Aspects of the marine ecology of Atlantic salmon (*Salmo salar* L.)

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Dr. scient. thesis

Department of Fisheries and Marine Biology
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"All that we do is touched with ocean, yet we remain on the shore of what we know."

from THE LIVING SEA

MacGillivray Freeman Films

PREFACE AND ACKNOWLEDGEMENTS

My interest in fish biology stems from childhood when my parents gave me the book "Havfisk" by Bent J. Muus[1] and illustrated by Preben Dahlstrøm, as a Christmas present in 1968. This book made a considerable impression on me, and it contained an ingenious "labyrinth" of the animal evolution that stimulated my curiosity about the development of our world.

The work presented here is the result of on-going research on Atlantic salmon at 'Fiskirannsóknarstovan' and a recent joint Nordic project on salmon in the Faroese area, supported by the Faroese government, 'Felagið Laksaskip', the Norwegian Directorate for Nature Management, the Nordic Council of Ministers (project no. 66.05.04), and Norwegian Institute for Nature Research. My gratitude especially to 'Nordisk forsker-utdanningsakademi' for a personal grant in 1996/1997, and to 'Granskingarráð Føroya', 'Vísindagrunnir Føroya Sparikassa' and 'Minningargrunnur Dánjal Niclasen' for financial support during the last part of my stay in Bergen.

I wish to express me deepest gratitude for the close co-operation with my supervisor Dr. Lars Petter Hansen. His valuable help and support through these years is greatly appreciated. I am thankful for all the help and support received from Prof. Gunnar Nævdal during my stay at Department of Fisheries and Marine Biology. Furthermore, I acknowledge my co-authors Eilif Gaard, Roar A. Lund and Niall O'Maoileidigh for fruitful co-operation, as well as the support received from Dr. Sigurd Stefansson.

I would also like to thank Hjalti í Jákupsstovu for his support and patience during my work with the thesis, and thanks are also due to the staff at 'Fiskirannsóknarstovan'. The help I received from those who collected the samples on-board and analysed the material is greatly appreciated: the late Jón Jákup Høisted, Rógvi Mouritsen, Arnold Hendriksen, Súni Lamhauge, Eydna Poulsen, Anna Johansen, Marit Pedersen, Ólavur Olsen, Høgni Debess, Gunnel Østborg and Berit Larsen. Thanks also to the skippers and crew onboard the salmon long-liners *Polarlaks* and *Hvítiklettur*.

The staff and fellow students at the Department of Fisheries and Marine Biology are gratefully acknowledged for their encouragement and help during my stay there. Finally I would like to thank the staff at 'Føroyska Viðskiftastovan' in Copenhagen for their kind hospitality, and the members of the ICES Working Group on Atlantic salmon for stimulating discussions.

I am deeply indebted to my wife Anna and our two children Hilmar and Konni for their love and enduring support—thank you all!

Bergen February 2000

Jan Arge Jacobsen

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[1] Muus, B.J. and Dahlstrøm, P. 1968. *Havfisk og fiskeri i Nordvesteuropa*. 2. udgave. GEC Gads Forlag, København.

ABSTRACT

The present thesis focuses on the oceanic life-history of Atlantic salmon (*Salmo salar* L.) in the Northeast Atlantic Ocean. The main aims were to study the spatial and temporal stock structure of salmon, their feeding habits in the high seas, and possible interactions of escaped farmed salmon with wild salmon. The productive frontal areas north of the Faroes Islands and in the Norwegian Sea are important feeding grounds for salmon, and a fishery for salmon has developed in these areas. The fish was sampled by floating long-lines during autumn (November–December) and winter (January–March), and a total of about 25,000 salmon have been examined during this study.

Salmon that had escaped from fish farms were found intermingled with wild salmon in the high seas. The proportion of escaped fish in the fishery was low until 1988, when it increased and reached a peak around 1990 and decreased again in recent years. It is concluded that if farmed components in catches are not accounted for, catches of wild salmon will be overestimated resulting in erroneous stock assessments of wild salmon.

Fish originating from the entire salmon distribution area may occur at Faroes in parts of their sea phase. Most of the wild salmon tagged at Faroes were recaptured in Norway, but significant number of returns were observed in Scotland and Russia as well. The incidence of salmon originating from other countries around the Northeast Atlantic and Canada was low. Most of the fish farm escapees originated from Norwegian fish farms. It is suggest that significant numbers of salmon caught in the Faroes area during autumn originate from southern European countries and that fish from northern regions appear to be more abundant in the winter. Recaptures in the Faroese fishery during autumn and winter of salmon tagged as smolts in different countries support this.

The salmon feed mainly on hyperiid amphipods, euphausiids, shrimps, lanternfishes, pearlsides and barracudinas, and less on larger pelagic fish and squid. However, if available they tend to select larger prey and prefer fish to crustaceans. Escaped farmed salmon were feeding and growing as efficiently as wild salmon, indicating that those fish that survived until capture were completely adapted to feed in the marine environment. It is still an open question whether food is a limiting factor for growth and survival in the sea. However, the wide variety of food in different areas and periods suggests that salmon abundance is unlikely to be very sensitive to annual changes in the availability of any particular prey.

The sea lice (*Lepeophtheirus salmonis*) were found to infest salmon in the open ocean. Practically all fish were infested with on average 30 lice per salmon. Most lice were adult ovigerous females. Escaped farmed salmon had significantly higher load of lice than wild salmon.

CONTENTS

LIST OF PAPERS

This thesis is based on the following papers:

I. Hansen, L.P., Jacobsen, J.A. and Lund, R.A. 1999. The incidence of escaped farmed Atlantic salmon, *Salmo salar* L., in the Faroese fishery and estimates of catches of wild salmon. ICES Journal of Marine Science 56: 200-206.

II. Jacobsen, J.A., Lund, R.A., Hansen, L.P. and O'Maoileidigh, N. 2000. Seasonal differences in origin of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea based on estimates from age structures and tag recaptures. (Submitted for publication)

III. Hansen, L.P. and Jacobsen, J.A. 2000. Origin, migration and growth of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands. (Submitted for publication)

IV. Jacobsen, J.A. and Hansen, L.P. 2000. Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. (Submitted for publication)

V. Jacobsen, J.A. and Gaard, E. 1997. Open-ocean infestation by salmon lice (*Lepeophtheirus salmonis*): comparison of wild and escaped farmed Atlantic salmon (*Salmo salar* L.). ICES Journal of Marine Science, 54: 1111-1119.

GLOSSARY

Wild salmon. Salmon that have spent their whole life cycle in the wild and were the result of natural spawning.

Farmed or escaped salmon. Salmon of farmed origin escaped at various stages from captivity or from smolt rearing farms.

Smolt[1]. Salmon when it is ready to leave fresh water and enter the sea phase of its life, usually in spring or early summer (May/June).

Post-smolt[1]. Salmon the first few (2-4) months after sea-entry as smolt during spring.

1SW salmon[1]. One sea-winter salmon, i.e. salmon in its first winter in the sea, defined to be the period from autumn the year of sea-entry to the autumn the year after.

2SW salmon[1]. Two sea-winter salmon, i.e. salmon in its second winter in the sea, defined to be the period from the second autumn to the third autumn after sea-entry.

3SW salmon[1]. Three sea-winter salmon, i.e. salmon in its third winter in the sea, defined to be the period from the third autumn to the fourth autumn after sea-entry.

2+SW salmon or MSW salmon[1]. Multi-sea-winter salmon, i.e. salmon older than 1SW.

Grilse. Salmon returning to spawn as 1SW salmon.

Forklength and total length. Forklength is length from snout to cleavage of the fork in the tail fin. Total length is length from snout to tip of tail fin.

EEZ. Exclusive Economic Zone.

CPUE. Catch per unit effort, e.g. number of salmon caught per 1000 hooks fished per day.

Discards. Salmon below 60 cm total length (approximately 57 cm forklength) obligatory to release at sea when caught.

TAC. Total allowable catch.

SST. Sea-surface temperature.

ICES. The International Council for the Exploration of the Sea.

NASCO. The North Atlantic Salmon Conservation Organisation.

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[1] See Allan & Ritter (1977) for a detailed salmonid terminology.

INTRODUCTION

Atlantic salmon (*Salmo salar* L.) are distributed widely in the North Atlantic Ocean and have been harvested for many years by anglers in freshwater, by commercial fishermen in fjords and coastal areas as well as at the feeding areas in the high seas. The oceanic phase of salmon begins when they leave freshwater as newly transformed smolts during spring and commence their seaward migration to their oceanic feeding areas. The salmon spend normally one to three years, occasionally up to five years feeding in the open ocean, before returning "home" to their natal river to spawn (Mills, 1989).

The freshwater phases of Atlantic salmon's life history have been extensively studied. In contrast much less is known about their life in sea, especially in the oceanic phase (e.g. Reddin, 1988; Shearer, 1992; Friedland & Reddin, 1993; Mills, 1993; Hansen & Quinn, 1998). The oceanic phase of salmon has frequently been referred to as a 'black box' in recognition of our lack of understanding and knowledge of this important life stage (Figure 1). However, it is surprising considering the importance of the high seas fisheries for salmon that there is a scarcity of information on life history in the sea. The occurrence of escaped farmed salmon in coastal (e.g. Lund *et al.*, 1991; Youngson & Verspoor, 1998) and oceanic areas (Hansen *et al.*, 1993a) has only underlined the need for further data on their biology to address possible interactions with wild salmon.

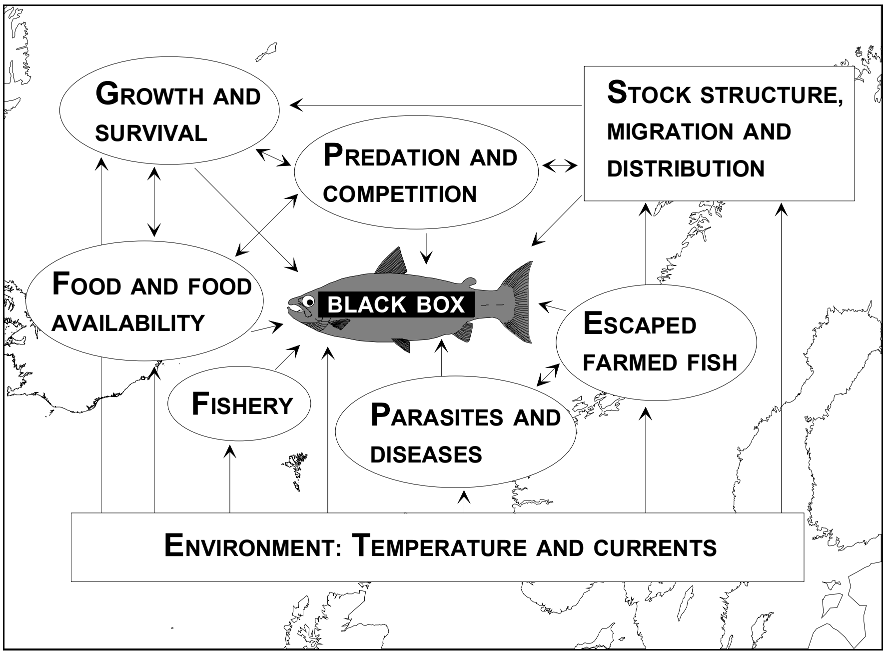

Figure 1. The lack of knowledge of the marine phase of wild Atlantic salmon has often been symbolised as a 'black box'. Here exemplified as various factors and their interactions affecting the salmons' life in the sea.

Smolt tagging programmes in many countries and adult tagging experiments at sea during since 1960s have provided information of the composition of country of origin of salmon in the North Atlantic. The general pattern is that salmon from the Northwest Atlantic is mainly confined to the western area, while salmon from the Northeast Atlantic is found both in the eastern and western part of the Atlantic (e.g. Parrish & Horsted, 1980; Jákupsstovu, 1988; Reddin, 1988). The analyses show that salmon in the fishery off West Greenland are split fairly even between North America and Europe (Reddin, 1988; Reddin & Friedland, 1999), however with temporal and spatial variations (Lear & Sandeman, 1980; Parrish & Horsted, 1980). Canada probably accounts for most of the North American component and Scotland (and the southern European regions) accounts for most of the European fish (Ruggles & Ritter, 1980; Swain, 1980; Jensen, 1980a). In the Northeast Atlantic the results show that in the northern Norwegian Sea salmon from Norway is most dominant with salmon from UK, Sweden and Russia also present (L.P. Hansen, NINA, Norway, unpublished data), while recaptures in the central and southern Norwegian Sea indicate higher proportions of salmon from the southern European regions present (Jákupsstovu, 1988; ICES, 1996). However, in retrospect the results from the previous major sea tagging experiment conducted in the sea around the Faroe Islands in 1969–1975 (Jákupsstovu, 1988) indicated an overweight of recaptures from the southern European regions as compared with later estimates of fish tagged as smolts and recaptured in the Faroese fishery (ICES, 1996). Thus a more representative distribution of the origin of the salmon stocks in the Norwegian Sea was justified (ICES, 1984; 1996).

For the management of salmon stocks, it is of great importance to identify precisely the country of origin of the stocks fished on the high seas, and to obtain better knowledge of their temporal and spatial population structure. In this way the fishery could target the effort towards less threatened stock complexes in the sea, by e.g. temporal and spatial restrictions in the fishery.

The food and feeding habits of salmon in the Northeast Atlantic are only poorly known (see Hislop & Shelton, 1993 for a review). In general salmon probably spend most of its time pelagically in the ocean close to the sea surface (Templeman, 1967; Reddin, 1985; Dutil & Coutu, 1988) preying on different pelagic animals such as fish, crustaceans and squids, and has been suggested to feed opportunistically (Hansen & Pethon, 1985; Reddin, 1988; Hislop & Shelton, 1993). However, there is no information available to compare the distribution of food organisms available with what salmon really eat. The studies so far in the Norwegian Sea mainly give a qualitative picture of the importance of the prey species for salmon, and some suffer from low number of stomachs examined (Struthers, 1970; 1971; Thurow, 1973; Hislop & Youngson, 1984; Hansen & Pethon, 1985). A more detailed study of the feeding habits of salmon in the sea was warranted. Such studies could shed light on their trophic position in the pelagic ecosystem, i.e. link their feeding preferences to growth and condition at sea; compare differences in feeding with respect to size or age; evaluate possible changes in feeding habits with changes in the environment (temperature) and season; and assess the likelihood that food might be a limiting factor for growth and survival in the sea. Furthermore, the occurrence of escaped farmed salmon among the wild fish had to be addressed with respect to their possible interactions, such as food competition and transmission of parasites.

Escaped farmed salmon have been observed in wide areas of the north Atlantic (Lund *et al.*, 1991; Gausen & Moen, 1991; Webb & Youngson, 1992; Carr *et al.*, 1997; Stokesbury & Lacroix, 1997; Youngson *et al.*, 1997), as well as in the high seas salmon fisheries in the Norwegian Sea (Hansen *et al.*, 1993a). Several detrimental effects on wild stocks have been suggested from the escapees, of which interbreeding and transmissions of parasites and diseases in coastal areas were considered the most severe (e.g. Hindar *et al.*, 1991; Håstein & Lindstad, 1991; McVicar, 1997; Sægrov *et al.*, 1997; Bakke & Harris, 1998). Of the harmful parasites in the sea, particularly sea lice (*Lepeophtheirus salmonis*) have caused great controversy, especially in the coastal areas of the significant fish farming production countries such as Norway, Scotland and Ireland, where large runs of wild salmon also occur (Hutchinson, 1997). Sea louse is a naturally occurring parasite on salmon, but there are few studies of their natural occurrence and levels of infection on salmon in undisturbed coastal areas (but see Youngson *et al.*, 1997). In the offshore areas of the North Atlantic only few studies of infection on wild salmon have been reported (Pippy, 1969; Wootten *et al.*, 1982; Berland, 1993; Holst *et al.*, 1993), and none from the central Norwegian Sea. There is thus a paucity of information on lice infestations of wild salmon during their high seas feeding phase.

The number of wild salmon have declined demonstrative throughout their native range for at least two decades (e.g. Parrish *et al.*, 1998), and this has intensified the research on salmon to find possible clues to the decline in the stocks (ICES, 1999b). The current status of the rivers in both North America and Europe show a clear geographical pattern, with most populations in the southern portions of the salmon range in severe conditions or extirpated; in the north the populations are stable; and at intermediate latitudes, populations are declining (Figs 1 and 2: Parrish *et al.*, 1998). Many of these declines or extirpations could be attributed to the construction of mainstream dams, pollution (including acid rain), and total dewatering of streams. Along with overfishing and recently, changing ocean conditions, and intensive aquaculture (Parrish *et al.*, 1998).

ICES has during many years estimated the exploitation rates of various homewater stocks in the Faroese high seas fishery (e.g. ICES, 1984; 1996). In the assessment of salmon stocks at the sea, it is evident that catch records from fisheries exploiting both wild fish and farm escapees will confound the assessment of stock status of wild fish, and it is therefore of great importance to identify the proportion of farmed fish and adjust catch records accordingly.

One important feeding area for salmon in the Northeast Atlantic is the central and southern Norwegian Sea, i.e. the area to the north of the Faroe Islands (Jákupsstovu, 1988), where a high seas fishery for salmon has developed. This area also hosts other pelagic fish species of large biomasses such as herring (*Clupea harengus*), blue whiting (*Micromesistius poutassou*) and Atlantic mackerel (*Scomber scombrus*) (ICES, 1999a; 1999c).

Objectives and aims

The present thesis focuses on the oceanic life-history of Atlantic salmon based on material from the Norwegian Sea. The main aims were to study the spatial and temporal stock structure of salmon and their feeding habits in the high seas. Further, possible interactions of escaped farmed salmon intermingled with the wild salmon in the high seas has been investigated. Thus, the aims were to:

- estimate the proportions of escaped farmed salmon in the Faroese high seas fishery (**Paper I**),
- study the migration, dispersal and origin of wild and farmed salmon (**Paper II and III**),
- describe qualitatively and quantitatively the feeding habits of wild and escaped farmed salmon (**Paper IV**),
- examine whether salmon are selective feeders and assess whether food is a limiting factor for growth and survival in the sea (**Paper IV**),
- estimate the sea lice infestation in the ocean and compare the level of infection of wild and escaped farmed salmon (**Paper V**), and
- assess the likelihood that fish farm escapees might transfer increased number of salmon lice from the coastal areas to the wild salmon in the ocean (**Paper V**).

THE HIGH SEAS FISHERY FOR SALMON

Since the discussion in the present thesis is focused on the ecology of salmon from the high seas, some basic background is provided of the major sea fisheries for salmon, i.e. the Norwegian Sea fishery and the fishery off West Greenland. This overview emphasises the Faroese fishery for salmon in the North Atlantic, beginning with a brief description of the fishery off West Greenland and continuing with a more detailed account of the Norwegian Sea fishery, including the fishery north of the Faroe Islands.

Atlantic salmon have been exploited throughout the whole geographical range of the species in the North Atlantic, with catches fluctuating between 6,000 and 12,000 tonnes through 1960 and 1990, but decreased considerably during the 1990s to the present level of approximately 3,000 tonnes, including 1,000 tonnes unreported catches (Figure 2). The high seas fishery has gradually diminished in recent years and today practically all salmon are taken in coastal and inshore areas and in rivers, except a small amount (<50 tonnes) taken at West Greenland and north of the Faroes (ICES, 1999b).

The offshore fishery at West Greenland

In the late 1950s an autumn salmon fishery developed gradually off the west coast of Greenland. Until 1965 only Greenlandic vessels took part in the fishery using fixed gillnets. During the period from 1965 to 1975 vessels from the Faroes, Norway and Denmark participated in the fishery introducing drift nets (Christensen & Lear, 1980; Jensen, 1988). The catches ranged from 1,000 to 2,700 tonnes during this period and increased partly due to the switch from multifilament to monofilament nylon in the drift nets permitting fishing also during daylight (Jensen, 1988). From 1976 foreign vessels were not allowed to fish for salmon at Greenland and the fishery became quota regulated. The fishery off West Greenland remained high until late 1980s, and has dropped considerably in recent years, and is below 50 tonnes today (Figure 2).

The salmon caught during autumn in the West Greenland area consisted of mainly 1SW non-maturing salmon (90-99%), destined to return as MSW salmon to spawn (ICES, 1984), i.e. the salmon will spend at least one more year in the sea before return.

The high seas fishery for salmon in the Norwegian Sea

In the mid 1960s a high seas fishery in the northern Norwegian Sea commenced (Christensen & Lear, 1980; ICES, 1984) followed by the development of a fishery around the Faroe Islands in late 1960s (Jákupsstovu, 1988).

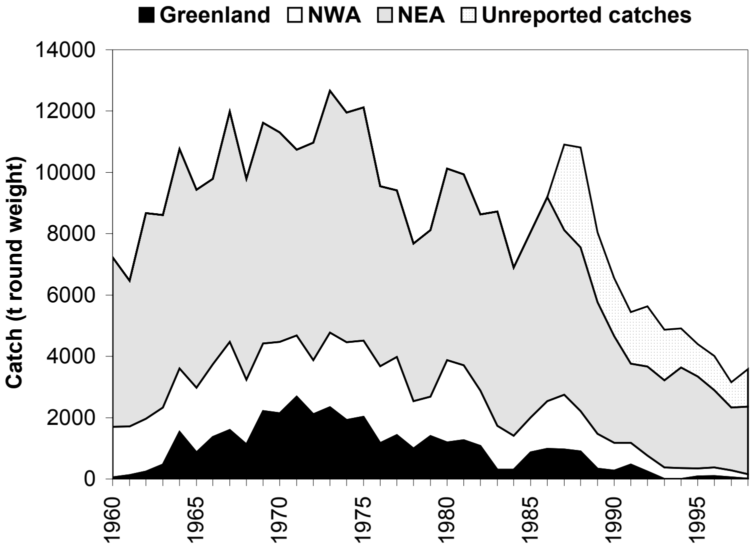

Figure 2. Total catches of salmon in homewaters and on the high seas in the North Atlantic since 1960 divided by area: the Northwest Atlantic (excluding Greenland), at Greenland (West Greenland), and in the Northeast Atlantic. Estimates of unreported catches available from 1987 are also shown (ICES, 1999b).

The fishery in the northern Norwegian Sea (Figure 3) was initiated by Danish vessels in 1967 using long-lines, and they were subsequently joined by Norwegian vessels and to a smaller extent vessels from Sweden, Faroes, Finland, and Federal Republic of Germany. The catches rose to approximately 1,000 tonnes in 1969 and 1970 and levelled off at about 500 tonnes up to 1975 (Figure 4). However, as a consequence of a national ban on salmon long-lining by Norway in 1975, the fishery was again carried on primarily by Danish vessels with catches between 200 and 500 tonnes up to 1984, when the fishery in the northern Norwegian Sea ceased.

Simultaneously as the northern Norwegian Sea fishery commenced, a small long-line fishery was developed by Faroese fishermen in the coastal waters around the isles, following successful experimental long-line cruises around the Faroes in April 1968 and 1969 by R/V *Jens Chr. Svabo* (Jákupsstovu, 1988). Initially, the area fished was relatively close and around the isles with annual catches ranging between 20 and 40 tonnes consisting of mainly one sea-winter (1SW) fish (60-90%). However, in 1979, two years after the establishment of the 200 nm Exclusive Economic Zone (EEZ) around the Faroes, the fishery increased substantially and peaked in 1981 with a catch of 1,025 tonnes (Figure 4) and the fishery had extended northwards off the Faroes with practically no fishery south of the isles, resulting in significantly higher proportions of 2SW salmon (80%) in the catches (Jákupsstovu, 1988).

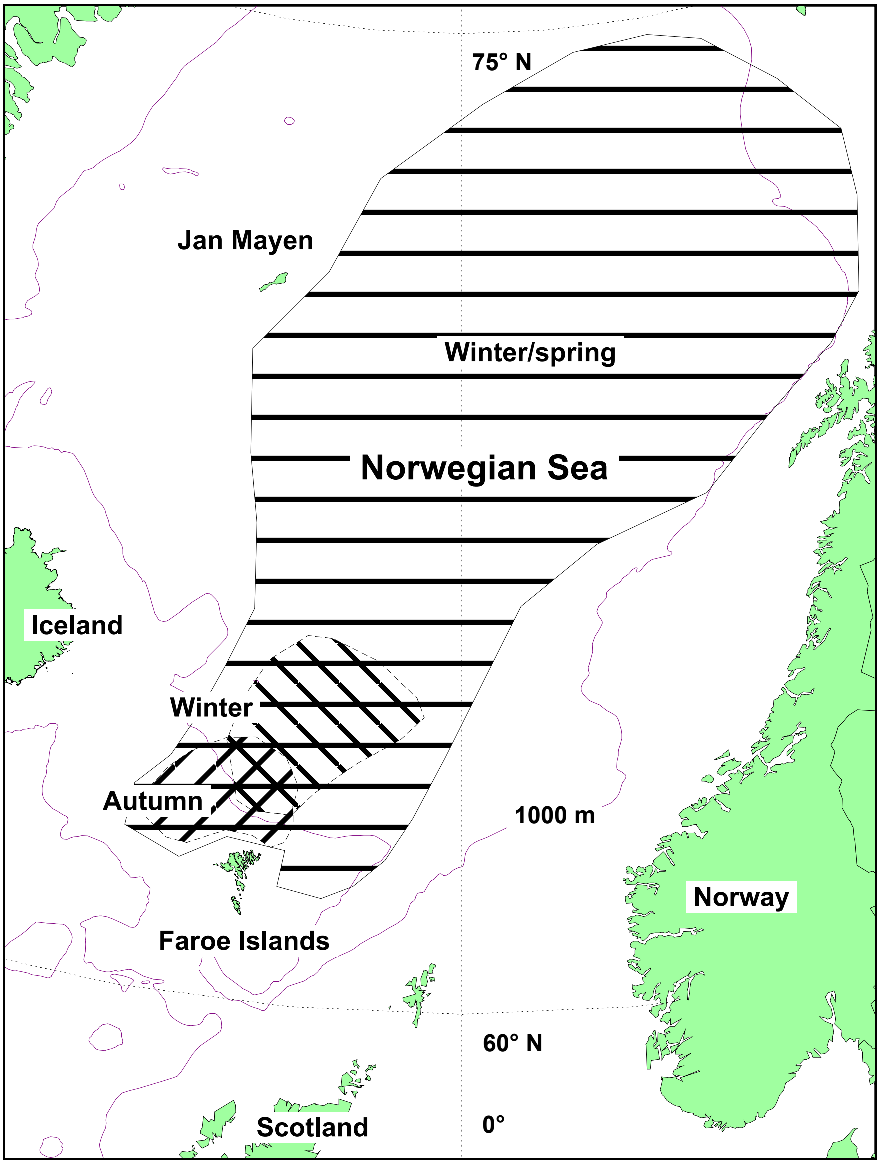

Figure 3. Approximate high seas fishing areas for salmon in the Northeast Atlantic since 1965. The large area in the Norwegian Sea indicates multinational fishing areas prior to 1984. The fishery in the northern part of the Norwegian Sea was carried out during winter and spring. In recent years the fishery was confined inside the Faroese 200 nm fishing limit, with the autumn fishery usually being carried out closer to the isles than the winter fishery.

After the formation of the North Atlantic Salmon Conservation Organisation (NASCO) in 1984, a quota was put on the Faroese fishery and it has been regulated since then. The regulation consisted of a TAC (total allowable catch) and various effort limitations, e.g. total number of hooks allowed, number of vessels per year and restricted fishing periods. The catches decreased from 630 tonnes in 1984 to around 300 tonnes in 1990. From 1991 and onwards the salmon boat owners organisation, "Felagið Laksaskip", has agreed on a buy-out compensation for the quota from various parties around the North Atlantic. The

Faroese Government, however, has continued to supervise sampling inside the EEZ to monitor the salmon present in the Faroese area and to obtain biological samples (e.g. size, age and weight distributions, recaptures of tagged fish), and to update time series of catch, catch per unit effort (CPUE), and of the proportion of escaped farmed fish in the area. The annual catches between 5-30 tonnes since 1991 was due to this research activity (Figure 4).

In the Norwegian Sea between 80 and 90% of the salmon caught were sexually maturing and destined to return to freshwater spawn the following autumn, irrespective of sea age (Youngson & McLay, 1985; Jákupsstovu, 1988).

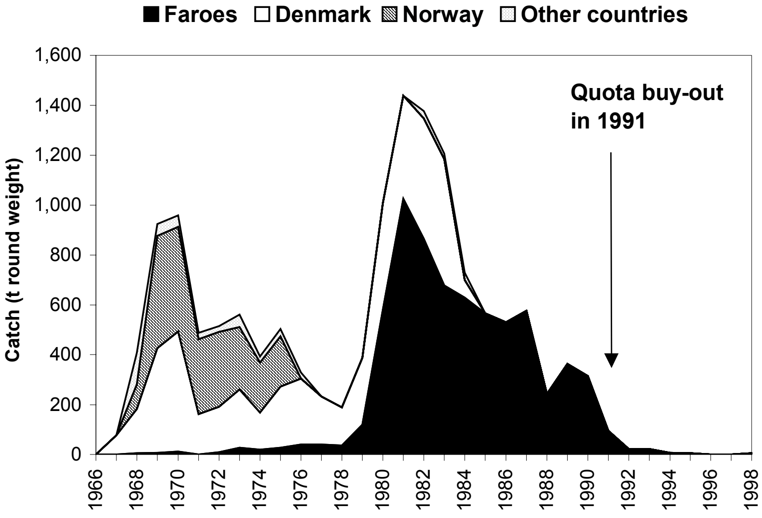

Figure 4. Catches of Atlantic salmon in the Norwegian Sea since 1966, showing the rise and fall of this high seas fishery (ICES, 1984; 1999b). After 1984 only the Faroese fished for salmon in the high seas. An unknown amount of unreported catches were presumably taken in the area north of the 200 nm fishing limit in the early 1990s. The Faroese quota has been purchased since 1991.

Fishing gear and methods used in the Faroese high seas fishery

The Faroese fishery for salmon is carried out by wooden boats (20-50 GRT) and by larger steel vessels up to 290 GRT. One of the largest salmon long-liner, M/S *Hvítiklettur*, is shown in Figure 5. The fishery in the early days began in late winter and early spring north of the Faroes and continued until June/July as far north as Jan Mayen (Figure 3). However, during the 1980s the fishing period gradually started earlier in the year, and at present the fishery begins in November and continues until the end of March, with a break of two weeks during Christmas. The trips lasted from 9 days (maximum for vessels with no freezing capacity) to one month for the largest vessels. The floating long-line used is essentially a replicate of the gear used by Danish fishermen in the Baltic (Figure 6). The number of hooks set during a fishing day varies between 1500 and 2500 hooks, and the total length of the line in the sea thus ranged from 25 to 45 km. The whole length of line is referred to as a set. A radio-transmitting "Dhan" buoy is attached at intervals to the line. The snood is weighted down approximately at its midpoint by a barrel lead to separate it from the main line (Figure 6). The long-line is usually set before dusk and the hooks are baited during setting with sprat (12 cm average length). Hauling starts approximately at noon and is completed between 5 and 10 hours later, depending on weather conditions and possible complications, e.g. breaking of the line, which frequently occurs. In those cases the remaining line can be found by picking up the radio transmissions from one of the Dhan buoys.

Figure 5. The Faroese long-liner M/S *Hvítiklettur*, one of the largest salmon fishing vessels in the fleet (105 feet, 279 GRT) and the one used in the research fishing during the project (Photo by Sigbjørg Justesen).

In the commercial fishery salmon below 60 cm total length (discards) were not permitted to land and were discarded if caught. Catches tend to be best in rough weather (Jan Arge Jacobsen, unpublished data), and this tendency has also been reported in the Northwest Atlantic (Christensen & Lear, 1980; Reddin & Friedland, 1993) and in the Baltic (Thurow, 1974). Further details on the fishing methods, gear and vessels can be found elsewhere (Mills & Smart, 1982).

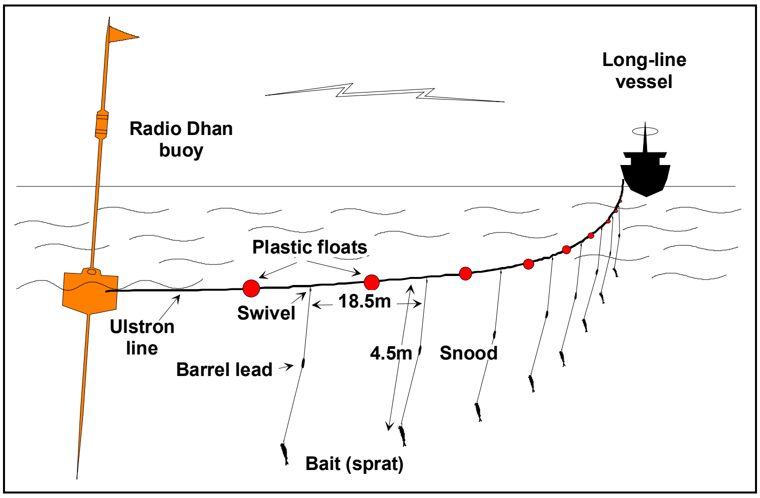

Figure 6. Schematic drawing of a salmon long-line as used in the Faroese high seas fishery.

This thesis is based on samplings from the Faroese high seas fishery, either during the commercial salmon fishery or during a directed research fishery with a hired salmon long-liner north of the Faroes.

SUMMARY OF RESULTS

Fishing periods: autumn is defined as November-December and winter as February-March.

Paper I. **Trends in the incidence of farmed Atlantic salmon in the Norwegian Sea**

The proportion of Atlantic salmon escaped from fish farms and caught in the Faroese salmon fishery (1980/1981–1995/1996) was estimated using scale analysis. The estimated proportion of farmed salmon in the fishery was relatively low from 1980/1981 to 1986/1987, but increased considerably thereafter, and reached a peak in the 1989/1990 fishing season when more than 40% of the catch was estimated to be of farmed origin. Later, the proportion declined, and in recent seasons the proportions of farmed salmon were estimated to be around 20%. The development in the proportion of escaped farmed salmon in the fisheries is thus relatively consistent with the increase in overall production of farmed salmon in the Northeast Atlantic, which increased considerably in 1988 and 1989, with Norway (74%) and Scotland (17%) accounting for the majority of the production. The exception being the years after 1992 where the proportion in the fisheries levelled off while the aquaculture production has increased considerably, totalling 410 thousand tonnes in 1995, which was 115 times the nominal catch of salmon in the North Atlantic. The estimated proportions of fish farm escapees were used to split the Faroese catch into wild and farmed components. It is concluded that if farmed components in salmon catches are not accounted for, catches of wild salmon will be overestimated and assessments of fisheries and stocks of wild salmon confounded. Furthermore, the increase observed in catch per unit of effort (CPUE) in the 1980s and early 1990s might have been caused by an increasing abundance of farmed salmon.

Paper II. **Seasonal differences in origin of Atlantic salmon in the Norwegian Sea based on estimates from age structures and tag recaptures**

To test if the population structure of salmon at the feeding areas in the Norwegian Sea north of the Faroes is stable throughout autumn and winter, river and sea age distribution was estimated from 2,350 scale samples obtained in the autumn and winter during four fishing periods 1991/1992–1994/1995. In addition, the origin of recaptures of salmon tagged as smolts in different European countries was compared between the two seasons. The fish classified as being of farmed origin from scale characteristics was excluded from the analyses. Age compositions in samples from the four fishing periods showed consistent patterns. The average smolt age (±SE) was significantly lower in the autumn than in the winter (2.5 ± 0.04 and 2.7 ± 0.03, range 1-5) as was average sea age (1.9 ± 0.03 and 2.2 ± 0.02, range 1-6). As salmon from southern European countries tend to smolt at an earlier age and produce more one-sea winter salmon than in northern Europe, we suggest that a significant proportion of the salmon caught in the Faroes area during autumn originate from southern European countries and that fish from northern regions appear to be more abundant in the winter. Recaptures in the Faroese fishery during autumn and winter of salmon tagged as smolts in different countries support this.

