 245–349. Ed. by O. Kinne. John Wiley, New York.

Garmendia Nunez, E. A., and Garcia-Sanchez, A. L. 1990. Shrimp culture status in Mexico 1989. *In* Abstracts of the 10–14 June 1990 World Aquaculture meeting, Halifax, NS, Canada, p. 115.

Holloway, Jr., J. D., Browdy, C. L., Richardson, III, J. R., King, C. O., Stokes, A. D., Hopkins, J. S., and Sandifer, P. A. 1990. IHHN virus and intensive culture of *Penaeus vannamei*: effects of stocking density and water exchange rates on production and harvest size distributions. *In* Abstracts of the 10–14 June 1990 World Aquaculture meeting, Halifax, NS, Canada, p. 73.

Kalagayan, G., Godin, D., Kanna, R., Hagino, G., Sweeney, J., Wyban, J., and Brock, J. 1991. IHHN virus as an etiological factor in runt-deformity syndrome of juvenile *Penaeus vannamei* cultured in Hawaii. J. World Aquaculture Soc., 22: 235–243.

Lightner, D. V. 1983. Diseases of cultured penaeid shrimp. *In* CRC handbook of mariculture, vol. 1, Crustacean aquaculture, pp. 289–320. Ed. by J. P. McVey. CRC Press, Boca Raton, FL.

Lightner, D. V. 1988. Diseases of cultured penaeid shrimp and prawns. *In* Disease diagnosis and control in North American marine aquaculture, pp. 8–127. Ed. by C. J. Sindermann and D. V. Lightner. Elsevier, Amsterdam.

Lightner, D. V., and Redman, R. M. 1991. Hosts, geographic range and diagnostic procedures for the penaeid virus diseases of concern to shrimp culturists in the Americas. *In* Frontiers of shrimp research, pp. 173–196. Ed. by W. J. Dougherty and M. A. Davidson. Elsevier, New York.

Lightner, D. V., Redman, R. M., and Bell, T. A. 1983a. Infectious hypodermal and hematopoietic necrosis (IHHN), a newly recognized virus disease of penaeid shrimp. J. Invertebrate Pathol., 42: 62–70.

Lightner, D. V., Redman, R. M., Bell, T. A., and Brock, J. A. 1983b. Detection of IHHN virus in *Penaeus stylirostris* and *P. vannamei* imported into hawaii. J. World Mariculture Soc., 14: 212–225.

Lightner, D. V., Redman, R. M., Danald, D. A., Williams, R. R., and Perez, L. A. 1984. Major diseases encountered in controlled environment culture of penaeid shrimp at Puerto Penasco, Sonora, Mexico. *In* Proceedings of the Ninth and Tenth US–Japan Meetings on Aquaculture. Ed. by C. J. Sindermann. NOAA Tech. Rep. NMFS 16: 25–33. US–Japan Meeting on Aquaculture, Symp. on Crustacean Culture, Kyoto.

Mahler, L. E., Groh, J. E., and Hodges, C. N. 1974. Controlled environment aquaculture. Proc. World Mariculture Soc., 4: 379–384.

Pantoja-Morales, C., and Lightner, D. V. 1991. Status of the presence of IHHN virus in wild penaeid shrimp from the coast of Sonora, Mexico. *In* Program and Abstracts of XXIV Annual Meeting of the Society for Invertebrate pathology. 4–9 August 1991, Flagstaff, AZ.

Rosenberry, B. (ed.). 1987. Marine Culture Enterprises. Aquaculture Digest. Shrimp Farming Int., 12 (11.30): 17, Nov. 1987.

Rosenberry, B. (ed.). 1988. Marine Culture Enterprises. Aquaculture Digest. Shrimp Farming Int., 13 (1.16): 12, Jan. 1988.

Rosenberry, B. (ed.). 1990. Shrimp Farming in the Western Hemisphere. Aquaculture Digest, vol. 15, June 1990.

Salser, B., Mahler, L., Lightner, D., Ure, J., Danald, D., Brand, C., Stamp, N., Moore, D., and Colvin, B. 1978. controlled environment aquaculture of penaeids. *In* Drugs and Food from the Sea, Myth or Reality?, pp. 345–355. Ed. by P. N. Kaul and C. J. Sindermann. University of Oklahoma Press, Norman, Oklahoma.

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Impact of *Eichhornia* and *Hydrilla* in the United States[1]

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The history of the introduction of two severe aquatic weed species – the waterhyacinth (*Eichhornia crassipes*) and hydrilla (*Hydrilla verticillata*) – is reviewed along with case histories of their economic and environmental impacts. Expensive management programs and regulatory controls have been implemented after introduction and establishment; however, these programs have not stopped the spread of the plants throughout the United States. Future programs must be more aggressive in their attempt to determine weedy potential prior to any purposeful introductions.

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Introduction

In a recent article, C. D. K. Cook stated, "There often seems to be an almost blind belief that really troublesome aquatic weeds have been introduced from elsewhere and that the main reason for their aggressiveness is that they have been relieved of the ecological restraints within their native range" (Cook, 1990). Cook further indicated that the cause of the weed problem is invariably man-induced changes to the aquatic habitat which allows the alien species to expand. Cook also estimated that 172 species of aquatic plants have become established outside their native range and that only a few have become seriously troublesome but all are potential weeds (Cook, 1990).

There is no complete agreement within the lake management community over Cook's statement relative to the problematic nature of these plants being due to man-induced changes. Experience in the United States with two plants in particular, waterhyacinths (*Eichhornia crassipes*) and hydrilla (*Hydrilla verticillata*), form the basis for much of this disagreement. These two plants have become serious pests in the United States not due to man's manipulation of the aquatic habitat but through their growth form, physiology, and reproductive capabilities.

[1] Florida Agricultural Experiment Stations Journal Series No. N-00381.

History of introduction

The waterhyacinth was introduced into the United States in 1884 at the Cotton States Exposition in New Orleans. The Japanese were distributing the plants as souvenirs, and, as the story goes, the plants were placed in ornamental ponds by the attendees. As the plants filled the ponds, the excess was thrown into nearby creeks and lakes (Barrett, 1989). The introduced plants quickly affected navigation and other water activities in southeastern lakes and rivers. By 1898 the plants had increased to the point that steamboats and other vessels were unable to reach docks or pass through navigation openings in bridges or narrow points on rivers. Public concern over the economic impact of this plant resulted in the passage of the River and Harbor Act of 1899, which authorized the US Army Corps of Engineers to construct and operate vessels and log booms in navigable waters of Florida and Louisiana in an attempt to manage the impact of the plant. These methods proved inadequate and seasonal climatic conditions provided the only real relief for several decades. The public outcry was so great that agencies resorted to such drastic efforts as spraying the plants with sodium arsenite. This was later prohibited due to the poisoning of applicators and livestock. More scientifically based and environmentally compatible management efforts utilizing safer herbicides and host-specific biocontrol insects were eventually developed. Today the waterhyacinth is not a serious pest due to the continuous efforts of many management agencies.

Another major aquatic plant in the United States, hydrilla, was introduced about 1959 in the Miami and Crystal River areas of Florida. The assumption has been that it was introduced by the aquarium industry as *Elodea* sp. and was called Florida Elodea for years. Hydrilla quickly became a problem in Florida due to its rapid growth rate and the physiological capability of requiring less sunlight for photosynthesis than native submersed plants. Hydrilla was able to grow in much deeper waters than native species and completely occupy the majority of the submersed habitat of many lakes and rivers. This niche was previously unoccupied by any native aquatic vegetation. This growth characteristic created serious water use, recreation, fish and wildlife and flood control problems which were rarely encountered with native plants.

Impacts of aquatic weeds

An example of the ecological impacts of these two plants is the increased contribution of organic material to lake sediments generated either through natural growth or treatment with herbicides. Table 1 indicates that the amount of organic sedimentation generated by waterhyacinths or hydrilla is greatest when the plants are allowed to completely cover a waterbody and no spray operations are conducted. The more intensive management activities (<30% coverage) significantly reduces this contribution (Joyce, 1985). Because of this and ecological impacts of these species, many biologists now consider them as "biological pollutants" of our water resources.

There are few disagreements over the impacts of severe infestations of aquatic weeds; however, there are many disagreements and concerns over the management techniques utilized and the magnitude and effects of some of the plant populations. For example, those individuals responsible for ensuring navigation, recreational boating, water recreation, flood control, public health, or irrigation would desire to have as little vegetation as possible. Whereas, those who are more concerned about fish and wildlife values would argue for more vegetation. The main disagreement involves the level of vegetation necessary to support a healthy fish and wildlife population, while not disrupting native species diversity or interfering with man's other uses. With exotic plants such as hydrilla and waterhyacinths, which display rapid expansion capabilities, the management at this "optimum" level becomes difficult and expensive.

Table 1. Annual organic sedimentation by aquatic weeds.

Percent coverage	Tons/acre (dry weight)	
	Waterhyacinths	Hydrilla
0	0.9	0.6
<30	1.5	0.9
100% (sprayed)	4.2	1.1
100% (unsprayed)	6.5	1.3

Two recent experiences at Lake Okeechobee and Orange Lake, Florida with these two species indicate the magnitude of the problem, the environmental and economic impacts, and the cost of containment.

Lake Okeechobee

Lake Okeechobee, located in South-central Florida, ranks as the second largest freshwater lake in the United States after Lake Michigan. The natural watershed has been highly modified to provide flood control and water supply benefits for agricultural and urban interest, as well as recreation and commercial navigation. In respect to these water resource uses, unmanaged waterhyacinths have shown the ability to cause severe economic and ecological damage by disruption of these water resource objectives.

As early as 1905, waterhyacinth problems were reported on Lake Okeechobee. Initial control operations consisted of mechanical removal or destruction. These methods were ineffective except on a localized, short-term basis. The development of 2,4-D in 1941, improvements in herbicide application techniques, discovery and introduction of biological suppressants (insects), and higher levels of funding led to the development of successful management programs. In today's management programs, plant populations are aggressively kept below problematic levels. The approach is commonly known as maintenance control.

Table 2 provides an analysis of waterhyacinth control on Lake Okeechobee since 1978 (Bodle, 1990; US Army Corps of Engineers, 1989; Zattau, 1990). Under maintenance control, it can be seen that maintaining the plants at low levels (FY 80–81, 81–82, 88–89, and 89–90) results in lower overall costs, fewer acres sprayed (thus less herbicide used), fewer plants present, but higher per acre costs. However, waterhyacinth populations on Lake Okeechobee have sometimes been allowed to exceed maintenance control levels when aquatic plant management programs were interrupted by the lack of adequate resources (FY 83–84, 84–85), or by policies (FY 86–87, 87–88) that were based upon factors other than many years of operational experience and scientific data. One such situation occurred in 1986 when waterhyacinth management was halted as a theoretical means to reduce phosphorus concentrations in the lake. In the absence of control programs, waterhyacinth coverage increased by 94% between August and November 1986 and caused emergency conditions on the lake which disrupted navigation and water movement, and destroyed

Table 2. Lake Okeechobee waterhyacinth control expenditures and operations Corps of Engineers and South Florida Water Management District 1978–1990.[1]

Fiscal year	Total expenditures ($ × 1000)	Acres controlled	Cost ($ per acre)	Acres present[2]
78–79	280.5	8 949	31.34	630
79–80	330.3	7 703	42.88	400
80–81	338.1	3 509	96.35	N/A
81–82[3]	252.3	3 306	76.32	694
82–83	450.6	8 117	55.51	7610
83–84	638.0	16 604	38.42	6449
84–85	383.5	11 995	31.97	1265
85–86	388.0	6 327	61.32	5542[4]
86–87	625.4	10 139	61.68	900
87–88	715.0	11 744	68.88	525
88–89	481.7	5 256	91.65	50
89–90	363.6	4 650	78.20	65

[1] Data obtained from U.S. Army Corps of Engineers, Jacksonville, Florida and South Florida Water Management District, West Palm Beach, Florida (Bodle, 1990; US Army Corps Eng., 1989; Zattau, 1990).

[2] Data obtained from annual surveys in August of each year by Florida Department of Natural Resources.

[3] The SFWMD assumed control operations on the Lake and tributaries from the COE in June, 1982.

[4] Acreage reaches record level of 7700 acres in December 1986.

native plant communities. As predicted by previous experience, high costs associated with large amounts of herbicides and manpower (FY 86–87 and 87–88) were necessary to regain maintenance control levels.

Orange Lake

Orange Lake is a 5400-hectare, shallow, eutrophic lake in North-central Florida which undergoes wide annual fluctuations in water level and surface area. The lake is a nationally renowned sportfishing lake and annually attracts a large number of non-local anglers. The lake supports 20 full-time fish camps that provide services such as lodging, guides, boat rentals, tackle, live bait, and food. The lake shoreline is relatively undeveloped and has an extensive littoral area which has historically been covered with spatterdock (*Nuphar luteum*), maidencane (*Panicum hemitomon*), knotgrass (*Paspalidium germinatum*), coontail (*Ceratophyllum demersum*), southern naiad (*Najas quadalupensis*), and bladderwort (*Utricularia* sp.) (Colle, *et al.*, 1987). The predominant industry in the immediate area is associated with agriculture (pasture lands) and sportfishing.