Paper III. **Origin, migration and dispersal of wild and farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands**

The distribution, migration, origin and growth of wild and escaped farmed Atlantic salmon was examined in the area north of the Faroe Islands. Between November 1992 and March 1995 a total of 5,448 salmon (3,811 wild and 1,637 fish farm escapees) were individually tagged and released back into the sea. A total of 106 fish (87 wild and 19 farmed) have been reported recaptured. The recapture rate of wild salmon (2.3 %) was significantly higher than that of farmed salmon (1.2 %). Recoveries of wild salmon were reported from homewater in nine north Atlantic countries, and in a number of different rivers throughout the distribution range of Atlantic salmon included Russia, Iceland, Spain and Canada. Most tags were recovered in Norway, but significant number of returns were observed in Scotland and Russia as well. Fish tagged in the autumn tended to return to areas closer to the Faroes than fish tagged in the winter. This strongly suggests that salmon originating from most areas of the distribution range are at some life stage present in this area, but in variable proportions at different times. Most of the salmon returned home to spawn the next autumn, and the fish that stayed for another year originated from northern areas of Europe. All recoveries of farmed salmon were done in Norway except one at the west coast of Sweden, suggesting that they mainly had escaped from Norwegian fish farms. Assessment of the proportion of wild salmon from different countries present in this area revealed that 40% of the fish were of Norwegian origin, and Scotland and Russia accounted for about 20% each. Four tags of wild fish were reported from Canada (7%), all in the same year when they were tagged. This demonstrates that adult Atlantic salmon can cross the north Atlantic ocean in less than 6 months. Estimated migration speed of wild fish and farmed fish returning to Norway and their specific growth rate was not different.

Paper IV. **Feeding habits of wild and escaped farmed of Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic**

The stomach contents of 2992 wild and 863 escaped farmed Atlantic salmon caught during autumn and winter in the Northeast Atlantic during three fishing periods 1992/1993–1994/1995 were analysed. The salmon fed mainly on hyperiid amphipods, euphausiids, shrimps, lanternfishes, pearlsides and barracudinas, and less on larger pelagic fish and squid. Crustaceans accounted for 95% in number (30% by weight) and fish for 5% in number (66% by weight). There was no difference in condition factor, number and weight proportions of prey, or in diet overlap between wild and farmed salmon, which suggests that farmed salmon that survive until they were captured are completely adapted to feed in the marine environment. The proportion of stomachs containing food was significantly lower during autumn (53%) than during winter (78%). The ambient sea-surface temperature is ca 7°C in autumn compared to ca 3°C in winter; therefore temperature dependent evacuation rate could explain the apparent lower stomach content during the autumn. The significantly higher condition of 3+SW salmon compared to the smaller 1 and 2SW fish, irrespective of season, might be a reflection of higher tolerance to low temperatures, greater forage potential or prey capture success. Although salmon show patterns of opportunistic feeding behaviour, there was also evidence of selective foraging. Generally fish were preferred over crustaceans, and amphipods were chosen over euphausiids. Large salmon tended to be more piscivory than smaller fish.

Paper V. **Open ocean infestation by salmon lice (*Lepeophtheirus salmonis*): comparison of wild and escaped farmed Atlantic salmon**

The infestation of salmon lice (*L. salmonis*) was investigated on 128 salmon caught on long-line in the Norwegian Sea between during November–March 1993–1995. The overall prevalence was 99%, the mean intensity and abundance was 30 lice per salmon. Most lice were adults (90%), with 2/3 being adult ovigerous females. These adult lice are estimated to be at least 3 months old at the prevailing sea-surface temperatures in the area: 7°C in November and 3°C in March. The prevalence and abundance of lice on one sea winter salmon were significantly higher on escaped farmed fish than on the wild salmon. However, no difference in abundance was observed between two sea winter wild and farmed salmon. The average number of lice per surface area of fish (density) was significantly higher in two sea winter salmon than in one sea winter salmon, indicating an accumulation of lice on the salmon in the oceanic phase (i.e. infestation). The prevalence of *Caligus elongatus* was 6% with an abundance of 1 lice per salmon, however, with one farmed salmon carrying 94% of all *C. elongatus* observed.

SYNOPTIC DISCUSSION

The discussion is divided into three sections, 1) temporal and spatial stock structure of wild and escaped farmed salmon in the ocean, 2) feeding habits of wild and escaped farmed fish in the sea with emphasis on whether salmon is an opportunistic feeder, and 3) possible interactions between fish farm escapees and wild salmon on the high seas. In the discussion I frequently refer to the autumn (November-December) and winter (February-March) fishing periods and fishing areas in the Norwegian Sea (Figure 3, page 11).

Temporal and spatial stock structures of wild and escaped farmed salmon

In the Norwegian Sea north of the Faroes it is evident that many salmon populations are present (**Paper II and III**). Fish are of different sea ages, river ages (**Paper II**), and large numbers of fish that had escaped from fish farms were also present (**Paper I**). It is also evident that salmon migrate and disperse in the sea, apparently not randomly, but rather in relation to environmental factors (currents and SST), food availability, predation risk, competition, and temporal and spatial constraints due to their origin as smolt as well as to their homing migration (**Paper II, III and IV**). In order that the population characteristics of the wild stocks should not be confounded, it is necessary to account for the proportion of escaped farmed fish in the various analyses presented (**Paper I-V**).

Why do salmon migrate to oceanic feeding areas before returning to freshwater again? The anadromy of salmon has been considered an evolutionary response to low productivity in freshwater, resulting in fish migrating towards more productive marine habitats in temperate and high latitudes (Gross *et al.*, 1988). However, with variations and exceptions (e.g. McDowall, 1988; Fleming & Gross, 1990). Thus, in order to maximise its lifetime reproductive rate, salmon have to balance the various cost and risks of freshwater and marine migration to reach favourable oceanic feeding grounds that can support rapid growth in habitats with acceptable environmental conditions. Furthermore, in the marine phase, the residence have to be adjusted according to the growth rate in the sea, the maturation schedule and the distance home.

Geographic origin

The tagging results positioned Norway as the main contributor of salmon to the southern Norwegian Sea, with significant contributions also from Scotland and Russia (**Paper III**). Only minor contributions were estimated from the other European countries and Canada. The majority of the salmon (91%) were recovered in home waters the same year as they were tagged. Most of the fish farm escapees originate from Norway (**Paper III**), which is in line with the fact that Norway accounts for about two thirds of the total aquaculture production of farmed Atlantic salmon in the Northeast Atlantic in recent years (ICES, 1999b). High proportions of fish farm escapees are also observed in Norwegian homewater fisheries (Lund *et al.*, 1991; 1996), and tagged farmed salmon released on the Norwegian coast have been recaptured in the Faroese fishery (Hansen *et al.*, 1987). It has been shown that the farmed fish home to the general areas of escapement from deliberate releases of tagged farmed fish in Norway (Hansen & Jonsson, 1991). It seems unclear whether farmed fish escaping from cages in Scotland, Faroes and Ireland also contribute to the Faroese fishery. Webb and Youngson (1992) found that about 20% of the catches on the west coast of Scotland were escapees, while they have not been detected in catches on the east coast (Youngson *et al.*, 1997). Thus, it cannot be ruled out that some of the Scottish escapees might migrate further north into the Norwegian Sea.

In the following discussion the recaptures from the countries around the Northeast Atlantic were grouped by two main geographical regions, i.e. a northern European group (Norway, Russia, Sweden, Denmark, Iceland and Faroe Islands) and a southern European group (Ireland, Scotland, England/Wales, Northern-Ireland, France and Spain) to reveal possible spatial differences in proportions of recaptures. The recaptures in the Northwest Atlantic included Canada and West Greenland, and escaped farmed fish were excluded.

Previous sea tagging experiments in the Norwegian Sea have shown that in the northern parts of the area salmon from Norway are most dominant with salmon from UK, Sweden and Russia also present (unpublished data, L.P. Hansen, Norway). The previous major sea tagging at Faroes in 1969–1975 (Jákupsstovu, 1988), indicates a much higher proportion of salmon from the southern regions compared with the other tagging results (Table 1). The 90 recaptures, of which 90% were reported in homewaters the same year as they were tagged, indicated that salmon from Scotland and Norway, and to a lesser extent Ireland, were the main contributors to the stock around Faroes, with only a few tags recovered in England/Wales, Sweden, Russia, and off West Greenland (Table 1). The present sea tagging results (**Paper III**) give a higher proportion of salmon from the northern region compared to the previous tagging at Faroes (Table 1). The main reason for the difference seems to be that the previous tagging was conducted relatively close to the isles, and even south of the isles, resulting in mainly 1SW salmon (85%) being tagged, while in the present tagging mainly 2SW salmon (80%) were tagged (**Paper III**). The higher proportion of 2+SW in the commercial catches in the 1980s were due a northward shift of the fishing areas, resulting in larger salmon (ICES, 1984; Jákupsstovu, 1988).

Table 1. Recapture proportions (%) of wild Atlantic salmon from various tagging programmes in the North Atlantic since 1960 by country of origin. The countries were grouped into southern and northern European countries for comparisons, as well as in the Northwest Atlantic and Northeast Atlantic. The results from the present tagging experiment is shown as raw recapture numbers [c] to be comparable to the other results, and as adjusted recaptures [d], i.e. corrected for tag reporting rates and exploitation rates in homewaters (**Paper III**).

	No. re-	. . . . Northern group						. . . . Southern group						NWA Region		NEA Region		N. Atlantic	
Tagging area	captured	NO	SW	RU	DK	FO	IC	IR	SC	EN/WA	NI	FR	SP	CA	W GR	N EU	S EU	NWA	NEA
Homewaters[a]	249	59.4	5.6			1.2	1.2	23.7	2.8	4.4	0.8	0.4	0.4			67.5	32.5	0	100
Faroes[b]	90	34.4	2.2	1.1				16.7	36.7	5.6					3.3	37.8	58.9	3.3	96.7
Norwegian Sea[c]	87[g]	54	4.6	6.9	2.3		1.1	10.3	13.8	1.1			1.1	4.6		69.0	26.4	4.6	95.4
Norwegian Sea[d]	87[g]	39.6	2.3	18.2	4.7		0.6	5.7	19.2	2.3			0.6	6.8		65.4	27.8	6.8	93.2
Average NEA[e]	426	44.5	3.4	6.5	1.6	0.4	0.6	15.3	19.6	4.1	0.3	0.1	0.3	2.3	1.1	56.9	39.7	3.4	96.6
West Greenland[f]	93							17.2	32.3	15.1		2.2	3.2	30.1		0	69.9	30.1	69.9

[a] smolt tagging 1991–1995 (**Paper II**), [b] previous sea tagging 1969–1975 (Jákupsstovu, 1988), [c] present sea tagging 1992–1995 (**Paper III**), [d] present sea tagging adjusted (corrected) for tag reporting rates and exploitation rates in homewaters (**Paper III**), [e] Average percentage recapture rates in the Norwegian Sea based on the three data series: Homewaters (**Paper II**), Faroes (Jákupsstovu, 1988) and Norwegian Sea corrected (**Paper III**). [f] previous sea tagging 1965–1972 at West Greenland, excluding recaptures in the fishery during tagging (Jensen, 1980a). [g] In total 106 fish were recaptured, but 19 were of farmed origin and were excluded from the table.

It is clear from Table 1 that the recaptures of salmon tagged as smolts in homewaters (**Paper II**) obviously reflect only those countries that tag smolts. For example Russia practically does not tag smolts, which is also evident in their absence in the recaptures from the homewater tagging programme (Table 1). However, their presence became evident in the recent sea tagging experiment (Table 1) (**Paper III**). It should be noted that only the wild component was used in the recapture proportions in the present tagging experiment, and that in the period 1969–1975 practically no fish farm escapees were in the sea (aquaculture were in its infancy in the early 1970s).

In the Northwest Atlantic approximately 2/3 of the salmon present were estimated to originate from Northeast Atlantic and the remainder from Canada (Table 1). However, more recent analysis of scale characteristics have revealed a more even split between North American and European salmon present in the West Greenland area (Reddin *et al.*, 1988), but with proportions of North American salmon varying from 34% in 1971 to 75% in 1990 (Reddin & Friedland, 1999). Scotland, England and Wales seem to be main countries of origin of the European component in the West Greenland area (Swain, 1980). It should be noted that probably very few salmon from the northern European regions migrate to West Greenland, although single recaptures from Norway and Sweden have been made in this area (Swain, 1980).

Temporal and spatial stock structures

In the Norwegian Sea there is evidence for a seasonal change in stock complexes entering and departing the feeding areas north of the Faroes (**Paper II**). Particularly salmon from areas in southern and mid part of Europe are observed in higher numbers in the autumn than in winter, when fish from northern areas were more abundant (**Paper II and III**).

There may be several explanations for the apparent change in the stock composition of salmon from autumn to winter. Smolts from different areas move into the ocean at different times. Fish from southern Europe may leave their home rivers as early as beginning of April (e.g. Baglinière, 1976), whereas smolts from northernmost Norway go to sea in late June or in the beginning of July (e.g. Hvidsten *et al.*, 1995). Advection and active movement would displace salmon post-smolts from different regions differently in the ocean during their first months at sea (**Paper II**). Such considerations have been made for salmon in the West Greenland area (Jensen, 1980a; Reddin & Shearer, 1987; Reddin *et al.*, 1988) and in the Gulf of St. Lawrence (Reddin & Short, 1991; Friedland *et al.*, 1999). Due to the earlier smolt runs in the south and the great influence of the northward flowing North Atlantic Current in the Norwegian Sea (Hansen *et al.*, 1998), the majority of the north European post-smolt might be located further to the north in November–December than those from the southern countries. Thus the northern group is expected to be less represented in the autumn catches compared to later in the fishing season (**Paper II**).

The recapture of relatively large southern European post-smolts north of Scotland and in the Norwegian Sea in June and July (Shelton *et al.*, 1997; Holm *et al.*, 2000), at a time when the majority of the e.g. Norwegian smolts just have left their rivers (Hvidsten *et al.*, 1995) and are smaller, indicate that there are sequential/temporal and spatial differences in the salmon stocks in the sea during the early period after seaward migration (Holm *et al.*, 1998). This is also suggested for salmon in the West Greenland area (Reddin & Burfitt, 1980; Reddin *et al.*, 1988) and in the Gulf of St. Lawrence (Reddin & Short, 1991). It should therefore not be surprising to find that these fish tend to keep their segregation into November, maybe more "diluted" at this later stage, when they recruit the fishery in the Faroese area. However, when they have entered the area north of the Faroes late in the year, no sign of schooling behaviour could be detected (Jákupsstovu, 1988). Some segregation, however, may be persistent during their feeding phase, as indicated further below.

A simple calculation of fish density in the feeding area support the view of solitary predatory behaviour during the marine feeding phase. In **Paper I**, the average CPUE (number of salmon per 1000 hooks per day) of 55 salmon (range 30-80) during the period 1981/1982–1994/1995, is equivalent to an average of 55/18 = 3 salmon per kilometre long-line fished (range 1.7-4.4), since there are 18 m between the hooks (see Figure 6, page 14). Furthermore, the fish are generally not clustered on the line when caught (Jákupsstovu, 1988). Depending on assumptions of the distance the baited long-line attract salmon (e.g. 1-2 km), the density in the sea would range from 1 to 3 salmon per square kilometre. Hansen (1984) found the density to be about one salmon per square kilometre calculated from a diffusion model, and Thurow (1973) calculated an average density of 1.5 salmon per square kilometre off northern Norway. Thus the density of salmon in the oceanic feeding areas is low compared to other major pelagic stocks (herring, mackerel and blue whiting) feeding in the area from late winter (Vilhjálmsson *et al.*, 1997; Holst *et al.*, 1998; ICES, 1999a; 1999c).

It was hypothesised (**Paper II**) that the spatial segregation was the result of a trade-off between food availability and thermal limitations, with the smaller salmon requiring higher ambient temperature. Thus, significant parts of the 1SW stocks might be confined to the southern and warmer side of the subarctic front in the southern Norwegian Sea during winter. This front is located in east-west direction approximately between the autumn and winter feeding areas and turns northward in a north-eastern direction into the eastern part of the winter feeding area (Hansen, 1985). Such a distribution would lead to a shift in the smolt age distribution and in the proportions of country of origin from the autumn area to the winter area, in the ways observed in **Paper II**. However, the suggestion of temporal segregation relies on the assumption that the movement of the fishery reflects a migration of salmon from the autumn to the winter feeding areas. Which might be a reasonable assumption, because fishing fleets usually concentrate in areas with highest CPUE (e.g. Healey *et al.*, 1990). However, since the division between the warmer and the colder side of the front coincide with the autumn and winter sampling areas that were not fished synoptically, we cannot verify our suggestions from the present data.

Although the spatial changes in the shift of the centre of seasonal distribution involved are not great (60 nm), the relatively large drop in SST from autumn to winter might indicate that two different water masses were exploited (**Paper II**). Thus, if the above assumption on temporal segregation does not hold, the results could indicate a stock segregation in the feeding areas north of the Faroes throughout the seasons. An indirect support for the alternative suggestion was given in **Paper II**, and was based on the earlier sea tagging experiment in the Faroese area (Jákupsstovu, 1988). This tagging was performed during winter in the area south of the present winter feeding area (i.e. closer to the Faroes), where mainly 1SW fish was caught and tagged as opposed to the present sea tagging (**Paper III**). The tag returns from the previous tagging experiment indicated a more southern origin of the fish in this area, as compared to the results from the present sea tagging (see Table 1). Thus, the observed stock segregation, at least in the winter feeding areas, might be the result of environmental conditions and the geographic origin of the fish.

Salmon have been observed to feed heavily on crustaceans, especially on the hyperiid amphipod *Themisto* spp. as well as on mesopelagic fish species in these feeding areas (**Paper IV**). Although the abundance of prey does not seem to be limiting, salmon have to compete with other major pelagic fish species, i.e. blue whiting, herring and mackerel, which are present in large numbers from early spring (ICES, 1999a; 1999c). The longer photoperiod to the north and novel feeding areas were suggested to be the main driving forces for horizontal migrations in these pelagic fish and furthermore the largest fish would benefit most energetically from such migrations (Nøttestad *et al.*, 1999). The abundance of *T. libellula*, which is a relatively large and important crustacean prey for salmon (**Paper IV**), is very high in the water mass on the colder side of the front (Dalpadado *et al.*, 1998). Since neither herring, mackerel nor blue whiting enter the colder areas during their feeding migrations (Vilhjálmsson *et al.*, 1997; Holst *et al.*, 1998; ICES, 1999a), it is possible that large salmon might find an area with less competition during late winter (**Paper II**). Thus, competition might also play a role to segregate the various age groups of salmon feeding in the sea.

Others have found thermally dependent segregation of salmon in the sea. Jákupsstovu (1988) found that the proportions of 1SW salmon compared to MSW salmon were higher in areas with SST above 4°C while the proportions MSW were higher in the colder areas with less than < 4°C. Reddin and Shearer (1987) found that the low temperature (< 4°C) seemed to limit salmon distribution and alter their migration routes in the Northwest Atlantic, and Reddin (1988) also found a more restricted distribution of the 1SW salmon compared to the wide distribution of MSW fish in the Northwest Atlantic. At West Greenland in mid 1980s, lower SST were associated with higher mean sea ages in the catches, mainly because a decline in the proportions of 1SW fish (ICES, 1985).

In **Paper IV** it was found that the condition factor of large (3+SW) salmon was significantly higher than of 1 and 2SW fish, and furthermore, that the condition of the large fish was independent on season, while the condition decreased from autumn to winter for the smaller fish. This indirectly support the suggested trade-off between food and thermal limitations with lower profitability for the small salmon during the winter period.

It is well known that the MSW stock components from many southern areas utilise other main feeding areas in addition to the Norwegian Sea. For example the West Greenland area is a major feeding area for MSW stocks from Scotland, England/Wales and Ireland (Swain, 1980; Jensen, 1980a; 1980b). The Irminger Sea and East Greenland areas probably host many European stocks (Jensen, 1967; Jensen & Lear, 1980; Horsted, 1988; Scarnecchia, 1989). The recaptures of salmon tagged as 1SW fish in the Faroese area and recaptured in the Irminger Sea the following year (only 2 recoveries), and conversely a salmon tagged in Irminger Sea in spring and recovered in the Faroese area the following autumn (ICES, 1984), indicate that some stocks, probably the MSW components of those stocks, might have a two-stage or even a three-stage migration and feeding cycle in the ocean: They might use the southern Norwegian Sea as a pathway to, from or during both ways to the feeding areas in the western Atlantic. Such migrants might explain parts of the observed temporal and spatial changes in the age structure and recovery proportions in the areas north of the Faroes. Turrell and Shelton (1993) gave a scenario of a hypothesised 'life-trajectory' of a British salmon migrating to West Greenland via Faroes, south Iceland and south Greenland, and they found such migration routes to fit spatially within the 4-8°C isotherms and temporally into the availability to the Faroese fishery in the Norwegian Sea and to the West Greenland fishery the following autumn. This conform to the multi-stage migration suggestion above.

In conclusion, there seem to be substantial evidence for a succession of stock complexes entering and departing the feeding areas in the Norwegian Sea. Partly due to differences in timing of smolt runs from the various geographical regions in the Northeast Atlantic as well as temporal and spatial constraints for the homeward migration due to maturation, and partly due to a segregation of salmon in a trade-off between food availability and thermal limitations, probably intensified by higher competition from other major pelagic stocks on the warmer side of the front.

Migration and dispersal

In the Norwegian Sea between 80 and 90% of the salmon caught during autumn and winter are maturing during the year and destined to return to freshwater the forthcoming autumn, irrespective of sea age (Youngson & McLay, 1985; Jákupsstovu, 1988; Paper III). The distance home from the feeding areas north of the Faroes to the home countries is shortest for Norwegian salmon (600 km) and longest for the Canadian salmon (4550 km). Average values of distance, speed and growth rates by country are shown in Table 2, which is an extract of the recapture details in **Paper III**. The migration speed was estimated from the distance home divided by the time from early March until recapture the same year (**Paper III**). However, for several reasons the estimates of migration speed are minimum estimates. The distance is the shortest strait line in the sea from tagging to recapture, and might furthermore be biased if the time of departure from the feeding area is dependent on the distance home. It is also probable that the fish continue to feed in the area at least until May before the onset of anorexia (Stead *et al.*, 1999) as most of the recaptures were made in July (90% recovered from June–September). Therefore it is difficult to limit the period to that used for active homeward migration. Furthermore, fish slow down in coastal waters and fjords (Hansen *et al.*, 1993b) and do not necessarily ascend the river immediately upon return to coastal waters (Jonsson *et al.*, 1990).

The results from Table 2 indicate that the migration speed was apparently higher for fish from distant areas. However, if fish from distant areas leave the feeding area earlier than those from nearby areas, then their true average migration speed might be the same. Average swimming speed of one body lengths per second (BL/s) of homing salmon were reported in the Pacific (Hartt, 1966; Quinn, 1988; 1990; Ogura & Ishida, 1995), which is considered the optimal long-distance migration speed (Weihs, 1973; Ware, 1978). By adopting a swimming speed 1 BL/s as the optimal homing migration speed (Weihs, 1973), the journey home as well as the average number of days feeding in the area prior to homeward migration (last two columns in Table 2) could be estimated. These estimates show that on average the fish could feed for four more months before the onset of homeward migration, of course varying according to the different countries involved (Table 2). The estimated minimum duration of the active homeward journey would be 10 days to Iceland to over two months to Canada from the feeding areas.

The growth in length ranged from nil to a maximum of 34 cm for a Canadian 2SW salmon, and the average daily growth in length of 0.045 cm, or 0.19% gain in body weight per day (G) (**Paper III**). There was no significant differences in growth rates among salmon from different regions, neither between wild and farmed salmon nor between fish that stayed for another year at sea and those that left the area within 12 months (**Paper III**). The average growth rate in the present work corresponds to the growth rates of salmon tagged in West Greenland and recaptured in North America (0.03 cm per day) and in Europe (0.05 cm per day) (Jensen, 1980a). A growth of about 500 g (from 3.3 to 3.8 kg) in three months was reported for 2SW salmon in the area north of the Faroes from February to end of April 1983 (ICES, 1984). This correspond to an average length increase of 3.4 cm, using the length-weight regression of 2SW salmon in **Paper III** ($w = 7.261 \cdot 10^{-6} l^{3.052}$, n= 645, $r^2 = 0.78$, $p < 0.001$).

Of fish recaptured relatively close to the tagging site there was no apparent difference in the distribution of salmon that was tagged in the autumn or in the winter (**Paper III**). This does not seem to be the case of fish that were recaptured relatively far away from the tagging sites. They were all tagged in the winter. This may suggest that salmon from distant areas are not present at the Faroes during autumn, and corresponds to the suggestion in **Paper II** that the northern group arrived at the feeding areas later in the season. This might also be true for the distant western group. The wild salmon that stayed for another year in the ocean were all 3SW fish upon return belonging to the northern region (Norway, Russia and Sweden) (**Paper III**).

Fish that were tagged in the winter seem to survive better than fish tagged in the autumn. There may be several explanations for this. First the size distribution of the fish that were tagged in the autumn were smaller than of those tagged in the winter, and smaller fish may thus be more vulnerable to handling and tagging stress (Fowler & Stobo, 1999) and subsequent predation. Second, these fish will spend on average three months longer in the sea than fish tagged in the winter, and may be exposed to different marine mortality factors for a longer period of time. Furthermore, based on smolt age and sea age distribution of salmon, **Paper II** suggested that fish originating from stocks in southern Europe were more abundant in the autumn than in winter. If this holds true, the possibility cannot be ruled out that the apparent differences in survival observed may reflect the trends observed in last decade that mortality of salmon stocks from southern Europe has increased more than for salmon from intermediate and northern regions in the Atlantic (Parrish *et al.*, 1998; ICES, 1999b). The low recapture rate of wild salmon (2.3%) in the present sea tagging experiment (**Paper III**) compared to the previous sea tagging (4.6%) (Jákupsstovu, 1988) might further indicate an overall decrease in marine survival in recent years. In the Baltic McKinnel and Karlström (1999) reported that the most recent smolt tagging releases have had the lowest recapture rates in 40 years, which also indicate poorer conditions for salmon in recent years in the Baltic.

Table 2. Average migration distance, migration speed and growth rate (G, specific growth rate) by type of fish (wild and farmed) and country of origin. Data from **Paper III**. N is number recaptured and the entries are average values. The rightmost two columns show the number of days left for feeding prior to homeward migration and the number of days to travel home with one BL/s.

Country	N	Distance km	Speed[a] km/d	Speed[a] BL/s	G % w/d	Days[b] feeding	Days[b] travelling
Wild salmon							
Norway	47	918	6.7	0.11	0.18	128	15
Scotland	12	838	10.4	0.18	0.17	82	15
Ireland	9	1207	10.3	0.18	0.20	101	21
Russia	6	2597	15.8	0.32	0.14	113	53
Sweden	4	1403	14.7	0.22	0.08	98	21
Canada	4	4548	22.4	0.35	0.33	133	70
Denmark	2	1311	6.5	0.10	0.22	184	20
Spain	1	2491	27.1	0.44	0.15	52	40
Iceland	1	626	4.6	0.06	0.22	128	9
England	1	1029	16.1	0.27	0.57	47	17
Total wild:	87	1267	9.6	0.16	0.19	116	21
Farmed salmon							
Norway	18	903	6.0	0.09	0.19	139	14
Sweden	1	1377	9.4	0.15	0.21	125	21
Total farmed:	19	928	6.2	0.09	0.19	139	13
Grand total:	106	1206	9.0	0.15	0.19	120	20

[a] Migration speed in km per day and body lengths per s (BL/s) from March the first in the year of recapture. [b] Number of days corresponding to a swimming speed of 1 BL/s during homing migration (Weihs, 1973).

Only three of 19 farmed salmon were recovered from the autumn tagging (**Paper III**), which apparently is in contrast to the suggested poorer survival rates of salmon from the southern European region above, because the farmed fish apparently comes from Norway (**Paper I and III**). However, the survival (return rate) of fish farm escapees have been shown to depend heavily on the time of escape, i.e. the highest survival is observed if escaping in spring (Hansen & Jonsson, 1989; Hansen & Jonsson, 1991). Thus, this may help to explain the lower survival of farmed salmon.

During tagging many (32%) of the fish were released with the hook left in, to avoid excessive handling of the fish and if the removal was considered to damage the fish. Of the fish recovered, the return rates of fish with the hook left in when tagged was significantly higher than of fish with no hook when released (**Paper III**), which might indicate that for some of the fish the removal of the hook was lethal. However, there was a tendency that growth rate was lower in the releases with the hook left in (**Paper III**). However, long-line caught salmon at West Greenland have been reported to be in "excellent condition for tagging" (Munro & Swain, 1980).

Management considerations

Below is shown an example of practical use of the stock structure estimates from the previous sections on the Faroese high seas fishery. The knowledge of the temporal and spatial composition of the salmon stocks present in the Faroese area enable an admittedly coarse assessment of the expected exploitation rates on the various stock complexes fished in the long-line fishery for Atlantic salmon north of the Faroes.

From **Paper III** approximately 65% of the salmon in the Faroese fishery were estimated to originate from countries belonging to the northern European region and approximately 28% were estimated to originate from the southern European region. These figures add up to 93%, which is the sum of the northern and the southern stock complexes, the remaining 7% were estimated to originate from Canada (Table 1), discounting farmed salmon (representing 20% on average, **Paper I**). From recoveries of microtags and external tags in the same fishery (**Paper II**), the approximate sea age distribution for the northern group was 12% 1SW and 88% 2+SW salmon, respectively and for the southern group 70% 1SW and 30% 2+SW salmon, respectively. In the Northwest Atlantic only 2SW were recovered. Thus, the Faroese fishery exploits mainly the 2+SW northern stock complex (65% of 88% = 57%), secondly the 1SW southern stock complex (28% of 71% = 22%), thirdly the 2+SW southern stock complex (28% of 30% = 8%), and fourthly the 1SW northern stock complex (65% of 12% = 8%), and 7% from the Northwest Atlantic (Table 3). If the average recapture rates of country of origin based on the three data series described in Table 1 were used, i.e. 57% from the north, 40% from the south and 3% from Northwest Atlantic, the result would be as shown in second part of Table 3.

Table 3. Approximate proportions (%) of various stock components and age groups exploited by the Faroese fishery, as inferred from tag recaptures in the North Atlantic.

	Sea age			Sea age		
Region	1SW	2+SW	Total[a]	1SW	2+SW	Total[b]
Northern	8	57	65	7	50	57
Southern	20	8	28	28	12	40
NWA	0	7	7	0	3	3
Total	28	65	100	35	62	100

[a] Proportion by region from **Paper III**, and [b] average from Table 1.

This opens up the possibility for a rational management of the fishery. If for example certain stock components and age groups were considered threatened, the entries in Table 3 would indicate which components were fished and also where restrictions might have a desired effect. However, for an effective management, more detailed information about the temporal and spatial stock distributions is required.

Diet and feeding habits of wild and escaped farmed salmon in the sea

This section compares the diet of wild and escaped farmed salmon, among sea ages, between seasons, and from various geographic regions and life stages. Then it was examined whether salmon are opportunistic feeders, and finally I assess the likelihood of food being a limiting factor for salmon in the sea.

The diet of salmon

Important food for salmon are crustaceans (amphipods, euphausiids, pelagic shrimps), mesopelagic fish (pearlside, lanternfishes, barracudinas), larger fish (blue whiting, herring, capelin, and mackerel), and juvenile squid (**Paper IV**). Crustacean prey dominated in number while fish dominated in weight. Relatively few larger pelagic fish such as herring, blue whiting and mackerel were taken. Wild and farmed salmon seemed not to differ in these figures (**Paper IV**).

During autumn half of the stomachs contained food while ca 80% contained food during winter and this difference was consistent in the three fishing periods (**Paper IV**). Thus, there seemed to be a lower feeding rate in the autumn season compared to the winter season. Lower feeding in autumn have been reported for salmon in the Labrador Sea (Lear, 1980) and in the Baltic (Christensen, 1961; Thurow, 1966). However, the higher condition factor of salmon in the autumn than in winter seems to contradict the apparent lower feeding intensity during autumn (**Paper IV**). The explanation to the apparent ambiguity might be found in the fact that the gastric evacuation rate is highly positively correlated with temperature (Dos Santos & Jobling, 1991). The ambient temperature decreases from 7°C in autumn to 3°C in winter, and would result in a lower rate of emptying of the stomachs during winter. This would give the impression that during winter fewer stomachs were empty, and that the non-empty stomachs on average contained more food.

There was a shift in the prey species composition with age or size of the salmon. The smaller (1SW) salmon had mainly eaten amphipods, lanternfishes and some barracudinas, while the larger 3+SW salmon had mainly eaten barracudinas, lanternfishes and some larger fish. The 2SW salmon had eaten the various prey groups in intermediate proportions compared to the 1 and 3+SW salmon (**Paper IV**). The larger fish prey was thus preferred with increasing age of the salmon to the smaller mesopelagic fish and crustaceans. The shift in food composition was the same for wild and escaped farmed salmon (**Paper IV**). Size selective feeding was reported for salmon in the Labrador Sea and on the Newfoundland shelf during spring, where the proportion of mesopelagic shrimps increased with fish size on behalf of amphipods and lanternfishes (Lear, 1980). There was also a tendency that the proportion of capelin increased with fish size at West Greenland, again on behalf of amphipods and of euphausiids (Lear, 1980).

There were some indications that escaped farmed salmon fed more actively or was more eager to take the bait than wild salmon, since farmed salmon contained a higher proportion of bait than did wild salmon (**Paper IV**). However, the biological significance of this observation is not clear, but might indicate that farmed fish have greater appetite during winter. The proportion of farmed fish that contained food was also higher than that of wild fish, supporting the previous statement. Therefore, it might be speculated that the feeding behaviour of escaped farmed salmon differ from that of wild salmon due to their farmed prehistory (i.e. their genetic alteration from wild strains). For example behavioural differences could result in different hooking probability of the two groups, or alternatively farmed salmon have been selected for fast and efficient growth that may have resulted in a higher demand for energy (Thodesen *et al.*, 1999), and thus have made farmed salmon a more aggressive feeder.

Thus, wild and farmed salmon differed in very few if any aspects of feeding. No difference was observed in diet overlap, nor in frequency, number or weight proportions of prey between wild and farmed salmon (**Paper IV**). The indication of a more eagerly feeding behaviour, and the higher proportion of farmed fish containing food compared to wild fish, strongly suggests that farmed salmon that survive until they were captured, are completely adapted to feed in the marine environment.

Comparison of the marine feeding habits from other areas and life stages

A summary of published accounts on the food of Atlantic salmon is presented in Table 4 as the number of occurrences (%) of each prey type for various geographic areas in the North Atlantic, including the results from the present study (**Paper IV**). Table 4 is similar to Hislop and Shelton's (1993) Table 5.1, but with percentage of occurrences instead of the number of occurrences. Similarly the corresponding weight percentages of prey is given in Table 5, along with the new data from the Norwegian Sea (**Paper IV**). In the tables, immature salmon is termed as 'adults' when they are found in the feeding areas in the open sea and as 'homing adults' when they are maturing and have initiated their homeward migration and are found on the continental shelves and in coastal areas.

There seem to be systematic differences in diet composition at different life stages of salmon as well as geographical differences. The general picture is that the feeding intensity decreases towards the spawning time, and salmon usually become anorexic the last part of their oceanic stage (e.g. Kadri *et al.*, 1997; Stead *et al.*, 1999). This is reflected in the high percentage of empty stomachs in samples of maturing salmon in coastal and estuarine areas, as compared to immature salmon in oceanic areas (Table 4). The food of adult salmon in coastal areas returning to spawn (e.g. Blair, 1965; Grønvik & Klemetsen, 1987; Hislop & Webb, 1992), where fish are totally dominant as prey (se the two first columns in Table 4 and 5). However, with one notable exception (included in the data from the Canadian Shelf, Table 4 and 5), where amphipods were the main food (Neilson & Gillis, 1979).