Hydrilla was identified in Orange Lake in 1974. Prior to this approximately 2700 hectares of the lake was devoid of submersed aquatic vegetation. Hydrilla was first discovered at a public boat ramp and was probably inadvertently introduced by a boater not removing vegetation fragments from the boat trailer after leaving an infested lake. Hydrilla quickly increased in coverage such that by 1977 there was only 114 hectares of open water on the lake or 95% areal coverage by a dense surface mat of hydrilla (Colle, *et al.*, 1987). Hydrilla management activities during this period consisted of chemically and mechanically cutting boating trails from access ramps to the remaining open water areas. In 1978, the hydrilla coverage was drastically reduced due to a dense algal bloom caused by a large influx of surface water. This bloom and the sharp increase in water level drastically reduced hydrilla coverage. During subsequent years, hydrilla reinfested the lake from tubers produced by the plants. Due to intense management activities with a new herbicide, Sonar (active ingredient fluridone), hydrilla has not exceeded 70% of the lake area in spite of the water level fluctuations.

Fortunately, the Florida Game and Freshwater Fish Commission periodically conducts non-uniform-probability roving creel surveys on the lake (Pfeiffer, 1967; Ware, *et al.*, 1972) in order to obtain estimates of angler effort. This data, combined with estimates of sportfishing expenditures by resident and non-resident anglers, provided an estimated value of US$1.0 million during the 1978–1979 angling season (Colle, *et al.*, 1987). In 1977, sportfishing activity decreased by over 90% due to the hydrilla infestation, but fully recovered in 1979 after the hydrilla was reduced to low levels. Subsequently, more intensive surveys of economic activity (Milon, *et al.*, 1986; Milon and Welsh, 1989) estimated the total indirect benefit of sportfishing to the region in excess of US$10.0 million. Thus, it can be seen that severe hydrilla infestations which cause significant shifts in sportfishing activities can have severe localized economic impacts.

Regulatory controls

One of the major US points of entry and distribution of aquatic plants is the State of Florida. According to the 1990 Florida Agricultural Statistics Service estimates there are over 44 aquatic plant growers with net sales of over US$7.0 million. In order to avoid intentional introductions of additional potentially harmful species, various institutional controls, primarily on the aquatic plant importation and aquarium industry, have been enacted. In Florida, laws are in place which regulate the importation, transportation, cultivation, collection, sale, possession, and revegetation of aquatic plants. The Florida Department of Natural Resources is charged with developing lists of potentially nuisance species, promulgating rules and permitting procedures for plant culture and possession, inspection of imports and growout facilities, enforcement of violations, and conducting emergency eradication activities upon discovery of nuisance species.

At the national level, the Federal Noxious Weed Act of 1974 (Public Law 93–269) regulates the import and movement of noxious weeds under the auspices of the US Department of Agriculture, Animal Plant and Health Inspection Service. This act also lists prohibited nuisance weed species, established quarantine procedures, and specified penalties for violations of US$5000, one year in prison, or both. Unfortunately, proper enforcement of this act was never funded.

Future directions

Prevention of future adverse effects of alien aquatic plant species is similar to that for other plants or animals. Efforts must be intensified to (a) establish systems and mechanisms to provide a predictive capability of potential ecological and economic impacts of species prior to their introduction, and (b) provide a realistic, responsive system of enforcement. In the past, the magnitude of the damage was not known until after the species was introduced or released. New advances in tissue culture or bioengineering techniques may provide methods of determining the "weedy" nature of a species or the development of growth characteristics in ornamental species which will decrease their weed potential. Barring such advances, future efforts will require expanded, worldwide databases on the biological and ecological characteristics of potentially weedy species, and past experiences with the target species. The availability of this information and the level of key wording should also be such that those less able to conduct the necessary research will have free and easy access to the information. Enforcement of international importation and quarantine programs must also be adequately funded so that potentially harmful species are excluded. Further, it is important that these programs be responsive enough that potentially economically important species which pose limited potential for disruption of native diversity are not unduly restricted or excluded.

References

Barrett, S. C. H. 1989. Water weed invasions. Sci. Am. October, 1989: 90–97.

Bodle, M. 1990. Personal communication. South Florida Water Management District, W. Palm Beach, FL.

Colle, D. E. *et al.* 1987. Influence of hydrilla on harvestable sportfish populations, angler use, and angler expenditures at Orange Lake, Florida. N. Am. J. Fish. Manage., 7: 410–417.

Cook, C. D. K. 1990. Origin, autecology, and spread of some of the world's most troublesome aquatic weeds. In Aquatic Weeds. The Ecology and Management of Nuisance Aquatic Vegetation, pp. 31–38. Ed. by A. H. Pieterse and K. J. Murphy. Oxford University Press, New York.

Joyce, J. C. 1985. Benefits of maintenance control of waterhyacinths. Aquatics, 7(4): 11–13.

Milon, J. W., Yingling, J., and Reynolds, J. E. 1986. An economic analysis of the benefits of aquatic weed control in North-central Florida. Food and Resources Economics Department Report 113. Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Florida 32611. 52 pp.

Milon, J. W., and Welsh, R. 1989. An economic analysis of sport fishing and the effects of hydrilla management in Lake County, Florida. Food and Resources Economics Department Report 118. Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Florida 32611. 47 pp.

Pfeiffer, P. W. 1967. The results of a non-uniform probability creel survey on a small state-owned lake. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners, 20: 409–412.

US Army Corps of Engineers, Jacksonville District. 1989. FY 1988 Aquatic Plant Control Program District Survey.

Ware, F. J., Fish, W. V., and Prevatt, L. 1972. Five year creel survey of two Florida lakes. Q. J. Florida Acad. Sci., 35: 31–48.

Zattau, W. Personal communication. 1990. Aquatic Plant Control Costs. US Army Corps of Engineers, PO Box 4970, Jacksonville, Florida 32232.

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The ecological invasion of Hawaiian reefs by two marine red algae, *Acanthophora spicifera* (Vahl) Boerg. and *Hypnea musciformis* (Wulfen) J. Ag., and their association with two native species, *Laurencia nidifica* J. Ag. and *Hypnea cervicornis* J. Ag.

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Russell, D. J. 1992. The ecological invasion of Hawaiian reefs by two marine red algae, *Acanthophora spicifera* (Vahl) Boerg. and *Hypnea musciformis* (Wulfen) J. Ag., and their association with two native species, *Laurencia nidifica* J. Ag. and *Hypnea cervicornis* J. Ag. – ICES mar. Sci. Symp., 194: 110–125.

Acanthophora spicifera, a red seaweed, which was introduced to Hawaii in the 1950s, is well established on all the Hawaiian islands except Hawaii. It has a heterogeneous distribution limited primarily by water motion between DIF 10–80 and temperature (25–27°C). Salinity has been less limiting (19–36‰). Competition between *Acanthophora* and two native algal species (*Laurencia* spp. and *Hypnea cervicornis*) is discussed. Another introduction, *Hypnea musciformis* entered the *Laurencia* niche in 1977 and has partially displaced *H. cervicornis*. Changes within the *Laurencia* niche due to the introduction of two alien marine algal species are discussed.

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Introduction

Eighteen species of marine macro-algae have been introduced to Oahu, Hawaii, since 1950. Two are highly successful "weedy" species, nine are marginally successful and seven have failed to become established (Table 1). Recently, most of these introductions have been in conjunction with aquaculture projects where the algae have been transported by air from as far away as Florida and the Philippines to Hawaiian reefs in locations where they would most likely be successful. Currently, only the ecological effects of *Kappaphycus alvarezii* (=*Eucheuma striatum*) (Doty, 1988) have been researched (Russell, 1983). The effects introduced species have on the native species ecology are unique to each one that enters the Hawaiian Islands, and an understanding of how they may change the ecosystem is critical for the conservation and management of the reefs, just as it is for the terrestrial ecology (Lewin, 1987). The research presented here deals specifically with the ecology of *Acanthophora spicifera* (Vahl) Boerg. and *Hypnea musciformis* (Wulfen) C. Ag. (two highly successful introduced species) and their competition with *Laurencia nidifica* J. Ag. and *Hypnea cervicornis* J. Ag. (two native species).

Acanthophora spicifera is the most widespread and successful alien alga in Hawaii. It appeared for the first time in Hawaii in the early 1950s (Doty, 1961), perhaps entering on a barge from Guam, or possibly along with fish imported to the Waikiki Aquarium (Russell, 1987). It has a relatively continuous distribution in nearly all of the tropical and subtropical seas of the world: Panama (Earle, 1973), Cuba (Taylor, 1967), the Mediterranean (Feldmann, 1937) (where it was introduced via the Suez Canal), Bangladesh (Nurul-Islam, 1976), Viet Nam (Dawson, 1954), Indonesia (Atmadja, 1977), Philippines (Levring *et al.*, 1969), and locations in between. However, before 1950 there was a gap in its distribution across the Central Pacific until it arrived in Hawaii (Trono, 1968), a location for which it was well suited.

The physical parameters for *A. spicifera* habitation in other locations are broad and varied. It is found in sheltered bays (Taylor and Bernatowicz, 1969), on shores exposed to the open ocean (Kim, 1964; Taylor, 1967), and in moderate to strong wave action (Womersley and Bailey, 1970). *Acanthophora* occurs 1–3 m deep, near shore in the eulittoral, upper sublittoral or lower intertidal zone (Doty, 1970; Earle, 1973; Tabb and Manning, 1961; Taylor, 1967), cannot withstand prolonged exposure to air (Kilar and Lou, 1986), and is

Table 1. Marine macro-algae introduced to Oahu, Hawaii, since 1950.

Species	Introduced to new location	Time of introduction	Place of origin	Degree of success	Commercial value	Competition with native species
Acanthophora spicifera (Vahl) Boerg. (S,A)	Pearl Harbor and/or Waikiki	After 1950 26 Apr 1952	Guam	Highly successful	None	*Laurencia nidifica*
Eucheuma denticulatum (Burm.) Col. & Herv. (T)	Honolulu Harbor Kaneohe Bay, etc.	October 1970 to late 1976	Philippines	Successful	Kappa-Carrageenan	Unknown
*Eucheuma isiforme** (C. Ag.) J. Ag. (T)	Kaneohe Bay	Jan 1974	Florida	Not successful	Iota-Carrageenan	None
Gracilaria epihippisora Hoyle (T)	Waikiki Kaneohe Bay	Apr 1971 Sept 1978	Hawaii Is.	Marginal	Agar	Unknown
Gracilaria eucheumoides Harvey (T)	Kaneohe Bay	mid 1970s	Philippines	Unknown	Carrageenan	Unknown
Gracilaria salicornia (C. Ag.) Dawson (T)	Waikiki Kaneohe Bay	Apr 1971 Sep 1978	Hawaii Is.	Highly successful	Agar	Unknown
Gracilaria sp. (IT)	Honolulu Harbor	1971	Philippines	Unknown	Carrageenan	Unknown
Gracilaria tikvahiae McLachlan (T)	Kaneohe Bay Kahuku	mid 1970s	Florida	Successful	Carrageenan Fresh produce	Unknown
Hypnea musciformis (Wulfen) J. Ag. (T)	Kaneohe Bay	Jan 1974	Florida	Highly successful	Kappa-Carrageenan	*Hypnea cervicornis Acanthophora spicifera*
*Kappaphycus alvarezii*** (Doty) Doty (T)	Honolulu Harbor Kaneohe Bay, etc.	9 Sep 1974 to late 1976	Philippines	Successful	Kappa-Carrageenan	None known
*Kappaphycus striatum*** (Schmitz) Doty (T)	Honolulu Harbor Kaneohe Bay, etc.	5 Aug 1970 to late 1976	Pohnpei and Philippines	Successful	Kappa-Carrageenan	Unknown
Lola lubrica (S. & G.) Ham. & Ham. (CO)	Makapuu and Kahuku	1976	California	Not successful	None	None
Macrocystis pyrifera (L.) C. Ag. (T)	Makapuu Keahole Point	1972 1980s	California	Not successful	Alginates	None
Nemacystus decipiens (Suhr.) Kuck. (UK)	Waikiki	1950s?	Unknown	Successful	None	Unknown
Pilinella californica Hollenberg (CO)	Makapuu Kahuku	1976	California	Not successful	None	None
Porphyra sp. (T)	Oahu	(?)	Japan	Unknown	Nori	Unknown
Wrangelia bicuspidata Boerg. (UK)	Kaneohe Bay	1974(?)	Unknown	Successful	None	Unknown

Introduced by (S) = ship, (A) = aquarium activities, (T) = transplanted, (CO) = with clams and oysters, (UK) = unknown
*Two distinct forms of *E. isiforme* were introduced, both failed to survive (see Cheney, 1988).
***K. alvarezii = Eucheuma striatum* var. *tambalang*; *K. striatum = E. striatum* var. *elkhorn* (see Doty, 1988 and Glenn and Doty, 1990).

normally found below the mean low tide level (Rao and Sreeramalu, 1974). The substratum to which it attaches is also varied: sand and rock (Taylor and Bernatowicz, 1969), shells (Dawson, 1954), concrete (Varma, 1959), rubber bands (Mshigeni, 1978), logs (Dawes *et al.*, 1978), and buoys (Anand, 1940).

Trono (1968) suggested that *A. spicifera* may be limited to high islands, which may contain certain vital micronutrients (Doty, 1954). However, Tsuda (1964) found *A. spicifera* on Tarawa, Kiribati, a low calcareous atoll. Temperature has been suggested as a more important factor governing its distribution, since *Acanthophora* tends to disappear in mid-winter in Bermuda (Taylor and Bernatowicz, 1969) and Trono (1968) suggested that it may be limited to waters that remain above 23.5°C.

Tabb and Manning (1961) also found an increase in the amount of *Acanthophora* when salinity decreased, but found it could tolerate high salinity. Soegiarto (1972) also reported a correlation between the local distribution of *A. spicifera* in Kaneohe Bay, Hawaii, and low salinity, low water motion, sandy substrata, and municipal pollution. From these observations the distribution of *A. spicifera* in Hawaii was expected to be limited to areas with lower than normal salinity, moderate wave action or water motion, at a depth of 1–3 m or less, below low tide and within an average temperature of 23.5°C.

The algal species with which *A. spicifera* has been reported are also numerous, but only a few occur with it regularly in other geographical locations. *Laurencia* spp. are associated with *A. spicifera* in the Philippines (Doty, 1970), in Panama (Earle, 1973), Indonesia (Atmadja, 1977), and Florida (Kilar and Lou, 1986), while *Hypnea* spp. are associated with *A. spicifera* in the Gulf of Mexico (Kim, 1964), Viet Nam (Dawson, 1954), and the Philippines (Doty, 1970). In Hawaii, *Acanthophora* has colonized the reefs in zones occupied by *Valonia ventricosa* J. Ag., *Colpomenia sinuosa* (Roth) Derbes and Solier and *Bornetella sphaerica* (Zanard.) Solms-Laubach (Santelices, 1977), and *Hypnea cervicornis* J. Ag. (Mshigeni, 1974). This paper tests the hypothesis that *A. spicifera* forms associations with *Laurencia* and *Hypnea* species in Hawaii and competes, displaces, or replaces them on the reef.

After the majority of this study was completed, another alien alga was introduced to Hawaii, *Hypnea musciformis* (Table 1). This fast-growing, weedy species was introduced from Florida to Kaneohe Bay, Hawaii, early in 1974 (Abbott, 1987), along with *Eucheuma isiforme* (C. Ag.) J. Ag., for marine agronomy experiments. By 1977 it had entered the same niche with *Acanthophora*, *Laurencia*, and *Hypnea cervicornis* and significantly altered the ecology. The direction and extent of change due to this fourth member of the association is also discussed.

Materials and methods

A systematic survey of all accessible shores and a specific sampling method was used on six of the Hawaiian Islands. Seventy locations were sampled, including most of Hawaii's harbors and a wide selection of the shoreline types.

When *Acanthophora* was found, a 46-cm diameter ring was placed over the heaviest growth of the alga, all of the thalli present within the ring were removed by hand, sorted to species, and weighed wet and dry. The occurrence of *A. spicifera* along the shores was tested using 95% confidence intervals for a binomial distribution.

Salinity was measured at each location with an American Optical Corp. refractometer No. 10419, temperature with calibrated mercury-filled thermometers, depth with a meter stick, and water motion with calcium sulfate blocks (Doty, 1971). Water motion is represented as a Diffusion Increase Factor (DIF), a value based on the enhanced dissolution rate of calcium sulfate blocks in moving water compared to their dissolution rate in still water. Water motion was measured once at each location and analysis of variance was used to test the significance of differences between the data.

Data was also collected from three transects on the windward side of Oahu over a consecutive 31-month period. These transects are subjected to the same general weather conditions and represent high, medium, and low water motion habitats (Fig. 1). All of the algae inside a 46-cm diameter ring were sampled at regular intervals along each transect and weighed wet and dry.

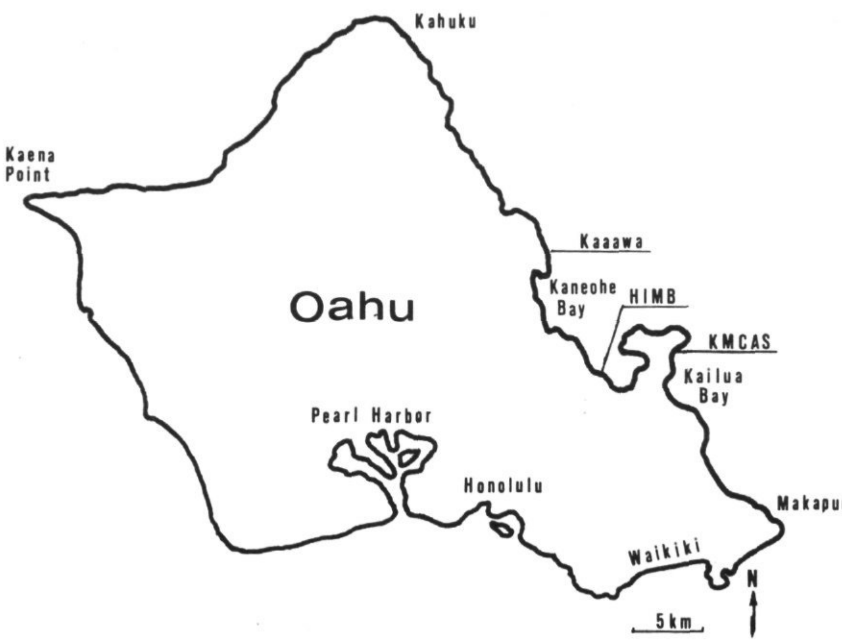

Figure 1. Map of Oahu, Hawaii, showing locations of the three transect sites (KMCAS, Kaaawa, HIMB) and important place names.

These same methods were used to determine the standing crop of species in other studies going on simultaneously (1973–1976) in Hawaii by other investigators (Santelices, 1977; Glenn *et al.*, 1990).

The Kaneohe Marine Corps Air Station (KMCAS) transect crosses a solution bench reef of solid amalgamated coral limestone, exposed to strong wave action and high water motion, on the Kailua Bay side of Ulupau Head on Mokapu Peninsula (Fig. 1). A line marked at 5-m intervals for 40 m (the width of the reef) was placed on the reef once a month, at the same location, and ring-samples made at each 5-m interval.

The transect at Kaaawa was located near a sugar mill ruins on State Highway No. 83 (Fig. 1). The 80-m long transect extended east from the shore perpendicular to the highway. The reef flat is in an area of moderate wave action and consists of sand, amalgamated coral limestone, and boulders. Samples were taken at 5-m intervals for the first 13 months, 10-m intervals for the next 7 months, and at 20-m intervals for the final 11 months.

The transect in Kaneohe Bay was on a sandy reef-flat 80 m east of Lilipuna Pier, used by the Hawaii Institute of Marine Biology (HIMB), 4 km inside the Kaneohe Bay barrier reef (Fig. 1). It is in an area of light wave action and low water motion and extended 110 m north from a retaining wall and terminated at the reef edge. Depth, water motion, temperature, and salinity were measured along each transect for the duration of the study.

Competitive interactions between *A. spicifera* and other algae were investigated by comparing the total and seasonal standing crop fluctuations of *A. spicifera* along the transects with the other algal species present. The Index of Diversity (Lewis and Taylor, 1967) was solved numerically on an HP28S calculator.

Competitive interactions between *A. spicifera* and *Laurencia nidifica* were tested both in the laboratory and in the field. The apparatus used was a $15 \times 25 \times 40$ mm block of plastic sponge (Magla Products, No. 2033-738) glued with contact cement to the top of an 8-mm diameter, 70-mm long tapered hardwood dowel which was wedged into a 6-mm diameter hole drilled into a $25 \times 25 \times 100$ mm, painted, mild steel bar (Fig. 2). Thirty of these units were placed into a $20 \times 68 \times 144$ cm tank filled with Kaneohe Bay sea water, which flowed over the experiment at $10 \, l \, min^{-1}$. Three liters per day of nutrient solution (10 g KNO_3 and 10 g $NH_4 NO_3$ 1^{-1}) was mixed at the rate of 250 ml h^{-1} with the incoming water once a day.

Both *A. spicifera* and *L. nidifica* were gathered from a reef in Kaneohe Bay. Each piece had a holdfast and was trimmed to weigh 1.0 g. Two slits were cut into each sponge and two thalli placed onto each slit at random, either as pairs of the same species (controls) or one of each species. Each pair was placed together so they were touching and secured to the sponge with a soft thread. These units were placed at random in the water tank, exposed to natural light (35 000–100 000 lux at noon), 13 h light and 11 h darkness, 24–28°C, a water flow that gave a DIF of 8 ± 2.

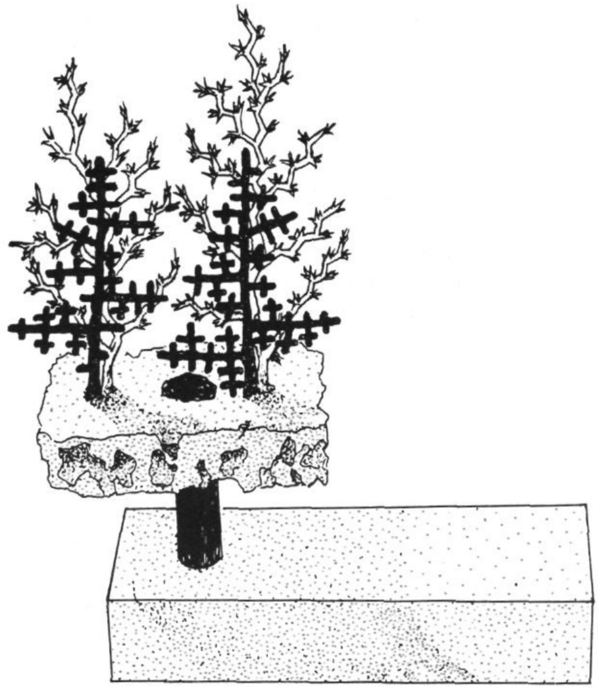

Figure 2. Apparatus used in the competition experiments between *Acanthophora* (light thallus) and *Laurencia* (dark thallus).

A duplicate experiment was conducted in the field on a Kaneohe Bay reef. Replicates were positioned on a cleared area normally inhabited by both *A. spicifera* and *L. nidifica*. The area was protected from grazing fish, rolling stones, and large drifting algae by a one-inch square mesh size plastic covered wire fence. The thalli were cleaned of epiphytes daily by hand. Growth rates of *Hypnea musciformis* thalli were studied at this same place. Temperature was 24–27°C and DIF was 58 ± 2. The experiments lasted nine days each and the results were tested using analysis of variance.

Results and discussion

Distribution of *Acanthophora* in the Hawaiian Islands

Acanthophora is well established on Oahu Island, but does not have a homogeneous distribution. Twenty-two of 33 sampling locations on Oahu had more than a trace of *A. spicifera* (Fig. 3). The largest quantities were on wide reef-flats at Wailupe and Ala Moana along the southern shore and Hauula and Punaluu along the northeastern shore (Table 2), but there was only a trace in samples from the southeastern shore and no thalli were present along the western shore, except in Pokai Bay.