The prey composition in the oceanic phase seems to be more varied, and includes capelin, sandeel, herring, barracudinas, lanternfishes, crustaceans and squid in varying proportions (Table 4 and 5). There seems, however to be a systematic difference in the oceanic food composition between the Northwest and Northeast Atlantic areas, and also within the regions. In the Northeast Atlantic fish account for approximately 66% in weight, whereas in the Northwest Atlantic fish constitute around 82% in weight, with mainly crustaceans contributing the rest (Table 5). Thus, there might be a higher reliance of fish as prey in the Northwest Atlantic as compared to the Northeast Atlantic. Hislop and Shelton (1993) proposed that the crustaceans were a much less important prey than fish in the North Atlantic. The present data was not available to them, but it emphasise the importance of crustacean prey in the oceanic areas in the Northeast Atlantic, contributing 30% in weight (Table 5). To assess the importance of various prey for salmon, it is necessary to account for the duration of the various oceanic life stages. Three life stages (feeding phases) might be considered, i.e. the post-smolt, open ocean, and homing phase. Thus, a phase duration × food composition principle could be used in such assessments (although not attempted here). I would, however, stress the importance of the hyperiid amphipods as prey for salmon beside various mesopelagic fish in the oceanic areas in the Northwest Atlantic (Table 4 and 5). Furthermore, especially in the autumn salmon seemed to rely on amphipods as food (**Paper IV**).

Differences in fish prey in the offshore areas within the Northwest Atlantic region are also evident (Table 4 and 5). Salmon off West Greenland mainly rely on capelin and sandeel as food while salmon in the Labrador Sea and Davis Strait areas feed on mesopelagic fish, which is more comparable to the fish prey types in the Northeast Atlantic (Table 5). This regional difference could be due to differences in availability and abundance of the various prey types. Jensen (1967) noted a similar contrast in the food content of salmon from the Irminger Sea and off West Greenland.

If the feeding habits differ between the Northwest and Northeast Atlantic, and even within the western Atlantic, it may affect the marine survival of salmon in the various areas differently. The high variance in the abundance of the short-lived capelin stock in the Northwest Atlantic (e.g. Methven & Piatt, 1989; Frank *et al.*, 1996), might have profound influences on the oceanic survival of salmon feeding in those areas. Thus it could be speculated that the ocean survival will fluctuate more in the Northwest Atlantic than in the Northeast Atlantic, due to the apparent higher reliance on capelin and sandeel as food in the Northwest Atlantic (off West Greenland) compared to a more "balanced" diet in the Northeast Atlantic (Table 4 and 5).

There seem to be evidence for a greater decline in the salmon stocks (particularly MSW stocks) in the Northwest Atlantic and in mid and southern Europe, than of stocks from the northern European region (e.g. Parrish *et al.*, 1998; ICES, 1999b). Large proportions of these MSW stocks feed in the Northwest Atlantic area and off West Greenland during some part of their oceanic phase (e.g. Shearer, 1992; Mills, 1993). Thus, I speculate that one reason for the decline might be deteriorating feeding conditions in the Northwest Atlantic during last decade, due to the harsh environmental conditions there since 1990 (DFO, 1998). However, with some improvement in the environmental conditions the last couple of years (DFO, 1998).

Table 4. Food of salmon in the North Atlantic. Frequency of occurrence (%) of prey in each major geographic area. From Table 5.1 in Hislop and Shelton (1993) and references therein, and from **Paper IV**. A + means less than 1%.

Life stage and period[a]	Homing adults	Homing adults	Adults winter	Adults autumn	Adults winter	Adults winter	Adults winter
Area	Canadian shelf	British Isles	Labrador Sea/David Strait	West Greenland	Norwegian Sea	Faroes 1983	Faroes 1992-95 **Paper IV**
No. examined	2267	3096	231	1503	1293	555	3848
No. empty or with only bait	1505	2719	35	152	600	258	1184
No. with food	762	377	196	1351	693	297	2664
Percentage with food	34	12	85	90	54	54	69
(1) FISH							
Clupeoids							
Clupea harengus	10	18	1	+	6	2	+
Sprattus sprattus		15					
Alosa pseudoharengus	+						
Clupeidae		1					
Capelin							
Mallotus villosus	68		+	45	2	2	+
Fry (mostly *Mallotus villosus*)							4
Sandeel							
Ammodyteidae	21	34		48	2	3	+
Lantern fishes							
Benthosema glaciale			1		7		10
Notoscopelus kroeyeri	+		3		+		+
Lampanyctus macdonaldi			1		+		
Lampanyctus crocodilus							+
Myctophum punctatum							+
Protomyctophum arcticum					+		
Hierops arctica			+				
Myctophidae				+	20	22	8
Barracudinas							
Paralepis c. borealis							+
Notolepis rissoi kroyeri					+		+
Paralepidae	+		30	2		1	3
Pearlside							
Maurolicus muelleri					+	3	18
Other fish	+	4		+	6	4	+
Unidentified fish	11	14	38	17	20	13	37
(2) INVERTEBRATES							
Annelids	1	1		1	+		
Insects	+	1					+
Crustaceans							
Copepoda						+	+
Amphipoda	3	6	37	24	12	61	66
Isopoda					3		
Euphausiids	2	+	5	22	36	32	51
Other crustaceans	+	2	4		+	8	25
Unidentified crustaceans					2		19
Mollusca							
Spiratella helicina	1						
Squid							
Gonatus fabricii			33	+	7		1
Unidentified/other squid	+		+		5	+	
Unidentified invertebrates	+		+	+			
(3) UNIDENTIFIED REMAINS					13		5

Table 5. Food of preadult and adult Atlantic salmon in the North Atlantic. Percentage composition by weight in the diet in each major geographic area. From Table 5.2 in (Hislop & Shelton, 1993) and references therein. Old Faroese data recalculated from Hislop and Youngson (1984) and new Faroese data from **Paper IV**. A + means less than 1%.

Life stage and period	Homing adults	Homing adults	Adults winter	Adults autumn	Adults winter	Adults winter
Area	Canadian shelf	British Isles	Labrador Sea/David Strait	West Greenland	Faroes 1983[a]	Faroes 1992-95 **Paper IV**
No. examined	2267	3096	231	1503	555	3848
No. empty or with only bait	1505	2719	35	152	258	1184
No. with food	762	377	196	1351	297	2664
Percentage with food	34	12	85	90	54	69
(a) Total stomach content						
Fish	98	99	83	82	66	66
Crustaceans	+	+	14	16	32	30
Molluscs	+					
Squid			3		2	2
Annelids	+	+	+	+		
Insects	+					
Unidentified	+		+	2		2
(b) Principal fish prey						
Clupeoids	13	57	+	+		18
Capelin	74		+	72	25	5
Sandeel	11	30	3	17		+
Lantern fishes	+		16		73	29
Barracudinas	+		59	2	2	22
Pearlside					1	16
Others	2	13	24	9		10
(c) Principal crustacean prey						
Amphipods	87	+	97	60	97	67
Euphausiids	+		+	40	1	17
Other	11	+	2		2	16

[a] The weight percentages from the Faroese area in 1983 (Hislop & Youngson, 1984) have been recalculated in order to conform to the species list in the present stomach data (**Paper IV**).

Is salmon an opportunistic feeder?

Several authors have suggested that Atlantic salmon are opportunistic feeders (Hansen & Pethon, 1985; Reddin, 1988; Pearcy, 1992; Hislop & Shelton, 1993; Sturlaugsson, 1994). However, in the Atlantic there is no information that compares the diet of salmon with the potential prey available. Although information from literature on plankton and micronekton distributions in the Northeast Atlantic (e.g. Dunbar, 1964; Johnson & Kitchell, 1996; Dalpadado *et al.*, 1998) might give a clue to the potential prey of salmon, the non-overlapping temporal and spatial nature of the data prevents any conclusion on prey selection. Furthermore, the vertical distribution of salmon in the sea is poorly known and have been mainly inferred from catching (Templeman, 1968; Reddin, 1985; Reddin &

Shearer, 1987; Dutil & Coutu, 1988). However, salmon is known to undertake deep dives, deeper than 150 m (Jákupsstovu, 1988) for shorter or longer periods. Thus, so far the feeding behaviour and forage strategy of Atlantic salmon has only been inferred from indirect measures such as stomach analysis.

In the present investigations (**Paper IV**) corresponding plankton samples (MIK net) from the upper 50 m were taken on 13 fishing locations to compare the diet of salmon to available food. Even if most of the species occurred in both data sets, their relative proportion differed greatly (see Table 5 in **Paper IV**). The results suggest that fish were preferred over crustaceans, and amphipods were preferred over euphausiids. Furthermore, of the three euphausiids present the larger *Meganyctiphanes norvegica* was preferred over the smaller *Thysanoessa inermis* and *Th. longicaudata* by salmon. The euphausiids ingested were larger than those from the habitat samples (**Paper IV**). The preference of fish to crustaceans, and of the larger *M. norvegica* over *Thysanoessa* spp. can be explained by size selective feeding of salmon. However, the preference of amphipods to euphausiids seems more subtle, as their sizes are comparable in the plankton samples, although in the stomachs the euphausiids were larger than the amphipods. The energetic content of euphausiids and amphipods might be different as well as their visual contrast in the sea, in particular the large and heavily pigmented compound eye of amphipods may make them more conspicuous (Zaret & Kerfoot, 1975), or their swimming and predatory escape behaviour might be different. It further seems that although there are numerous *Thysanoessa* spp. available in the upper 50 m from the plankton data, this genus is hardly preyed upon by salmon. In the Pacific, Peterson et al. (1982) also found a preference for amphipods to similar sized stages of a copepod of juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) off the Oregon coast, and Brodeur et al. (1992) estimated that the consumption of euphausiids as percentage of total biomass was quite low (0.01% d^{-1}) by coho and chinook, although the abundance of euphausiids from plankton tows were high.

Holst et al. (1996) found a tendency of size-selective feeding of salmon post-smolts of the hyperiid amphipods (*Themisto* spp.), as indicated by a positive relation between prey size in the stomachs and post-smolts size. This corresponds with the findings of a weak, but significant correlation between length of salmon and length of *Themisto libellula* prey (**Paper IV**). Furthermore, Holst et al. (1996) noted that given that O-group fish were available in the area as observed from the trawl catches and that amphipods also were available from parallel plankton sampling, the post-smolts fed mainly on O-group fish, indicating a selective feeding strategy. Selective feeding was also reported by Lear (1972) in the Northwest Atlantic, where salmon preferred herring to capelin, and the large salmon contained significantly more herring than small salmon.

Salmon did not feed on *Sagitta* spp., although it has been reported as food for salmon in the Pacific (Brodeur & Pearcy, 1990; Tadokoro *et al.*, 1996). It might be speculated that *Sagitta* spp. either is too transparent, unpalatable, or is a low energy prey.

At least two year classes (1 and 2+ group) of pearlside (*Maurolicus müelleri*) were present in the salmon stomachs, however, only the smaller 1 group was present in the plankton samples (**Paper IV**), apparently indicating size selective feeding. Alternatively, the larger 2+ group of pearlside might avoid the plankton sampler or being distributed below the sampling depth of 50 m. The pearlside has been reported in some areas to be separated into two vertical layers in the sea during winter, with the older individuals occupying the lower layer (Goodson *et al.*, 1995) and are reported to be most numerous below 200 m depth in the Norwegian Sea (Dalpadado *et al.*, 1998). Thus salmon probably also feed deeper than 50 m. Salmon are generally found to inhabit the upper surface layers (Templeman, 1967; Reddin, 1985; Dutil & Coutu, 1988) most of the time with occasional deep ascents for shorter or longer time periods, deeper that 150 m (Jákupsstovu, 1988). Pacific salmon also occasionally feed deeper than 150-200 m during day (Pearcy *et al.*, 1988).

In summary, although salmon show patterns of opportunistic feeding behaviour, there was also evidence of selective foraging. Generally fish were preferred over crustaceans, and amphipods were chosen over euphausiids. Furthermore, large salmon tended to be more piscivory than smaller fish. Such a feeding behaviour of salmon might influence the dispersal on the feeding areas. Although temperature constraints are indicated to be a strong decisive factor for oceanic distribution of salmon (Reddin, 1985). In **Paper II**, it was suggested that the spatial segregation of various stock complexes and age groups salmon in the feeding area was the result of a trade-off between food availability, age specific thermal limitations (or preferences), and possibly competition from other large pelagic stocks feeding in the area.

Is food a limiting factor for growth and survival of salmon?

Survival in the marine environment is a complex process, and Anderson (1988) summarised four major hypotheses that were used to explain marine mortality of fishes: starvation, predation, physical dispersal, and disease. The effect of temperature and size on development, mortality and survival rates of the early pelagic life stages of marine fishes was reviewed by Pepin (1991). Conditions that determine growth rate during larval phase, such as food availability and temperature, are thought ultimately to determine survival (Ware, 1975; Anderson, 1988; Pepin, 1991). It is likely that the growth-survival/mortality hypothesis put forward for other pelagic marine fishes (Anderson, 1988) also apply to the early marine phase of Atlantic salmon. There is, however, limited knowledge of the factors influencing the growth and survival of post-smolts (Friedland & Reddin, 1993; Friedland *et al.*, 1998), and it remains to be demonstrated that survival of salmon is a direct function of growth, mediated through size-dependent predation. Neither are the indirect effects of climate, such as food availability evident.

It has been shown that ocean climate conditions may affect marine survival of salmon (e.g. Friedland *et al.*, 1993; Friedland *et al.*, 1998). Presently there is no clear single factor that can be identified that cause mortality of salmon in the marine environment. Mortality is probably a combination of different factors as well as synergism between them. Traditionally it is assumed that the major mortality in salmon occur at an early phase of the post-smolt phase (Holtby *et al.*, 1990; Hansen & Quinn, 1998; Friedland, 1998).

Growth in salmonids is correlated with water temperature (Brett, 1979), and Friedland *et al.* (1998) also observed that enhanced growth was associated with years having favourable temperature conditions, which in turn resulted in higher survival (return) rate to the rivers. The suggested relationship between growth of salmon and temperature does not help to explain whether the reduced growth rates of Atlantic salmon in recent years (ICES, 1999b) were due to a reduced abundance of food of high quality, or a result of lower ocean temperatures. The slower growth rates may result in a higher predation pressure (Ware, 1975; Folkvord & Hunter, 1986; Pepin *et al.*, 1987).

The biomass of salmon in the ocean is very low compared with other fish species such as herring, mackerel and blue whiting. Furthermore, several studies suggest that marine mortality is density independent (Chadwick, 1988; Chadwick & Claytor, 1990; Crozier & Kennedy, 1993; Jonsson *et al.*, 1998). It is also suggested that salmon is an opportunistic feeder (**Paper IV**), and therefore should not be dependent on one particular prey. Food is therefore expected to be a limiting factor only in extreme cases.

An external and man made effect on food availability is the potential effect of the industrial fisheries (reduction fishery) mainly operating in coastal areas and on continental shelves, which is obviously the removal of potential prey for salmon. A change in age and size structure of the prey populations indirectly affects the salmon by changing the predator-prey relationship. However, the likely effect might be less than anticipated due to the presumed opportunistic forage behaviour of salmon, and the relatively low number of salmon in the sea, provided that the removal is less than the biomass needed as prey.

In summary, no conclusive statement can be made whether food is limiting for growth and marine survival, and it is suggested that only in extreme cases would food be limiting for salmon in the high seas. Furthermore, since the effect of temperature on survival is not clear, it is an open question whether salmon (in large number) might be lost due to lethal (low) temperatures in the sea.

Possible interactions between fish farm escapees and wild salmon in the ocean

In the following section possible interactions between fish farm escapees and wild salmon on the high seas are examined. This is approached by first giving an overview of suggested interactions and then a discussion of the various aspects covered by the papers in the present thesis.

Escaped farmed salmon have been observed in most areas of the north Atlantic where wild salmon are also found (Lund *et al.*, 1991; Gausen & Moen, 1991; Webb & Youngson, 1992; Carr *et al.*, 1997; Stokesbury & Lacroix, 1997; Youngson *et al.*, 1997), including the high seas fisheries in the Norwegian Sea (Hansen *et al.*, 1993a; Paper I). Several detrimental effects on wild stocks have been suggested from the fish farm escapees (Hindar *et al.*, 1991; Webb *et al.*, 1991; Gross, 1998; Youngson & Verspoor, 1998; Paper I, IV and V), which include:

- interbreeding and redd destruction,
- predation on outgoing smolts by escapees,
- food and space competition in coastal and oceanic areas, and
- source of diseases and parasites and possible transfer of increased levels to wild salmon.

Furthermore, incorrect catch statistics would confound assessment of wild salmon. Interbreeding and transmissions of parasites (especially *Gyrodactylus salaris*) and diseases in coastal areas were considered the most severe (e.g. Hindar *et al.*, 1991; Håstein & Lindstad, 1991; Crozier & Kennedy, 1993; McVicar, 1997; Sægrov *et al.*, 1997; Bakke & Harris, 1998). Of the harmful parasites in the sea, particularly sea lice (*Lepeophtheirus salmonis*) have caused great controversy, especially in the coastal areas of the significant fish farming production countries such as Norway, Scotland and Ireland, where large runs of wild salmon also occur (Hutchinson, 1997).

The effect of fish farming on the survival of salmon in the sea has been discussed extensively in recent years (McVicar, 1997), with the nearly exponential increase in fish farming industry since late 1980s (ICES, 1999b). However, the extent and severity of fish farming to ocean mortality of wild salmon is poorly known (McVicar, 1997; Bakke &

Harris, 1998). Gausen and Moen (1991) reported that high proportions of escaped farmed salmon (>20%) were found only in rivers having fish farms situated closer than 20 km from river outlet. However, it is difficult to draw conclusions on the severity of lice infestations on wild salmon on the coast in relation to numbers and proximity of the fish farms in an area, as no conclusive evidence is provided yet (McVicar, 1997).

Experiments with smolts kept in tanks show that salmon smolts suffer high stress with a load higher than about 10 preadult and adult salmon lice (Nolan *et al.*, 1999), which might render the fish more susceptible to secondary infections, as well as displaying depressed growth rates resulting in either direct or indirect mortality due to higher vulnerability to predators of the infected smolts. A burden of 30 copepodid lice on smolts becomes lethal when they transform into preadult stages on the smolt (Grimnes & Jakobsen, 1996). Thus, sea lice is an important pathogen responsible for high losses of sea-farmed Atlantic salmon (Brandal & Egidius, 1979; Grimnes & Jakobsen, 1996). However, in wild stocks in coastal areas, sea lice are rarely reported to cause severe pathology (White, 1940; Nagasawa, 1987; Johnson *et al.*, 1996). In the Northeast Atlantic there is a paucity of information on salmon lice infestations of wild salmon during their oceanic phase. In the offshore areas of the North Atlantic only four reports of infection on wild salmon have previously been presented (Pippy, 1969; Wootten *et al.*, 1982; Berland, 1993; Holst *et al.*, 1993), and they indicated a level of infestation of 8–20 lice per fish. However, these estimates are considered to suffer from a downward bias due to sampling methods. Nagasawa (1985) showed that Pacific salmon caught by long-line carried over four times as many lice as salmon from comparable gillnet catches and Holst *et al.* (1993) found an inverse correlation between scale losses and prevalence of lice on post-smolts from trawl catches, suggesting loss of lice during capture by these gears as a result of skin abrasion. The present estimate of an abundance of 30 lice per salmon (99.2% prevalence) is considered less biased due to the present sampling method with long-line (**Paper V**). It is thus suggested that a level of about 30 lice on a salmon (>40 cm) is not considered harmful for the survival of the fish in the oceanic feeding phase.

The levels of lice were denser on 1SW escaped farmed salmon than on 1SW wild salmon (**Paper III**). It is thus likely that these escapees carry higher load of lice from coastal areas to the high seas than wild salmon. Furthermore, the presence of both chalimus and pre-adult (juvenile) stages of lice on the salmon throughout the seasons and the increasing abundance and density of lice with sea age of wild salmon indicate that infestation occurs in the open sea (**Paper V**). Thus it is possible that escaped farmed salmon transfer increasing numbers of sea lice to wild salmon in the ocean. Unfortunately, no historic data exist to compare lice levels of salmon on the high seas, and furthermore it is not clear which and how the mechanisms might operate in high seas transmissions and infestations.

It is suggested that most of the fish farm escapees in the sea during autumn and winter have escaped from Norwegian fish farms (**Paper I and III**). Our results demonstrate that of the 1SW salmon the fish farm escapees had a significantly higher load of lice than the wild salmon (**Paper V**), and it might be speculated that the escapees caught in the high seas were the survivors, with the most heavily infected fish lost either directly due to predation or indirectly due to subsequent diseases. For example the observation of four heavily infected 1SW escaped farmed salmon with more than 100 adult lice, and one with nearly 300 lice, caught in an area far north of the traditional autumn fishing grounds (**Paper V**), were obviously in the wrong place at the wrong time, with lice levels that were considered lethal (Grimnes & Jakobsen, 1996). Furthermore, these four fish had a higher than average number of juvenile lice stages attached, indicating that they probably had escaped fairly recently.

There were no differences in the feeding habits between wild and escaped farmed salmon, and it was suggested in **Paper IV** that the escapees feed as efficiently as wild salmon and that they were completely adapted to the marine environment. Farmed salmon were also observed feeding in Scottish waters (Hislop & Webb, 1992). Thus, the farmed salmon might compete for food with wild salmon in the high seas, although it is suggested that food does not seem to be a limiting factor for survival of salmon in the sea.

Generally the ocean survival seems to be lower for hatchery reared and farmed salmon (Jonsson *et al.*, 1991; Paper III) than in wild fish and their reproductive success is inferior to wild salmon (Jonsson *et al.*, 1990; Lura & Sægrov, 1991; Fleming *et al.*, 1996). Thus it seems as reared salmon in general have lover fitness than wild.

ICES has during many years estimated the exploitation rates of various homewater stocks in the Faroese high seas fishery (e.g. ICES, 1984; 1996). In the assessment of salmon stocks at the sea, it is important to estimate the farmed and ranched component. Unless they are accounted for, the presence of a high proportion of such fish will result in an overestimate of the catches of wild salmon resulting in the size and status of the wild stocks being concealed. Had escaped fish not been accounted for, the assessments of the Faroese fishery would have been impaired, particularly from the 1988/1989 fishing period to the 1991/1992 fishing period, when the farmed proportion was very high. An example from the present thesis (**Paper I**) would be the statistically significant increasing trend in the overall CPUE observed in the Faroese fishery during the period 1980/1981–1992/1993 ($r_s = 0.81$, $p < 0.001$), which usually is interpreted as an increase in stock abundance. However, the apparent increasing abundance in the area could in fact be explained by an increasing abundance of farmed salmon in the area, rather than of wild fish. The adjusted CPUE of wild salmon only for the same period (**Paper I**) showed no trend with time ($r_s = 0.2$, $p > 0.05$).

The results from the present thesis show that (a low) infestation of salmon lice occur in the open ocean and further indicate that escaped farmed salmon may carry a greater number of lice to the sea due to it higher load of parasite compared to wild salmon. The presence of farmed fish in catches would confound stock assessments of wild salmon if not discounted for, and they may possibly affect wild salmon by competing for food on the high seas. Furthermore, there is an indication from tagging that the escapees do not "home" as precisely as do wild salmon and that ocean survival of farmed salmon might be lower than for wild salmon.

CONCLUSIONS AND PERSPECTIVES

This thesis provide new information on various aspects of the marine ecology of Atlantic salmon in the ocean. Further, I have examined possible interactions between wild and escaped farmed salmon in the high seas. This knowledge contribute to improved understanding of the general biology of salmon in the oceanic phase, and may help to develop reliable assessment models of wild salmon.

It is shown that farmed Atlantic salmon that escape from fish farms disperse in the ocean and are found intermingled with the wild salmon. Furthermore, I suggest that farmed salmon may simply be lost at sea (unable to home), experience higher mortality, or are subjected to lower catchability in homewaters because they entered homewaters at different times than wild salmon. Most of the fish farm escapees originate from Norwegian fish farms.

It is shown that wild salmon from large parts of their natural distribution range are present in the Faroes area during some stage of their oceanic feeding phase. Norwegian salmon are most abundant, but relative high number of salmon from Scotland and Russia are also present. Even fish of Canadian origin are found in the area.

Apparently there is a change in stock composition of wild salmon from autumn to winter, with an increasing proportion of fish from more northern areas present during winter. This is presumably related to geographic origin of the fish, timing of migration, food availability, competition and sea-surface temperature.

Escaped farmed fish feed and grow as effectively as the wild salmon in the sea, suggesting that the fish farm escapees that survived until captured have adapted to the marine environment. Evidence for both opportunistic and selective forage strategies of salmon have been provided, and food does not appear to be limiting.

It was documented that lice infestations occur in the high seas, however at a much lower levels than in coastal areas. There is a potential for transfer of lice from escaped farmed to wild salmon in the ocean, since the escaped farmed salmon had higher load of lice than wild salmon the first winter at sea.

Further research should emphasise the temporal and spatial aspects of distribution and migration in relation to biological and short- and long-term oceanographic and environmental factors. The large numbers of escaped farmed salmon in the sea should be further addressed, as there is still limited knowledge of their behaviour and ecology.

The biomass of salmon in the ocean is very small compared with the biomass of other pelagic marine species (e.g. herring, mackerel, blue whiting and capelin) and there is a need to examine whether these species interact with Atlantic salmon.

The effect of predation on salmon survival and abundance in the marine phase is virtually unknown, and is in many cases dominated by anecdotal evidence. Noting that predation on salmon is extremely difficult to document in the ocean, dedicated investigations on this subject are certainly needed.

In the present thesis I have focused on salmon of 'catchable' size, i.e. approximately a half year after ocean migration. However, recent work suggest that the post-smolt stage or early sea phase is very important in determining the survival of salmon in the sea, and therefore intensified study of this life-stage is encouraged. Further, the recent development of archival tags provide great opportunities to study details of behaviour of salmon in the sea.

Thus, I have tried to peer into the 'black box' and expose some of its contents, but still there are large areas in darkness. Much shall be learned from dedicated future research on the marine behaviour and ecology of Atlantic salmon.

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PAPER I

The incidence of escaped farmed Atlantic salmon, *Salmo salar* L., in the Faroese fishery and estimates of catches of wild salmon.

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The incidence of escaped farmed Atlantic salmon, *Salmo salar* L., in the Faroese fishery and estimates of catches of wild salmon

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Hansen, L. P., Jacobsen, J. A., and Lund, R. A. 1999. The incidence of escaped farmed Atlantic salmon, *Salmo salar* L., in the Faroese fishery and estimates of catches of wild salmon. – ICES Journal of Marine Science, 56: 200–206.

The proportion of Atlantic salmon escaped from fish farms and caught in the Faroese salmon fishery was estimated using scale analysis. Samples were obtained of fish landed in the commercial fishery from 1980/1981 to 1990/1991 fishing seasons and from research catches in the 1991/1992 to 1995/1996 seasons. The material collected was in some years limited to only part of the fishing season. The estimated proportion of farmed salmon in the fishery was relatively low from 1980/1981 to 1986/1987, but increased considerably thereafter, and reached a peak in the 1989/1990 fishing season when more than 40% of the catch was estimated to be of farmed origin. Later, the proportion declined, and in recent seasons the proportions of farmed salmon were estimated to be around 20%. These estimates were used to split the Faroese catch into wild and farmed components. It is concluded that if farmed components in salmon catches are not accounted for, catches of wild salmon will be overestimated and assessments of fisheries and stocks of wild salmon confounded. Furthermore, the increase observed in catch per unit of effort (c.p.u.e.) in the 1980s and early 1990s might have been caused by an increasing abundance of farmed salmon.

Key words: Atlantic salmon, wild salmon, escaped farmed salmon, Faroes, Norwegian Sea, scale analysis, long-line, assessment

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Introduction

In recent years, salmon farming has expanded considerably. In 1995, 411 580 t were produced in the North Atlantic, with Norway and Scotland accounting for the majority of the production (ICES, 1997). In comparison, the total nominal landings of salmon in commercial fisheries in the North Atlantic in 1995 were 3339 tonnes (ICES, 1997). This catch figure, however, also includes a proportion of salmon released as smolts for ranching, or for stock enhancement, and fish farm escapees (ICES, 1997). In any case, the total number of salmon in fish farms far outweigh the number of wild salmon. This must only heighten our interest in escapes into the wild of salmon from fish farms.

Evidence from the Norwegian fish farming industry indicates that losses from the cages can occur at any time after the fish are placed in the sea and at all life stages. Escaped fish are caught in fisheries and, when sexually mature, they enter fresh water to spawn (e.g. Hansen *et al.*, 1987; Gausen and Moen, 1991; Lura and Sægrov, 1991; Webb *et al.*, 1991).

Tagged farmed salmon released directly into Norwegian coastal waters were recaptured in the high seas fishery at Faroes (Hansen *et al.*, 1987), and Hansen *et al.* (1993) demonstrated that large numbers of escaped farmed Atlantic salmon were present in oceanic waters in the Northeast Atlantic ocean and accounted for a substantial part of the commercial salmon catches at Faroes.

The entry of fish farm escapees into most areas of the North Atlantic (e.g. Gausen and Moen, 1991; Lund *et al.*, 1991; Webb and Youngson, 1992; Hansen *et al.*, 1993; Carr *et al.*, 1997; Stokesbury and Lacroix, 1997;

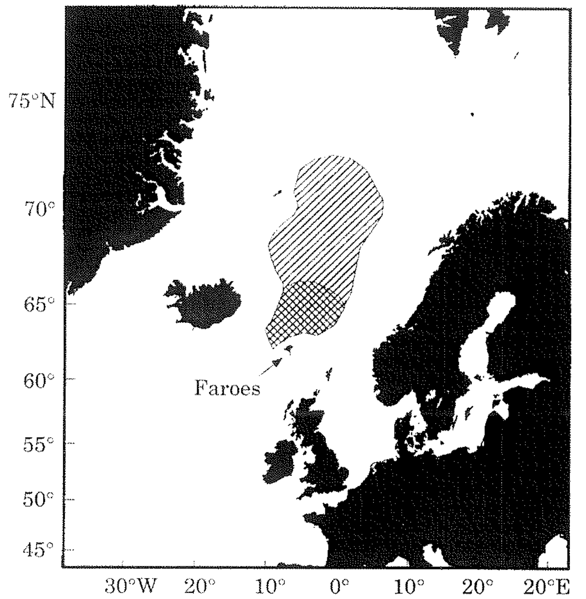

Figure 1. Map of the Northeast Atlantic showing the Faroese fishing areas for salmon where scale samples were obtained. Fishing areas prior to 1984 are shown as hatched areas and after 1984 as crosshatched areas, when quota restrictions were in force and the fishery was confined to the Faroese area.

Youngson *et al.*, 1997) where wild salmon are also found, poses several possible problems. First, interbreeding of farmed and wild salmon has been suggested to have negative effects on wild stocks (e.g. Hindar *et al.*, 1991). Second, transmission of parasites and diseases occurs between farmed and wild stocks (e.g. Håstein and Lindstad, 1991). Third, raw catch records from fisheries exploiting both wild fish and farm escapees will confound the assessment of stock status of wild fish. It is therefore of great importance to identify the proportion of farmed fish and adjust catch records accordingly.

The aim of the present paper is to develop a time series of the estimated proportion of escaped farmed salmon in the Faroese long-line fishery, and subsequently to estimate the number and catch per unit effort (c.p.u.e.) of farmed and wild salmon caught.

Material and methods

The Faroese Fishery Laboratory has systematically sampled scales from the commercial long-line fishery for Atlantic salmon north of the Faroes since 1980 to determine the smolt age and sea age of the salmon caught. These scale samples were re-examined in order to estimate the occurrence of farmed salmon in the fishery. The material analysed was collected from the 1980/1981 fishing season onwards to the 1995/1996 fishing season, and came mainly from the areas north of the Faroes (Fig. 1). In November to December sampling was carried out closer to the Faroes than in January to April, and in the years prior to 1984 part of the samples were taken far north of the Faroe Islands in international waters in the Norwegian Sea. From the 1980/1981 fishing season to the end of 1990, commercial salmon catches were sampled, whereas from 1991 to 1995 samples were obtained from a research fishery operated by only one vessel. During the whole period, scale samples were collected randomly from the catch, and the fish were measured (fork length; cm) and weighed to the nearest 0.1 kg.

Identification of farmed fish was carried out by scale analysis (Lund *et al.*, 1989; Lund and Hansen, 1991). This method has been developed by analysis of scales from Norwegian salmon of known origin, and the characters used were estimated smolt size, the characteristics of the transition zone from fresh water to salt water, the position of sea winter bands, the number of summer checks, and the proportion of replacement scales at the marine stage. To be classified as reared, at least two out of the six characters examined must indicate that the fish were of reared origin. This method has been shown to give good separation between farmed and wild salmon, but fish that escaped at the smolt stage or were released as smolts for ranching or enhancement are difficult to detect accurately, and their numbers are thus underestimated (Lund and Hansen, 1991).

Sampling was not carried out throughout the fishing seasons; in 11 out of 16 seasons only part of the season was sampled, and in two seasons sampling was carried out only in 1 month (Table 1). The number of scale samples collected on a monthly basis varied from 22 to 270 and on seasonal basis from 100 to 850 (Table 1).

Monthly variations within fishing seasons in the proportion of farmed fish were examined using χ^2 tests. The only significant differences occurred in the 1991/1992 ($p<0.001$) and 1993/1994 ($p=0.018$) fishing seasons, whereas in the 12 other fishing seasons, when data from two or more months were available, no signficant differences were detected. To split the total catch of salmon at Faroes by season into wild and farmed components, it was found appropriate to use the unweighted mean proportions by season of fish from these two groups in the calculations, as no clear trend could be observed within the seasons. Hence we treat the monthly samples as being random samples from the whole season.

To introduce confidence intervals on the estimated proportions of the farmed component each season, and on estimated catches of wild and farmed salmon, the binomial error function was calculated using Monte-Carlo simulation (@Risk, 2000 simulations) to estimate the 5 and 95% bounds assuming non-symmetrical variance around the mean proportions. The possible error due to non-random sampling by month within each season is not considered in this calculation. Confidence

Table 1. The material used for classification of salmon sampled in the Faroes long-line fisheries since 1980. *Samples only from latter part of the season (January to April); **Only 1 month sampled that season.