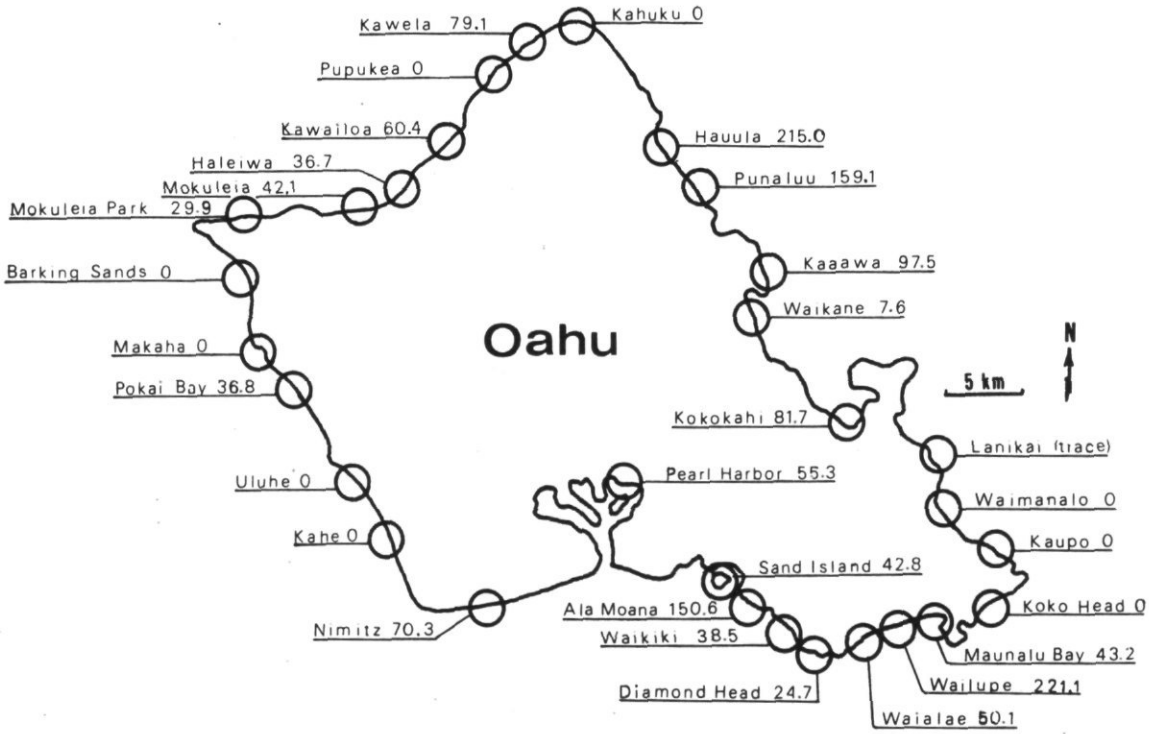

Figure 3. The distribution and quantities (g/m^2) of *Acanthophora* on Oahu, Hawaii.

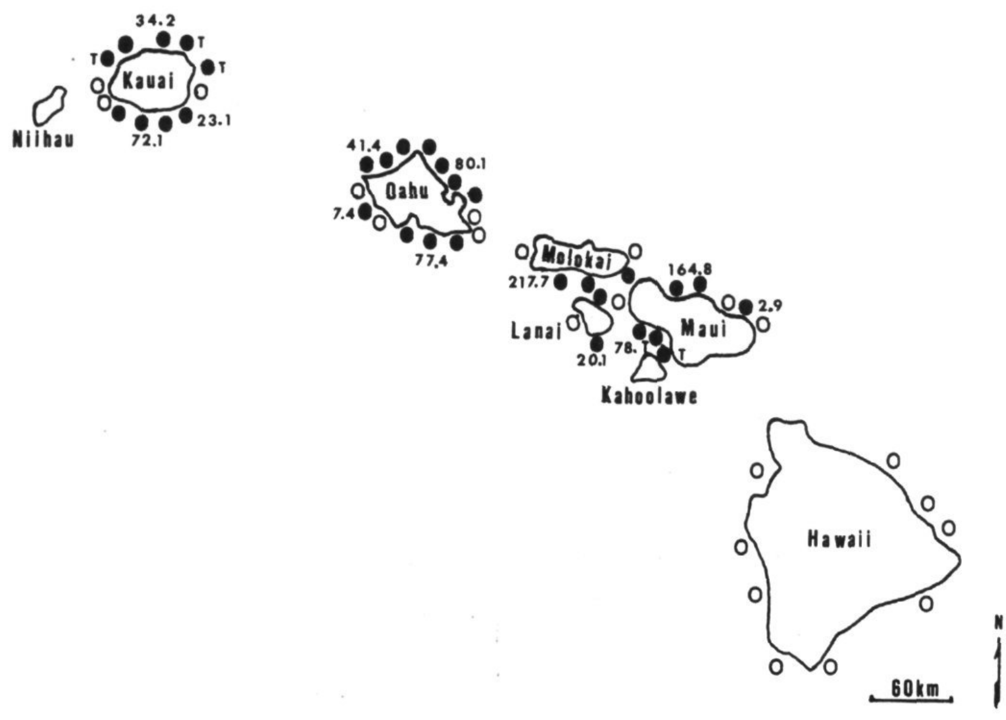

Figure 4. A summary of the distribution of *Acanthophora* on the major Hawaiian Islands. Solid circles indicate it was present, open circles indicate it was absent. The numbers are average quantities (g/m^2) of *Acanthophora* on the shores indicated.

Table 2. Amounts of *Acanthophora spicifera* and the physical features of locations surveyed in the island of Oahu.

Location	Dry wt. g/m²	DIF	°C	Salinity
Kaupo	0	66.5 ± 5.9	25	35.0
Waimanalo	0	74.2 ± 1.0	24	35.0
Lanikai	Trace	58.8 ± 2.6	28	35.0
Kailua	Trace	62.5 ± 15.4	28	35.0
Kokokahi	81.7	36.8 ± 0.3	28	35.5
Lilipuna Pier	122.7	45.0 ± 1.2	28	35.0
Waiahole	7.6	56.6 ± 3.1	28	19.5
Kaaawa	97.5	65.6 ± 3.5	27	35.5
Punaluu	159.1	50.3 ± 2.3	25	35.0
Hauula	215.0	48.9 ± 2.3	25	35.6
Kahuku	0	96.7 ± 6.3	25	35.6
Kawela	79.1	55.2 ± 4.5	23	23.9
Pupukea	0	Destroyed	25	34.2
Kaiwailoa	60.4	57.6 ± 4.7	25	33.1
Haleiwa	36.7	51.0 ± 1.8	26	35.0
Mokuleia	42.1	43.7 ± 1.6	25	34.3
Mokuleia Park	29.9	52.8 ± 2.7	25	35.0
Barking Sands	0	Destroyed	25	35.5
Makaha	0	88.1 ± 8.0	25	35.5
Pokai Bay	36.8	46.5 ± 1.8	26	35.0
Uluhi	0	91.4 ± 9.0	26	35.5
Kahe Point	0	61.3 ± 7.3	32*	35.5
Nimitz	70.3	Lost	28	35.0
Pearl Harbor	55.3	Lost	28	35.0
Sand Island	42.8	49.0 ± 2.5	28	35.0
Ala Moana	150.6	Lost	28	35.0
Waikiki	38.5	66.4 ± 2.6	28	35.0
Diamond Head	24.7	80.6 ± 1.9	28	35.5
Waialae	50.1	52.7 ± 2.1	28	35.0
Wailupe	221.1	40.6 ± 4.5	28	35.2
Maunalua Bay	43.2	43.8 ± 1.6	28	36.0
Koko Head	0	84.4 ± 4.5	25	35.0

*This reef was artificially heated by water from an electricity generating plant.

Table 3. Amounts of *Acanthophora spicifera* and the physical features of locations surveyed in the Hawaiian Islands.

Location	Dry wt. g/m²	Temp. °C	Salinity
KAUAI ISLAND			
Haena	Trace	25.5	34.0
Hanalei	46.4	21.0	28.0
Anini	90.4	22.0	35.0
Moloaa Bay	Trace	22.0	34.0
Waipouli	0	22.0	34.0
Hauula	Trace	21.5	34.0
Ahukini	115.6	22.0	34.0
Kalapaki	Trace	22.0	34.0
Nawiliwili	0	22.0	34.0
Poipu	137.2	25.5	35.0
Port Allen	85.6	23.0	35.0
Kikiloa	65.6	23.0	34.0
Kekaha	0	23.0	34.0
MOLOKAI ISLAND			
Halawa	0	22.0	35.0
Pohakuloa	269.2	22.0	35.0
Kamalo	150.8	23.0	34.0
Kaunakakai	234.0	24.0	34.0
Kepuhi	0	22.0	35.0
LANAI ISLAND			
Federation Camp	40.9	28.0	35.0
Manele Bay	20.1	27.0	34.0
Kamalapau	0	22.0	35.5
MAUI ISLAND			
Kahului	35.2	26.0	32.0
Hookipa	294.3	25.0	35.0
Waianapanapa	0	25.0	32.0
Hana	5.7	25.0	32.0
Maalaea	Trace	26.0	35.0
Polo Beach	Trace	26.0	35.0
Launiupoko	234.0	28.0	35.0
Lahaina	Trace	28.0	35.0
HAWAII ISLAND			
Laupahoehoe	0	25.0	35.0
Hilo Harbor	0	23.0	30.0
Leleiwi	0	23.0	33.0
Honaunau	0	26.0	35.5
Kailua-Kona	0	26.0	35.0
Kawaihae	0	25.0	35.0
Kalapana	0	24.0	34.0

Acanthophora is also well established on the outer islands, except on the island of Hawaii. It is distributed along the shores of Kauai, Molokai, Lanai, and Maui in patterns similar to those on Oahu (Fig. 4). The largest quantities (234.0–294.3 g/m²) were present on wide reef-flats, near shore, never in the breaker zone, but rather in areas protected from strong wave action (Table 3). Lesser amounts were found on bench reefs and little or no thalli were on shores exposed to the trade winds and high energy water motion. The only island *Acanthophora* was not found on was Hawaii (B. Magruder, Bishop Museum, has just recently found trace amounts at Kawaihae) (Fig. 4), which characteristically has unprotected shores of igneous rock exposed directly to wave action and no coral reef-flats. This heterogeneous distribution, however, could also be due to other factors, such as substratum type or availability, temperature, or salinity.

Distribution in relation to substrata and wave action

The habitats in which *A. spicifera* was found ranged from moderately exposed shores (Hauula and Haena, Kauai; Polo Beach, Maui) to protected bays (Kokokahi in Kaneohe Bay, Oahu). The five basic types of habitats which *Acanthophora* thalli occupy have been based on exposure to wave action and DIF values (Fig. 5). These are, (1) moderately exposed basaltic shores or seaward sides of jetties (Fig. 5a), (2) narrow bench reefs of eroded amalgamated coral limestone (Fig. 5b), (3) extensive coral reef-flats (Fig. 5c), (4) protected natural bays with a sand or silt covered bottom (Fig. 5d), and

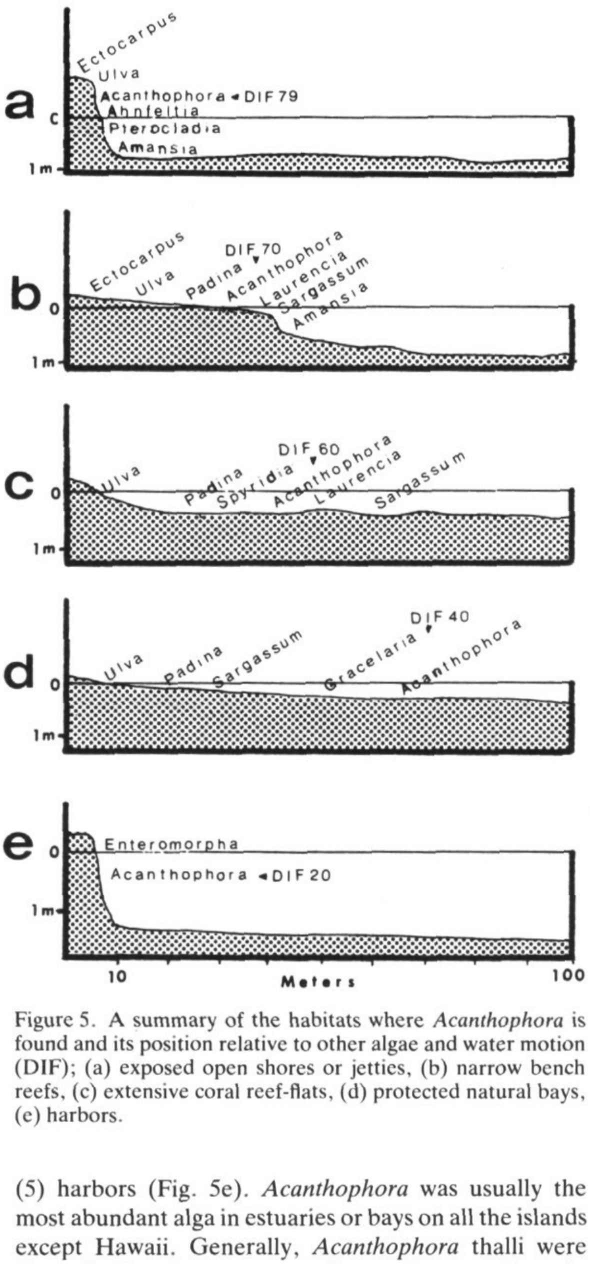

Figure 5. A summary of the habitats where *Acanthophora* is found and its position relative to other algae and water motion (DIF); (a) exposed open shores or jetties, (b) narrow bench reefs, (c) extensive coral reef-flats, (d) protected natural bays, (e) harbors.