Season	Time	Year	Wild	Reared	Unclassifiable	Total
1980/81	January	1981	153	4	1	158
	March	1981	124	3	5	132
1980/81*	January–March		277	7	6	290
1981/82	January	1982	74	3	1	78
	February	1982	70	0	0	70
	March	1982	44	1	1	46
	April	1982	22	0	0	22
1981/82*	January–April		210	4	2	216
1982/83	February	1983	48	1	1	50
	March	1983	63	2	1	66
	April	1983	63	0	5	68
1982/83*	February–April		174	3	7	184
1983/84	January	1984	147	4	5	156
	February	1984	52	5	2	59
1983/84*	January–February		199	9	7	215
1984/85	January	1985	71	8	1	80
	February	1985	47	4	1	52
	March	1985	90	6	3	99
	April	1985	35	2	2	39
1984/85*	January–April		243	20	7	270
1985/86	January	1986	52	2	3	57
	February	1986	53	4	3	60
	April	1986	75	2	1	78
1985/86*	January–April		180	8	7	195
1986/87	March	1987	134	4	2	140
	April	1987	66	2	1	69
1986/87*	March–April		200	6	3	209
1987/88	January	1988	45	3	2	50
	February	1988	73	10	0	83
	April	1988	82	4	1	87
1987/88*	January–April		200	17	3	220
1988/89	November	1988	75	23	2	100
	January	1989	91	20	8	119
	April	1989	83	12	6	101
1988/89	November–April		249	55	16	320
1989/90	January	1990	106	87	13	206
	February	1990	36	32	5	73
1989/90*	January–February		142	119	18	279
1990/91**	December	1990	49	42	8	99
1991/92	November	1991	71	47	4	122
	December	1991	117	69	10	196
	February	1992	100	102	6	208
	March	1992	87	40	2	129
	April	1992	133	56	9	198
1991/92	November–April		508	314	31	853
1992/93	November	1992	11	8	6	25
	December	1992	54	18	22	94
	March	1993	125	61	14	200
1992/93	November–March		190	87	42	319
1993/94	November	1993	132	58	10	200
	December	1993	124	65	9	198
	January	1994	15	5	5	25
	February	1994	112	27	10	149
	March	1994	153	50	13	216
1993/94	November–April		536	205	47	788
1994/95	November	1994	120	34	2	156
	February	1995	83	22	1	106
	March	1995	88	16	7	111
1994/95	November–March		291	72	10	373
1995/96**	December	1995	195	64	11	270

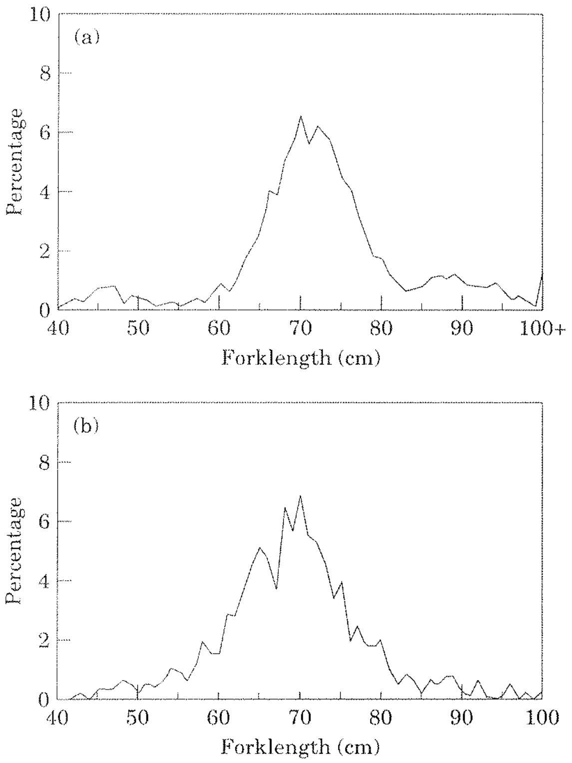

Figure 2. Fork length distribution of wild salmon (a) (n=3887) and salmon escaped from fish farms (b) (n=967), based on samples taken north of the Faroes for scale readings during the fishing seasons 1980/1981 to 1994/1995.

intervals for the c.p.u.e. estimates were calculated using the same method.

Results

The fork length distribution of the total number of salmon estimated to be of wild and farmed origin is shown in Figure 2. Although there were some variations among seasons, the majority of the wild fish were between 60 and 80 cm in length [Fig. 2(a)]. This corresponds to the size distribution of salmon in their second sea year which is the dominating component in the commercial fishery. Fish less than 60 cm and larger than 80 cm are usually in their first and third winter at sea. From the 1980/1981 to 1986/1987 fishing seasons the estimated number of farmed salmon was small, but increased thereafter. The great majority of farmed salmon were also between 60 and 80 cm [Fig. 2(b)].

The time series of the estimated proportions of farmed salmon in the Faroes fishery between the 1980/1981 and the 1995/1996 fishing seasons are shown in Figure 3, superimposed on the time series of the total production of farmed salmon in the Northeast Atlantic the same year (i.e. the proportion of farmed salmon in 1980/1981 season is compared to the production in 1981 etc.). The proportion of farmed fish was relatively low from 1980/1981 to 1986/1987, increased considerably thereafter, and reached a peak in the 1989/1990 and 1990/1991 fishing seasons, when more than 40% of the fish sampled were estimated to be of farmed origin. Thereafter, the proportion declined, and in the last three fishing seasons of the time series the proportion of farmed fish was estimated to be around 20%. This development reflects the trends in production of farmed salmon in the Northeast Atlantic until the 1992/1993 fishing season, but after that the proportion of farmed salmon at Faroes fell while farmed production continued to increase. The estimated proportion of farmed salmon in the Faroese fishery was significantly correlated with the total production of farmed salmon in the Northeast Atlantic (Spearman rank correlation analysis: $r_s=0.78$, $p=0.0006$).

Estimated catches at Faroes of wild and farmed salmon are shown in Figure 4. A decline in the catches of wild salmon from the 1988/1989 fishing season to the 1990/1991 fishing season is apparent when the catches have been corrected for farmed salmon. Since 1991 in Faroese boat owners have agreed to accept compensation for not fishing the salmon quota, allowing only one research vessel to operate in the area. Low catches from the 1991/1992 fishing season and onwards should therefore not be confused with low stock levels.

Catch per unit effort levels for wild and farmed salmon for the fishing seasons 1981/1982 to 1994/1995 are shown in Figure 5. During the time series the effort has declined, and since 1991 only one vessel has been operating. However, it appears that there is an increasing trend in c.p.u.e. for all salmon combined, from the 1981/1982 to 1992/1993 fishing season, which is explained by an increased c.p.u.e. of farmed salmon. In the 1993/1994 and 1994/1995 fishing seasons c.p.u.e. values were relatively low.

Discussion

The methodology used to classify the fish tends to underestimate the proportion of reared fish, in particular those escaped at the freshwater stage, or at an early marine stage (Lund *et al.*, 1989; Lund and Hansen, 1991). On the other hand, the method will also detect some of the salmon released for ranching or as smolts in stock enhancement programmes. However, a large part of these fish carry external or internal tags, often combined with fin clips. The salmon analysed in the present material were screened for tags, and tagged fish were not included in the analysis. Furthermore, the number of hatchery reared smolts released into rivers in the Northeast Atlantic is relatively small compared with the number of wild salmon present, except in Iceland where ranching has been established as an industry. However,

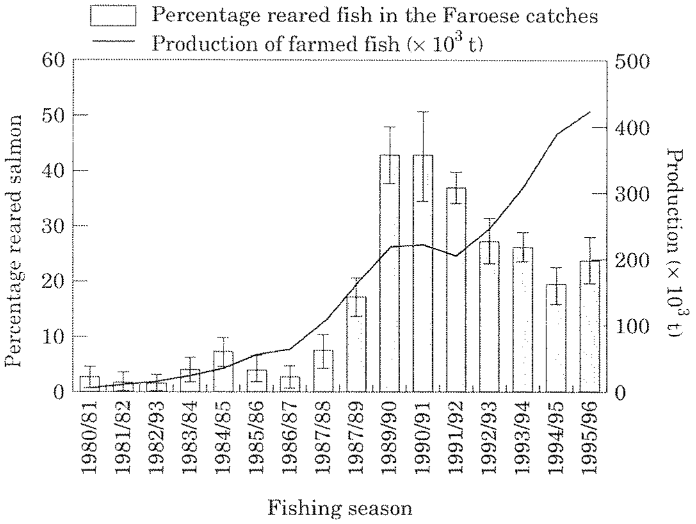

Figure 3. Production of farmed salmon in the Northeast Atlantic and estimated percentage of escaped farmed salmon caught in the Faroese long-line fishery for salmon. Error bounds (95% confidence limits) on the separation of catch into wild and farmed salmon are indicated (Monte Carlo simulation, 2000 simulations using @Risk).

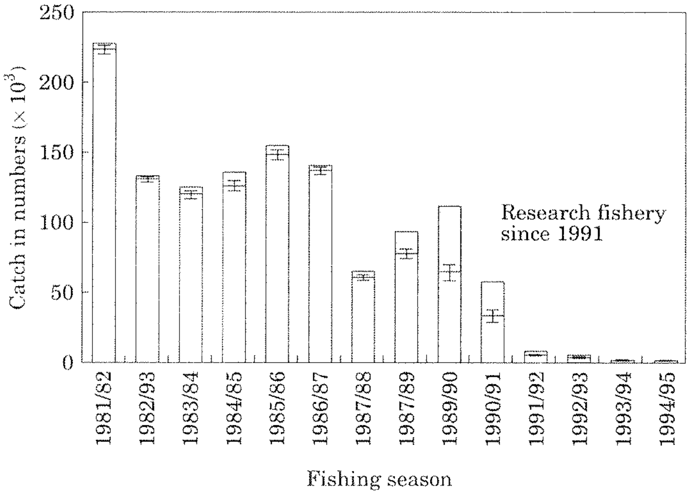

Figure 4. Estimated catches of wild (open bars) and farmed (shaded bars) Atlantic salmon in Faroese waters from the 1981/1982 fishing season. In the intersection between wild and farmed fish each year 95% confidence levels are shown (Monte Carlo simulation, 2000 simulations using @Risk). Low catches from 1991/1992 and onwards are due to the fact that the "fisheries" were conducted by a single research vessel.

very few fish tagged in Icelandic ranching operations have been reported from the Faroese fishery, suggesting that they exploit other feeding areas. All in all, this suggests that deliberately released salmon smolts are a relatively small component of the salmon sampled, and that escaped farmed salmon account for the major proportion.

A bias in the estimated proportions of farmed salmon might have been introduced due to the limited sampling in the first part of the time series where only the latter part of the fishing season (January to April) was sampled. Although in the 1993/1994 fishing season there was a significant downward trend in the proportion of farmed fish as the season progressed, i.e. from November to March, no clear trend was observed within the other seasons. We could therefore not provide any corrections to the time series due to data deficiency. Any bias would have had little effect prior to the 1988/1989 fishing season when the proportion of farmed fish was low. However, in the 1989/1990 fishing season and in particular in the 1990/1991 fishing season, when the proportion of farmed fish was at its maximum in the

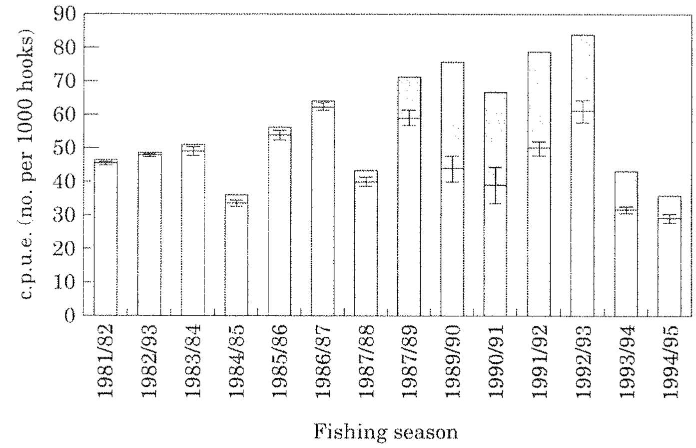

Figure 5. Catch per unit effort (c.p.u.e.; catch in number per 1000 hooks per day) of wild salmon (lower portion of the bars) and escaped farmed salmon (shaded bars) in the Faroese salmon fisheries since the 1981/1982 fishing season. Since 1991 only one research vessel has been operating in the area. Error bounds (95% confidence limits) on the separation of catch into wild and farmed salmon are indicated (Monte Carlo simulation, 2000 simulations using @Risk).

time series, the sampling was limited to only 2 months and 1 month, respectively. The estimated proportions of farmed fish in those two fishing seasons might therefore be more uncertain than in fishing seasons when sampling was more complete.

The variation in the proportion of farmed salmon among seasons in the salmon fisheries at Faroes is relatively consistent with the increase in overall production of farmed salmon in the Northeast Atlantic until the 1992/1993 fishing season. In the 1992/1993 to 1995/1996 fishing seasons however, the proportion of farmed salmon was significantly lower that in the previous three seasons, despite the fact that the production of farmed salmon increased considerably during the same period. The most likely reason for this is a reduction in number of fish escaping from fish farms. Alternatively, because the proportion of farmed salmon is also dependent on the number of wild salmon present in the area, this apparent inconsistency might also be explained by increased abundance of wild fish, although this is not supported by trends in c.p.u.e. (Fig. 5). Furthermore, recent assessments of salmon stocks in the North Atlantic strongly suggest a decline in the abundance of wild salmon in the area (ICES, 1997).

The total production of farmed salmon in the Atlantic in 1995 was 411 580 t (ICES, 1997). Of this, 95% were produced in Europe, and of the total production Norway and Scotland accounted for 72 and 17%, respectively. The production at Faroes was 9000 tonnes which represents about 2% of total production in the Atlantic. Salmon escape from cages in all areas where farms are present, and it is reasonable to assume that the largest number of fish escape from Norwegian farms.

In Norway, experimental releases of tagged farmed salmon during their first year in sea cages have shown that the survival to sexual maturity is highest when the fish are released in the spring. When they are released in late summer and autumn, survival is low (Hansen and Jonsson, 1989). Furthermore, in most cases these fish return to the general marine area from where they escaped. However, fish that escaped in March strayed to rivers far from the site of escape, although they were not reported from areas other than Norway and the west coast of Sweden (Hansen and Jonsson, 1991). The high proportion of farmed salmon observed in Norwegian home water fisheries (Lund *et al.*, 1996), combined with the fact that Norway accounts for the major production of farmed salmon in the Atlantic, strongly suggest that most farmed salmon occurring in the Norwegian Sea are of Norwegian origin. This is supported by the fact that tagged farmed salmon released on the Norwegian coast were recaptured in the Faroese fishery (Hansen *et al.*, 1987). However, we cannot rule out that farmed fish escaping from cages in Scotland, Faroes, and Ireland also contribute to the Faroese fishery.

When assessing salmon fisheries and wild salmon stocks, it is important to estimate the farmed and ranched component of the catch. If such fish are not accounted for, their presence will result in an overestimate of the catches of wild salmon and the size and status of the wild stocks will be obscured. Had escaped fish not been accounted for, assessments of the Faroese fishery would have been impaired, particularly from the 1988/1989 fishing season to the 1991/1992 fishing season, when the farmed proportion was very high. Furthermore, the increasing trend in c.p.u.e. for salmon caught from the 1981/1982 to 1992/1993 fishing season would have been attributed to an increasing abundance of farmed salmon, rather than wild fish.

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PAPER II

Seasonal differences in origin of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea based on estimates from age structures and tag recaptures.

Seasonal differences in the origin of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea based on estimates from age structures and tag recaptures

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Abstract

To test if the population structure of Atlantic salmon (*Salmo salar* L.) at the feeding areas in the Norwegian Sea north of the Faroes is stable throughout autumn (November–December) and winter (February–March), river and sea age distribution was estimated from 2,350 scale samples obtained in the autumn and winter during four consecutive fishing periods 1991/1992–1994/1995. In addition, we compared the origin of recaptures of salmon tagged as smolts in different European countries between the two seasons. The fish were classified as being of wild or fish farm origin from scale characteristics, and farmed salmon were excluded from the analyses. Age compositions in samples from the four fishing periods showed consistent patterns. The average smolt age (±SE) was significantly lower in the autumn than in the winter (2.5 ± 0.04 and 2.7 ± 0.03, range 1-5) as was average sea age (1.9 ± 0.03 and 2.2 ± 0.02, range 1-6). As salmon from southern European countries tend to smolt at an earlier age and produce more one-sea winter salmon than in northern Europe, we suggest that a significant proportion of the salmon caught in the Faroes area during autumn originate from southern European countries and that fish from northern regions appear to be more abundant in the winter. Recaptures in the Faroese fishery during autumn and winter of salmon tagged as smolts in different countries support this.

Keywords: Escaped farmed salmon; high seas fishery; country of origin; recaptures; *Salmo salar;* sea age; smolt age; tagging; wild salmon

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1. Introduction

Atlantic salmon (*Salmo salar* L.) are widely distributed in the Northeast Atlantic ocean, and one important feeding area for salmon is the central and southern Norwegian Sea, i.e. the area north off the Faroe Islands (Jákupsstovu, 1988). This area is characterised by a front that separates the warmer Atlantic water from south-west, and the colder and less saline Arctic water from north-west (Hansen, 1985). Salmon are typically distributed in or close to the frontal areas (Jákupsstovu, 1988). A high seas fishery for salmon developed in this area in the 1960s, and Faroese long-liners have exploited this resource since late 1970s (Jákupsstovu, 1988). From recaptures of externally tagged salmon in the Faroes fishery in the early 1980's, there is direct evidence that salmon of different smolt year classes originating from different rivers in Norway, Scotland and Sweden are caught together during the same time period in the same statistical rectangle (Hansen, 1993). Subsequent tagging programmes using external and coded wire tags (CWT) showed that salmon from Ireland, England and Wales (and to a lesser extent Iceland, France and Spain), were also caught together in these areas during the fishing season (ICES, 1996).

The catches consist mainly of fish spending their second winter in the ocean (2SW salmon; ca 80% of the catch), but some 1SW and 3+SW salmon are also caught (ICES, 1996). Reports from fishermen and from landing statistics suggest that fish caught during autumn are smaller than fish landed during the winter period. It is not clear whether this difference could be accounted for by growth, i.e. by the longer feeding period of fish that were sampled in the winter period, or whether this reflects changes in the population structure.

Smolt and sea age of salmon differ between salmon populations from different regions of Europe, tending to be lower in salmon stocks from the southern regions such as Spain, France, UK and Ireland than in northern regions like Norway and Russia (Templeman, 1967; Power, 1969; Baglinière, 1976; Munro and Swain, 1980; Metcalfe and Thorpe, 1990; ICES, 1996).

We tested the hypothesis that the population structure of Atlantic salmon at Faroes is stable throughout the autumn and winter by examining the temporal and spatial differences in smolt and sea age in salmon during their feeding period north of the Faroes. Furthermore, we compared the origin of salmon tagged as smolts in different European countries that were recaptured in this area in the autumn and winter.

2. Materials and methods

Scale samples of 2,350 Atlantic salmon were collected north of the Faroe Islands during autumn (November–December) and winter (February–March, a few samples were also taken in April 1992) in four consecutive fishing periods 1991/1992–1994/1995 (Fig. 1). The fish were sampled randomly from the long-lines during haul-back, and scale samples were collected from the dorso-lateral area on the left side of the fish as recommended by Shearer (1992). Fork lengths and total weights of the fish were recorded. The sea-surface temperature (SST) was measured four times a day, before and after setting, and before and after hauling of the long-line. There was a gradual shift in the fishing areas in a north-eastern direction from the beginning of the fishing period (early autumn) to the end of the period (late winter), this was accompanied by a shift in the ambient SST (±SD) at the fishing locations from 7.7ºC ± 1.1ºC (n = 29) in the autumn to 3.3ºC ± 0.8ºC (n = 27) in the winter.

A salmon which has spent its first winter in the sea is termed a one sea-winter (1SW) salmon. Salmon spending two, three or more winters at sea are termed two sea-winter (2SW) salmon, three sea-winter (3SW) salmon etc. When 3SW and older salmon have been pooled the term 3+SW is used. In order to interpret the results it should be noted that the sea age of the fish is defined as changing in September and not the beginning of the year, i.e. a salmon is assumed to be the same sea age throughout the autumn and winter seasons.

Since the late 1980's, the expanding fish farm industry in the Northeast Atlantic has resulted in the presence of fish farm escapees in the fishing areas (Hansen et al., 1993; 1999). These escapees were identified using scale analysis (Lund and Hansen, 1991). The number of scale samples collected in the different fishing periods is shown in Table 1. Of the 2,350 fish examined, 678 (29%) were judged to be of farmed origin and 1525 (65%) were identified as wild salmon. Approximately 6% of the fish could not be classified to either group. The farmed and the unclassified fish were excluded from the analysis. It was possible to estimate sea age from 1520 (99.7% of the number of scales available) fish and smolt age from 1335 (87.5%) wild fish. The reason for the relatively low number of samples with readable smolt age was due to the fact that a number of scales had incomplete annual zones at the freshwater stage.

During the sampling period all fish caught were screened for external Carlin tags and internal coded wire tags and 296 tagged salmon were recaptured. These tagged fish were released as smolts (during spring and summer) and originated from several countries. The recaptures were not weighted by the number of tagged fish released from each country. Instead, the proportions of recoveries were used for comparison between the autumn and winter seasons. Chi-square tests were used to analyse differences in smolt and sea age distributions between autumn and winter and t-tests were used to compare mean lengths between seasons.

3. Results

The smolt age of wild salmon varied between 1 and 5 years, and mean smolt ages during the four fishing periods varied between 2.3 and 2.6 years in the autumn samples and between 2.7 and 2.8 years in the winter samples (Table 2). The smolt age distributions were significantly different between autumn and winter, being higher in the winter samples in all fishing periods (χ^2 tests, df = 3 in all cases, 1991/1992: $p = 0.02$, 1992/1993: $p < 0.001$, 1993/1994: $p = 0.001$, 1994/1995: $p < 0.001$).

The sea age of wild salmon varied between 1 and 6 years, and mean sea age during the four fishing periods varied between 1.8 and 2.0 years in the autumn samples and between 2.1 and 2.4 years in the winter samples (Table 3). The sea age distributions were significantly different between the autumn and winter samples in all fishing periods (χ^2 tests, df = 2 in all cases, $p < 0.001$ for all four periods).

The size of the wild fish (total material) ranged from 38 to 118 cm, and the 1SW, 2SW and 3+SW age groups can be identified as three successive peaks in the length distributions (Fig. 2). The mean size at sea age (±SE) was significantly lower in the autumn samples (45 ± 0.4, 67 ± 0.2, 83 ± 1.2) than in the winter samples (48 ± 0.4, 72 ± 0.2, 88 ± 0.5) for age 1, 2 and 3SW, respectively (t-tests, $p < 0.001$ for all ages, pooled material, Fig. 3). This was consistent in all four fishing periods.

The tagged salmon recovered from the Faroese fishery in 1991 to 1995 were mainly tagged as smolts in Norway and Ireland (Table 4). This is not surprising as these countries account for most of the tagged smolts in the east Atlantic. To test possible spatial and temporal differences in population structures and hence in recaptures, the origin of the tag recaptures were grouped by two main geographical regions, i.e. a northern European group (Norway, Sweden, Iceland and Faroe Islands) and a southern European group (Ireland, Scotland, England/Wales, Northern-Ireland, France and

Spain). The proportions of salmon recaptured (Table 4) from the northern and the southern countries were significantly different between seasons ($\chi^2 = 54.0$, df = 1, $p < 0.001$). The recapture proportions of the northern and southern groups were similar during autumn (53.5 vs. 46.5%) whereas during winter the proportion of salmon from the southern European region was much lower (9.9%) than that from the northern region (90.1%) (Fig. 4).

To examine this difference more closely, we compared tag recaptures of salmon originating from the northern and southern group analysed by sea age (Table 5).

There were higher proportions of 1SW fish of northern origin recaptured in winter than of southern origin, which is opposite to the situation in the autumn ($\chi^2 = 17.5$, df = 1, $p < 0.001$). For 2+SW fish the same holds true with 2/3 of the northern fish recaptured in winter when only 1/3 of the southern fish were recaptured ($\chi^2 = 13.7$, df = 1, $p < 0.001$). Thus, for all ages, the proportions of salmon recovered from the northern region were lower during autumn (34%) than during winter (66%) while the proportion of fish from the southern region seem to be much lower during winter (85% in autumn and 15% in winter) ($\chi^2 = 54.0$, df = 1, $p < 0.001$). There were no significant seasonal differences in the recovery proportions between 1 and 2+SW salmon within each region ($p = 0.427$ and 0.188 for northern and southern group, respectively).

In total for both seasons, 87% of the fish from the northern region were recaptured as 2+SW and 13% as 1SW, and from the southern region the great majority of the fish was recovered as 1SW fish (74%) whereas 26% were recovered as 2+SW (Table 5). The difference in the proportion of 1 and 2+SW fish of northern and southern origin was highly significant ($\chi^2 = 93.0$, df = 1, $p < 0.001$). These results indicate a structural change from autumn to winter in both the total proportions of fish available as well as in the age distributions from the two fishing areas.

4. Discussion

Based on the data in the present paper we reject the null hypothesis that there are no temporal or spatial differences in population structure of Atlantic salmon during their feeding period north of the Faroes. Alternatively, there appears to be evidence for a change in stock complexes entering and departing these areas. Particularly salmon from areas in southern and mid part of Europe are observed in higher proportions in the autumn (November–December) than in winter (February–March) when fish from northern areas were more abundant.

We observed that salmon caught in the area north of the Faroes had lower smolt and sea ages during autumn than in the winter period. Because salmon from southern parts of Europe generally are of lower smolt ages as well as lower sea ages than from northern areas we suggest that our observations are at least partly due to a change in proportions of the salmon stocks present in the Faroes area with time, with the higher proportion during the autumn period originating from southern European countries while relatively more salmon from northern European countries inhabit the Faroese area during the winter period. The proportions of total tag recaptures of fish from the northern and southern region were not different in the autumn, whereas the proportion of fish from the southern region where considerably reduced during winter. For one-sea winter fish, salmon from the southern European countries predominated in the autumn, whereas in the winter, a higher proportion of fish from the northern countries were taken. Among the 2+SW fish, the predominant component was of northern origin, during both autumn and winter. This, together with the observed changes in river and sea age composition suggests a change in the stock composition in the area. Some of this difference, however, may be accounted for by the fact that the Faroes salmon fishery moves somewhat towards north-east during winter. The centre of distribution of the samples is shifted about 60 nm to the north-east from autumn to winter.

It might be suspected that the newcomers (1SW) from the northern areas, which have spent less time in the sea for growth than the southern European cohorts, are too small to be taken effectively by the long-lines in the autumn season. The size selectivity of the salmon long-line is not known, but generally for long-lines it has been suggested that bait size is the most important size selection factor followed by hook size in catching cod and haddock by long-lines (Løkkeborg, 1994). We used whole sprat (approximately 12 cm in total length) as baits, which might reduce the catch efficiency for smaller salmon. However, fish as small as 38 cm total length were taken by these long-lines. For the comparison between the autumn and winter seasons we would not expect any significant difference in catch efficiency of MSW fish due to their relatively large size (the mean length of 2SW fish increased by 3-5 cm from autumn to winter). However, for 1SW fish, there may be a threshold size where the catchability increases. If this is affecting the sampling, then the proportion of 1SW fish from the northern regions should have increased as the season progressed as the fish grew in length. If this was the only temporal change in stock structure in the area, this should have led to a decrease in the mean sea age during winter, but we observed an increase during this period.

Between 80 and 90% of the salmon present in the area north of the Faroes are estimated to become sexually mature during the year and spawn in the autumn, irrespective of age (Youngson and McLay, 1985; Jákupsstovu, 1988; Hansen and Jacobsen, 2000). The timing when these fish leave the Faroese area could explain the observed decline of 1SW fish of southern origin from autumn to winter. If so, then the southern component should depart rather early. However, evidence points to the opposite, e.g. for the River Dee, Scotland, the MSW salmon both return to and ascend the river earlier than the later returning grilse (Hawkins, 1987), and in Norway the MSW salmon approaches the coastal areas earlier than the 1SW salmon on their journey home (Jonsson et al., 1990). The grilse component of the Irish stock arrive back to the home coast sometime in early summer (from early May onwards). These fish arrive back to the coast later than the "spring" salmon which are generally large 2SW or more rarely 3SW fish and appear off the Irish coast from February to May. However, it has been suggested that only a relatively small number of salmon from Ireland are present at Faroes during the time of the fishery (Browne et al., 1994).

Spatial difference in post-smolt distribution were reported by Holm et al. (1998) who found large numbers of post-smolts with river age 1 and 2 far north in the Norwegian Sea during summer, suggesting that a large part of those originated in more southern areas of Europe, whereas the abundance of smolts with high river ages was low in the same area. Spatial changes in smolt age distributions have also been observed in other areas. Analyses of scale samples from a large multinational offshore research fishing at West Greenland in 1972, revealed a significant change from lower smolt ages in the north (Disco area) to higher smolt ages in the south, and in the Labrador area the smolt ages were significantly higher than at West Greenland (Munro and Swain, 1980). They suggested that the fish taken at Labrador originated "from rivers of the more northerly latitudes." (Munro and Swain, 1980). Reddin and Short (1991) also noted that the river ages of post-smolt salmon caught in the Labrador sea could be used to infer their origin due to the relationship of river age and latitude. Jensen and Lear (1980) found that only after discriminating between European and North American salmon in the Irminger Sea, a difference in smolt age became evident, with mean smolt age of European salmon being significantly lower (1.9, range 1.7–2.4) than for North American salmon (3.4, range 2–4).

There may be several explanations for the apparent change in the stock composition of salmon from autumn to winter. Smolts from different areas move into the ocean at different times; fish from southern Europe may leave their home rivers as early as beginning of April (e.g. Baglinière, 1976), whereas smolts from northernmost Norway go to sea in late June or in the beginning of July (e.g. Hvidsten et al., 1995). This different timing and location would probably result in a different distribution of post-smolts from different stock complexes. The recapture of relatively large southern European post-smolts north of Scotland and in the Norwegian Sea in June and July (Shelton et al., 1997; Holm et al., 2000), at a time when the majority of the e.g. Norwegian smolts just have left their rivers (Hvidsten et al., 1995) and are smaller, indicate that there are sequential/temporal and spatial differences in the salmon stocks in the sea during the early period after seaward migration. Holst *et al.* (1996) noted that post-smolts of river age 3 and especially 4+ seemed to be missing from pelagic trawl catches during summer in the Norwegian Sea and suggested that the northern post-smolt were outside their sampling area.

Jákupsstovu (1988) found that the proportions of 1SW salmon tended to be higher in areas with sea surface temperatures (SST) above 4°C, compared to MSW fish which showed a higher abundance in the colder areas (< 4°C). Reddin and Shearer (1987) found that low SST (< 4°C) seemed to limit salmon distribution and alter their migration routes in the Northwest Atlantic, and Reddin (1988) also found a more restricted distribution of 1SW salmon compared to the wide distribution of MSW fish in the Northwest Atlantic. Thus, significant parts of the 1SW stocks might be confined to the warmer side of the subarctic front in the southern Norwegian Sea during winter. This front is located in an east-west direction approximately between the autumn and winter sampling areas (Fig. 1), and turns northward in a north-eastern direction into the eastern part of the winter area (Hansen, 1985). However, during summer and autumn the upper 50 m are heated, resulting in the higher autumn temperatures in the area.

The suggestion of a temporal segregation relies on the assumption that the movement of the fishery (on average 60 nm) reflects a migration of salmon from the autumn to the winter feeding areas, and that the largest salmon migrate farthest into the colder winter area. Fishing fleets usually concentrate in areas with highest catch per unit effort (e.g. Healey et al., 1990). However, since the division between the warmer and the colder side of the front coincide with the autumn and winter sampling areas that were not fished synoptically, we cannot verify these suggestions from the present data.

The relatively large drop in SST from autumn to winter might indicate that two different water masses were exploited. Thus, if the above assumption on temporal segregation does not hold, our results could indicate a general stock segregation in the feeding areas north of the Faroes throughout the seasons. An indirect support for the alternative suggestion can be found from the age structure and origin of salmon tagged at sea during the winters of 1969–1975 in the Faroese area. Jákupsstovu (1988) noted that the high proportion of 1SW (85%) fish available for tagging, was the result of the relatively southern area fished during that period (i.e. south of the present winter feeding area), as opposed to further north where 2SW fish were more abundant. Furthermore, salmon from the southern European countries dominated in the returns from this tagging experiment (Jákupsstovu, 1988), as opposed to the observation in the present data, where approximately 90% of the recaptures originated from northern European countries during winter (Table 4). Thus, the observed stock segregation, at least in the winter feeding areas, is apparently related to environmental conditions and the geographic origin of the fish. A word of caution is warranted here, since the recapture rates from tagging of adult fish at sea are not directly comparable to recaptures of salmon tagged as smolt in homewaters. This is because the estimated recovery proportions from the various regions might be biased due to unequal mortality after tagging, different recapture probabilities and the fact that not all countries tag salmon.

Salmon have been observed to feed heavily on crustaceans, especially on the hyperiid amphipod *Themisto* spp. as well as on mesopelagic fish species in these feeding areas (Jacobsen and Hansen, 2000). Although the abundance of prey does not seem to be limiting, salmon have to compete with other major pelagic fish species, i.e. blue whiting, herring and mackerel, which are present in large numbers from early spring (ICES, 1999a; 1999b). The abundance of *T. libellula*, which is a relatively large and important crustacean prey for salmon (Jacobsen and Hansen, 2000), is very high in the water mass on the colder side of the front (Dalpadado et al., 1998). Since neither herring, mackerel nor blue whiting enter the colder areas during their feeding migrations (Vilhjálmsson et al., 1997; Holst et al., 1998; ICES, 1999a), it is possible that large salmon enter an area with few competitors. It could therefore be speculated that spatial segregation of salmon is a result of a trade-off between food availability, competition and thermal limitations. This prediction that could be tested in future investigations.

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Table 1

Number of scale samples collected north of the Faroes by fishing period (1991/1992–1994/1995) and by autumn (November–December) and winter (February–March) periods. The scale samples are split into wild, farmed and unknown type.

Fishing	Wild salmon		Farmed salmon		Unknown type		
Period	Autumn	Winter	Autumn	Winter	Autumn	Winter	Total
1991/1992	188	320	116	198	15	17	854
1992/1993	65	125	26	61	28	14	319
1993/1994	256	280	123	82	19	44	804
1994/1995	120	171	34	38	2	8	373
Total	629	896	299	379	64	83	2350

Table 2

Smolt age distribution of wild salmon in numbers (% in brackets) by season (autumn: November–December and winter: February–March) for each fishing period (1991/1992–1994/1995). Total by season in bold. Age group 4+ includes smolt age 4 and higher in samples. Mean smolt age is given for each period, SE is standard error and N is number of samples.

	Smolt age						
Season	1	2	3	4+	Mean	SE	N
Autumn 1991	14 (8)	70 (39)	68 (38)	27 (15)	2.6	0.06	179
Autumn 1992	5 (12)	21 (53)	12 (30)	2 (5)	2.3	0.11	40
Autumn 1993	32 (16)	74 (36)	68 (34)	29 (14)	2.5	0.06	203
Autumn 1994	7 (6)	57 (50)	31 (27)	20 (17)	2.6	0.08	115
Total autumn	**58 (11)**	**222 (41)**	**179 (33)**	**78[a] (15)**	**2.5**	**0.04**	**537**
Winter 1992	8 (2)	105 (41)	144 (51)	39 (6)	2.7	0.05	296
Winter 1993	0 (0)	34 (33)	57 (55)	12 (12)	2.8	0.07	103
Winter 1994	11 (4)	86 (37)	99 (44)	40 (15)	2.7	0.06	236
Winter 1995	1 (1)	66 (41)	67 (41)	29 (18)	2.8	0.06	163
Total winter	**20 (3)**	**291 (36)**	**367 (46)**	**120[a] (15)**	**2.7**	**0.03**	**798**

[a] Samples including eight individuals of smolt age 5.

Table 3

Sea age (SW) distribution of wild salmon in numbers (% in brackets) by season (autumn: November–December and winter: February–March) for each fishing period (1991/1992–1994/1995). Total by season in bold. Age group 3+ includes sea age 3 and higher in samples. Mean sea age is given for each period, SE is standard error and N is number of samples.