(5) harbors (Fig. 5e). *Acanthophora* was usually the most abundant alga in estuaries or bays on all the islands except Hawaii. Generally, *Acanthophora* thalli were short (4–10 cm), compact, and very dense on the substratum in high water motion areas (Fig. 5a, b), in contrast to thalli, which were tall (10–15 cm), more openly branched, and occurred in scattered clumps in moderate or low water motion areas (Fig. 5c, d, e). Its plastic morphology has allowed it to adapt to different conditions and invade a diversity of habitats.

Distribution in Hawaiian harbors

Acanthophora was present in 17 of 21 harbors surveyed (Tables 2 and 3), which means it is able to grow in areas where boats are available as substrata and disseminating agents. It was not present, however, at Nawiliwili Harbor, Kauai; Kaumalapau, Lanai; Kawaihae Boat Harbor; or Hilo Harbor, Hawaii. In addition, its thalli were found growing on a variety of substrata: basaltic jetty rock (Kahului, Maui), concrete abutments (Ahukini Landing, Kauai), on a concrete boat ramp (Hana, Maui), a seawall (Manele Bay, Lanai), on a wooden floating pier, hemp ropes, painted steel buoys, and the hulls of boats (Port Allen, Kauai; Kaunakakai, Molokai; Manele Bay, Lanai), and on mooring lines in Lahaina Harbor, Lahaina Harbor, Maui.

Acanthophora was attached to the hull of a tug boat (*Lihue III*) at the waterline in Port Allen, which made regular runs to Oahu and would drydock in Honolulu Harbor every two years. In addition, 28.4 g wet weight of *Acanthophora* was removed from a 15-m long sailing yacht, *Oriana*, from Honolulu, while it was moored at Kaunakakai, Molokai. Another sailing boat from Oahu, in Manele Bay, Lanai, also had *Acanthophora* growing on its hull. *Acanthophora* has the ability to colonize boat hulls and was probably carried to all the ports in Hawaii shortly after its introduction. Its present pattern of distribution on the island shores reflect its ability to survive the physical or biological conditions it encountered after being introduced and disseminated.

Distribution in relation to water motion, temperature, salinity, depth, and season

There was a highly significant difference between the average values of water motion in areas with and without *A. spicifera* on Oahu (Table 2). The average water motion was higher (DIF 78.9 ± 2.7) in locations without *A. spicifera* than in areas with it (DIF 52.8 ± 0.4). Water motion was also a prominent feature distinguishing the three transects from each other (Fig. 6). The average water motion values along the KMCAS transect were significantly higher at the 5% level and more variable than at either the Kaaawa or HIMB transects (Fig. 6). There was also an abrupt and significant increase in DIF values at KMCAS at 30 m from shore, which coincided with an abrupt decrease in the biomass of *Acanthophora* (Fig. 7). At 25 m the DIF value was 66.6 ± 4.1 and at 30 m it was 84.8 ± 5.3, and at 25 m the biomass of *Acanthophora* was high (82.7 g/m^2), while at 30 m it was only 46.4 g/m^2. The fore-reef, with stronger water motion, did not support the growth of *Acanthophora*, even though the depth, temperature, salinity, and substratum were

Table 4. Average depth, water motion, temperature, and salinity at the three transects.

Parameter	KMCAS	Kaaawa	HIMB
Transect length (m)	40	80	110
Depth (cm)	3.6 ± 1.9	23.4 ± 7.7	43.1 ± 11.5
Water motion (DIF)	63.3 ± 20.3	45.1 ± 3.2	21.6 ± 4.6
Temperature (°C)	27.6 ± 1.7	25.1 ± 0.3	24.9 ± 0.2
Salinity	34.4 ± 0.6	33.0 ± 1.6	33.3 ± 0.9

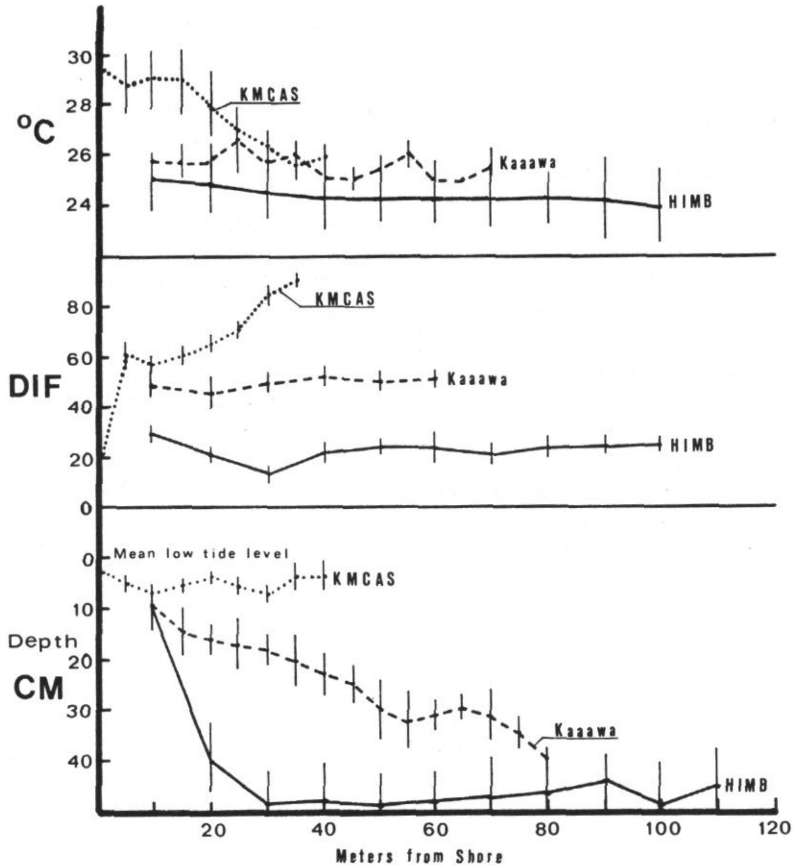

Figure 6. Average temperatures, water motion (DIF) and depths at mean low tide along the transects at KMCAS, Kaaawa, and HIMB.

nearly the same. Water motion, with an upper value of ca. DIF 80, appears to prevent the growth of *Acanthophora* in certain high wave action areas on the reef and exposed shores of Hawaii.

The lowest recorded water motion value where *Acanthophora* was growing (DIF 13.0 ± 3.0) was 30 m from shore at the HIMB transect (Fig. 6). The average at this transect was DIF 21.6 ± 2.9, the lowest of the three transects. Difficulties in culturing *Acanthophora* were also related to water motion. Thalli would not grow without added fertilizer in the competition experiment at DIF 7.8 ± 1.0. Together, these data indicate *Acanthophora* requires water motion of at least DIF 10 before growth will occur. This means *Acanthophora* is limited to habitats in Hawaii within the limits of a DIF 10–80 range.

The monthly *Acanthophora* standing crop fluctuated in relation to temperature changes, although to a lesser extent than for water motion. The months with a maximum standing crop of *A. spicifera* correspond with the warmer months (Fig. 8). The greatest growth occurred when the temperatures were 26.7 ± 1.2°C at Kaaawa and 24.9 ± 1.2°C at HIMB. An indication of the upper limits of its growth was seen at the KMCAS transect, where the average water temperature was significantly higher. Here the standing crop of *A. spicifera* increased when the water temperature decreased from 28.0°C to 26.7°C (Fig. 8). *Acanthophora* was also absent from the artificially heated reef (32°C) at Kahe Point (Table 2). *Acanthophora* grows best in a temperature range of ca. 25–27°C. This is higher than the 23.5°C suggested by Trono (1968) and also higher than the optimum temperature for growth of *Acanthophora* and *Gracilaria* in Florida (Dawes *et al.*, 1978). However, it is closer to the range in which *Acanthophora* grows in Indonesia, 26.5–33.0°C (Atamadja, 1977). Attempts to verify these field results in the laboratory failed because the high water motion values, also required for good growth by *Acanthophora*, could not be duplicated in the growth chambers available.

Although the average salinity between shores without *Acanthophora* was significantly higher (35.1 ± 0.3‰) than the salinity of shores with it (33.8 ± 0.9‰) (Table 3), there was no correlation between the standing crop of *A. spicifera* and salinity at the three transects during the seasonality study. It was found in locations with low salinity (19.5‰) at Waiahole and Kawela, Oahu (23.9‰) (Table 2) and was not affected by seasonal rains, which temporarily significantly lowered the salinity to 23.4 at Kaaawa and 28.8 at HIMB, during one unusually rainy season in February. The correlation between the occurrence of *Acanthophora* and low salinity suggested by Soegiarto (1972) was not substantiated by this study and *Acanthophora* appears to have a much broader salinity tolerance range (ca. 19–36‰) than previously suspected. In Florida, *Acanthophora*'s photosynthetic peak was at 20‰ and its photosynthetic output was ten times higher than the other algae over a range of 20–30‰ (Dawes *et al.*, 1978). Salinity did not correlate with differences in *Acanthophora* standing crop between locations or the seasons and is probably not an important limiting factor contributing to the distribution of *Acanthophora* in Hawaii.

The relation between *Acanthophora* and other algae on the reef

Laurencia nidifica J. Ag. and *Hypnea cervicornis* J. Ag. were the two most common species observed growing next to and physically attached to *A. spicifera*. *Laurencia nidifica* was attached to the same substatum with *Acanthophora* and was commonly physically fused to *Acanthophora* by natural grafts to such an extent both thalli had to be broken or torn to separate them completely during sorting and weighing. *Hypnea cervicornis* was also closely associated with *Acanthophora*, especially at the HIMB transect, but it was usually entangled in its upper branches as an epiphyte.

Five patterns of distribution were seen between *A. spicifera*, *L. nidifica*, and *H. cervicornis*. (1) Each species was found as solitary thalli attached to the substratum. (2) *Acanthophora* and *L. nidifica* were found attached to the substratum and to each other at the same time. (3) Either *L. nidifica* or (4) *Acanthophora* were found with *H. cervicornis* entangled as an epiphyte in their branches, and (5) often all three species were found growing together, *A. spicifera* and *L. nidifica* tangled and fused to each other with *H. cervicornis* epiphytic in both their branches.

These same patterns were reflected in herbarium specimens. One herbarium specimen of *Laurencia* spp. collected in Hawaii before 1950 had *H. cervicornis* entangled in its upper branches. Five out of 50 herbarium specimens of *A. spicifera* from Hawaii and other places in the Pacific had *Laurencia* spp. mixed with them on the same sheets and three of them also had *H. cervicornis* attached (Russell, 1981). This implies the specimens were together on the reef when they were collected, especially if one considers how difficult it is to separate them completely. The *Laurencia nidifica*, *Hypnea cervicornis*, *Acanthophora spicifera* association mentioned above appears to be supported by these observations.

Other species that were less directly associated with *A. spicifera* were *Ulva fasciata* and *Ahnfeltia concinna* J. Ag., in areas with nearly vertical basaltic substrata and

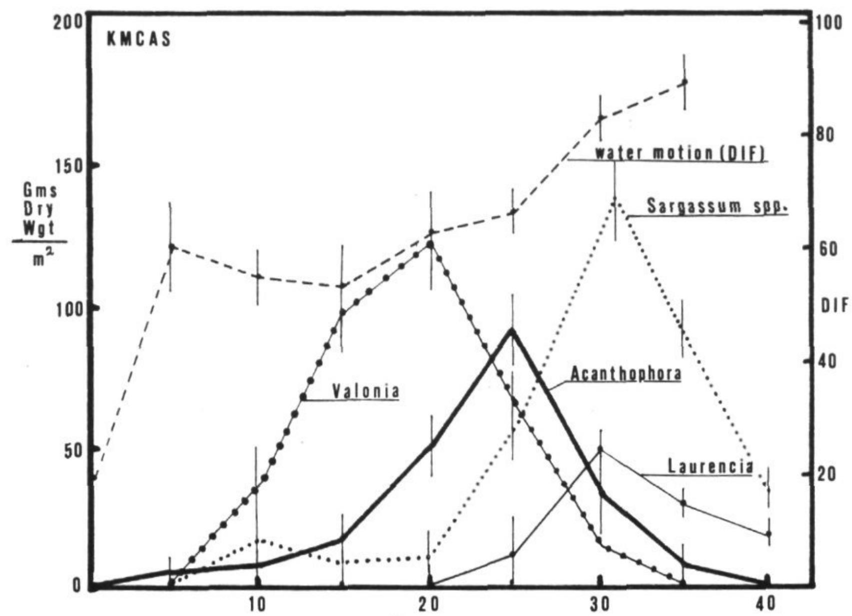

Figure 7. Distribution of *Valonia aegagropila*, *Acanthophora spicifera*, *Laurencia* spp., and *Sargassum* spp. across the reef at the KMCAS transect (n = 16) compared to water motion (DIF).