	Sea age					
Season	1SW	2SW	3+SW	Mean	SE	N
Autumn 1991	15 (10)	159 (86)	14 (4)	2.0	0.03	188
Autumn 1992	20 (31)	41 (63)	4 (6)	1.8	0.07	65
Autumn 1993	20 (12)	212 (73)	22 (15)	2.0	0.04	254
Autumn 1994	23 (19)	93 (78)	3 (3)	1.8	0.05	119
Total autumn	**78 (12)**	**505 (81)**	**43[a] (7)**	**1.9**	**0.03**	**626**
Winter 1992	2 (1)	252 (80)	64 (19)	2.2	0.03	318
Winter 1993	1 (1)	75 (60)	49 (39)	2.4	0.05	125
Winter 1994	65 (23)	140 (48)	75 (29)	2.1	0.04	280
Winter 1995	5 (3)	137 (80)	29 (17)	2.2	0.04	171
Total winter	**73 (8)**	**604 (68)**	**217[b] (24)**	**2.2**	**0.02**	**894**

[a] Samples including five individuals of sea age 4 and 5.

[b] Samples including 32 individuals of sea age 4, 5, and 6.

Table 4

Number of tag (external and internal) recaptures 1991/1992 to 1994/1995, by season and country of origin. The countries of origin are grouped into southern and northern European regions (in bold) for comparisons. Column percentages in brackets.

Country/region	Autumn (%)	Winter (%)	Total (%)
Norway	49 (38.6)	99 (81.8)	148 (59.7)
Sweden	6 (4.7)	8 (6.6)	14 (5.6)
Faroes	1 (0.8)	2 (1.7)	3 (1.2)
Iceland	3 (2.4)	-	3 (1.2)
Northern region:	**59 (46.5)**	**109 (90.1)**	**168 (67.7)**
Ireland	51 (40.2)	8 (6.6)	59 (23.5)
Scotland	6 (4.7)	1 (0.8)	7 (2.8)
England/Wales	7 (5.5)	3 (2.5)	11 (4.0)
N. Ireland	2 (1.6)	-	2 (0.8)
France	1 (0.8)	-	1 (0.4)
Spain	1 (0.8)	-	1 (0.4)
Southern region:	**68 (53.5)**	**12 (9.9)**	**80 (32.3)**
Total	127 (100)	121 (100)	248 (100)

Table 5

Tag recaptures by season (autumn and winter) and sea age (1 and 2+SW) of smolts tagged in northern and southern European region from the period 1991/1992–1994/1995. Percentages in brackets: column percentages in the main body of the table and row percentages in the bottom row.

	Northern region			Southern region			
Season	1SW	2+SW	Total	1SW	2+SW	Total	Grand total
Autumn	9 (43)	50 (34)	59 (34)	52 (88)	16 (76)	68 (85)	126 (51)
Winter	12 (57)	97 (66)	109 (66)	7 (12)	5 (24)	12 (15)	121 (49)
Total	21 (13)	147 (87)	168 (68)	59 (74)	21 (26)	80 (32)	247 (100)

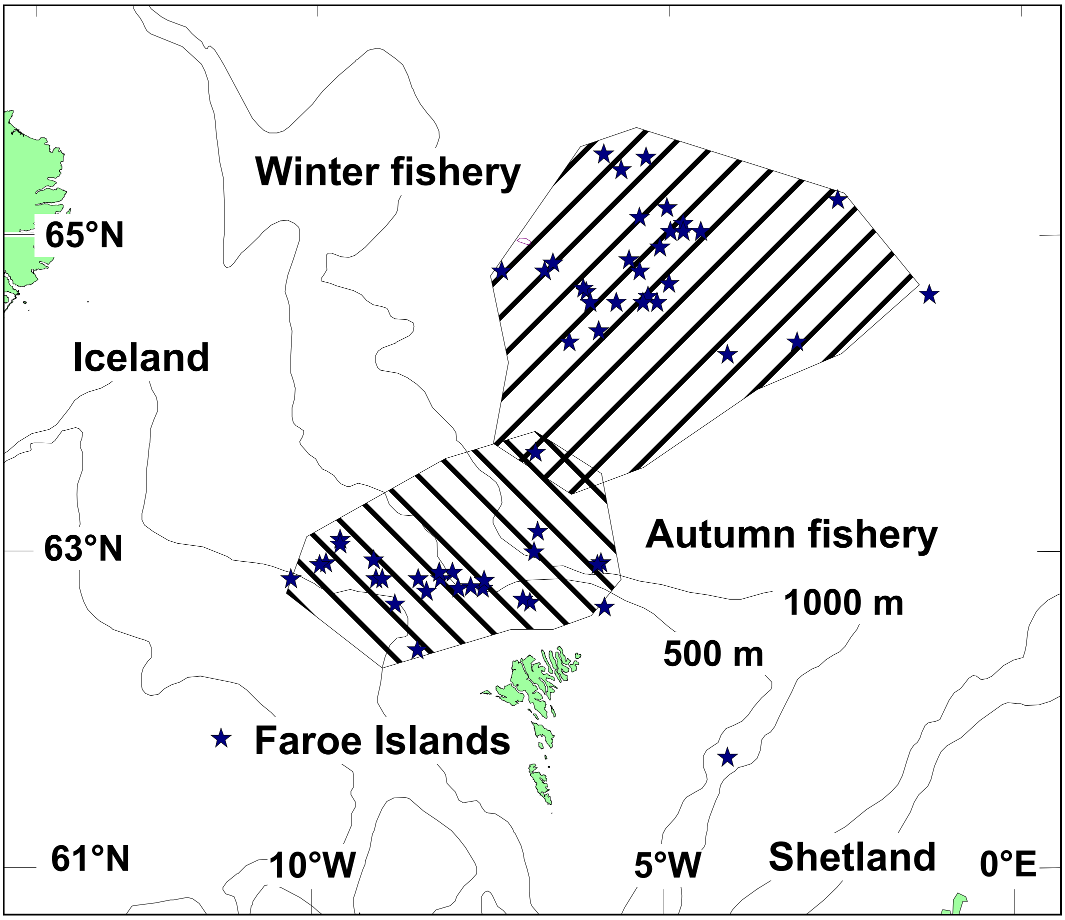

Fig. 1. Fishing locations and main areas fished during the sampling programme at Faroes were 2350 salmon were sampled for scale analyses during four fishing periods 1991/1992–1994/1995. In some locations a star represent several fishing operations (i.e. long-line sets). The autumn fishery (November–December) is located closer to the isles and more westerly than the winter fishery (February–March), which is located further to the north-east. There is some overlap between autumn and winter fishing stations, not shown on the map.

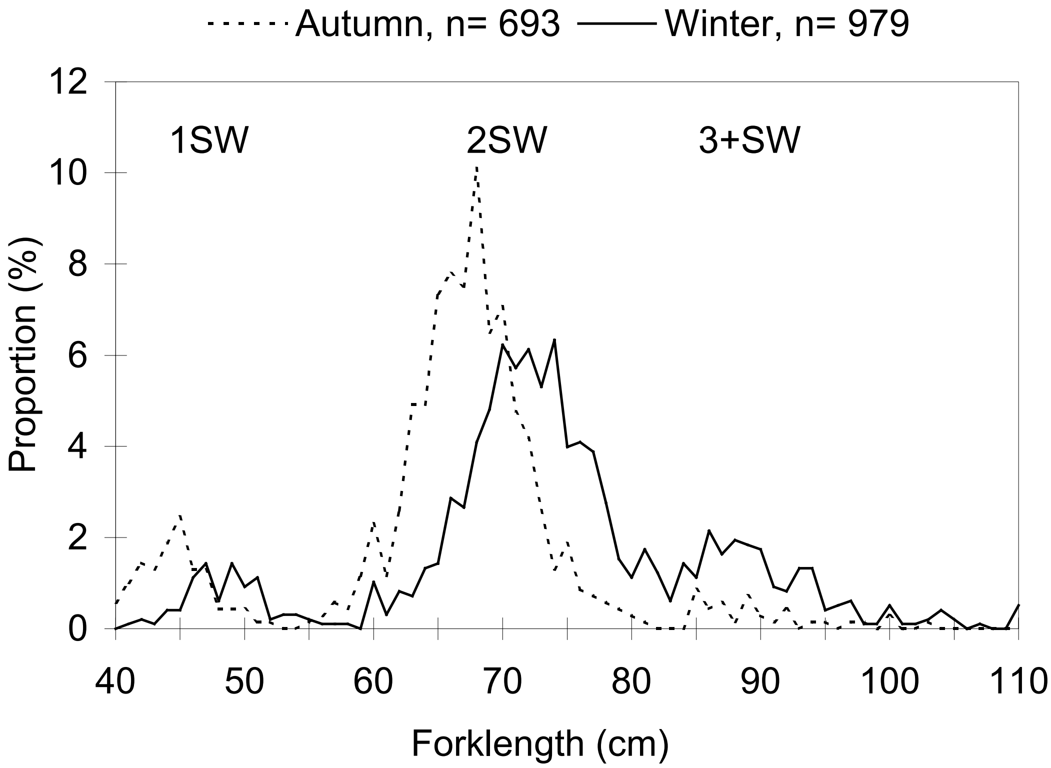

Fig. 2. Length frequency (%) distribution (forklength) of wild salmon caught during autumn (November–December) and winter (February–March) north off the Faroes in four fishing periods 1991/1992–1994/1995. The 1SW, 2SW and 3+SW age groups can be identified as 3 successive peaks in the length distribution with modes around 45-48 cm, 67-72 cm and 85-88 cm during autumn and winter, respectively.

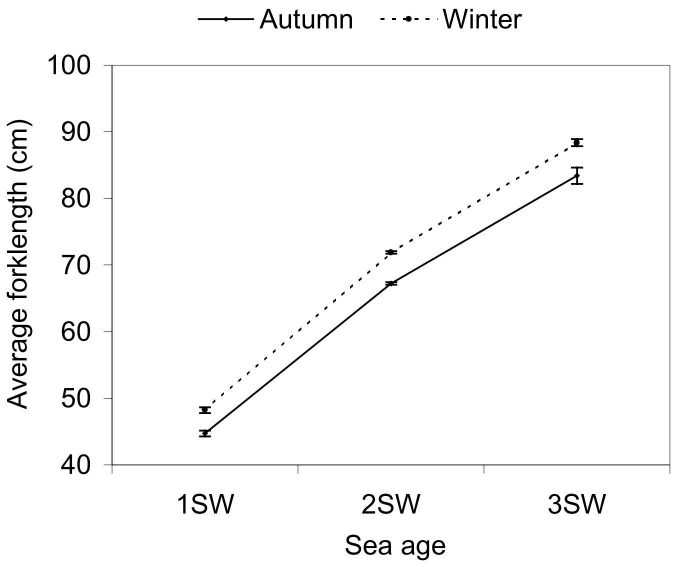

Fig. 3. Average forklength (±SE) by sea age (SW) of wild salmon caught during autumn (November–December) and winter (February–March) north of the Faroes in four fishing periods 1991/1992–1994/1995.

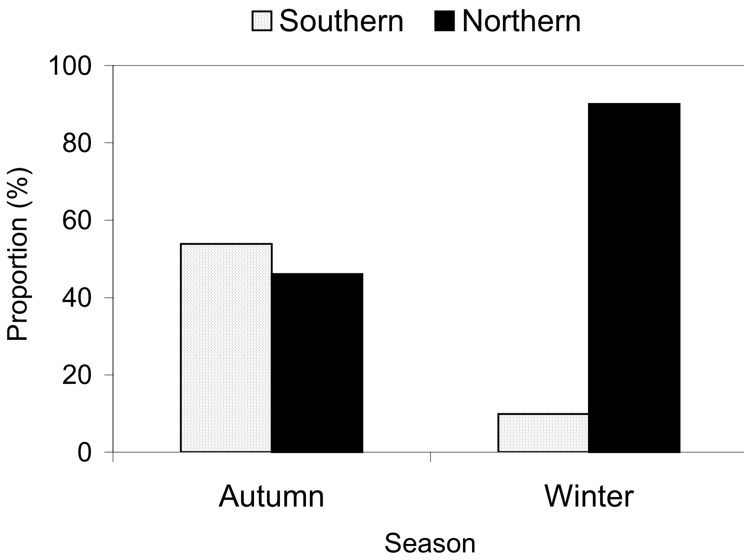

Fig. 4. Tag recapture proportions (%) by season and geographic regions, i.e. the southern and northern European countries for comparisons. Data from recaptures in the Norwegian Sea 1991–1995.

PAPER III

Origin, migration and growth of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands.

Origin, migration and growth of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands

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Abstract: We examined the distribution, migration, origin and growth of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the north east Atlantic ocean north of the Faroe Islands. Between November 1992 and March 1995 a total of 5,448 salmon (3,811 wild and 1,637 fish farm escapees) were caught by floating long-lines, individually tagged and released back into the sea. A total of 106 fish (87 wild and 19 farmed) have been reported recaptured. The recapture rate of wild salmon (2.3 %) was significantly higher than that of farmed salmon (1.2 %). Recoveries of wild salmon were reported from homewater in nine north Atlantic countries, and in a number of different rivers throughout the distribution range of Atlantic salmon included Russia, Iceland, Spain and Canada. Most tags were recovered in Norway, but significant number of returns were observed in Scotland and Russia as well. No fish were recaptured at Faroes. Fish tagged in the autumn tended to return to areas closer to the tagging site than fish tagged in the winter. This strongly suggests that salmon originating from most areas of the distribution range are at some life stage present in this area, but in variable proportions at different times. Most of the salmon returned home to spawn the next autumn, and the fish that stayed for another year originated from northern areas of Europe. All recoveries of farmed salmon were done in Norway except one at the west coast of Sweden, suggesting that they mainly had escaped from Norwegian fish farms. Assessment of the proportion of wild salmon from different countries present in this area revealed that 40% of the fish were of Norwegian origin, and Scotland and Russia accounted for about 20% each. Four tags of wild fish were reported from Canada, all in the same year when they were tagged. This demonstrates that adult Atlantic salmon can cross the north Atlantic ocean in less than 6 months. Estimated migration speed of wild fish and farmed fish returning to Norway and their specific growth rate was not different.

Key words: migration, growth, tagging, ocean, farmed salmon, wild salmon

Running head: Migration of wild and escaped farmed salmon

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INTRODUCTION

Atlantic salmon are distributed over large areas in the Northeast Atlantic, but there is still relatively little information on the distribution and migration patterns of this species in the ocean (e.g. Hansen & Quinn, 1998). Inside the Faroes Exclusive Economic Zone (EEZ) salmon have been exploited for a relatively long period of time (Jákupsstovu, 1988). This fishery exploits mainly two-sea-winter (2SW) fish, although some 1 and 3SW fish are also caught. Recaptures at Faroes of salmon tagged as smolts in different countries have revealed that salmon from many countries are present in the area, but no quantitative analysis of stock distribution has been carried out. Most of these recaptures, however, originate from hatcheries. From recaptures of tagged salmon in the Faroes fishery in the 1980s there is direct evidence that salmon of different smolt year classes originating from different rivers in Norway, Scotland and Sweden are caught side by side during the same time period in the same area (Hansen, 1993).

A tagging experiment at sea around the Faroe Islands was carried out during the period 1969 to 1976 (Jákupsstovu, 1988). Most of the salmon tagged was small (1SW), and may thus not reflect the composition of stocks in the area. Most recaptures of the tagged fish were reported from Scotland and Norway, and there were also several fish recovered from Ireland.

In recent years large numbers of farmed salmon have been observed at Faroes (Hansen *et al.*, 1993a), accounting for a significant proportion of the Faroese salmon catch (Hansen *et al.*, 1999). There is direct evidence that farmed salmon escaping from net pens in Norway enter this area (Hansen *et al.*, 1987), but there is no information on the movement, survival and growth of these fish in the ocean.

The main goal of this paper is to examine the origin, migration and growth of wild and escaped farmed salmon utilising the Faroese area during parts of their oceanic feeding phase.

MATERIAL AND METHODS

As a part of a salmon research project in the north east Atlantic ocean at Faroes from 1992 to 1995, wild and farmed Atlantic salmon were tagged and released back into the sea. The salmon were caught north of the Faroe Islands using commercial floating long-lines that were baited with sprats. The lines were usually set early in the morning, hauling started approximately at noon and was completed between 5 and 10 hours later. The average number of hooks in each set was about 2000. The fishing took place between November and March during the three fishing periods 1992/93, 1993/94 and 1994/95. The area fished during the autumn part (November-December) was closer to the Faroes than the area fished in the winter (February-March) (Fig. 1).

Immediately after capture the salmon that were judged to have a fair probability of survival were individually tagged with numbered Lea tags. The fish were measured (fork length) and a few scales were removed from the dorso-lateral area as recommended by Shearer, (1992). If possible, the hook was removed, but in cases where removal could seriously damage the fish, the hook was left in the fish. The salmon were kept in a tank with a continuos inflow of sea water onboard the vessel for some time allowing the fish to recover after handling and tagging. If the fish appeared fit by visual inspection, it was released.

All fish were determined to be of wild or farmed origin by examining whether they showed external characters like e.g. fin erosion which is common on reared salmon (Lund *et al.*, 1989), and by analysis of scales (Lund & Hansen, 1991). In total 3811 wild and 1637 farmed salmon were tagged and released (Table I), and Fig. 2 shows the length distribution in the autumn and winter of both groups of fish. It can be observed that the length distribution of wild and farmed salmon is similar.

The sea age of wild salmon was estimated by splitting the length frequencies into sea age cohorts (see e.g. ICES, 1996), i.e. fish less than 57 cm forklength were taken to be one sea winter (1SW), fish between 57 and 82 cm forklength were taken to be 2SW, and fish larger than 82 cm were 3SW. Among the wild salmon 2SW fish are the dominating sea age group as it accounts for more than 80% of the wild fish tagged. It should be noted that the incidence of 1SW fish is more pronounced in the autumn than in the winter, whereas 3 SW fish occurred in a higher proportion in the winter.

Tags were reported from commercial fishermen operating in home waters, and from anglers in rivers, and they were asked to submit information about date, time and site of recapture, the size of the fish and the gear used for catching the fish. The distance between tagging and recapture site (migration distance) was estimated using the shortest distance (straight line between the two sites), and are thus minimum distances.

To estimate the origin of wild salmon in this area we corrected the observed number of recaptures by country with their respective mean exploitation rates in homewaters plus and minus 10% error (ICES, 1996). The recaptures from each country were also adjusted for their respective homewater tag reporting rates (as provided by the ICES North Atlantic Salmon Working Group members, 1997). Furthermore, error estimates due to small number of recaptures were introduced using the binomial distribution model. 'At Risk' simulations were used to estimate error bounds (95% confidence limits) on the estimated proportion of fish returning to different countries. Farmed salmon were not included in this analysis.

Weight (g) of individual fish was estimated from length-weight regression (log-log regression) of fish that were not tagged ($W = 0.0047863L^{3.1479}$, $r^2 = 0.92$, n = 3643, $p < 0.001$). Specific growth rate G (percent gain in weight per day) was calculated $(\ln W_r - \ln W_t)100/D$, where W_r and W_t is weight at recapture and tagging, respectively, and D is number of days in liberty.

RESULTS

RECAPTURE RATES

The overall reported recapture-rate of the number of salmon tagged was small, only 106 fish were recovered which is 1.9% of the number of salmon tagged. Of wild fish 87 individuals (2.3% of the number tagged) were recaptured, whereas 19 (1.2%) of the fish identified as fish farm escapees were recovered (Table II). The recapture rates of fish of farmed origin was significantly lower than for wild fish (χ^2= 6.8, df= 1, p= 0.009). For both wild and farmed salmon, the recapture rates were lower of fish tagged in the autumn than in winter (χ^2= 7.3, df= 1, p= 0.007). Tags were reported from many countries in the North Atlantic (Table III), both from marine fisheries and in freshwater. No tags were recovered from the research fishery at Faroes nor from West Greenland.

The recapture rate of wild salmon increased significantly with sea age at tagging (Fig. 4) (G= 15.4, df= 2, p< 0.001). However, the power of the test might be questioned, as only two 1SW fish were recovered, but the recapture rate of 3SW was significantly higher than of 2SW fish (χ^2= 10.6, df= 1, p= 0.001).

The recapture rates of fish with the hook left in when released was significantly higher than of fish with no hook when released (χ^2= 7.5, df= 1, p= 0.006), which might indicate that for some of the fish the removal of the hook prior to release was lethal.

GEOGRAPHICAL DISTRIBUTION OF RECAPTURES

In wild fish there was an apparent difference in the geographical distribution of recaptures of fish tagged and released in the autumn (Fig. 5) and the winter (Fig. 6). Fish tagged in the autumn were recaptured relatively close to the site of release, in south Norway, Scotland, Ireland and Iceland, whereas fish tagged in the winter were also recaptured in more distant areas such as Russia, north Norway, Sweden, Denmark and Spain and Canada. This suggests that fish from distant areas are more abundant in the Faroese area in the winter than in the autumn. Tag returns were scattered over large areas of Norway and Scotland suggesting that fish from large areas of these countries were present in the same areas at Faroes. Tag recaptures were also reported from major salmon rivers in these countries such as River Numedalslågen, R. Drammenselv, R. Gaula, and R. Namsen in Norway; R. Spey, R. Brora, R. Tay, R. North Esk, and R. Dee in Scotland.

It is interesting to note that four tags were reported from Canada, one tagged in March 1993 and recaptured in River Miramichi in September 1993, three tagged in February/March 1995 and of those two subsequently recaptured in the Miramichi in September 1995 and one in Kouchibouguac River (close to Miramichi) in October 1995. This demonstrates that salmon are able to cross the north Atlantic ocean in 6 months or less.

Of the 19 fish farm escapees recaptured, 18 were recovered from Norway, and one from the west coast of Sweden (Table IV). The geographical position of the recaptures demonstrates that the fish were distributed over large areas of coastal Norway (Fig. 7).

ORIGIN OF SALMON

Overall estimates of the proportion of wild salmon originating from different countries in the research fishery during these three fishing periods are presented in Table 5 together with the assumptions and approximations made. It is not surprising that Norway accounts for the major proportion (40%), whereas the mean estimated proportion of salmon from Scotland and Russia is close to 20 %. The estimates indicate that there are only a relatively small number of fish from other countries in the area. No similar analysis was carried out for the farmed fish, but the great majority appear to be of Norwegian origin.

SEXUAL MATURITY

Of the wild fish tagged and released, 7 individuals of a total of 87 fish recaptured in home waters (8.0 %), stayed for an additional year in the sea before returning to home waters (Table III). This is due to the fact that these fish grew 10-22 cm in length until they were recaptured more than one year after they were tagged. Five of these fish originated from Norway, one from Sweden and one from Russia. They were all tagged as 2SW fish, and thus they returned home as 3SW fish. The recaptures from mid and southern part of Europe returned home during the same season they were released. Of the farmed fish 2 of a total of 19 fish recaptured (10.5%) stayed for an additional year in the sea.

MIGRATION DISTANCE AND SPEED

The bulk of the fish were recaptured between 3 and 11 months after release, ranging from 48 days for a Scottish 2SW wild salmon (tagged 17 March and recaptured 1 May 1993) to nearly two years of a Norwegian 2SW wild salmon (Fig 8). Two escaped farmed fish stayed for 1½ year at sea before returning to Norway. The shortest journey home was made by a salmon homing to the west coast of Norway (600 km), and the longest migration distance was to Canada (4500 km). Estimated migration speed (shortest distance travelled/number of days from tagging till recapture) was highly variable between individual fish, and the estimated speed was higher in fish that were tagged in the winter than fish tagged in the autumn (Fig 9). The estimated migration speed was approximately 5 km/day for Norwegian, Scottish and Irish fish tagged in the autumn, whereas fish of the same origin tagged in the winter were estimated to move with a speed of 7-10 km/day. Fish from more distant waters like Russia and Canada tagged in the winter moved 15-25 km/day. There was no difference in estimated migration speed of farmed and wild salmon returning to Norway.

GROWTH

The specific growth rate (G, % weight gain per day) was highly variable among individual fish. The overall mean G was 0.19, ranging from 0 to 0.64. The G of wild salmon recaptured during autumn (0.17, n= 19) and winter (0.20, n= 64) was not different (t-test, df= 81, p= 0.472). Neither was there any difference between wild salmon recaptured less than one year (G= 0.19, n= 76) and after two years (G= 0.14, n=

7) at sea (t-test, df= 81, p= 0.403), nor between wild (*G*= 0.19, n= 83) and farmed (*G*= 0.19, n= 19) salmon (t-test, df= 100, p= 0.995).

DISCUSSION

Fish that were tagged in the winter seem to survive better than fish tagged in the autumn. There may be several explanations for this. Firstly, the fish that were tagged in the autumn were smaller than those tagged in the winter, and may thus be more vulnerable to handling and tagging stress (Fowler & Stobo, 1999) and subsequent size selective predation. Secondly, these fish will spend longer time in the sea than fish tagged in the winter, and may thus be exposed to marine mortality factors for a longer period of time. Furthermore, based on smolt age and sea age distribution of salmon at Faroes, Jacobsen *et al.* (2000) suggested that fish originating from rivers in mid and southern Europe were more abundant in the Faroese area in the autumn than in winter. If this holds true, we cannot rule out the possibility that the apparent differences in survival reported in the present paper may reflect a trend observed in last decade, that marine mortality rates of salmon stocks from southern Europe has increased more quickly than for salmon from northern regions in the Atlantic (Parrish *et al.*, 1998; ICES, 1999).

The relatively low recapture rate of wild salmon (2.3%) in the present sea tagging experiment compared with the previous sea tagging project in the Faroese area (4.6%) (Jákupsstovu, 1988) might further indicate a decrease in marine survival. However, in recent years significant reductions in fishing efforts have been made both at Faroes as well as in home waters which have resulted in a decline of exploitation rates (ICES 1999).

Atlantic salmon home with high precision to the rivers they left as smolts (e.g. Thorpe, 1988; Hansen *et al.*, 1993b). Thus it is highly reasonable to conclude that salmon tagged at Faroes and subsequently recaptured in freshwater are most likely to have returned home. It is also reasonable to assume that salmon caught in coastal areas in homewater have returned to their country of origin.

The estimated proportions of salmon from different countries in the research fishery show that Norwegian salmon stocks account for the major part of the stock complex, although there are also significant numbers of Scottish, Russian and Irish salmon. Because 1SW fish accounts for most of Irish salmon runs, it is likely that the proportion of Irish salmon north of the Faroes is underestimated. The reason for this is the apparent high handling and tagging mortality of the 1 SW salmon released. This is further supported by the observed presence of many microtagged 1 SW salmon of Irish origin reported from the Faroes fishery during autumn (Jacobsen *et al.*, 2000). All in all, the geographical distribution of tag returns to homewaters, strongly suggests that fish from most areas of the distribution range of Atlantic salmon at some life stage are present in the Norwegian Sea area north of the Faroe Islands. This does not mean that all stocks are systematically abundant in the area, but pass through occasionally, or that components of stocks use the area for feeding. This is supported by the fact that tagged wild fish were recovered in Canada, Spain and eastern part of European Russia, as well as in all major salmon producing countries in Europe.

Over 90 % of the fish recaptured were reported from home waters the same season as they were tagged, and relatively few fish stayed in the ocean for another year. This shows that a large proportion of the salmon in the area was indeed sexually maturing the next autumn. This figure is an overestimate as fish that stay in the ocean for another year are subjected to a higher natural mortality than fish that returned home one year earlier. Indirect estimates of the incidence of maturity of salmon caught in the Faroes fishery in 1982 and 1983 suggested that 80% of the MSW fish were maturing, (ICES, 1984), which corresponds to the figure in the present paper. It was interesting to note that fish that stayed for another year in the ocean were of northern origin (Norway, Sweden and Russia). The material is relatively small, but it could be speculated if fish from the northern countries mainly stay in the north east Atlantic during the marine phase, whereas fish from mid and southern Europe stay in the area for a limited time arriving from other oceanic areas. As support for this, it has been shown that fish from south and mid Europe are much more abundant at Greenland than fish from the northern countries (Jensen, 1980b).

The distribution of salmon at Faroes has earlier been assessed from sampling the fishery for a number of years. Some of the results have been reported by Jákupsstovu (1988), who also reported on a tagging program during the period 1969 to 1976 where in total 1,946 salmon caught on long line were tagged and released back into the sea. A total of 90 recaptures were reported, 33 in Scotland, 31 in Norway and 15 in Ireland suggesting that salmon from these countries were most abundant around Faroes, followed by England/Wales (5), Sweden (2), Russia (1), and 3 from West Greenland.

These results are somewhat different than those in the present study, and the main reason for this may be that the previous tagging was conducted relatively close to the Faroes, and even south of the islands, and the fact that the great majority of the salmon tagged was 1SW fish (85% of the total number tagged), whereas the present tagging experiment was conducted further north and mainly 2SW salmon (80%) where tagged. The size distribution of salmon in the area north of the Faroes generally increases with latitude (Jákupsstovu, 1988; ICES, 1996).

Among the fish tagged during 1969–1976 (Jákupsstovu, 1988) it is worth noting that some fish in the area may have been on their way westwards, as they were reported from West Greenland later the same year. Conversely salmon tagged at West Greenland have been reported in the area north of the Faroes the following year (ICES, 1984). From this it may be suggested that salmon of European origin may move through the Faroese area on their way to the feeding areas in the west Atlantic as well as on their way home. The fact that there were no tag returns in Greenland from the present experiment is probably caused by the very significant reduction in the fishing effort in this area in recent years (ICES, 1996). It is well known that MSW fish of European origin are present at both west and east Greenland (Jensen, 1967; Swain, 1980; Jensen & Lear, 1980; Jensen, 1980a; 1980b; Horsted, 1988; Scarnecchia, 1989).

The abundance of farmed fish in the ocean has been relatively high in recent years (Hansen *et al.*, 1999). In several countries a large salmon farming industry has developed, particularly in Norway and Scotland, which account for most of the total production (540,000 tonnes in 1998) in the North Atlantic (ICES, 1999). Escapees of farmed fish have been observed in several areas in the Northeast Atlantic, and contribute to a relatively large extent to salmon fisheries in Norway and Faroes. Hansen and Jonsson (1991) showed that reared salmon kept in saltwater, tagged and released into a Norwegian fjord every month throughout a year, tended to return to the geographical area of release and enter nearby rivers to spawn, except when released in late winter when they tended to stray farther away from the release site. When the fish were released in late summer and autumn, their survival was poor (Hansen & Jonsson, 1989). These observations have recently been supported by sequential releases of individually tagged large farmed salmon from two fish farms in Norway (L.P. Hansen personal observations). Thus this may help to explain the observed lower recapture rate of farmed salmon in the present study. Alternatively, it has been observed that escaped farmed salmon enter fjords and freshwater later in the season than wild fish (Lund *et al.*,

1991) which may result in a lower exploitation rate on farmed than wild fish, and thus lower number of tags recovered if a large proportion of the farmed fish enter home waters after the fishing season has closed. The observation that most of the tagged farmed salmon in the present experiment were recaptured in Norway, suggest that these fish escaped from Norwegian fish farms.

The estimates of migration speed are minimum estimates, and are of course highly dependent on when the fish decide to go home, how long time they have been in home waters before capture. Furthermore, the estimated distance travelled is based on the shortest distance between site of release and site of recapture which is definitely not the actual migration route. Apparently the estimated migration speed of fish tagged in the autumn was lower than for those tagged in the winter. However, Atlantic salmon tagged off Norway travelled on average only between 9 and 14 km/d (Hansen *et al.*, 1993b), which compares to our estimates of salmon tagged in the winter, either indicating a systematic difference between the areas or more likely the inherent problems in such analyses to limit the period used for active homeward migration. Probably the main reason for the difference between fish tagged in the autumn and winter is due to the possibility that salmon return home later in the winter. Furthermore, salmon slow down in coastal waters and fjords (Hansen *et al.*, 1993b) and do not ascend the freshwater immediately upon return to coastal water (Jonsson *et al.*, 1990). Thus swimming speed of salmon caught in freshwater are therefore further underestimated.

The specific growth rate was similar for wild and farmed salmon. This is supported by observations of feeding habits of salmon in this area where no difference in number or weight proportions of different prey between wild and farmed salmon was observed (Jacobsen & Hansen, 2000). Furthermore, there was no difference in condition factor between the two groups. This strongly suggests that fish farm escapees that survive until capture in the Faroes area have adapted to the marine environment.

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Table I. Number of wild and escaped farmed salmon tagged and released by month in Faroese waters November 1992 to March 1995.

Month	No. wild salmon	No. farmed salmon	Total
November 1992	469	212	681
December 1992	204	62	266
March 1993	1311	793	2104
November 1993	126	50	176
December 1993	102	41	143
February 1994	80	26	106
March 1994	132	57	189
November 1994	392	106	498
December 1994	149	36	185
February 1995	311	100	411
March 1995	535	154	689
Total	3811	1637	5448

Table II. Reported recapture rates of salmon in number (% in brackets) tagged at Faroes in the autumn (November-December) and winter (February-March).

Season	Wild	Farmed	Total
Autumn 1992	11 (1.6)	1 (0.4)	12 (1.3)
Winter 1993	36 (2.7)	8 (1.0)	44 (2.1)
Autumn 1993	3 (1.3)	1 (1.1)	3 (1.3)
Winter 1994	5 (2.4)	2 (2.4)	7 (2.4)
Autumn 1994	7 (1.3)	1 (0.7)	8 (1.2)
Winter 1995	25 (3.0)	6 (2.4)	30 (2.8)
Total	87 (2.3)	19 (1.2)	106 (1.9)

Table III. Recaptures in number of wild salmon in different countries tagged in the Norwegian Sea, north of the Faroes during the 1992/1993, 1993/1994 and 1994/1995 fishing periods.

Country	Tagged 1992/1993		Tagged 1993/1994		Tagged 1994/1995		Total	
	Rec.93	Rec.94	Rec.94	Rec.95	Rec.95	Rec.96	No	%
Norway	23	2	2		17	3	46	54.1
Scotland	8		1		3		12	13.8
Ireland	3		2		4		9	10.3
Russia	1	1	3		1		5	5.9
Sweden	2	1			1		4	4.6
Canada	1				3		4	4.6
Denmark	2						2	2.3
England	1						1	1.1
Iceland	1						1	1.1
Spain	1						1	1.1
Total	43	4	8	0	29	3	87	99.8

Table IV. Number of escaped farmed salmon recaptured by country. The fish were tagged at Faroes during the 1992/93, 1993/94 and 1994/95 fishing periods.

Country	Tagged 1992/1993		Tagged 1993/1994		Tagged 1994/1995		Total	
	Rec.93	Rec.94	Rec.94	Rec.95	Rec.95	Rec.96	No	%
Norway	8	0	3	0	5	2	18	94.7
Sweden	1	0	0	0	0	0	1	5.3
Total	9	0	3	0	5	2	19	100.0

Table V. Results of 'At Risk' simulation to estimate proportion (%) of fish tagged at Faroes returning to different countries. Confidence limits (95%) were applied based on 1000 simulations. Recoveries were adjusted for homewater exploitation rates and tag reporting rates as provided by the North Atlantic Salmon Working Group members, 1997.

Country	No.	Tag reporting rate		Exploitation rate		Estimated	Simulation		
	recapt.	min	max	min	max	recapt.	'-5%	Mean(%)	'+95%
Norway	47	0.4	0.60	0.50	0.80	145	27.2	39.6	51.7
Scotland	12	0.8	1.00	0.10	0.30	67	8.8	19.2	32.5
Russia	6	0.6	0.80	0.10	0.15	69	7.6	18.3	30.5
Canada	4	0.65	0.85	0.15	0.28	25	1.6	6.9	13.6
Ireland	9	0.6	0.80	0.50	0.75	21	2.5	5.7	9.4
Denmark	2	0.4	0.60	0.14	0.34	17	0	4.7	11.8
England	1	0.4	0.60	0.15	0.35	8	0.6	2.3	4.7
Sweden	4	0.55	0.75	0.55	0.90	8	0	2.3	7.1
Spain	1	0.6	0.80	0.55	0.85	2	0	0.6	1.8
Iceland	1	0.8	1.00	0.40	0.60	2	0	0.6	1.7
Total	87					364		100.2	

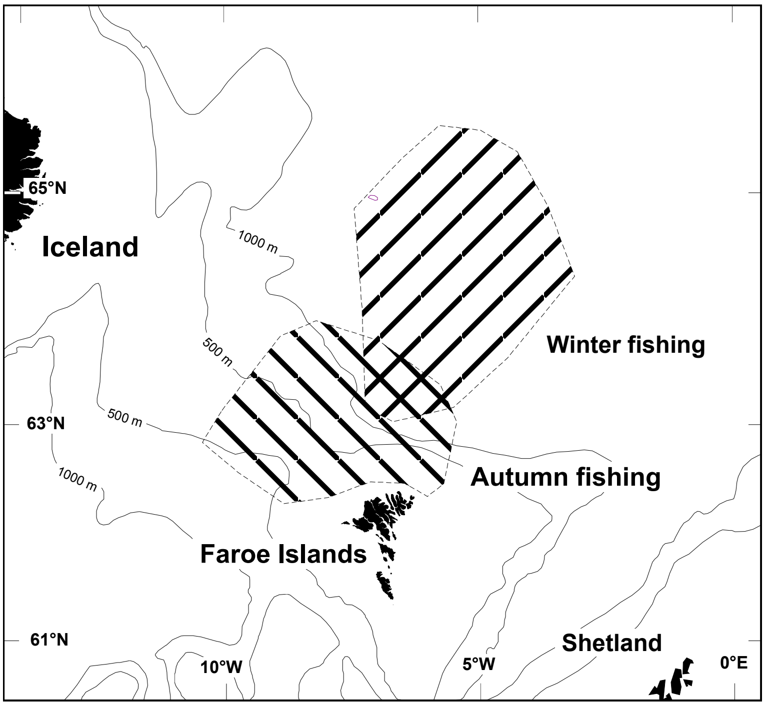

Fig. 1. Areas of tagging north of the Faroes. The autumn fishery is located closer to the isles and as the season progresses the fishery moves in a north-eastern direction farther into the Norwegian Sea.

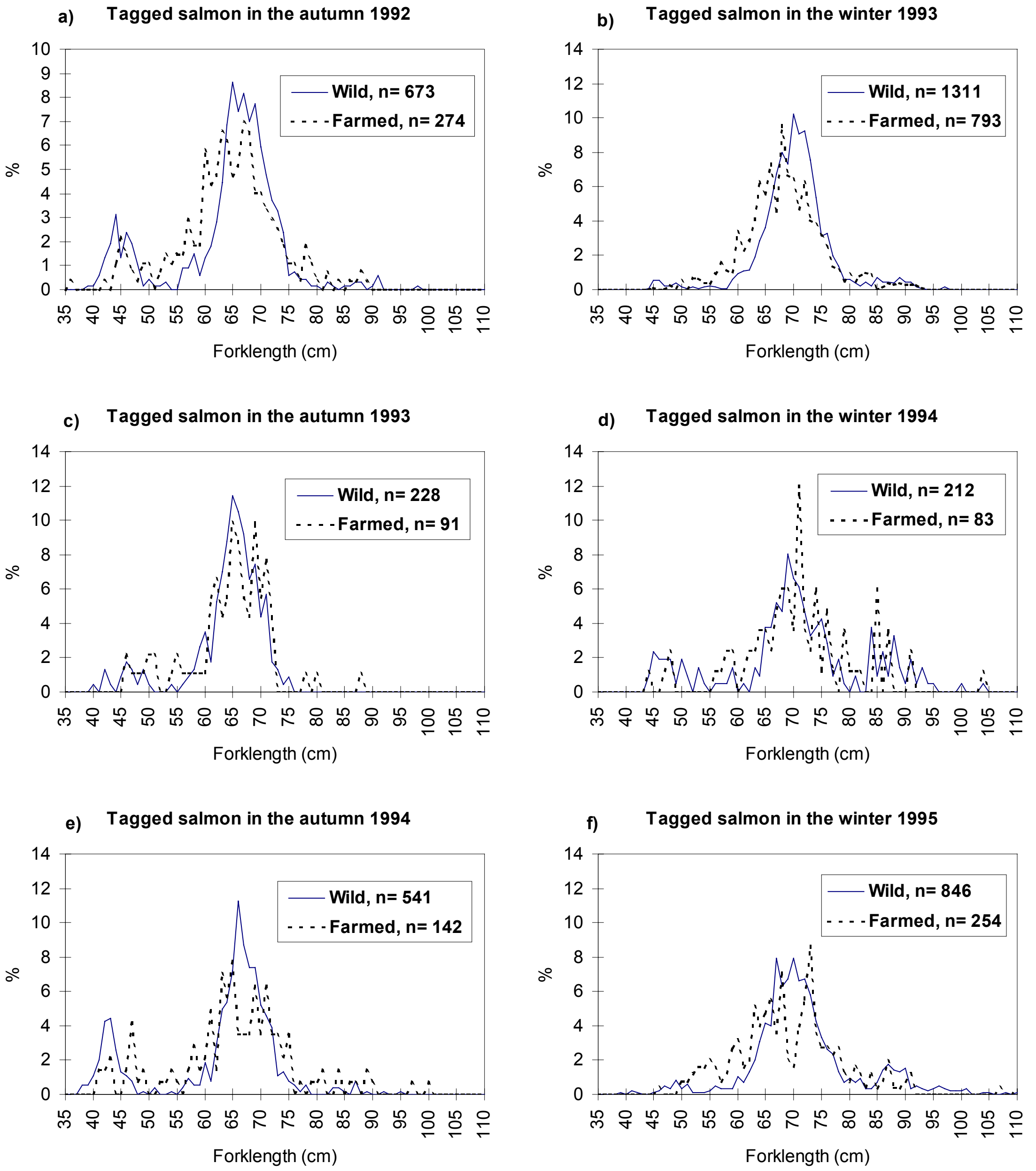

Fig. 2. Forklength distributions of wild and farmed salmon tagged north of the Faroes during three fishing periods 1992/93–1994/95. The fishing period is divided into an autumn (November-December) and winter (February-March) season.

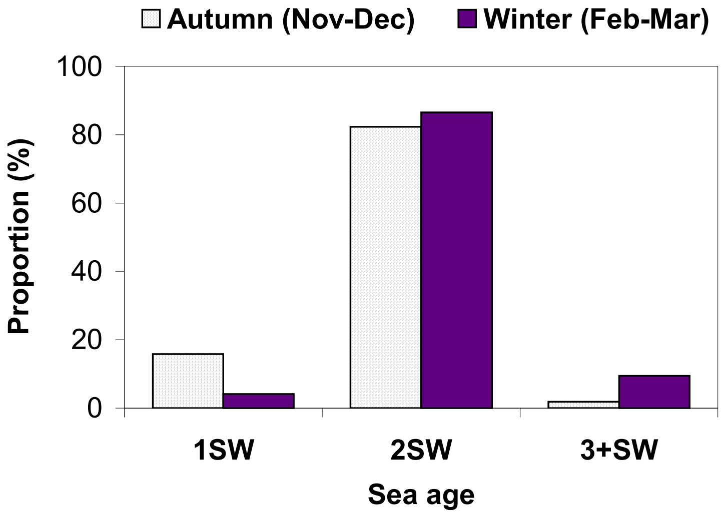

Fig. 3. Estimated sea age distribution of wild Atlantic salmon tagged north of the Faroes by season. Total number of observations is 3811 fish.

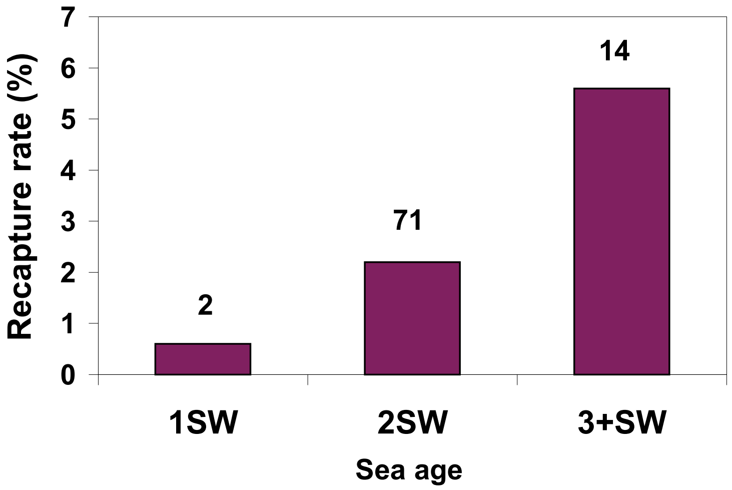

Fig. 4. Recapture rates by sea age of wild salmon tagged and released north of the Faroes during 1992/1993–1994/1995. The figures show the number of observations.

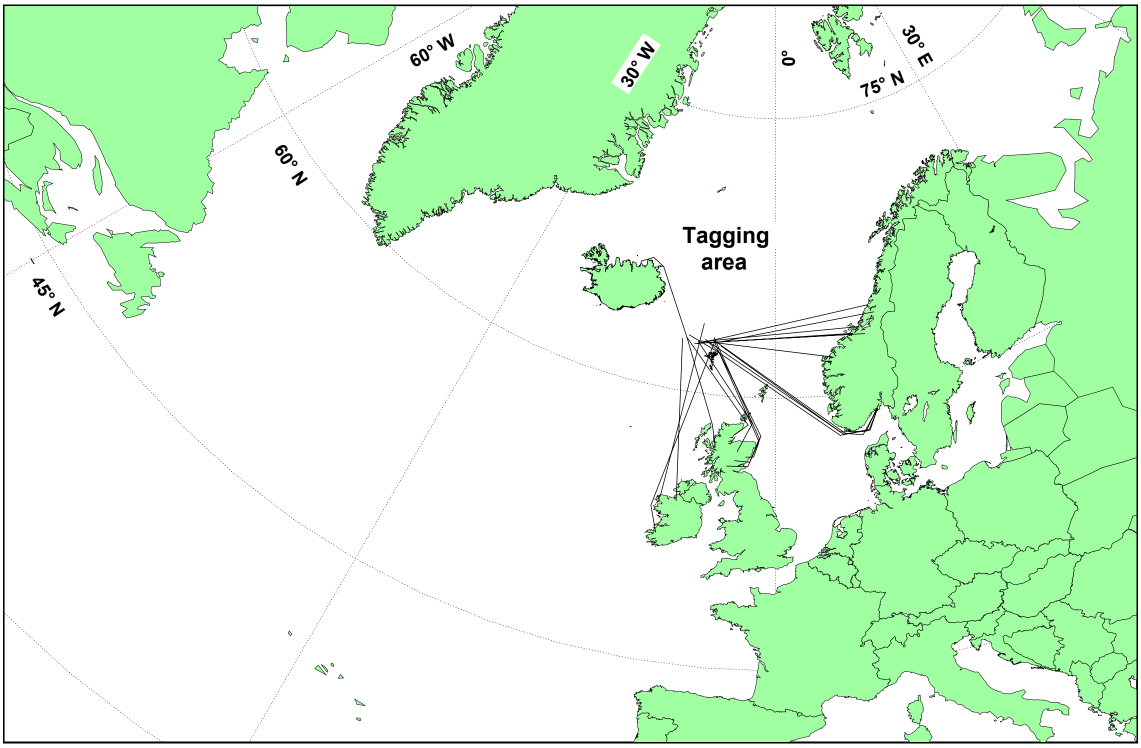

Fig 5. Geographical distribution of wild salmon tagged and released north of the Faroe Islands in the autumn and recaptured in home waters. The lines indicate the shortest direct migration route home.

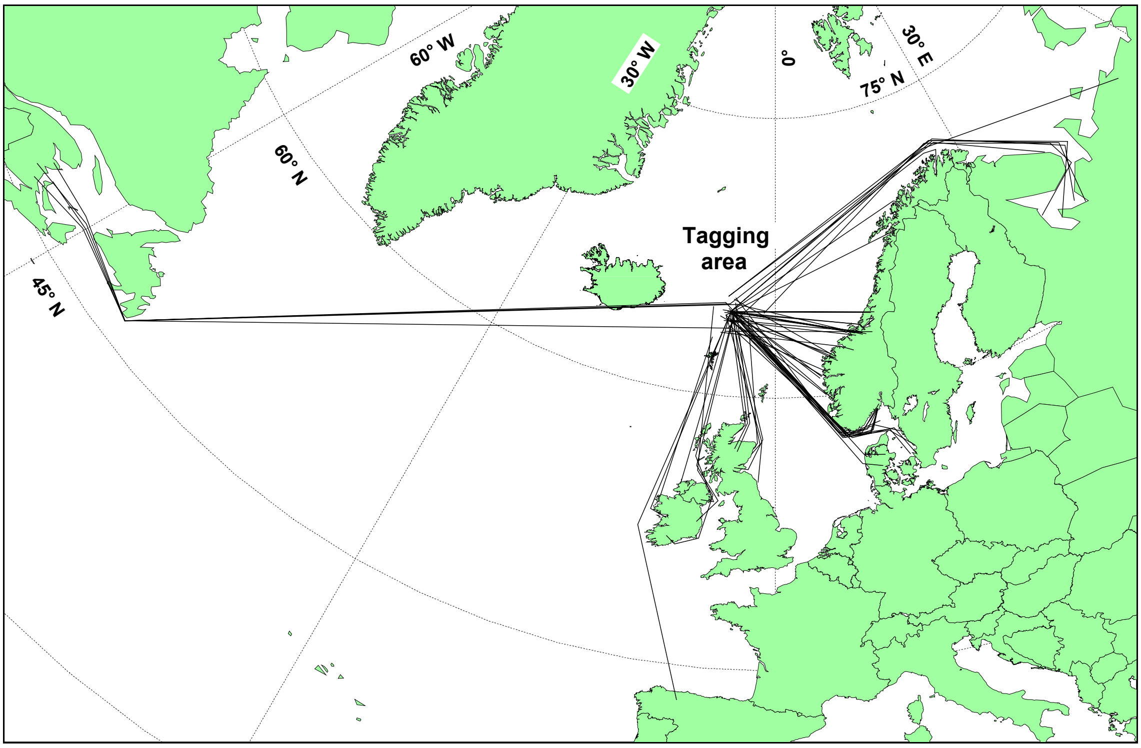

Fig. 6. Geographical distribution of wild salmon tagged and released north of the Faroe Islands in the winter and recaptured in home waters. The lines indicate the shortest direct migration route home.

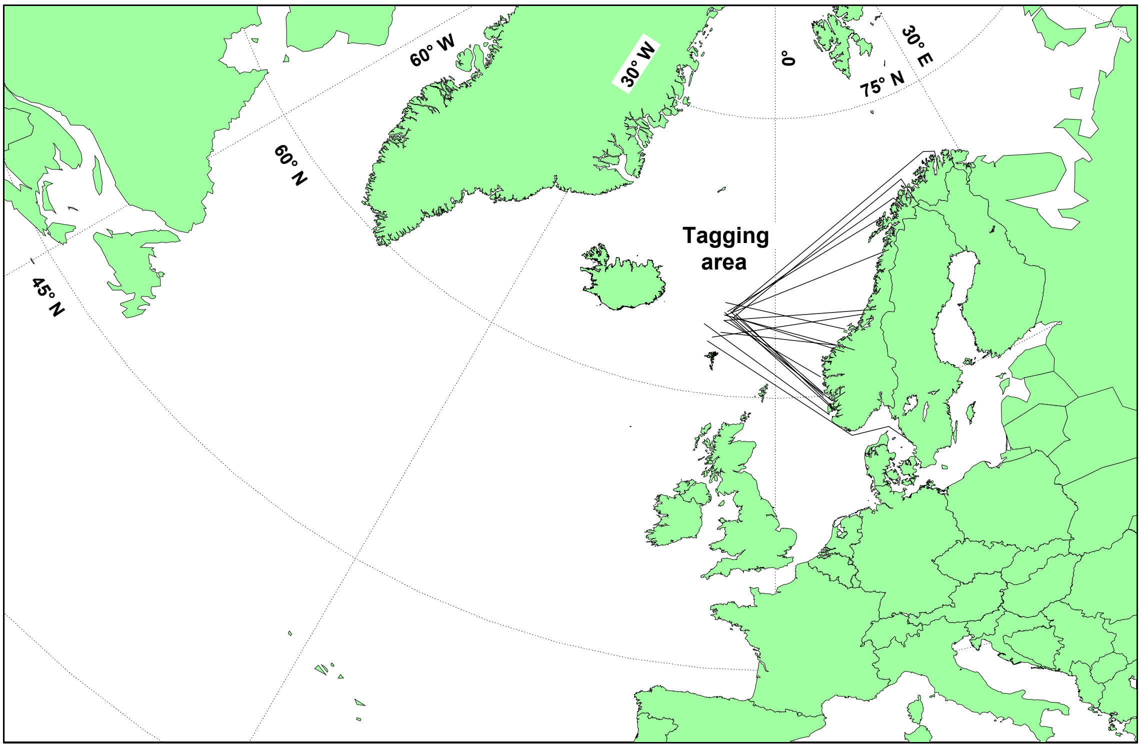

Fig. 7. Geographical distribution of escaped farmed salmon tagged and released north of the Faroe Islands in the autumn and recaptured in home waters. The lines indicate the shortest direct migration route home.

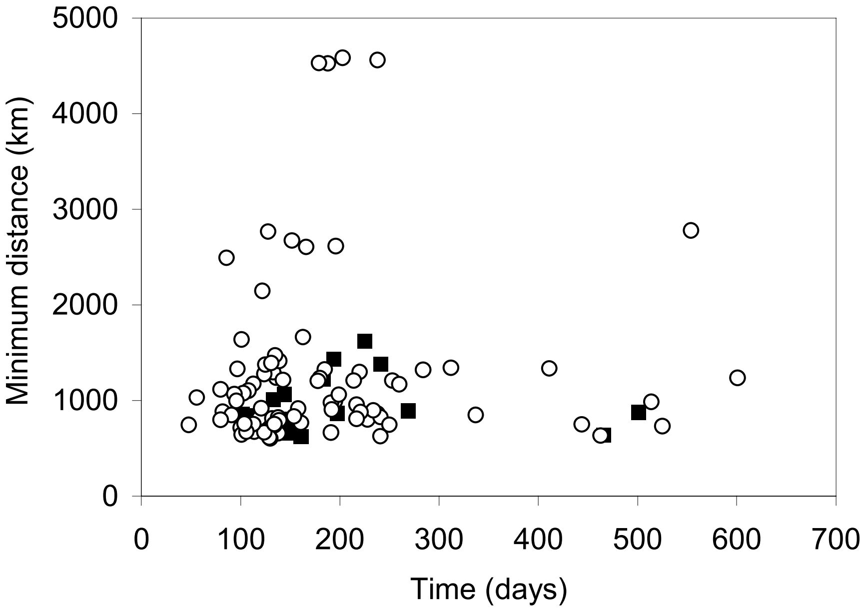

Fig. 8. Minimum distances travelled versus days in liberty. Wild salmon is shown as open circles and escaped farmed salmon as filled squares.

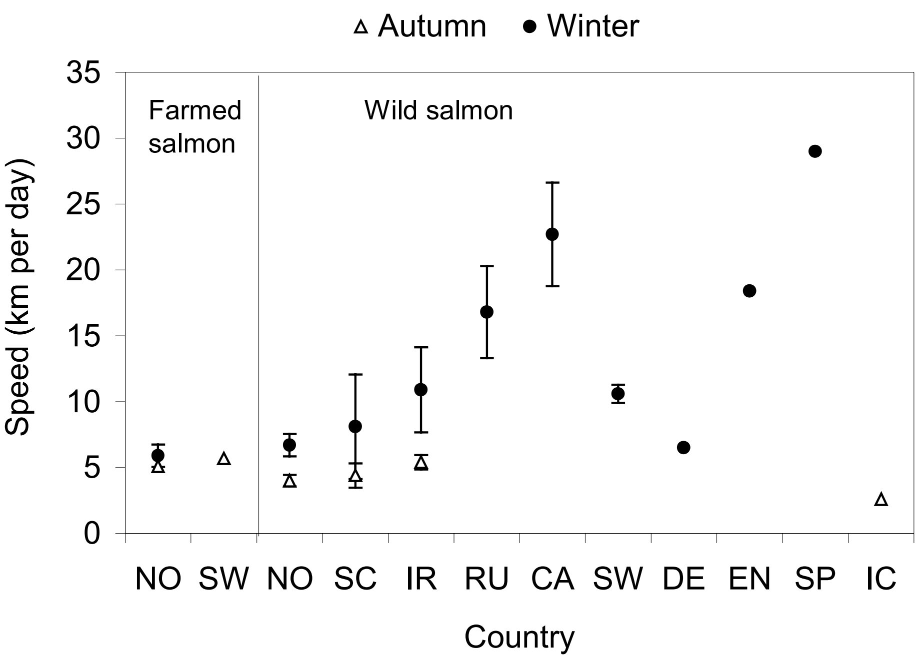

Fig. 9. Estimated migration speed (km per day) of farmed and wild salmon by country of origin. Speed was calculated as the average speed from tagging in the Northeast Atlantic to recapture in the home countries. Confidence intervals (95%) are indicated where number of recoveries were greater than two fish.

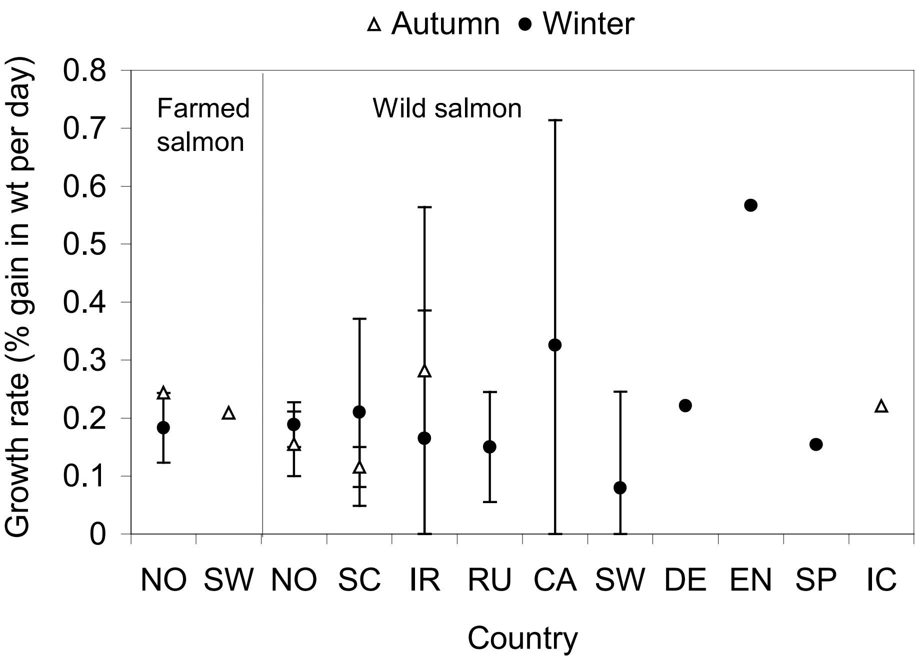

Fig. 10. Estimated specific growth rates (G, % gain in weight per day) of farmed and wild salmon by country of origin. Confidence intervals (95%) are indicated where number of recoveries were greater than two fish.

PAPER IV

Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic.

Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic

Jan Arge Jacobsen and Lars Petter Hansen

Abstract: The stomach contents of 2992 wild and 863 escaped farmed Atlantic salmon caught on floating long-lines in a Faroese research fishery in the late autumn (November–December) and winter (February–March) feeding areas in the Northeast Atlantic (63–66°N and 1-10°W) during three consecutive fishing periods 1992/1993–1994/1995 were analysed. The salmon fed mainly on hyperiid amphipods, euphausiids, shrimps, lanternfishes, pearlsides and barracudinas, and less on larger pelagic fish and squid. Crustaceans accounted for 95% in number (30% by weight) and fish for 5% in number (66%) by weight. There was no difference in condition factor, number and weight proportions of prey, or diet overlap between wild and farmed salmon, which suggests that farmed salmon that survive until they were captured are completely adapted to feed in the marine environment. The proportion of stomachs containing food was significantly lower during autumn (53%) than during winter (78%). The ambient sea-surface temperature is ca 7°C in autumn compared to ca 3°C in winter; therefore temperature dependent evacuation rate could explain the apparent lower stomach content during the autumn. The significantly higher condition of 3+SW salmon compared to the smaller 1 and 2SW fish, irrespective of season, might be a reflection of higher tolerance to low temperatures, greater forage potential or prey capture success. Although salmon show patterns of opportunistic feeding behaviour, there was also evidence of selective foraging. Generally fish were preferred over crustaceans, and amphipods were chosen over euphausiids. Large salmon tended to be more piscivory than smaller fish.

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Introduction

The abundance of Atlantic salmon (*Salmo salar* L.) has generally decreased during the last two decades (Parrish et al. 1998; ICES 1999). There are a number of reasons for this, included degradation of freshwater habitat suitable for salmon, pollution, effects of parasites and diseases, and perhaps overfishing (Parrish et al. 1998; see Mather 1998). Furthermore, it has been observed that surface temperatures in the ocean have declined, and effects of this has been suggested to increase post-smolt mortality (Friedland et al. 1993; Reddin and Friedland 1993; Friedland et al. 1998).

Although more information about Atlantic salmon in the marine phase has been gained in recent years (e.g. Mills 1993), still little is known about the food and feeding habits of salmon in the Northeast Atlantic (see Hislop and Shelton [1993] for a review). The few studies so far in the Faroese area and the Norwegian Sea mainly give a qualitative assessment of the importance of the prey species for salmon (Struthers 1970; Struthers 1971; Thurow 1973; Hislop and Youngson 1984; Hansen and Pethon 1985). Salmon probably spend most of its time pelagically in the ocean close to the sea surface (Templeman 1967; Reddin 1985; Dutil and Coutu 1988) preying on different pelagic animals such as fish, crustaceans and squids.

The seaward migration of young salmon post-smolts occurs in spring. The salmon spend normally one to three years, occasionally up to five years in the open ocean. One important feeding area for salmon in the Northeast Atlantic during the autumn and winter months is in the central and southern Norwegian Sea, i.e. the area to the north of the Faroe Islands. This area is characterised by a front that separates the warmer Atlantic water from south-west and the colder and less saline Arctic water from north-west (Hansen 1985). Salmon are typically distributed in or close to the frontal areas (Jákupsstovu 1988).

Due to the large fish farming effort in the Northeast Atlantic, significant numbers of fish farm escapees have been observed mingled with the wild salmon in oceanic waters north of the Faroes (Hansen et al. 1993; 1999). The fate of the escaped salmon is poorly known, and we do not know how well escaped farmed salmon adapt to the marine environment.

Several authors have suggested that Atlantic salmon are opportunistic feeders (Hansen and Pethon 1985; Reddin 1988; Pearcy 1992; Hislop and Shelton 1993;

Sturlaugsson 1994). However, in the Atlantic there is no information that compares the diet of salmon with the potential prey available. Although information from literature on plankton and micronekton distributions in the Northeast Atlantic (e.g. Dunbar 1964; Dalpadado et al. 1998) might give a clue to the potential prey of salmon, the non-overlapping temporal and spatial nature of the data prevents any conclusion on prey selection. So far the feeding behaviour and forage strategy of Atlantic salmon has only been inferred from indirect measures such as stomach analysis.

In this paper we tested the hypothesis that Atlantic salmon that escape from fish farms adapt to the marine environment as do wild fish. This was done by comparing the qualitative and quantitative feeding habits of wild and escaped farmed salmon during autumn and winter in the sea north of the Faroes. Furthermore, we tested if there were differences in stomach contents among fish of different sea ages, and between seasons. Finally we tested whether Atlantic salmon are selective or opportunistic feeders by comparing stomach contents with available prey.

Materials and methods

Sampling

Atlantic salmon were caught in an experimental fishery with floating long-lines in the Norwegian Sea (north of the Faroes) between 63–66°N and 1–10°W (Fig. 1). Sampling took place during the autumn (November-December) and winter (February-March) fishery in the three fishing periods 1992/1993, 1993/1994 and 1994/1995. The experimental fishery followed the general pattern of the commercial salmon fisheries, which usually starts in November in the north-western area relatively close to the Faroes, and as the season progresses the fishery moves gradually in an north-eastern direction (Fig. 1). Normally there is a period of one to two months (late December to mid February) separating the autumn and winter fishery when fishing is difficult due to bad weather.

The long-lines (2000 hooks baited with sprat) were set early in the morning before dusk. Hauling started approximately at noon and was completed between 5 and 10 hours later, depending on the weather conditions and complications, such as breaking of the line. Usually the first 50 salmon caught from each set were sampled for stomach analysis. The sea-surface temperature (SST) was measured four times a day, before and after setting and hauling of the long-line, respectively.

There was no indication of that salmon regurgitates after capture. This cannot be completely verified, but neither the scientific staff onboard the research vessel nor the salmon fishermen noted any remains of stomach content on deck or in the water when hauling the line.

From catches in a total of 106 fishing sets 3855 stomachs were collected (Table 1), and they were removed and frozen immediately after capture. Fork lengths and gutted weights were measured and a scale sample was collected from each fish. On 13 fishing locations concurrent plankton samples were obtained (Fig. 1, encircled points) using a modified Isaackid midwater trawl (MIK), which is a framed 2 m diameter plankton net with 2.5 mm meshes in the foremost 11 m and 0.5 mm in the hindmost 2 m. The net was towed with a speed of 2.5 knots for 10 minutes at three depths, 5 m, 25 m, and 50 m, respectively. This sampling was carried out in the morning (about 07.00 and 08.00 h a.m.) just after the setting of long-lines were completed, except on the first station when the sample was taken at 18.00 h.

Wild and farmed salmon and sea age

Scales were used to identify if the fish was of wild or farmed origin (Lund and Hansen 1991). Salmon during its first winter in sea is termed one sea-winter (1SW) salmon. Salmon during its second winter in sea is termed two sea-winter (2SW) salmon, and similarly for 3SW and older salmon (Fig. 2). Scale samples from a total of 1112 (37%) wild and 369 (43%) farmed salmon were available. When no scale samples were available the fish was determined to be of wild or farmed origin by examining the presence of external characters like fin erosion which is common on reared salmon (Lund et al. 1989). The sea age of those fish was estimated from the material with sea age calculated from scales using the following simple discrimination algorithm. A length (length-split) was chosen from the known sample that separated the 1 and 2SW and 2 and 3+SW (3SW and older) wild salmon most efficiently, i.e. with lowest misclassification rate (Fig. 2). The estimated length-split between 1 and 2SW fish was 57 cm and between 2 and 3+SW fish 81 cm. The total misclassification was 6% (67 out of 1112 wild salmon). For farmed fish, however, the same rules could not be used with same efficiency due to considerable overlap in length at various sea ages (Fig. 2). It was therefore decided to use the length splits obtained from the wild salmon. In doing so, the number of 1SW fish was underestimated and the number of 2 and 3+SW salmon was overestimated (Fig. 2) with 22.5% misclassification (83 out of 369 farmed salmon). The relatively large discrepancy in the sea age of the escaped farmed fish is mainly due to the variable size at time of escape from sea cages at the coast and the fact that reared salmon is larger at-age than wild salmon due to the high growth rate under rearing conditions. Furthermore, the age of the farmed fish tend to be overestimated due to marks or checks in the scales being erroneously interpreted as winter bands (Lund et al. 1989). The decision to use the same length splits for both wild and farmed salmon, however, facilitates comparisons between different sea age groups in the analyses.

Stomach analysis

The identifiable stomach content was separated on species, measured and weighted individually if possible, or divided into length groups, which were weighted and counted. The remaining food items were grouped by the degree of digestion to genus, family or taxon, leaving the most digested material impossible to identify either to fish remains, crustacea remains or organic remains.

For quantitative analyses of the feeding habits of salmon, it is important that the number and corresponding weight of each prey species or prey group is available, to enable calculations of relative abundances. In 9% of the cases only weights or lengths of prey were recorded, in those cases were corresponding mean weights or mean lengths, respectively, used of prey from less digested stomachs in the same set. In the numerical analyses (i.e. diet overlap) stomachs containing remains were excluded, and judging from the frequency of the unidentified matter (2-13%, mean 6% of number and 5-33%, mean 16% of weight) in the various categories in the analyses, no one data set was likely to be more affected than the other. It is thus assumed that the total prey species distribution in the stomachs containing remains is similar to those stomachs containing only identifiable material.

For statistical analyses the data were grouped by several categories: season (autumn and winter), type of fish (wild and farmed) and sea age (1, 2, and 3+SW salmon). We further performed analyses by year (actually by fishing period lasting from November to March) where data permitted such analyses, and unless otherwise stated all three years were pooled.

Sprats that were obviously baits were observed in nearly half of the stomachs, and some salmon had taken more than one sprat. Furthermore, bird feathers and different inorganic material, such as nylon gut, sheets of plastic, dry paint etc. were also present in a few stomachs. Stomachs that contained bait, feathers or inorganic material only were considered as being empty.

Condition

The condition factor (K) for each category to be compared was calculated as $K = 10^5 w/l^3$, w is gutted weight in kg and l is forklength in cm. Data were log transformed prior to ANOVA to normalise the data.

Feeding intensity and diet overlap

The feeding intensity was examined by use of the proportion of empty stomachs to the total number of stomachs examined, as well as by the ratio of the average stomach content of prey (g) to body weight (g 10^3), the data were log-transformed to ensure normality.

Relative abundance of each species was studied by use of three frequently used measures: (1) the percentage frequency of occurrence (%F), based on the number of stomachs in which each food item occurred in relation to the total number of stomachs sampled (including empty stomachs), (2) the percentage in number (%N) of each prey item in all stomachs in a sample, and (3) the weight percentages (%W) of each prey item in all stomachs in a sample.

The intraspecific diet overlap between wild and farmed salmon, among sea ages of salmon, and between seasons was investigated using the simplified Morisita overlap index (Horn 1966) between predator j and k, $C_H = 2\ \ p_{ij}\, p_{ik} / (\ \ p_{ij}^2 + \ \ p_{ik}^2)$, where p_{ij} and p_{ik} are the proportions (number or weight) of prey species i in the stomach contents of the predator j and k, respectively. The diet overlap was estimated for several pairs of predator groups, dependent on the problems addressed, i.e. between wild and farmed salmon, between sea ages, between autumn and winter samples. To assess the degree of diet overlap, the prey species (i) were grouped into 10 ecological meaningful prey groups based on taxonomic adherence and size: 1 = amphipods, 2 = euphausiids, 3 = shrimps, 4 = other crustaceans, 5 = silverside, 6 = lanternfishes, 7 = other small fish, 8 = barracudinas, 9 = other large fish, and 10 = squids.

The overlap indices are critically dependent on the taxonomic resolution of the prey species groups (Krebs 1989; Hansson et al. 1996). High degree of pooling gives a high index and *vice versa*. Because of this sensitivity, we do not present statistical significance of the results, but use them for descriptive purposes and give a qualitative discussion of the results. However, Zaret and Rand (1971) considered values larger than 0.6 biologically significant, Langeton (1982) classified the values of the percentage overlap index as low (<30%), medium (30-60%), or high (>60%), and Pearcy et al. (1988) considered values larger than 75% as high. These classifications where, however, not based on statistical considerations.

Prey availability and prey selection

The simplified Morisita overlap index was used to compare the MIK plankton samples and the salmon stomach samples. However, due to avoidance problems of large fish such as herring, barracudinas and the larger capelin (>50 mm) from the MIK plankton sampler, these groups were excluded from the comparative analysis, as well as jellyfish and remains of fish and crustaceans, that could not be enumerated.

Results

Of the 3855 stomachs collected, 1176 (31%) were empty or contained only bait, unidentified or inorganic material. On average only half of the stomachs sampled in the autumn (53%) contained food while during winter 78% contained food. This difference was consistent in the three fishing periods. The frequency of farmed fish containing food was significantly higher than in wild fish in winter samples: farmed 85% and wild 76% ($\chi^2 = 18.74$, $df = 1$, $p < 0.001$), but were marginally non-significant in the autumn samples: farmed 57% and wild 51% ($p = 0.057$). There was no conclusive trend with age in the proportion of empty stomachs.