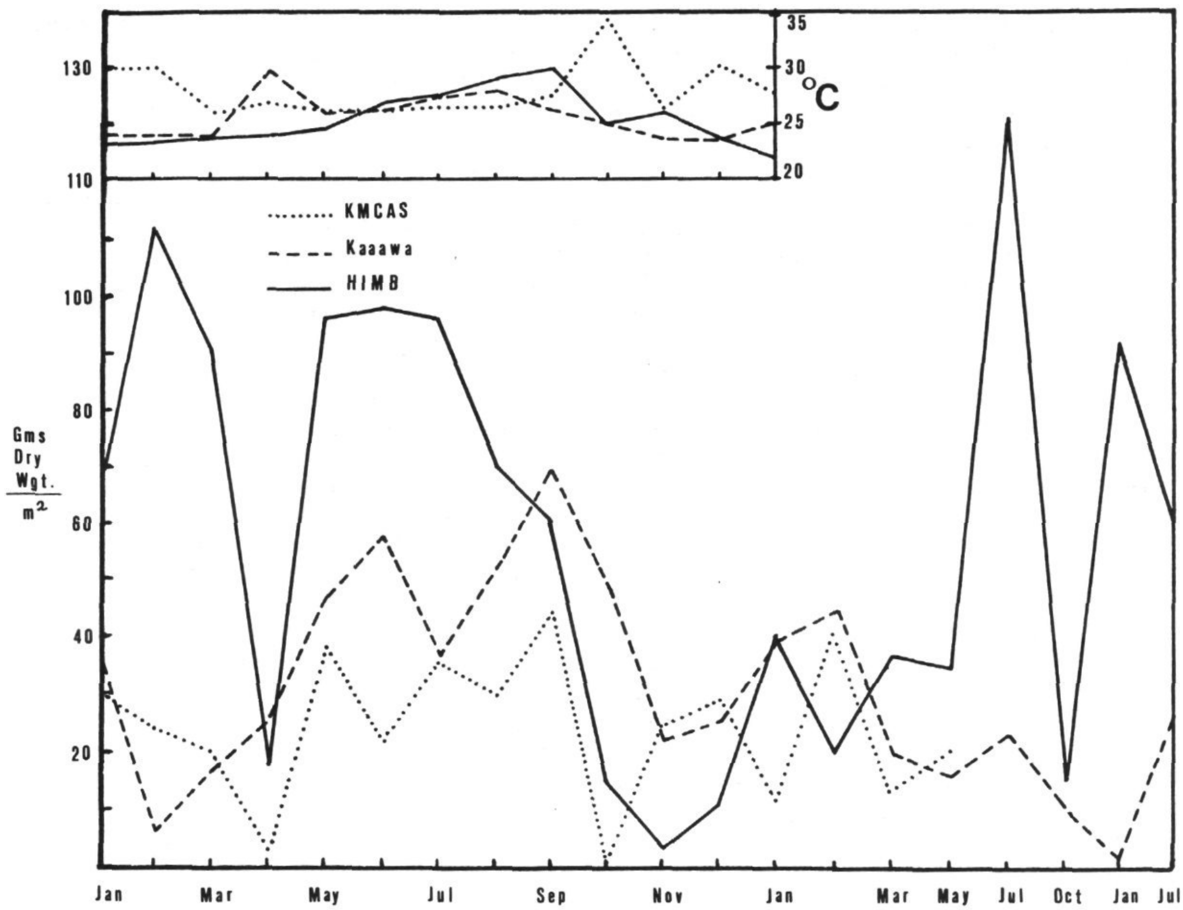

Figure 8. Seasonal comparison of *Acanthophora* standing crops at the KMCAS, Kaaawa, and HIMB transects in relation to temperature.

high water motion (Fig. 5a), *Padina japonica* Yamada and *L. nidifica* on solid eroded coral substrata (Fig. 5b, c), and *Gracilaria coronopifolia* and *Enteromorpha* spp. in sandy or silted locations (Fig. 5d, e). These were common members of the community, but were not in direct competition with the greater mass of *Acanthophora* on the reefs.

The distribution of different species across the nearly flat shallow reef at the KMCAS transect occurred in distinctly visible zones. Of the 26 species of algae present, only *Sargassum polyphyllum* J. Ag. and *Valonia aegagropila* C. Ag. were present during each month of the study, were in the same number of samples, but were distributed on different portions of the reef. The average maximum biomass for *V. aegagropila* was located 20 m from shore, for *A. spicifera* it was 25 m from shore, and for *Sargassum* spp. (*S. polyphyllum*, *S. obtusifolium* J. Ag. and *S. echinocarpum* J. Ag.) it was 30 m from shore (Fig. 7). *Laurencia nidifica* and *L. obtusa* var. *rigidula* Grun. were also present, directly seaward from *A. spicifera* (Fig. 7), where they formed a turf or densely arranged dwarf plants characteristic of fore-reefs subjected to strong wave action (Kilar and McLachlan, 1986). The distribution of *Laurencia* between *Acanthophora* and *Sargassum* puts it in direct competition for space, especially with *Acanthophora*, with which it also forms a turf. This turf is nearly all *Acanthophora* thalli at 25 m, but blends with *Laurencia* at 30 m. Before *Acanthopora* entered Hawaii, *Laurencia* probably formed a turf between *Valonia* and *Sargassum*, but after the introduction of *Acanthophora*, *Laurencia* was forced seaward by competition as *Acanthophora* colonized the surfaces most suitable for its growth.

These zones have also been reported from Panama by Kilar and McLachlan (1986), where the fore-reef is referred to as the *Laurencia* Zone and the back-reef as the *Acanthophora* Zone. The authors also attribute this zonation to differences in water motion and *Acanthophora*'s mode of reproduction by vegetative fragmentation, which allows it to rapidly colonize available space. The reef studied by Santelices (1977) at Hauula, Oahu, only had a back-reef *Valonia* Zone and the *Acanthophora* Zone, but no *Laurencia* Zone, because that reef did not have a DIF over 60 during the course of

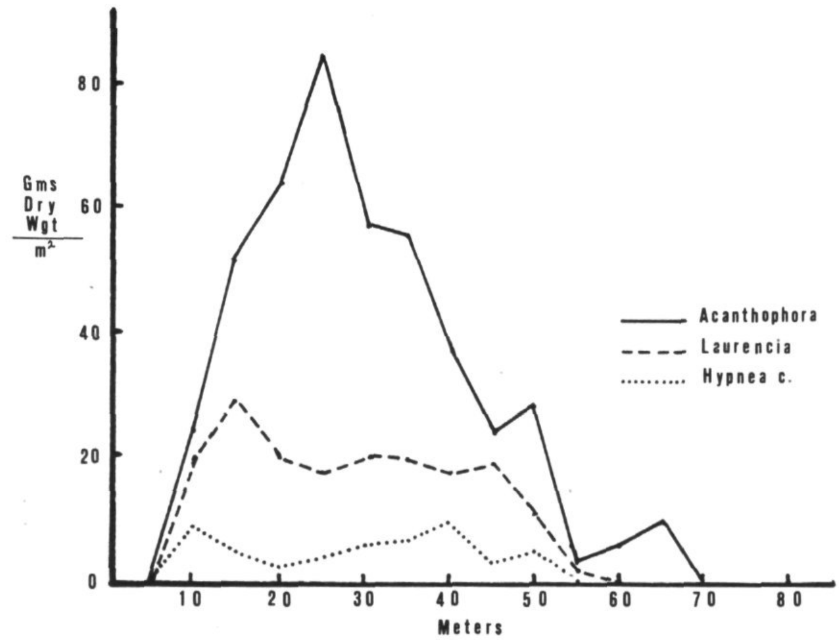

Figure 9. Distribution of *Acanthophora*, *Laurencia nidifica* and *Hypnea cervicornis* across the reef at the Kaaawa transect: based on average amounts (n = 20).

the study. The optimum DIF value for *Acanthophora* is 66.6 (Fig. 7). Zonation only appears on a reef between *Acanthophora* and *Laurencia* when the DIF gradient approaches 80. The KMCAS reef (a solution bench) is an ideal location for further competition studies in light of what Olson and Lubchenco (1990) have suggested, because the water motion gradient is extensive (DIF 20-90) and represents the only major physical parameter that changes from the back-reef to the fore-reef.

Additional evidence indicating competition between *Acanthophora* and *Laurencia* was also seen at the Kaaawa transect. *Laurencia nidifica* was one of three

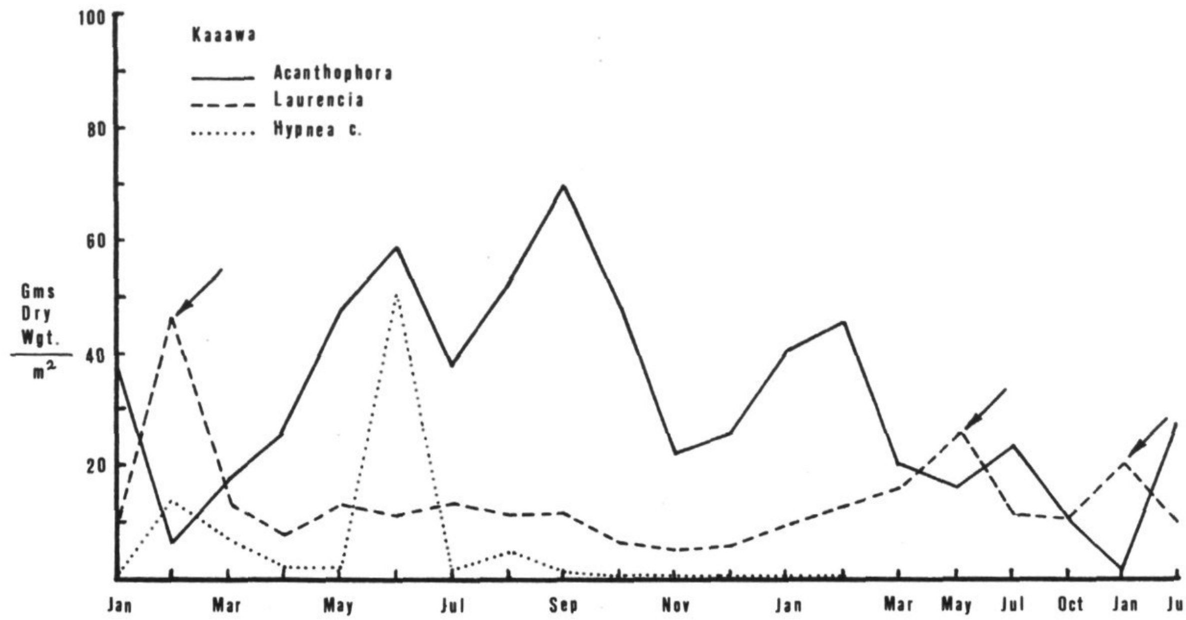

Figure 10. Seasonal comparison of *Acanthophora*, *Laurencia nidifica*, and *Hypnea cervicornis* standing crops at the Kaaawa transect; based on average amounts (n = 20).

Table 5. The number of samples in which various species were present at the three transects. Most frequent species listed first.

Species	KMCAS	Kaaawa	HIMB
Acanthophora spicifera	68	107	160
Laurencia nidifica	30	107	3
Hypnea cervicornis	4	53	41
Ulva spp.	0	21	74
Lyngbya majuscula	5	85	5
Padina japonica	46	28	0
Gracilaria bursapastoris	0	6	59
Sargassum echinocarpum	30	18	14
Valonia aegagropila	60	1	0
Hypnea pannosa	0	0	58
Gelidiella acerosa	50	0	0
Sargassum polyphyllum	39	0	0
Ceramium fastigiatum	0	8	30
Cladophora socialis	35	0	0
Spyridia filamentosa	24	7	0
Bornetella sphaerica	23	6	0
Dictyosphaeria versluysii	18	9	0
Dictyota acuteloba	0	26	0
Sargassum obtusifolium	19	0	0
Halimeda discoidea	4	11	0
Cladophora fasciculata	0	13	0
Microdictyon japonicum	13	0	0
Bryopsis pennata	0	0	11
Pterocladia capillacea	10	0	0
Enteromorpha intestinalis	1	3	4
Grateloupia filicina	0	1	5
Sphacelaria tribuloides	5	0	0
Galaxaura spp.	1	3	0
Centroceros clavulatum	0	0	3
Dictyosphaeria cavernosa	1	2	0
Gracilaria coronopifolia	0	3	0
Hypnea spinella	2	0	1
Neomeris annulus	1	2	0
Rosenvingea orientalis	0	0	3
Dictyota crenulata	0	2	0
Griffithsia sp.	0	0	2
Jania capillacea	2	0	0
Symploca hydnoides	0	2	0
Wrangelia penicillata	0	2	0
Chnoospora miniata	1	0	0
Cladophora luxuriens	0	1	0
Codium edule	0	1	0
Ectocarpus indicus	1	0	0
Lobophora variegata	0	1	0
Tolypiocladia calodictyon	0	0	1
Total samples	493	527	474
Total species	26	29	17
Index of species diversity*	6 ± 1.0	7 ± 1.2	3 ± 0.9

*S = aLog (1 + N/a), a is the Index of Diversity, S is the total number of species, N is the total number of occurrences (Lewis and Taylor, 1967).

species present during all the months studied at Kaaawa. The other two were *Hypnea cervicornis* and *Lyngbya majuscula* Gomont; however, only *Laurencia* occurred in each of the 107 samples containing *Acanthophora* (Table 5) and only *Laurencia* and *Hypnea* had the same distribution as *Acanthophora* across the reef (Fig. 9). None of the other 23 species had this high correlation. *Laurencia* was also the only species that increased in

Table 6. Standing crop of *Hypnea musciformis*, in relation to other algal species on Checker Reef in Kaneohe Bay, Oahu.