The dietary importance of different food by seasons of wild and farmed salmon is shown in Tables 2 and 3. The most important crustaceans were amphipods (*Themisto libellula, T. compressa, T. abyssorum* and *Eusirus holmi*), shrimps (*Hymenodora glacialis*) and krill (*Meganyctiphanes norvegica* and *Thysanoessa inermis*). The most important fishes were pearlside (*Maurolicus muelleri*), lanternfishes (*Benthosema glaciale* and *Notoscopelus kroeyeri*), barracudinas (*Notolepis rissoi kroyeri*, *Paralepis coregonoides borealis*), blue whiting (*Micromesistius poutassou*), herring (*Clupea harengus*), capelin (*Mallotus villosus*), and mackerel (*Scomber scombrus*). Apparently there was no difference in the prey species composition between wild and farmed salmon.

The abundance of the various prey species differed between seasons, but were also highly dependent on whether frequency of occurrence, number or weight percentages were calculated. The occurrence and numerical representations favour the importance of numerous small and frequently occurring prey (e.g. crustaceans) whereas the weight representation favour the larger and often infrequent prey such as fish. Crustaceans including *Themisto* spp., euphausiids and pelagic shrimps accounted for 95% of the food in number, but by weight to about 30%. By weight 66% of the stomach content was fish, particularly mesopelagic fish such as lanternfishes, pearlsides, barracudinas, and silverside, corresponding to only 5% in number. Some larger pelagic fish such as herring, blue whiting and mackerel were also present (0.1% by number and 13% by weight). Fish and crustacean prey accounted for 96% of the weight of all prey taken, the remainder was equally divided by unidentified organic remains and squid. These figures were similar for wild and farmed salmon (Tables 2 and 3).

Condition

The multiple ANOVA of K-factor on season (autumn and winter), type (wild or farmed) and sea age (1, 2, and 3+SW) resulted in season and sea age being highly significant, with no difference in condition between wild and escaped farmed salmon during the feeding phase in the sea (Table 4). The significant difference between the age groups was due to a large increase in the K-factor from the smaller 1 and 2SW salmon (which were not significantly different) to the larger 3+SW fish (by comparison of the overlap of the 95% confidence intervals, Fig. 3). Both 1 and 2SW salmon had significantly higher K-factor in autumn than in winter, but the condition of 3+SW salmon did not depend on season (Fig. 3).

Food content

From a regression analysis with log transformed data of the non-empty stomachs the average food content, s (g), was found to be proportional to the length, l (cm), of the fish, $s = 3.153 \cdot 10^{-4} l^{2.238}$ ($r^2 = 0.58$, $p < 0.001$, Fig. 4). The value of the allometric exponent (2.238) suggests that neither the weight nor length in third power would have standardised the data with respect to size of the fish. The resulting exponent would be negative and produce a hyperbolic decreasing trend with fish size. In our case since the weight (g) of the salmon is proportional to the length of the fish as $w = 3.542 \cdot 10^{-3} l^{3.22}$ ($r^2 = 0.95$, $p < 0.001$), the stomach content/body weight ratio as a function of fish length would be $s/w = 8.902 \cdot 10^{-2} l^{-0.982}$, or approximately inversely related to fish length. Thus all quantitative of comparisons stomach content were restricted to length or age groups to avoid ontogenetic dependencies.

Quantitative differences in stomach contents were observed between autumn and winter. A separate ANOVA by sea age of the logarithm of the stomach content/body weight ratio, $\ln(s/w)$, on season and type of salmon (Fig. 5), showed no difference between wild and farmed salmon, but significantly higher ratio in the winter than in the autumn for age group 1 (1.966 vs. 0.599, $F_{1,276} = 26.0$, $p < 0.001$) and 2 (1.053 vs. 0.297, $F_{1,1913} = 162.3$, $p < 0.001$), but was marginally insignificant for 3+SW salmon (0.416 vs. 0.215, $F_{1,478} = 3.5$, $p = 0.060$). It seems that the feeding rate of the larger 3+SW salmon is less dependent on season than for the smaller salmon.

The increase in the average food content per salmon from autumn to winter was mainly due to a relative increase of mesopelagic fish (lanternfishes, silverside and barracudinas) in the diet (Table 2 and 3).

Bait

Of the 3855 salmon caught and analysed, sprats that were obviously baits were observed in 1554 (40%) stomachs, 1164 (30%) wild and 390 (10%) farmed salmon. Of these 114 (3%) salmon, 78 (2%) wild and 36 (1%) farmed, had taken more than one sprat, and even a few salmon had taken up to four baits prior to capture.

We anticipated that the frequency of fish that contained bait *versus* no bait when caught would be independent of season, type of fish and size or age of fish. However, there were significantly higher proportion of salmon that contained bait during winter (43%) than during autumn (35%) ($\chi^2 = 27.3$, $df = 1$, $p < 0.001$), as well as significantly higher proportion of farmed salmon (45%) containing bait compared to wild salmon (39%) ($\chi^2 = 11.0$, $df = 1$, $p < 0.001$). There were also significant differences in the proportions that contained bait *versus* no bait among sea ages of salmon ($\chi^2 = 30.0$, $df = 2$, $p < 0.001$), both during autumn and winter and for wild and farmed salmon. Bonferroni adjusted posteriori tests showed that the proportion of the smaller 1SW (22%) salmon containing bait was significantly lower than for the larger 2 (41%) and 3+SW (52%) salmon, irrespective of season and type of fish ($\chi^2 = 77.2$, $df = 1$, $p < 0.001$). The 2 and 3+SW salmon were not significantly different (average 43%).

The proportion of salmon that had taken two or more baits prior to capture *versus* those containing only one bait was significantly higher during winter (9%) than during the autumn (3%) ($\chi^2 = 17.4$, df = 1, $p < 0.001$), and this difference was highly significant for wild salmon: winter (2%) and autumn (8%) ($\chi^2 = 15.1$, df = 1, $p < 0.001$), although the same tendency was observed for farmed salmon, the results were non-significant: winter (5%) and autumn (11%) ($p = 0.064$). No differences were observed among sea ages of salmon in this respect.

Prey type versus sea-surface temperature

Seasonal differences in temperature regimes were observed between the autumn and wintering feeding areas (Fig. 1), with a shift in the ambient sea-surface temperature (SST±SD) at the fishing locations (sets) from 7ºC ± 1.6ºC (n = 48) in the autumn to 3ºC ± 1.3ºC (n = 70) in the winter.

The species composition of *Themisto libellula* and *T. compressa* f. *compressa* (the 'short-legged' form of *T. compressa* [Schneppenheim & Weigmann-Haas 1986], a phenotype developing in warmer water than the 'long-legged' form [Sheader 1975]), two of the three hyperiid amphipods of the genus *Themisto* observed as prey, showed an inverse relationship of abundance (number and weight) in the stomachs of both wild (Table 2) and farmed salmon (Table 3). When *T. compressa* f. *compressa* is present in large numbers, then the number of *T. libellula* is low and vice versa. Linear regressions of the natural logarithm of prey weight percentages of *T. libellula* and *T. c.* f. *compressa*, respectively on ambient SST (Fig. 6), showed that the abundance of *T. libellula* was significantly positively related to ambient SST ($F_{1,63} = 14.8$, $r^2 = 0.196$, $p < 0.001$) and the abundance of *T. c.* f. *compressa* were significantly negatively related to ambient SST ($F_{1,43} = 21.6$, $r^2 = 0.315$, $p < 0.001$). Thus, of the amphipods *T. libellula* dominated in the stomachs of salmon caught in the colder areas or periods while *T. c.* f. *compressa* dominated in salmon from the warmer areas.

Diet overlap

There was no difference in the food content between wild and farmed salmon, the simplified Morisita overlap index was 0.995, indicating a very high degree of overlap in choice of prey species or prey species groups. The high overlap was also evident between seasons (autumn, 0.994 and winter, 0.991) and among sea age groups 1, 2 and

3+SW (0.876, 0.984, and 0.981, respectively). Thus we pooled wild and farmed salmon in the further analyses.

The seasonal index was 0.584, indicating a moderately low overlap in the stomach content between autumn and winter. The seasonal overlap within each age group was 0.706, 0.527, and 0.728 for sea age 1, 2 and 3+SW, respectively, indicating that the differences between seasons was mainly due to 2SW salmon, which also is the main age group caught (72%). The seasonal differences in prey (Fig. 7) show that mainly amphipods and the group "Other large fish" were eaten during autumn, while the contribution to the weight percentages were more evenly distributed by lanternfishes, barracudinas, silverside, "Other large fish" and amphipods during winter.

A closer examination of the seasonal differences of the large fish prey, i.e. the groups barracudinas and "Other large fish" show that mainly blue whiting, *Micromesistius poutassou*, and to a lesser extent herring, *Clupea harengus*, mackerel, *Scomber scombrus*, and Paralepidae (Table 2 and 3) were eaten during autumn, while mainly Paralepidae and herring, and some fry of capelin, *Mallotus villosus* were eaten during winter (Fig. 8). Although the contribution in weight is high of the larger fish prey, only 136 salmon (3.5%) had taken those prey.

The 1 and 2SW salmon had a relatively high diet overlap (0.764). However, the moderate diet overlap between 2 and 3+SW salmon (0.648) and the low overlap between 1 and 3+SW (0.359) indicated a shift in prey composition among age (size) groups of salmon. The smaller 1SW salmon had mainly eaten amphipods and lanternfishes, and some barracudinas, while the larger 3+SW salmon had mainly eaten large fish, barracudinas and lanternfishes, and the 2SW salmon had eaten the various prey groups in intermediate proportions compared to the 1SW and 3+SW salmon (Fig. 9). The larger fish prey was thus preferred with increasing age (size) of the predator to smaller mesopelagic fish and crustaceans. The age distribution of salmon containing large prey (3% 1SW, 66% 2SW, and 31% 3+SW) was significantly larger than for the remaining fish (11% 1SW, 72% 2SW, and 17% 3+SW) (χ^2, df = 2, $p < 0.001$), the difference between each proportion within each age was significant (χ^2 tests adjusted for multiple comparisons). The reported age specific changes towards fish with increasing age were evident both in the autumn and winter season.

Prey size to fish size

The relationships between average prey size and fish size for *Themisto libellula*, *Meganyctiphanes norvegica*, *Hymenodora glacialis* and *Maurolicus muelleri* were examined. Generally the average prey size in the stomachs did not depend on fish size, except for *T. libellula*, where a significant positive relationship was observed ($r^2 = 0.039$, df = 426, $p < 0.001$). The prey length data of *T. libellula* were transformed to natural logarithms to assure that they were normally distributed. However, the regression had a very low explanatory value (4%).

Prey availability and prey selection

In total 319 non-empty salmon stomachs were observed at the 13 fishing stations where corresponding MIK plankton samples were available. The abundance of prey species and their weight percentages show that the plankton tows generally included the same species as found in the stomachs, i.e. the hyperiid amphipods, euphausiids, shrimps, lanternfishes and pearlsides (Table 5). However, *Sagitta* spp. and a few individuals of the small copepod, *Calanus finmarchius*, that were observed in the plankton samples, were absent from the stomachs. On the other hand, large fish such as herring, barracudinas and the larger capelin (>50 mm) found in the salmon stomachs were not caught with the net probably due to avoidance. The data set for calculating overlap index was thus limited by excluding larger fish as well as jellyfish and remains of fish and crustaceans that could not be enumerated (Table 5). Although most of the species occurred in both data sets, their relative proportion differed greatly resulting in a low overlap index (0.3). Atlantic salmon appeared to select small pelagic fish to crustaceans, and furthermore to prefer amphipods (*Themisto* spp.) to euphausiids, although the availability of the euphausiids was significantly higher as indicated from the plankton samples (Table 5). On average the salmon had taken twice as much amphipods than euphausiids while the plankton sampler caught 13 times more euphausiids than amphipods. There were also great variations and low overlap between the two prey groups at the individual sampling stations, but the preference of amphipods to euphausiids was also evident at sampling station level (Fig. 10). Of the euphausiids, it seems as salmon prefer the larger *Meganyctiphanes norvegica* to the smaller *Thysanoessa longicaudata* and *T. inermis*, suggesting size selective feeding (Fig. 10).

To further explore possible selective feeding behaviour by salmon, the percentage length distribution of six species or groups were studied in more detail (Fig. 11a-f). The pearlside, *Maurolicus müelleri* (Fig. 11a); the amphipods *Themisto libellula* (Fig. 11b), *T. compressa*, including both forms, i.e. *T. c.* f *compressa* and *T. c.* f *bispinosa* (Fig. 11d), and *T. abyssorum* (Fig. 11e); the Euphausiids *Meganyctiphanes norvegica* (Fig. 11e), and *Thysanoessa* spp., including both *Thysanoessa inermis* and *Thysanoessa longicaudata* (Fig. 11a). These groups were chosen due to available length distributions in both the plankton and the stomach samples. For four of the six groups the size distribution of the prey eaten by salmon was larger than that of the animals caught in the corresponding plankton samples. This was especially true for the *M. müelleri*, where the 1 and 2+ groups were eaten by salmon but only the 1 groups was caught in the plankton net (Fig. 11a). Of the amphipods there was an almost perfect overlap between the samples, i.e. *Themisto libellula* and *T. compressa*, respectively (Fig. 11b-c), but the salmon had taken exclusively larger *T. abyssorum* than were caught in the environment (Fig. 11d). Similarly the euphausiids eaten were larger than those caught in the plankton net (Fig. 11e-f).

Discussion

Stomach contents

Oceanic waters north of the Faroes and in the southern Norwegian Sea are important feeding areas for salmon in the Northeast Atlantic during winter (Jákupsstovu 1988), and in October/November the first 1SW salmon appear in the long-line catches north off the isles. However, salmon in their second winter at sea (2SW) are the dominating component in this fishery.

The results of the present study revealed that crustaceans including *Themisto* spp., euphausiids and pelagic shrimps accounted for more than 95% of the food in number, but by weight 66% of the stomach content was fish, particularly lantern fishes, pearlsides, barracudinas, and silversides. Some larger pelagic fish such as herring, blue whiting and mackerel were also present (0.1% by number and 13% by weight).

Hislop and Shelton (1993) proposed that the crustaceans were a much less important prey than fish in the North Atlantic. However, the extensive material studied here places more emphasis on crustacean prey in the Northeast Atlantic, particularly the hyperiid amphipods and to a lesser extent euphausiids as the average prey in salmon beside mesopelagic fishes. Especially in the autumn salmon seemed to rely on amphipods as food. This is in contrast to the food of adult fish in coastal areas returning to spawn (Blair 1965; Grønvik and Klemetsen 1987; Hislop and Webb 1992), where fish totally dominate, however with one notable exception where crustaceans were the main food (Neilson and Gillis 1979).

Condition

It appears that the condition factor (K-factor) for salmon in the sea is relatively high, especially for 3+SW salmon, and is comparable to salmon in e.g. West Greenland waters (Lear 1972; Munro and Swain 1980), but higher than those observed by Dwyer and Piper (1987). The higher condition during autumn than in winter is consistent with the observations made by Dwyer and Piper (1987), although the level of the predicted K-factors around 0.82 and 0.85 with ambient temperatures of 3 and 7°C, respectively (Dwyer and Piper 1987), were lower than our estimates of 0.9 and 0.94 respectively, for the same temperature ranges.

The significantly higher condition of 3+SW salmon than of the smaller salmon, irrespective of season, might be a reflection of higher tolerance (due to its size) to low temperatures, greater potential to forage over a wide area and improved capture success of various prey available. In addition, the feeding rate (stomach content/body weight ratio) of the larger 3+SW salmon is more independent of season than for the smaller salmon. Since about 90% of the salmon present in the area north of the Faroes were estimated to mature, irrespective of age (ICES 1984; Youngson and McLay 1985; Jákupsstovu 1988), most of the fish will undertake the homeward migration sometime during winter of spring. Thorpe (1994) and Kadri *et al.* (1995; 1997) indicated that in maturing salmon a certain threshold level of energy reserves have to be achieved at a certain date for the fish to mature. Because salmon feed less during homing migration, we suggest that the large fish have stored sufficient energy earlier in the season than younger fish, due to the observation that older individuals home earlier in the season than younger fish (Hawkins 1987; Jonsson et al. 1990).

Feeding intensity

On the assumption that the proportion of empty stomachs is indicative of the intensity of feeding (Rae 1967; Bowman and Bowman 1980), then salmon feed more intensively in winter than in autumn, when nearly half of the stomachs were empty. Of the stomachs containing food, the feeding rate in weight increased from autumn to winter for the 1 and 2SW fish, but not for 3+SW salmon. The increase was mainly due to higher proportions of fish in the diet in winter, particularly of mesopelagic fish. The apparent low feeding rate in late autumn could be an indication of reduced food availability in the sea during this period. In comparison salmon sampled in the Labrador Sea (Lear 1980) had less food in their stomachs in the autumn than in the spring (3.1 g and 5.7 g food per kg of salmon, respectively) and were feeding less actively (28% and 8% empty stomachs, respectively). Lower feeding rates during winter were also observed in the Baltic (Christensen 1961; Thurow 1966).

The higher condition factor of salmon in the autumn than winter seems to contradict the statement above on lower food availability during autumn. The explanation to the apparent ambiguity might be found in the fact that the gastric evacuation rate is highly dependent on temperature (Dos Santos and Jobling 1991). The lower rate of emptying of the stomach during winter caused by lower ambient temperature would give the impression that fewer stomachs were empty and, that the non-empty stomachs on average would contain more food due to slow digestion.

We observed a significantly lower proportion of the salmon containing bait during autumn than in winter, and similarly a significantly lower proportion of salmon that had taken two or more baits prior to capture compared to only one bait during autumn than in winter. However, the biological significance of these observations is not clear, but might indicate that the fish have greater appetite during the winter.

The observation that a higher proportion of escaped farmed fish containing bait than wild salmon is difficult to explain. The probability that salmon take the bait depends on whether the bait and hook was approached and swallowed in one bout or the capture was a result of hooking without swallowing. If the feeding behaviour of the escaped farmed salmon was different, e.g. due to its farmed prehistory, it might result in different behaviour when approaching the bait. Alternatively farmed salmon have been selected for fast and efficient growth. This may have resulted in a higher demand for energy (Thodesen et al. 1999) and thus made farmed salmon a more aggressive feeder.

If the escaped farmed fish behave different compared to wild salmon in the sea, either having problems to adapt to the wild or being more eager to take food due to their farmed prehistory, it could be expected that the condition factor of two groups were different. However, no difference in condition was observed between wild and escaped farmed salmon during the feeding phase in the sea. Neither were any differences observed in frequency, number or weight proportions of prey between wild and farmed salmon, nor in diet overlap. Furthermore, a higher proportion of farmed fish contained food than wild fish. This strongly suggests that fish farm escapees that survived until capture have adapted to feed in the oceanic environment.

Farmed salmon caught in Scottish coastal waters have also been observed to feed on natural prey (Hislop and Webb 1992). Reiriz et al. (1998) found that naive hatchery-reared juvenile Atlantic salmon parr exposed to natural prey had a fast learning response towards novel prey so it matched the efficiency of wild-caught fish. The fast learning response would allow fish to maintain a high foraging efficiency when faced with frequent changes in the availability of different prey types (Fisher and Pearcy 1996; Orr and Bowering 1997; Cortés 1997; Andersen 1999).

Prey availability and stomach content

The comparative material from the salmon stomachs and the plankton samples might contain several potential sources of bias, including avoidance from the towed net sampler, limiting sampling range (0-50 m) and uncertainty in the interpretation of gut samples on how accurately they represent relative abundance of prey as consumed (Kohler and Ney 1982). The validity of the plankton samples as to be representative of prey availability could not be addressed. However, all but one net sample was taken in the morning between 07 and 08 h, after setting of the line and before hauling, thus minimising possible diurnal variations in the material and further ensuring that the plankton samples were obtained while the long-line was fishing. However, not necessarily when the salmon was feeding.

Although the large fish species such as herring, barracudinas and the larger capelin (>50 mm) were excluded prior to the comparative analysis, the resulting overlap index was low (0.3), which might indicate at least a partly selective feeding strategy of salmon. Though possible, we tend to rule out that avoidance from the net could have caused the observed differences in the proportions between the net and the stomachs. Judging from the fact that pearlside up to 40 mm and capelin fry (40-50 mm) were caught in the plankton net, the avoidance of crustaceans (mainly < 30 mm) from the net should be negligible. We further assume no difference in avoidance behaviour between amphipods and euphausiids of similar size. Other researchers have reported avoidance of large zooplankton and fish (> 45 mm) from the MIK plankton net sampler and similar sampling devices (Munk 1988; Dalpadado et al. 1998).

Even if most of the species occurred in both data sets, their relative proportion differed greatly. Our results suggest that fish were preferred over crustaceans, of crustaceans the amphipods were preferred over euphausiids, and of the three species of euphausiids the larger *Meganyctiphanes norvegica* was preferred over the smaller *Thysanoessa inermis* and *Th. longicaudata*. Furthermore, within each of the three euphausiids species, the prey ingested was larger than from the habitat samples. The preference of fish to crustaceans, and of the larger *M. norvegica* over *Thysanoessa* spp. can be explained by size selective feeding of salmon. However, the preference of amphipods to euphausiids seems more subtle, as their sizes are comparable in the plankton samples, although in the stomachs the euphausiids were larger than the amphipods. The energetic content of euphausiids and amphipods might be different as well as their visual contrast in the sea, in particular the large and heavily pigmented compound eye of amphipods may make them more conspicuous (Zaret and Kerfoot 1975), or their swimming and predatory escape behaviour might be different. It further seems that although there are numerous *Thysanoessa* spp. available in the upper 50 m from the plankton data, this genus is hardly preyed upon by salmon. In the Pacific, Peterson et al. (1982) also found a preference for amphipods to similar sized stages of a copepod of juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) off the Oregon coast, and Brodeur et al. (1992) estimated that the consumption of euphausiids as percentage of total biomass was quite low (0.01% d^{-1}) by coho and chinook, although the abundance of euphausiids from plankton tows were high.

Holst et al. (1996) found a tendency of size-selective feeding of salmon post-smolts of the hyperiid amphipods (*Themisto* spp.), as indicated by a positive relation between prey size in the stomachs and post-smolts size. This corresponds with our findings of a weak, but significant correlation between length of salmon and length of *Themisto libellula* prey. Furthermore, Holst et al. (1996) noted that given that O-group fish were available in the area as observed from the trawl catches and that amphipods also were available from parallel plankton sampling, the post-smolts fed mainly on O-group fish, indicating a selective feeding strategy. Selective feeding was also reported by Lear (1972) in the Northwest Atlantic, where salmon preferred herring to capelin, and the large salmon contained significantly more herring than small salmon.

Salmon did not feed on *Sagitta* spp., although it has been reported as food for salmon in the Pacific (Brodeur and Pearcy 1990; Tadokoro et al. 1996). It might be speculated that *Sagitta* spp. either is too transparent, unpalatable, or is a low energy prey.

At least two year classes (1 and 2+ group) of pearlside (*Maurolicus müelleri*) were present in the salmon stomachs, however, only the smaller 1 group was present in the plankton samples, apparently indicating size selective feeding. Alternatively, the larger 2+ group of pearlside might avoid the plankton sampler or being distributed below the sampling depth of 50 m. The pearlside has been reported in some areas to be separated into two vertical layers in the sea during winter, with the older individuals occupying the lower layer (Goodson et al. 1995) and are reported to be most numerous below 200 m depth in the Norwegian Sea (Dalpadado et al. 1998). Thus salmon probably also feed deeper than 50 m depth. Salmon are generally found to inhabit the upper surface layers (Templeman 1967; Reddin 1985; Dutil and Coutu 1988) most of the time with occasional deep ascents for shorter or longer time periods, deeper that 150 m (Jákupsstovu 1988). Pacific salmon also occasionally feed deeper than 150-200 m during day (Pearcy et al. 1988).

A shift in prey composition among age (size) groups of salmon was also indicated, the smaller 1SW salmon had taken higher proportions of amphipods compared to the larger 2+SW fish, while the proportion of fish prey, particularly barracudinas and other large fish increased with age, indicating a higher degree of piscivory with age.

The tendency that the warmwater phenotype, *Themisto compressa* f. *compressa* (Sheader 1975) was more abundant in salmon stomachs then the *T. libellula* (considered an arctic or subarctic species) in warmer water and *vice versa* in colder water may lend support to the hypothesis that salmon are opportunistic feeder in the sense of a capability to feed on whatever prey organisms were available. However, the relatively low overlap between salmon diet and the available prey in our study, and the preference of amphipods to euphausiids and of the larger *Meganyctiphanes norvegica* to the smaller *Thysanoessa* spp. (both euphausiids), seems to render salmon as a selective feeder.

We conclude that crustaceans and particularly the hyperiid amphipods of the genus *Themisto*, euphausiids and mesopelagic shrimps are important sources of food for salmon in the autumn period and equally important becomes the different mesopelagic fish as lantern fishes, pearlsides and barracudinas during the late winter period. The occasional presence of larger fish in the stomachs, such as herring, blue whiting and mackerel is not considered as a main source of food for salmon in the sea. We were not able to assess whether food is a limiting factor for salmon in the sea. We suggest that salmon feed opportunistically, however, selecting the larger size range of available prey. Finally we conclude that escaped farmed salmon that survive until capture adapt well to the "wild" life in the ocean.

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Table 1. The salmon stomachs collected from 106 fishing sets in the Faroese research fishery during three fishing periods 1992/1993–1994/1995. The number of salmon stomachs sampled by season, by type of fish (wild or farmed), and by sea age (1, 2 and 3+ sea winters) are shown. Sea age 3+ includes some fish older that 3SW.

Fishing Period	Season	Type	1SW	Sea age 2SW	3+SW	Total
1992	Autumn	Farmed	6	15	4	25
		Wild	30	63	5	98
1993	Winter	Farmed	24	173	44	241
		Wild	26	549	341	916
Subtotal:			86	800	394	1280
1993	Autumn	Farmed	27	103	10	140
		Wild	27	260	23	310
1994	Winter	Farmed	25	85	11	121
		Wild	112	228	101	441
Subtotal:			191	676	145	1012
1994	Autumn	Farmed	19	120	1	140
		Wild	126	467	15	608
1995	Winter	Farmed	31	148	17	196
		Wild	48	506	65	619
Subtotal:			224	1241	98	1563
Grand total:			501	2717	637	3855

Table 2. Diet of wild salmon: frequency of occurrence (%*F*, including empty stomachs), number (%*N*), and weight percentages (%*W*) of prey items in salmon by autumn (A, November-December), winter (W, February-March) and in total. The entries 0 means < 0.1%. Data were collected from 2992 wild salmon stomachs of which 961 (32%) were empty.

		%*F*			**%*N***			**%*W***	
Prey groups	**A**	**W**	**Total**	**A**	**W**	**Total**	**A**	**W**	**Total**
Crustaceans:									
Hyperiid amphipods:									
Themisto spp.	16.1	14.9	15.3	22.6	21.6	22.2	11.6	4.0	5.3
Themisto libellula	14.6	26.7	22.6	5.2	27.8	14.1	4.2	6.6	6.2
Themisto compressa	23.2	19.4	20.7	70.3	19.8	50.2	31.5	1.4	6.7
Themisto abyssorum	1.0	3.3	2.5	0	0.3	0.1	0	0	0
Euphausiids:									
Euphausiidae	5.9	6.2	6.1	0.5	2.6	1.3	0.8	0.6	0.6
Meganyctiphanes norvegica	16.8	36.9	30.1	0.9	12.0	5.3	2.6	3.7	3.5
Thysanoessa inermis	0.7	2.2	1.7	0	0.4	0.2	0.1	0.1	0.1
Thysanoessa longicaudata	0.3	0.2	0.2	0	0	0	0	0	0
Shrimps:									
Hymenodora glacialis	2.7	23.0	16.1	0.1	2.4	1.0	0.8	4.5	3.8
Sergestes arcticus	0.4	0.2	0.3	0	0	0	0.1	0	0
Pasiphea tarda	-	0.1	0	-	0	0	-	0	0
Other crustaceans:									
Paraeuchaeta norvegica	0.3	-	0.1	0	-	0	0	-	0
Gammaridea	-	0.2	0.1	-	0	0	-	0	0
Aristias tumidus	0.1	-	0	0	-	0	0	-	0
Eusirus holmi	-	2.0	1.3	-	0.1	0.1	-	0.2	0.1
Crustacea remains:	2.4	17.7	12.5	0.1	1.1	0.5	0.5	4.0	3.4
Fishes:									
Silversides:									
Maurolicus muelleri	2.4	16.8	11.9	0.1	3.6	1.5	1.3	10.0	8.5
Baracudinas:									
Paralepidae	0.3	2.3	1.6	0	0.2	0.1	2.6	8.2	7.2
Notolepis rissoi kroyeri	0.1	0.9	0.6	0	0.1	0	0.5	3.9	3.3
Paralepis coregonoides borealis	0.4	0.2	0.3	0	0	0	2.5	0.9	1.2
Lanternfishes:									
Myctophidae	0.4	8.1	5.5	0	1.2	0.5	0.3	6.8	5.7
Lampanyctus crocodilus	-	0.1	0	-	0	0	-	0.1	0.1
Notoscopelus kroeyeri	0.6	0.3	0.4	0	0	0	2.8	0.4	0.8
Myctophum punctatum	0.1	0.6	0.4	0	0.1	0	0.1	0.5	0.4
Benthosema glaciale	0.9	10.3	7.1	0	1.7	0.7	0.9	10.1	8.5
Other fish:									
Ammodyteidae	-	0.2	0.1	-	0	0	-	0	0
Mallotus villosus	-	0.2	0.1	-	0.1	0	-	0.9	0.8
Fry (mostly *Mallotus villosus*)	0.5	3.5	2.5	0.1	2.3	1.0	0.2	1.6	1.4
Clupea harengus	0.2	0.6	0.4	0	0	0	5.5	9.0	8.4
Micromesistius poutassou	0.7	-	0.2	0	-	0	18.5	-	3.3
Onogadus argentatus	-	-	-	-	-	-	-	-	-
Lycenchelys sp.	-	0.1	0	-	0	0	-	0.1	0.1
Scomber scombrus	0.3	0.1	0.1	0	0	0	7.3	0.5	1.7
Belone belone	-	0.1	0.1	-	0	0	-	0.6	0.5
Gasterosteus aculeatus	-	0.1	0.1	-	0	0	-	0.1	0.1
Fish remains:	6.1	34.4	24.8	0.1	2.2	1.0	4.2	17.1	14.8
Squid:									
Gonatidae	0.1	0.9	0.6	0	0.1	0	0	2.4	2.0
Gonatus fabricii	-	0.1	0	-	0	0	-	0.2	0.1
Remains organic:	2.2	2.8	2.6	0	0.2	0.1	1.1	1.2	1.2
Birds and bird remains:	0.3	0.4	0.3	-	0	0	-	0.2	0.1

Table 3. Diet of farmed salmon: frequency of occurrence (%*F*, including empty stomachs), number (%*N*), and weight percentages (%*W*) of prey items in salmon by autumn (A, November-December), winter (W, February-March) and in total. The entries 0 means < 0.1%. Data were collected from 863 farmed salmon stomachs of which 215 (25%) were empty.

		%*F*			**%*N***			**%*W***	
Prey groups	**A**	**W**	**Total**	**A**	**W**	**Total**	**A**	**W**	**Total**
Crustaceans:									
Hyperiid amphipods:									
Themisto spp.	20.3	19.0	19.5	23.2	24.0	23.5	11.6	3.6	4.8
Themisto libellula	13.8	28.5	23.3	10.9	22.3	15.6	6.5	4.8	5.1
Themisto compressa	25.6	24.6	24.9	60.8	17.9	43.1	25.7	1.4	5.0
Themisto abyssorum	1.3	4.5	3.4	0.1	0.4	0.2	0.1	0	0.1
Euphausiids:									
Euphausiidae	7.5	8.2	8.0	3.1	4.1	3.5	5.2	0.7	1.4
Meganyctiphanes norvegica	21.6	43.2	35.6	1.4	14.7	6.8	4.0	3.9	3.9
Thysanoessa inermis	1.0	2.7	2.1	0	0.3	0.1	0.1	0.1	0.1
Thysanoessa longicaudata	1.0	0.2	0.5	0	0	0	0	0	0
Shrimps:									
Hymenodora glacialis	2.3	26.5	18.0	0.1	2.9	1.2	1.2	4.2	3.8
Sergestes arcticus	0.3	0.2	0.2	0	0	0	0.1	0.2	0.1
Pasiphea tarda	-	-	-	-	-	-	-	-	-
Other crustaceans:									
Paraeuchaeta norvegica	0.7	-	0.2	0	-	0	0	-	0
Gammaridea	-	0.4	0.2	-	0	0	-	0	0
Aristias tumidus	-	-	-	-	-	-	-	-	-
Eusirus holmi	0.3	2.7	1.9	0	0.2	0.1	0.1	0.2	0.2
Crustacea remains:	20.3	19.0	19.5	0	1.3	0.6	0.7	4.8	4.2
Fishes:									
Silversides:									
Maurolicus muelleri	2.3	20.8	14.3	0.1	3.4	1.4	2.2	7.6	6.8
Baracudinas:									
Paralepidae	0.3	3.2	2.2	0	0.2	0.1	4.3	9.6	8.8
Notolepis rissoi kroyeri	-	0.7	0.5	-	0	0	-	2.0	1.7
Paralepis coregonoides borealis	-	0.4	0.2	-	0	0	-	0.6	0.5
Lanternfishes:									
Myctophidae	2.0	8.6	6.3	0.1	1.3	0.6	2.2	6.1	5.5
Lampanyctus crocodilus	-	-	-	-	-	-	-	-	-
Notoscopelus kroeyeri	-	0.2	0.1	-	0	0	-	0.4	0.4
Myctophum punctatum	-	0.4	0.2	-	0	0	-	0.6	0.5
Benthosema glaciale	1.0	9.9	6.7	0	1.6	0.7	0.9	7.2	6.3
Other fish:									
Ammodyteidae	-	-	-	-	-	-	-	-	-
Mallotus villosus	0.7	0.5	0.6	0	0	0	1.5	0.7	0.8
Fry (mostly *Mallotus villosus*)	0.3	4.1	2.8	0	2.3	0.9	0	1.4	1.2
Clupea harengus	0.3	0.7	0.6	0	0.1	0	6.7	10.8	10.2
Micromesistius poutassou	1.0	-	0.3	0	-	0	20.4	-	3.0
Onogadus argentatus	0.3	-	0.1	0	-	0	0.7	-	0.1
Lycenchelys sp.	-	-	-	-	-	-	-	-	-
Scomber scombrus	-	-	-	-	-	-	-	-	-
Belone belone	-	-	-	-	-	-	-	-	-
Gasterosteus aculeatus	-	-	-	-	-	-	-	-	-
Fish remains:	6.2	39.1	27.5	0.1	2.5	1.1	4.1	22.7	19.9
Squid:									
Gonatidae	-	1.6	1.0	-	0.1	0	-	2.3	1.9
Gonatus fabricii	-	-	-	-	-	-	-	-	-
Remains organic:	1.6	6.5	4.8	0	0.4	0.2	1.6	3.8	3.5
Birds and bird remains:	-	0.4	0.2	-	0	0	-	0.5	0.4

Table 4. ANOVA of K-factor ($K = 10^5 w/l^3$) for 3855 salmon grouped by season (autumn or winter), type (wild or farmed) and sea age (1, 2 or 3+SW). *** = 0.1% significance level.