		Wet wt.		Dry wt.	
Species*	Month	(g/m^2)**	%	(g/m^2)	%
Hypnea musciformis	Apr	1212.3	60.2	136.9	50.1
	May	356.6	21.8	36.6	16.5
	Jun	173.0	13.0	18.9	12.8
Acanthophora spicifera	Apr	19.5	0.9	4.4	1.6
	May	978.0	59.8	115.1	51.9
	Jun	571.3	43.1	69.0	46.8
Laurencia nidifica	Apr	167.7	8.3	39.6	14.5
	May	112.6	6.9	15.9	7.2
	Jun	227.9	17.2	21.6	14.7
Sargassum echinocarpum	Apr	84.4	4.2	24.8	9.0
	May	48.3	3.0	9.8	4.4
	Jun	114.7	8.6	23.6	16.0
Dictyosphaeria cavernosa	Apr	518.7	25.8	63.3	23.2
	May	93.9	5.7	14.2	6.4
	Jun	172.0	13.0	23.4	15.9
Halimeda discoidea	Apr	12.1	0.6	4.1	1.5
	May	46.9	2.9	30.0	13.5
	Jun	67.5	5.1	14.3	9.7

*Species not included if found in only one sample.
**Averages based on four ring samples.

biomass as *Acanthophora* biomass decreased (Fig. 10). Kilar and Lou (1986) found that *Acanthophora* was dominant over *Laurencia* on the reef, but in periods of stress, when *Acanthophora* is damaged, *Laurencia* becomes dominant, because it better withstands exposure to air. These observations support the hypothesis that *Acanthophora* is probably suppressing the growth of *Laurencia*.

In contrast to KMCAS and Kaaawa, *Laurencia* was rarely found on the HIMB transect, while *Hypnea cervicornis* was more abundant here than at the other two transects. *Hypnea* was the most common species in direct physical contact with *Acanthophora* at HIMB, usually as an epiphyte (Table 5). The other species common on this reef (*Ulva fasciata* and *U. reticulata*) were mainly distributed on portions of the reef away from *Acanthophora*. However, competition between *Acanthophora* and *Hypnea* did not appear to be happening, since the seasonal standing crop peaks of *Hypnea* generally corresponded with the peaks of *Acanthophora* (Fig. 11).

At HIMB, *Acanthophora* utilizes worm tubes, that rise from the sand, as a substratum, a resource not used by other algae (Brostoff, 1985). The *Acanthophora* thalli, in turn, provide a substratum to *Hypnea cervicornis* (which does not attach directly to worm tubes). In addition, as *Acanthophora* grows it provides more sur-

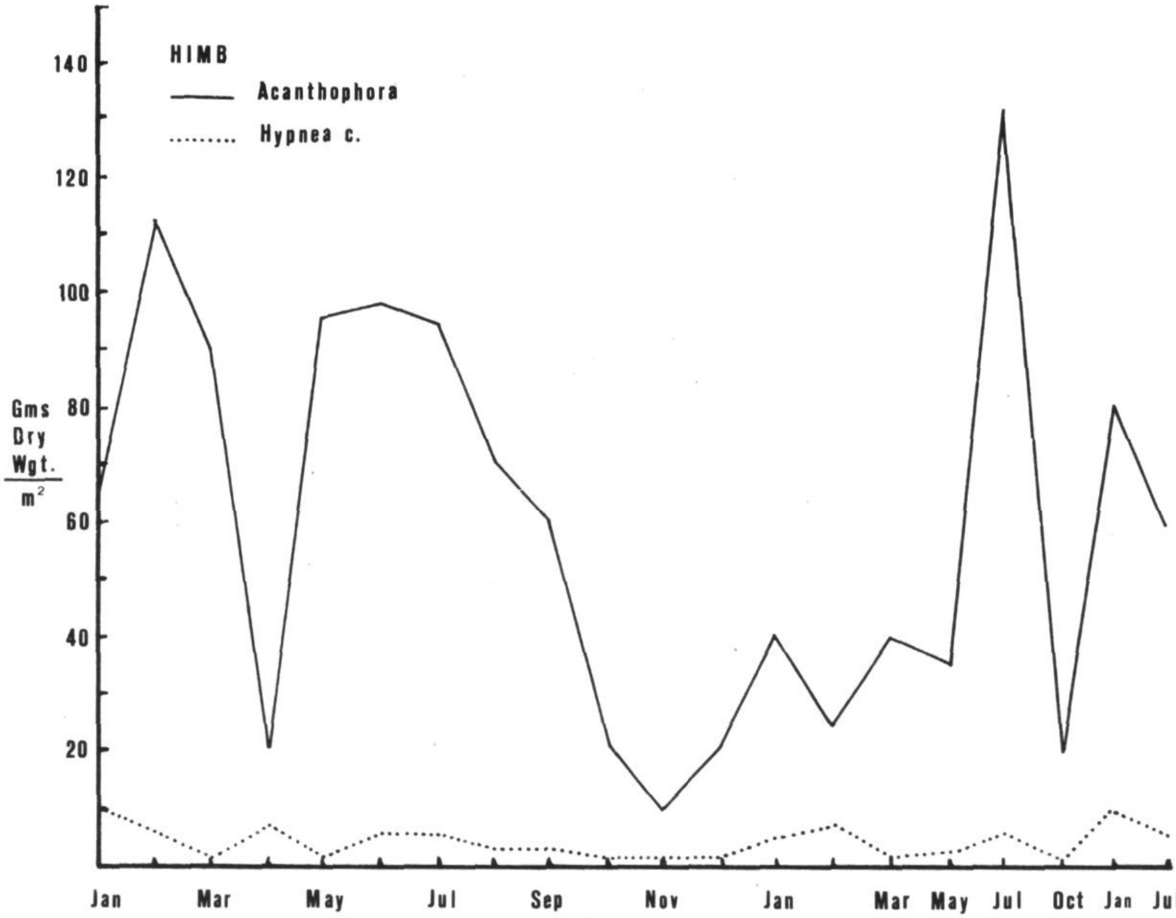

Figure 11. Seasonal comparison of *Acanthophora* and *Hypnea cervicornis* standing crops at the HIMB transect; based on average amounts (n = 20).

face for *Hypnea* and carries it higher into the water column, where its growth is enhanced. Another epizoic utilization by *Acanthophora* and *Laurencia* occurs on decorator crab carapaces (Kilar and Lou, 1986). In addition, the crab prefers to eat *Laurencia* rather than *Acanthophora*, a competitive advantage for the latter.

Competition between *Acanthophora* and *Laurencia*

Similar results were observed in each experiment designed to test competition between *Acanthophora* and *Laurencia*. When *Acanthophora* and *Laurencia* were grown together there was a depression of growth (Fig. 12). Although the results were not statistically significant at the 5% level, each experiment in a controlled environment and in the field gave the same subtle suppression of growth. Since all thallus sizes were the same and shading was not a factor, the competitive mechanism used here is most likely chemical.

Although *Acanthophora* has a much wider range of habitats than *Laurencia*, the evidence supports the hypothesis that *Acanthophora* invaded the niche in the reef community occupied primarily by *Laurencia nidifica*. Competition between these species is probably occurring since: (1) both are in close physical contact with each other (frequent fusions occur), (2) they both occurred in every sample at Kaaawa, (3) they are present together in a variety of herbarium samples, (4) they have the same or overlapping distribution on the reefs at Kaaawa and KMCAS, (5) the growth of *Laurencia* increased only when *Acanthophora* biomass on the reef declined, and (6) there is a suppression of growth when the two species are grown together that is not present when each is grown separately. *Acanthopora* and *Laurencia* appear to be competing for that space on the reef which is in the position of optimum water motion for each.

Introduction of *Hypnea musciformis* to the *Laurencia* niche

After much of the work on *Acanthopora* was finished, *Hypnea musciformis* was introduced to Oahu and began its spread throughout the islands. Although it was intro-

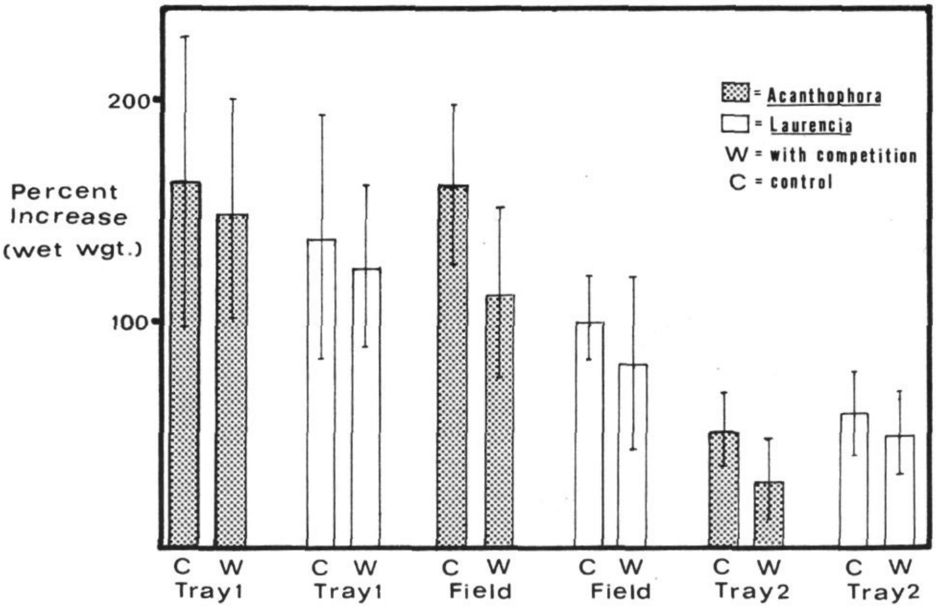

Figure 12. Percentage increase in weight of *Acanthophora spicifera* and *Laurencia nidifica* grown alone and with each other for ten days under three different growing conditions.

duced in early 1974 there was a lag phase of about three years; then in 1977 it became a dominant feature on several of the Kaneohe Bay reefs. It has a high growth rate (10–12% day^{-1} was recorded for it in Kaneohe Bay) although this was difficult to determine in the field since it fragments easily and also gathers fragments of *H. musciformis* thalli from the drift. Humm and Kreuzer (1975) reported a growth rate for *H. musciformis* of 50% day^{-1} (at 28–29°C, 34–35‰) and Dawes (1987) reported 20% day^{-1}. Humm and Kreuzer (1975) also recognized the difficulty in determining its growth rate in the field because of fragmentation and predation.

Hypnea musciformis completely took the place of *H. cervicornis* as the predominant epiphyte on *Acanthopora* on Checker Reef (Table 6). The task of accurately separating and sorting species became nearly impossible as *H. musciformis* attached to dozens of *Acanthophora* branches by tenacious hooks. Additionally, its morphology, except for the hamate branches, is nearly the same as *H. cervicornis*. These two introduced algae (*A. spicifera* and *H. musciformis*) represented between 56.1 and 81.6% of the bulk of algae growing on the reef. The success of *Acanthophora* in Hawaii was soon surpassed by *H. musciformis*, as it spread to Waikiki in 1980 (Abbott, 1987) and was being washed up in windrows at Launuipoko Beach park on Maui in December 1984. In June 1986 it was also collected from the reef at Kauhau, Lanai.

Before 1950 a simple association between *Laurencia* and *Hypnea cervicornis* was well established. When *Acanthophora* was introduced after 1950 it entered this same niche, competed with *Laurencia* (depressing its growth slightly), but enhanced the productivity of *H. cervicornis* and the reef as a whole (Fig. 13). When *H. musciformis* invaded it also entered this niche, by epiphytizing *Acanthopora*, and had the ability to compete well against *H. cervicornis*. *Hypnea musciformis* is also an epiphyte on *A. spicifera* and *L. scoparia* J. Ag. in Brazil (Schenkman, 1990). It again increased the total productivity of certain reefs in Hawaii. As the four algae grow together the system becomes top heavy and the increased drag causes the upper branches of *Acanthophora* to break and enter the drift, resulting in windrows of algae on the beach. The holdfasts of *Laurencia* and *Acanthophora* remain behind and continue to grow as the cycle begins again.

These two alien species possess traits that favor them over the native species (Carpenter, 1990). They have high growth rates, high spore production, effective vegetative propagation, self-thinning, are effective epiphytes, have high surface to volume ratios, morphological plasticity, one has a persistent holdfast, and they resist herbivory. *Acanthophora* and *H. musciformis* are competitively dominant over *L. nidifica* and *H. cervicornis* in Hawaii and provide good working material for competition studies in the field. The complexity of effects that alien seaweeds have on the ecology of an area after they are introduced needs to be understood to help predict the impacts that other alien algae may have on native marine flora and fauna.

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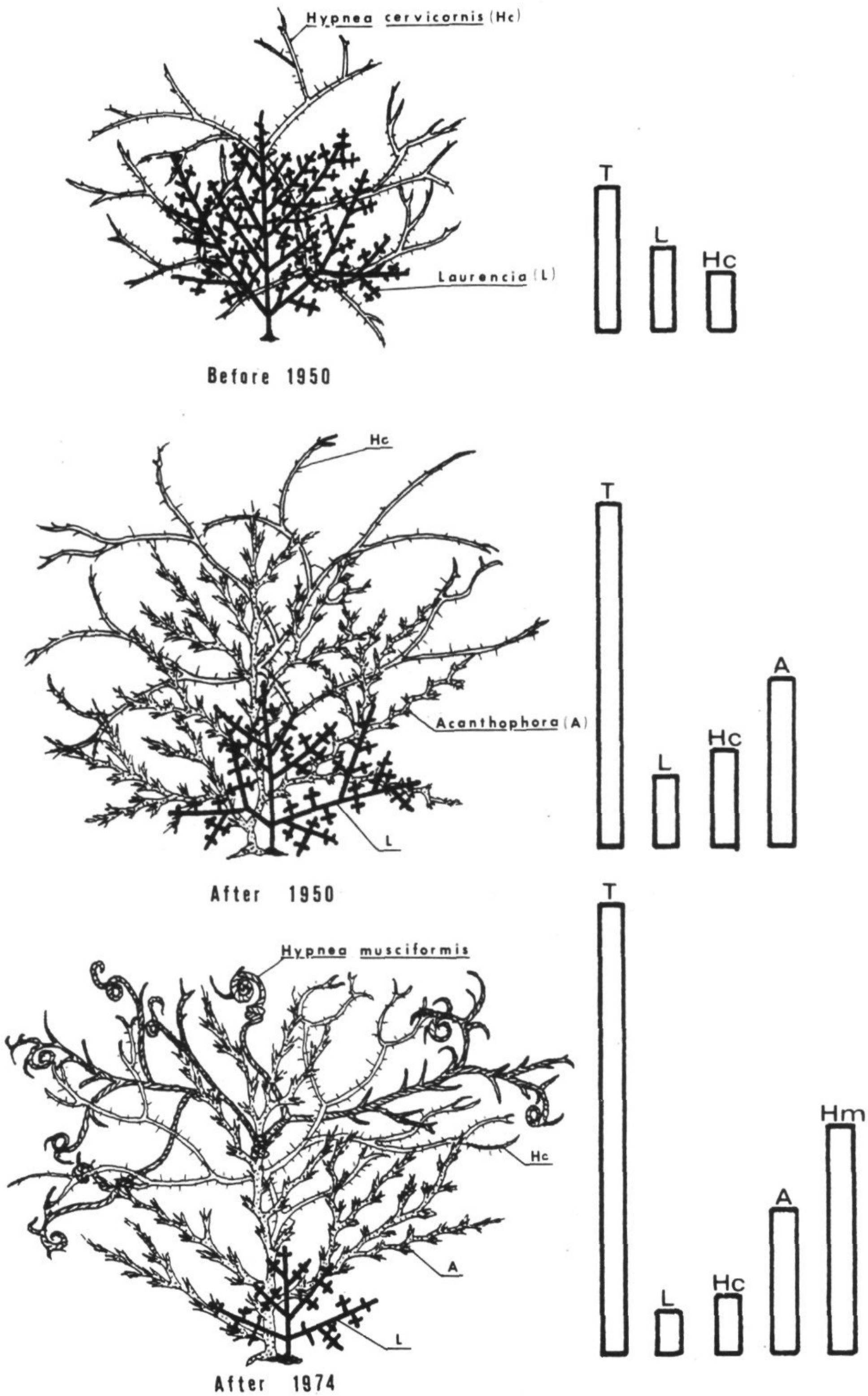

Figure 13. The relative positions and quantities (histograms) of the two native species, *Laurencia nidifica* and *Hypnea cervicornis*, before alien algae were introduced to Hawaii, after *Acanthophora spicifera* was introduced, and after *Hypnea musciformis* was introduced.

References

Abbott, I. A. 1987. There are aliens among the algae, too – or limu malihini. Newsl. Hawaiian Bot. Soc., 26: 60–63.

Anand, P. L. 1940. Marine algae from Karachi, Part I: Chlorophyceae. Panjab Univ. Bot. Publ., Lahore. 76 pp.

Atmadja, W. S. 1977. Notes on the distribution of red algae (Rhodophyta) on the coral reef of Pari Islands, Seribu Islands. Mar. Res. Indonesia, 17: 15–27.

Brostoff, W. 1985. Seaweed grazing and attachment by the nereid polychaete *Platynereis dumerilii*. Proceedings of Fifth International Coral Reef Congress, Tahiti, 1985, 4: 3–8.

Carpenter, R. C. 1990. Competition among marine macroalgae: a physiological perspective. J. Phycol., 26: 6–12.

Cheney, D. P. 1988. The genus *Eucheuma* J. Agardh in Florida and the Caribbean. *In* Taxonomy of economic seaweeds, pp. 209–219. Ed. by I. A. Abbott. California Sea Grant College Program Report No. T-CSGCP-018.

Dawes, C. J. 1987. The biology of commercially important tropical marine algae. *In* Seaweed cultivation for renewable resources, pp. 155–190. Ed. by K. T. Bird and P. H. Benson. Elsevier, Amsterdam.

Dawes, C. J., Moon, R. E., and Davis, M. A. 1978. The photosynthetic and respiratory rates and tolerances of benthic algae from a mangrove and salt marsh estuary; a comparative study. Estaur. Coast. Mar. Sci., 6: 175–185.

Dawson, E. Y. 1954. Marine plants in the vicinity of the Institut Oceanographique de Nha Trang, Viet Nam. Pacific Sci., 8: 372–481.

Doty, M. S. 1954. Distribution of the algal genera *Rhipilia* and *Sargassum* in the central pacific. Pacific Sci., 8: 367–368.

Doty, M. S. 1961. *Acanthophora*, a possible invader of the marine flora of Hawaii. Pacific Sci., 15: 547–552.

Doty, M. S. 1970. The red alga genus *Eucheuma* in the Philippines, University of Hawaii, Hawaii Botanical Science Paper No. 18, i-xiii, 358 pp.

Doty, M. S. 1971. Antecedent event influence on benthic marine algal standing crops in Hawaii. J. Exp. mar. Biol. Ecol., 6: 161–166.

Doty, M. S. 1988. *Prodromus ad Systematica Eucheumatoideorum*: a tribe of commercial seaweeds related to *Eucheuma* (Solieriaceae, Gigartinales). *In* Taxonomy of economic seaweeds, pp. 159–208. Ed. by I. A. Abbott. California Sea Grant College Program Report No. T-CSGCP-018.

Earle, S. A. 1973. A review of the marine plants of Panama. Bull. Biol. Soc. Wash., 2: 69–87.

Feldmann, J. 1937. Recherches sur la végétation marine de la Méditerranée. La Côte des Albéres. Thèses Présentées a la Faculté des Sciences de l'Université de Paris, Série A, No. 1757, Order No. 2623, 10: 1–339.

Glenn, E. P., and Doty, M. S. 1990. Growth of the seaweeds *Kappaphycus alvarezii*, *K. striatum* and *Eucheuma denticulatum* as affected by environment in Hawaii. Aquaculture, 84: 245–255.

Glenn, E. P., Smith, C. M., and Doty, M. S. 1990. Influence of antecedent water temperatures on standing crop of a *Sargassum* spp. dominated reef flat in Hawaii. Mar. Biol., 105: 323–328.

Humm, H. J., and Kreuzer, J. 1975. On the growth rate of the red alga, *Hypnea musciformis*, in the Caribbean Sea. Carib. J. Sci., 15: 1–3.

Kilar, J. A., and Lou, R. M. 1986. The subtleties of camouflage and dietary preference of the decorator crab, *Microphrys bicornutus* Latreille (Decapoda: Brachyura). J. Exp. Mar. Biol. Ecol., 101: 143–160.

Kilar, J. A., and McLachlan, J. 1986. Branching morphology as an indicator of environmental disturbance: testing the vegetative fragmentation of *Acanthophora spicifera* and the turf morphology of *Laurencia papillosa*. Aquat. Bot., 24: 115–130.

Kim, C. S. 1964. Marine algae of Alacian Reef, Southern Gulf of Mexico. Dissertation Abstract, Dept. of Botany, Duke University.

Levring, T., Hoppe, H. A., and Schmid, O. J. 1969. Marine algae. Cram, DeGruyter and Co., Hamburg, i–v. 421 pp.

Lewin, R. 1987. Ecological invasions offer opportunities. Science, 238: 752–753.

Lewis, T., and Taylor, L. R. 1967. Introduction to experimental ecology. Academic Press, New York. 401 pp.

Mshigeni, K. E. 1974. The biology and ecology of selected species in the Hypneacaea (Rhodophyta, Gigartinales), PhD dissertation, University of Hawaii, Honolulu. 739 pp.

Mshigeni, K. E. 1978. Field observations on the colonization of new substrata and denuded intertidal surfaces by benthic macrophytic algae. Bot. Mar., 21: 49–57.

Nurul-Islam, A. K. M. 1976. Contribution to the study of the marine algae of Bangladesh. Bibliotheca Phycologica 19: 1–253.

Olson, A. M., and Lubchenco, J. 1990. Competition in seaweeds: linking plant traits to competitive outcomes. J. Phycol., 26: 1–6.

Rao, M. U., and Sreeramalu, T. 1974. Observations on changes in the growth of four intertidal algae at Visakkapatram. Bot. Mar., 17: 52–54.

Russell, D. J. 1981. The introduction and establishment of *Acanthophora spicifera* (Vahl) Boerg. and *Eucheuma striatum* Schmitz in Hawaii. PhD dissertation, University of Hawaii, Honolulu. 508 pp.

Russell, D. J. 1983. Ecology of the imported red seaweed *Eucheuma striatum* Schmitz on Coconut Island, Oahu, Hawaii. Pacific Sci., 37: 87–107.

Russell, D. J. 1987. Introduction and establishment of alien marine algae. Bull. Mar. Sci., 42: 641–642.

Santelices, B. 1977. Water movement and seasonal algal growth in Hawaii. Mar. Biol., 43: 225–235.

Schenkman, R. P. F. 1989. *Hypnea musciformis* (Rhodophyta): Ecological influence on growth, J. Phycol., 25: 192–196.

Soegiarto, A. 1972. The role of benthic algae in the carbonate budget of the modern reef complex, Kaneohe Bay. PhD dissertation, Botany Department, University of Hawaii. 313 pp.

Tabb, D. C., and Manning, R. B. 1961. A checklist of the flora and fauna of northern Florida Bay and adjacent brackish waters of the Florida mainland, collected during the period, July, 1957, through September, 1960. Bull. Mar. Sci. Gulf and Caribbean, 11: 552.

Taylor, W. R. 1967. Marine algae of the eastern tropical and subtropical coasts of the Americas. Univ. Mich. Press, Ann Arbor, i–ix. 870 pp.

Taylor, W. R., and Bernatowicz, A. J. 1969. Distribution of marine algae about Bermuda. Bermuda Biol. St. Res. sp. Publ., 1: 1–42.

Trono, G. 1968. The taxonomy and ecology of the marine benthic algae of the Caroline Islands. PhD dissertation, University of Hawaii, Honolulu. 387 pp.

Tsuda, R. T. 1964. Floristic report on the marine algae of selected islands in the Gilbert Group. Atoll Res. Bull., 105: 1–12.

Varma, R. P. 1959. Studies on the succession of marine algae on a fresh substratum in Palk Bay. Proc. Indian Acad. Sci., 49: 245–263.

Womersley, H. B. S., and Bailey, A. 1970. Marine algae of the Solomon Islands. Phil. Trans. Roy. Soc. Lond., 259: 257–352.

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