Source of variation	Sum of Squares	df	Mean-Square	F-ratio	P	Sign.
Season	0.558	1	0.558	48.234	0.000	***
Type	0.027	1	0.027	2.325	0.127	
Sea age	0.033	2	1.517	131.103	0.000	***
Season * Type	0.001	1	0.001	0.064	0.800	
Season * Sea age	0.034	2	0.017	1.467	0.231	
Type * Sea age	0.005	2	0.002	0.209	0.811	
Error	44.483	3845	0.012			

Table 5. Total wet-weight percentages of different prey groups in the salmon stomachs and in the MIK plankton samples from 13 corresponding fishing locations. Table entries marked with a dash (–), means that prey species/group were not found in the sample. Total wet-weights (g) of all samples are given at the bottom row in parenthesis. Remains of a crustacea and fish were found in the stomach content due to advanced digestion, while in the MIK samples the material was fresh and identifiable to species or family. To calculate the simplified Morisita overlap index between the prey species in the stomachs and in the MIK samples, the data set was reduced by excluding large fish that avoided the plankton net, and remains and jellyfish that could not be enumerated, i.e. the entries marked with a star (*) in the two rightmost columns.

Species/group	Category	Stomachs weight %[a]	MIK samples weight %[b]	Stomachs Weight %	MIK samples weight %
Scyphosoa	Jellyfish	–	2.17	*	*
Tomopteris sp.	Polychaeta	–	0.05	–	0.05
Bivalvia	Mussels	–	0.01	–	0.01
Sagitta sp.	Chaetognatha	–	0.98	–	1.01
Lepeophtheirus salmonis [c]	Crustaceans	–	0.01	–	0.01
Calanus finmarchicus	Crustaceans	–	0.10	–	0.10
Aristias tumidus	Crustaceans	0.003	–	0.006	–
Eusirus holmi	Crustaceans	0.25	–	0.43	–
Pareuchaeta norvegica	Crustaceans	0.002	1.25	0.003	1.27
Themisto spp.	Crustaceans	16.37	6.82	31.85	6.97
Ephausiidae	Crustaceans	8.72	87.54	14.90	89.47
Hymenodora glacialis	Crustaceans	5.15	0.05	8.90	0.05
Crustacea remains	Crustaceans	5.62	–	*	*
Gonatus fabricii	Squid	0.02	0.03	0.03	0.03
Maurolicus müelleri	Fish -small	4.74	0.54	8.10	0.56
Myctophidae	Fish -small	18.25	0.03	31.17	0.03
Mallotus villosus [d]	Fish -small	2.70	0.44	4.61	0.44
Mallotus villosus [d]	Fish -large	0.44	–	*	*
Paralepidae	Fish -large	9.45	–	*	*
Clupea harengus	Fish -large	15.90	–	*	*
Fish remains	Fish	12.38	–	*	*
Total wet-weight (g)		(1719)	(837)	(1006)	(819)

[a] Total weight % in 319 non-empty salmon stomachs (of 481 sampled) from 13 fishing locations.

[b] Total weight % in the MIK plankton samples taken on the 13 fishing locations as above.

[c] A few salmon lice have been found in salmon stomachs from other samples in the same area.

[d] Only capelin fry (< 50 mm) was caught in the MIK samples while both fry and adult specimens were found in the salmon stomachs.

Fig. 1. Fishing locations where 3855 stomachs of Atlantic salmon were sampled during the autumn (November-December) and winter (February-March) fishery in 1992/1993, 1993/1994, and 1994/1995 north off the Faroes. Plankton samples were taken on 15 locations in 1994 and 1995 (MIK plankton net). The main fisheries take place in the autumn closer to the Faroes than the in the winter season (inside the stippled area). The 500 and 1000 m depth contours are shown.

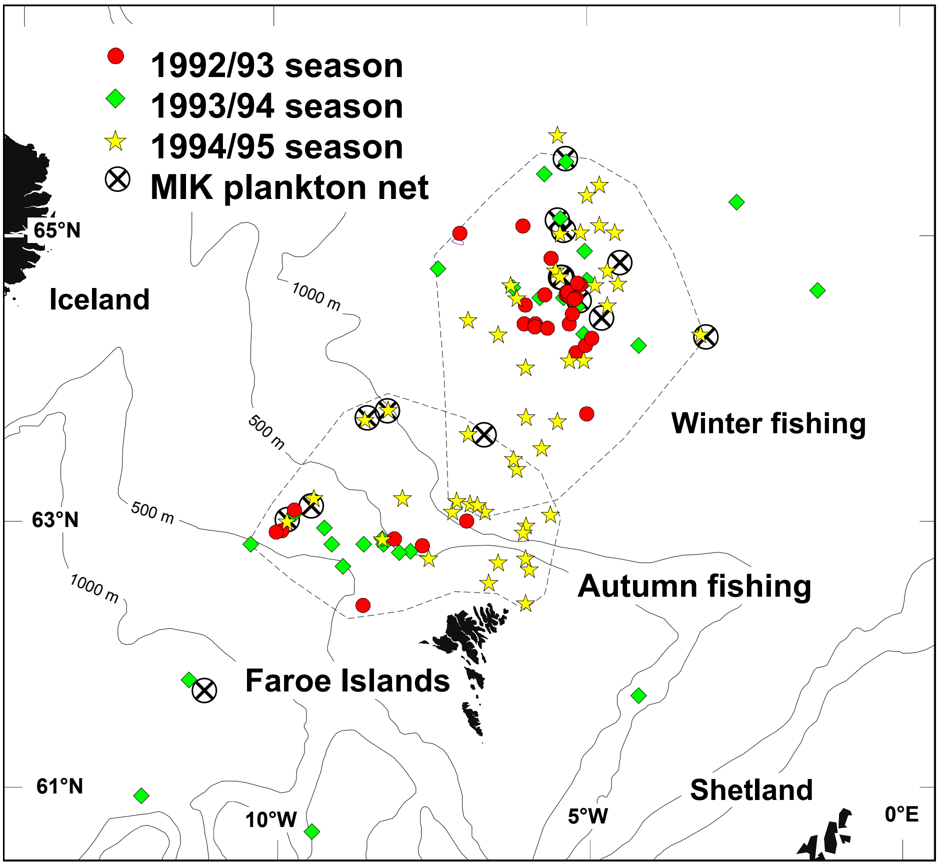


Fig. 2. Size distribution (forklength) by sea age of wild salmon (upper panel) and escaped farmed salmon (lower panel) during 1992/93–1994/95 fishing seasons north of the Faroes (autumn and winter samples pooled). Sea age was determined by scale readings of 1112 wild and 369 farmed salmon, respectively. Sample percentages of total number of each type are shown in brackets.

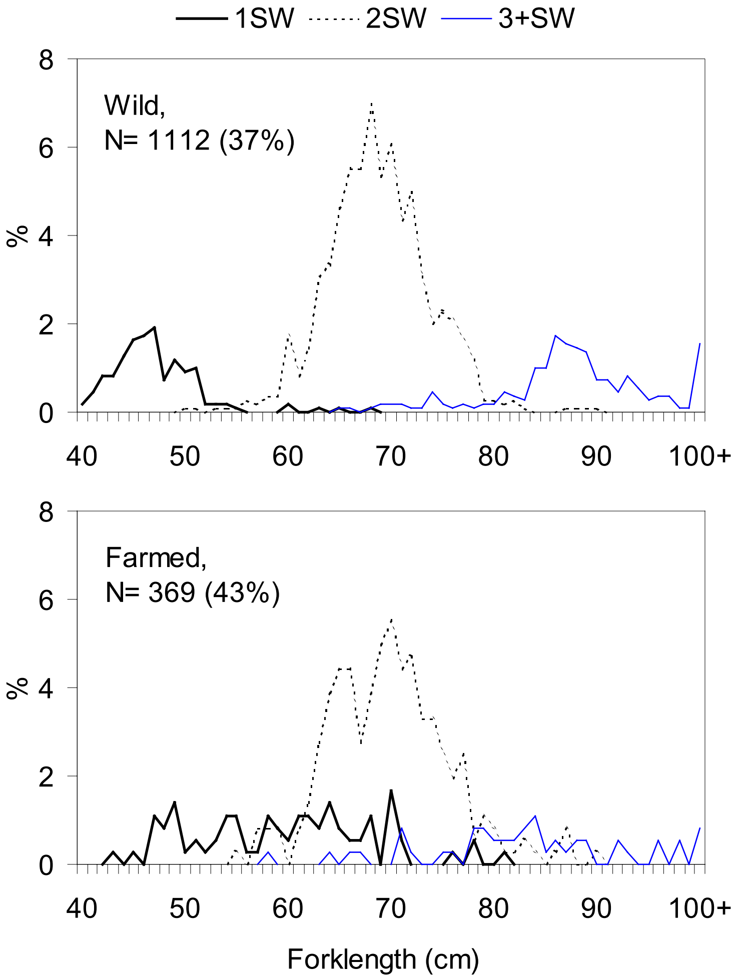


Fig. 3. K-factor ($K = w10^5/l^3$) in 3855 salmon grouped by season (autumn or winter) and sea age (1, 2 or 3+SW). Wild and farmed salmon were pooled due to no difference in K-factor. Confidence intervals (95%) are indicated around the estimates and a star (*) under a pair of observations indicate significant differences between seasons.

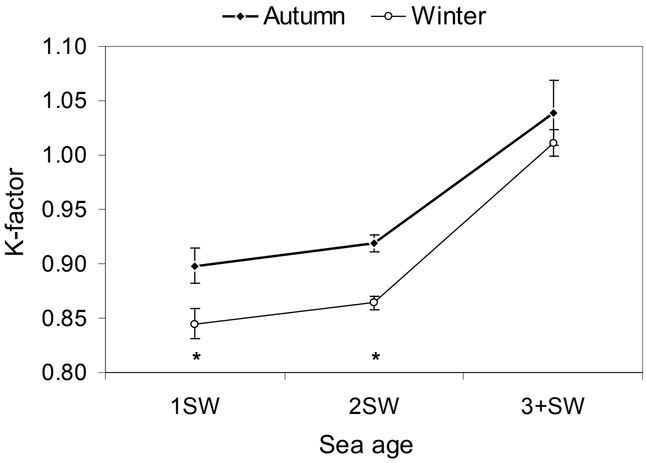


Fig. 4. Regression of forklength on average stomach food content per cm group (log-log regression with 95% confidence bounds on the regression line). Data were obtained from 2679 non-empty salmon stomachs sampled during autumn and winter 1992/1993, 1993/1994, and 1994/1995 north off the Faroes.

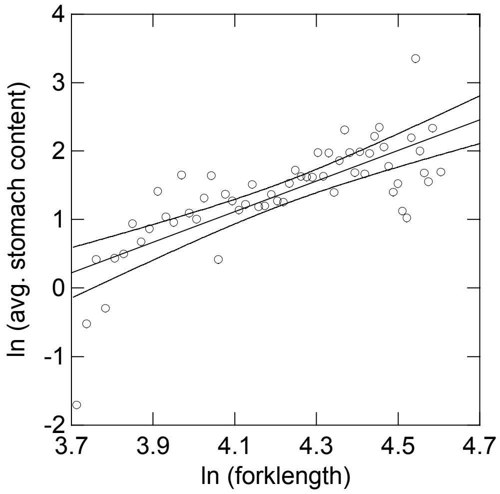


Fig. 5. Average stomach content of prey (g) 10^3 / body weight (g) ratio ($s10^3/w$) by sea age 1, 2 and 3+SW, respectively, grouped by season (autumn or winter). Wild and farmed salmon were pooled as there were no differences between them. Confidence intervals (95%) are indicated around the estimates and a star (*) indicate significant differences between seasons.

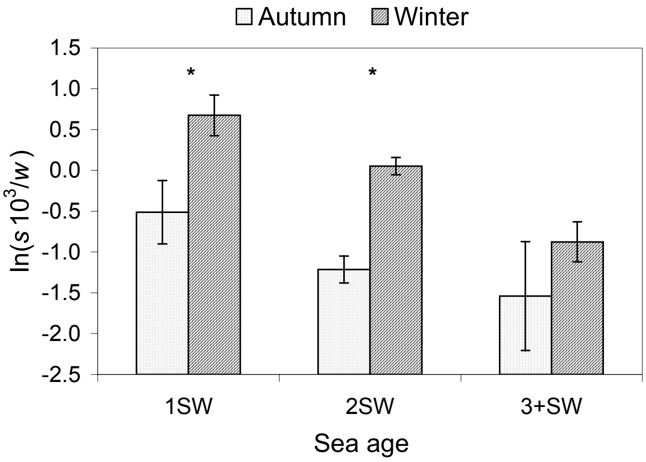


Fig. 6. Percentage weight distribution of two hyperiid amphipods *Themisto libellula* and *T. compressa* f. *compressa*, respectively, in the salmon stomachs grouped by SST (sea-surface temperature) from the period 1993–1995. The 95% confidence intervals on the regression lines are indicated.

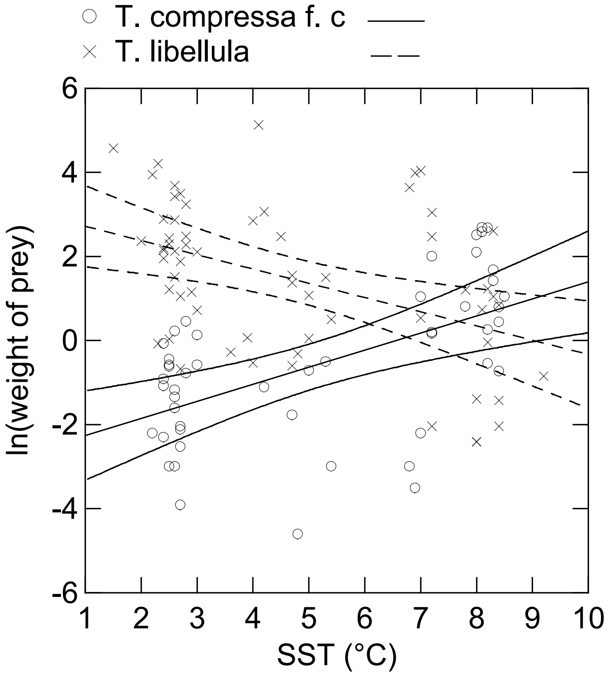


Fig. 7. Diet of salmon by weight proportions between autumn and winter, for the 10 prey groups defined and used in the calculation of diet overlap. Mean prey length (mm) is indicated below each prey group. Squid were not measured, but were juveniles.

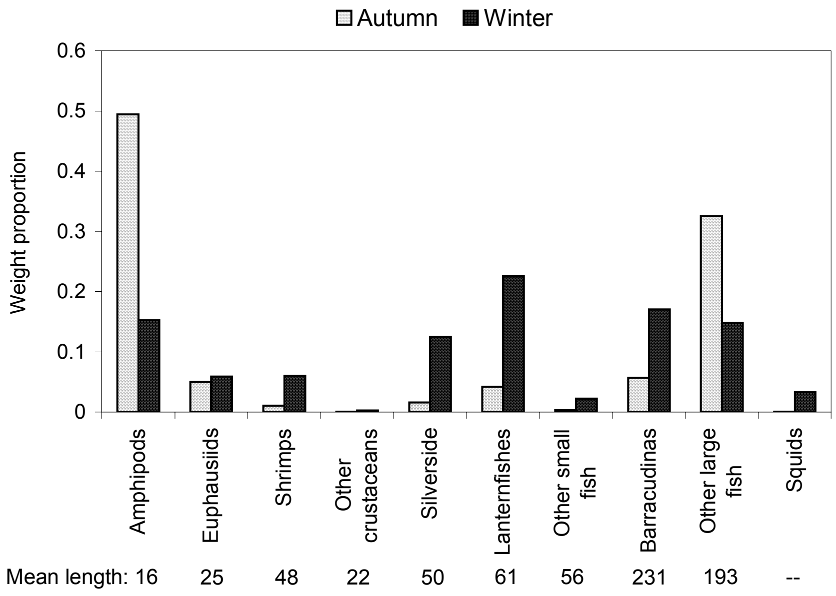


Fig. 8. Weight proportion of large fish prey taken by salmon by season (autumn and winter). Mean prey length (mm) is indicated below each prey group. Only one *Belone belone* was measured.

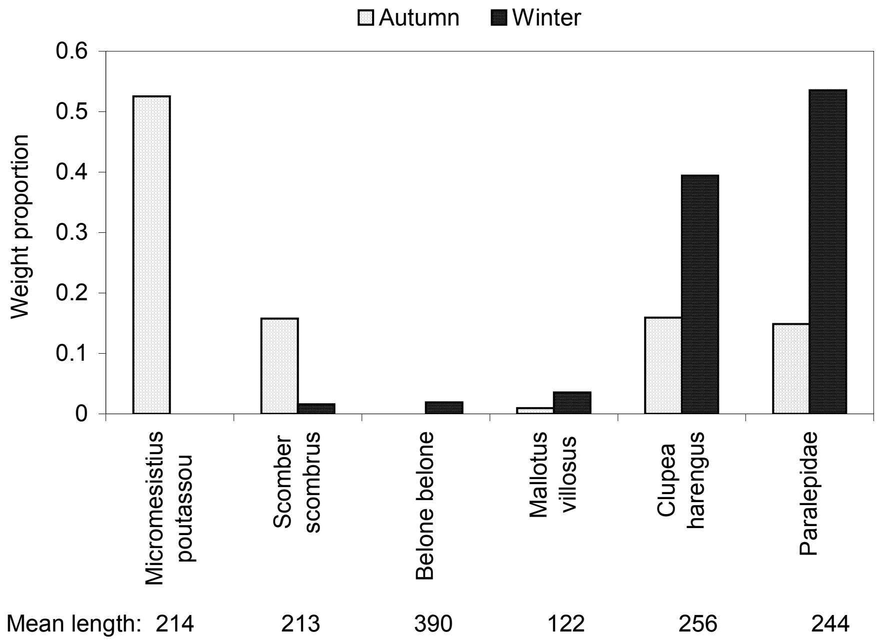


Fig. 9. Diet of 1, 2, and 3+SW salmon by weight proportions in the 10 prey groups defined and used in the calculation of diet overlap. The smaller 1SW salmon had taken higher proportions of crustaceans (amphipods) while the proportion of fish, particularly barracudinas and other large fish increased with sea age. Mean prey length (mm) is indicated below each prey group. Squid were not measured, but were juveniles.

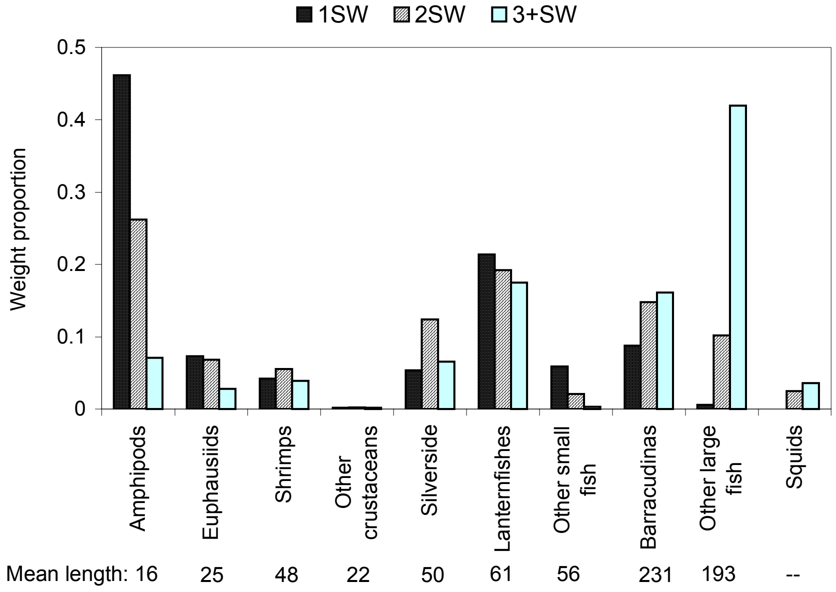


Fig. 10. Relative weight distribution (%) of two *Themisto* spp. species and three euphausiids species from MIK plankton net samples, 0-50 m depth (upper panel) and from corresponding salmon stomachs samples (lower panel), at 9 of the 13 fishing locations with detailed species segregation of euphausiids and amphipods in both samples. Simplified Morisita overlap indices are shown on top of upper panel, a star indicates high overlap. Number of stomachs are labelled on top of lower panel.

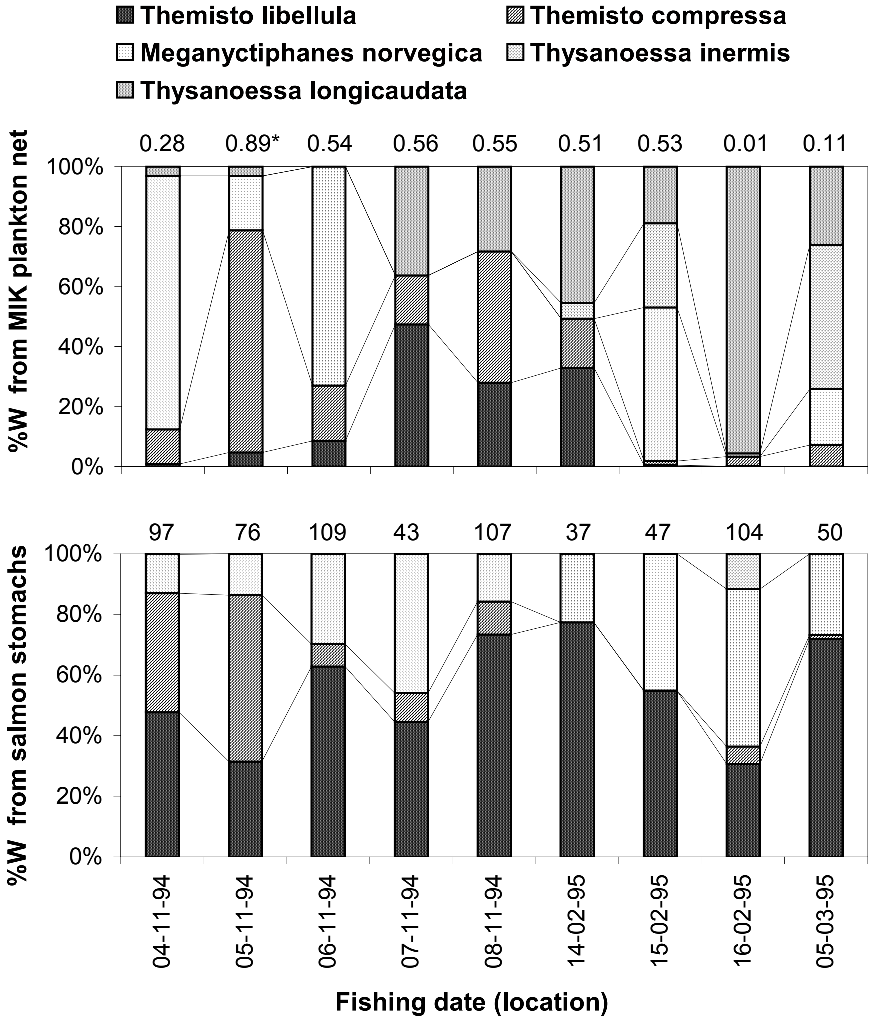
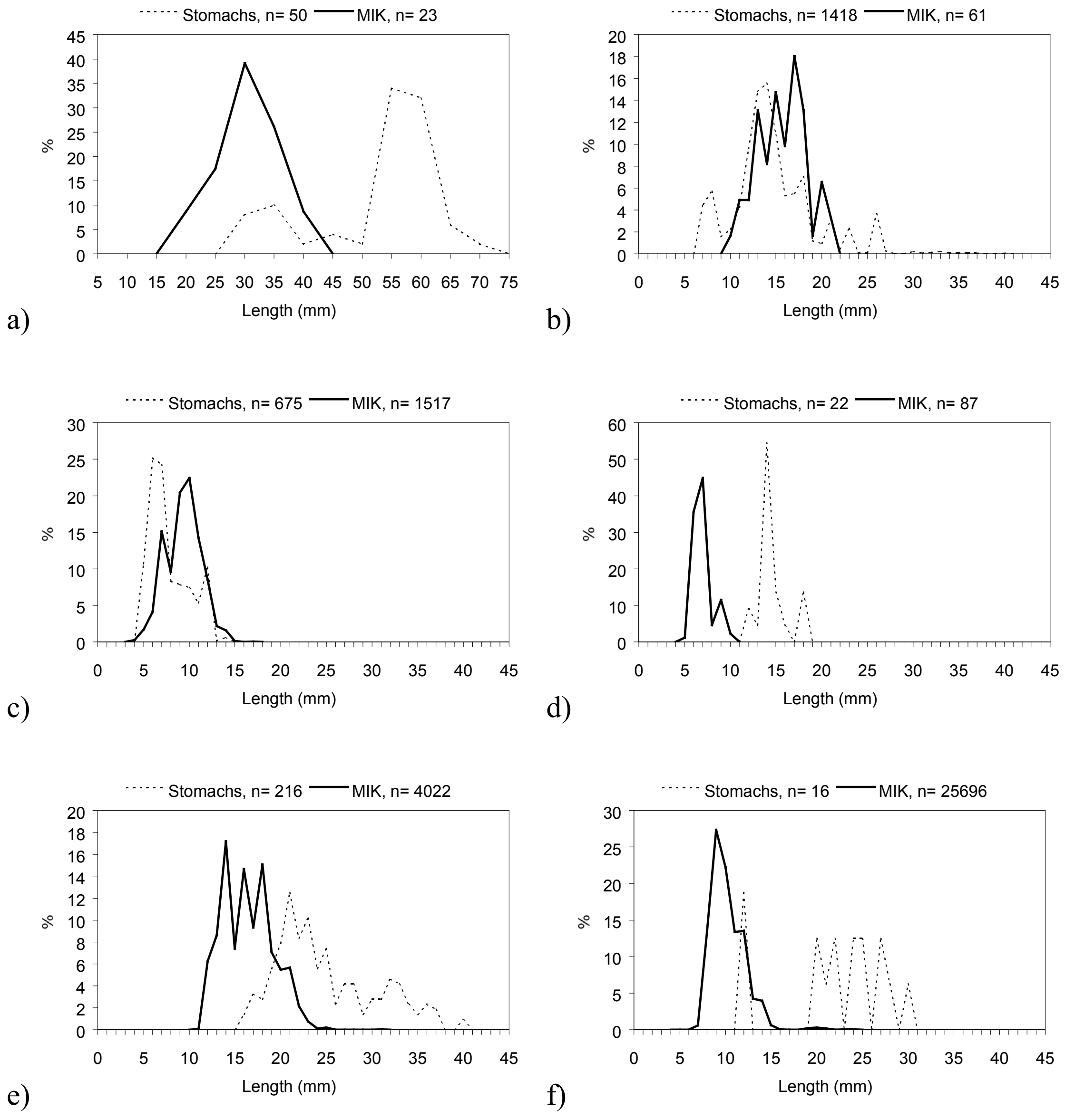


Fig. 11. Length distribution of various prey from corresponding stomach samples and MIK plankton net samples (0-50 m depth), at 9 of the 13 fishing locations with detailed species segregation of euphausiids and amphipods in both samples: a) *Maurolicus müelleri*, b) *Themisto libellula*, c) *Themisto compressa*, i.e. *T. c.* f *compressa* and *T. c.* f *bispinosa*, d) *Themisto abyssorum*, e) *Meganyctiphanes norvegica*, and f) *Thysanoessa* spp., i.e. both *Th. inermis* and *Th. longicaudata*.



PAPER V

Open-ocean infestation by salmon lice (*Lepeophtheirus salmonis*): comparison of wild and escaped farmed Atlantic salmon (*Salmo salar* L.).

ICES Journal of Marine Science, 54: 1113–1119. 1997

Open-ocean infestation by salmon lice (*Lepeophtheirus salmonis*): comparison of wild and escaped farmed Atlantic salmon (*Salmo salar* L.)

J. A. Jacobsen and E. Gaard

Jacobsen, J. A. and Gaard, E. 1997. Open-ocean infestation by salmon lice (*Lepeophtheirus salmonis*): comparison of wild and escaped farmed Atlantic salmon (*Salmo salar* L.). – ICES Journal of Marine Science, 54: 1113–1119.

Salmon lice (*Lepeophtheirus salmonis*) infestation was investigated in 128 salmon (*Salmo salar* L.) caught on floating long-lines in the Norwegian Sea during November–March 1993–1995. Overall prevalence was 99.2% and abundance 29.5 lice per salmon. Most lice were adults (90%), and 72% of these were ovigerous females. These adult lice were estimated to be at least 3 months old based on prevailing sea-surface temperatures at the sampling site: 7°C in November and 3°C in March. The prevalence and abundance of lice on one sea winter (1SW) salmon were significantly higher on escaped farmed fish than on wild salmon. However, no difference in abundance was observed between 2SW farmed and wild salmon. The average number of lice per surface area of fish (density) was significantly higher in 2SW wild salmon than in 1SW wild salmon, indicating an accumulation of lice on the salmon in the oceanic phase. No differences in density were observed between 1SW and 2SW farmed salmon. The prevalence of *Caligus elongatus* was low (5.5%), with an abundance of 0.9 lice per salmon.

Key words: Atlantic salmon, *Caligus elongatus*, escaped farmed salmon, *Lepeophtheirus salmonis*, open-ocean infestation, *Salmo salar*, sea age, sea lice, wild salmon.

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Introduction

Two species of sea lice, *Lepeophtheirus salmonis* (Krøyer, 1938) and *Caligus elongatus* von Nordmann, 1832, infest the Atlantic salmon (*Salmo salar* L.) in the North Atlantic and adjacent seas. The salmon louse (*L. salmonis*) is an important pathogen responsible for high losses of sea-farmed Atlantic salmon (Brandal and Egidius, 1979; Grimnes and Jakobsen, 1996). In wild stocks, sea lice are commonly present in low numbers and are rarely the cause of severe pathological symptoms (White, 1940; Nagasawa, 1987; Johnson *et al.*, 1996). In spite of their known presence on wild salmon returning from the sea, there is a paucity of good data on the infestation of Atlantic salmon in the open ocean. For *L. salmonis*, abundance estimates of less than eight lice per fish have been reported from the high seas on fish caught by gillnet and pelagic trawl (Pippy, 1969; Holst *et al.*, 1993) and less than 20 lice per fish from gillnet samples from the coastal areas of Norway (Berland, 1993). In the North Pacific, abundance estimates of less than 13 have been reported on Pacific salmon (*Oncorhynchus* spp.) (Nagasawa, 1985, 1987; Nagasawa *et al.*, 1993). Some of these estimates suffer from a downward bias of infestation levels due to the sampling methods. Nagasawa (1985) showed that Pacific salmon caught by long-line carried over four times as many lice as salmon from comparable gillnet catches and Holst *et al.* (1993) found an inverse correlation between scale losses and prevalence of lice on post-smolts from trawl catches, suggesting loss of lice during capture by these gears as a result of skin abrasion.

Salmon from most countries bordering the North Atlantic utilize the area north of the Faroes during their oceanic feeding phase (Jacobsen and Hansen, 1996; ICES, 1997). This feeding area is characterized by a front that separates the warmer Atlantic waters from the south-west and the colder and less saline Arctic waters from the north-west (Hansen, 1985). Salmon are typically distributed in or close to the frontal areas (Jákupsstovu, 1988; Jacobsen and Hansen, 1996), and in recent years large numbers (20–40%) of fish-farm escapees have been observed in this feeding area (Hansen *et al.*, 1993; ICES, 1997). It is possible that escaped farmed salmon transfer increasing numbers of sea lice to wild salmon in the open ocean but

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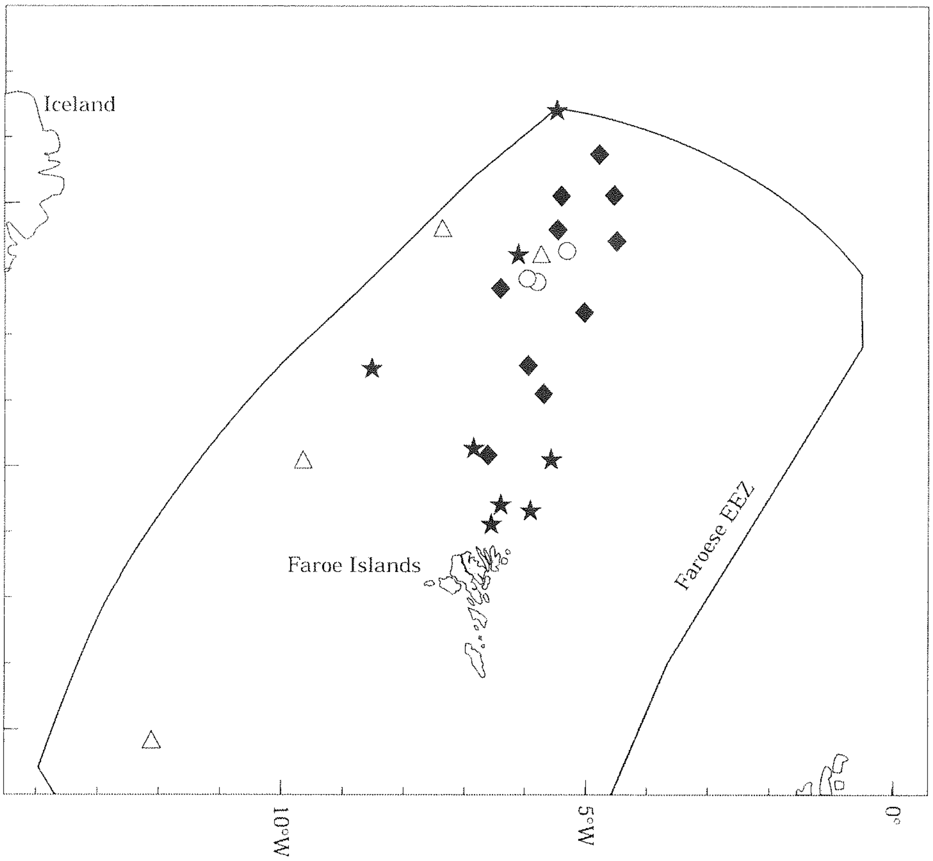

Figure 1. Sampling locations of 128 Atlantic salmon caught using long-lines during the period from March 1993 to March 1995: March 1993—3 salmon (○), February–March 1994—13 salmon (△), November–December 1994—50 salmon (★), and February–March 1995—62 salmon (◆).

unfortunately no historic infestation data are available from the high seas to study this question.

The level of infestation of salmon in the feeding areas and post-smolts in the sea may provide information about possible causes of mortality during the oceanic phase. Moreover, basic information, which is necessary for understanding the epizootiology of the salmon lice, is still lacking. Of special interest are life-history parameters such as the longevity and mortality of adult lice under the conditions experienced by salmon in the open ocean. Such knowledge is important in understanding the possible interactions between escaped farmed salmon as lice carriers and wild salmon in feeding areas in the open sea.

This paper describes the infestation of *L. salmonis* and *C. elongatus* on Atlantic salmon caught by long-line in the open ocean during the winter. The sea lice burdens of wild and escaped farmed salmon are compared, the rate of infestation in the sea is estimated, and possible mechanisms of transmission of lice in relation to the distribution of salmon in the sea are discussed.

Materials and methods

In total, 128 salmon caught on 25 long-line sets in the Norwegian Sea (north of the Faroes) between 62°30′N–66°00′N and 10°00′W–2°00′W during November–March 1993–1995 (Fig. 1) were examined for sea lice. This sample was part of a larger research programme in the Faroes area ongoing since 1992 (ICES, 1997). Most of the fish were caught in November–December 1994 (50 salmon) and February–March 1995 (62 salmon). In addition, three fish from March 1993 and 13 from February–March 1994 were examined. To minimize the loss of sea lice, live salmon were taken directly from the long-line with a gaff and, without touching the side of the vessel or deck, were placed in individual plastic bags. The snood was cut off, leaving the hook in the fish. The salmon to be examined for sea lice were randomly selected off the line. Sea-surface temperature (SST) was measured four times a day, before and after setting and hauling of the long-line.

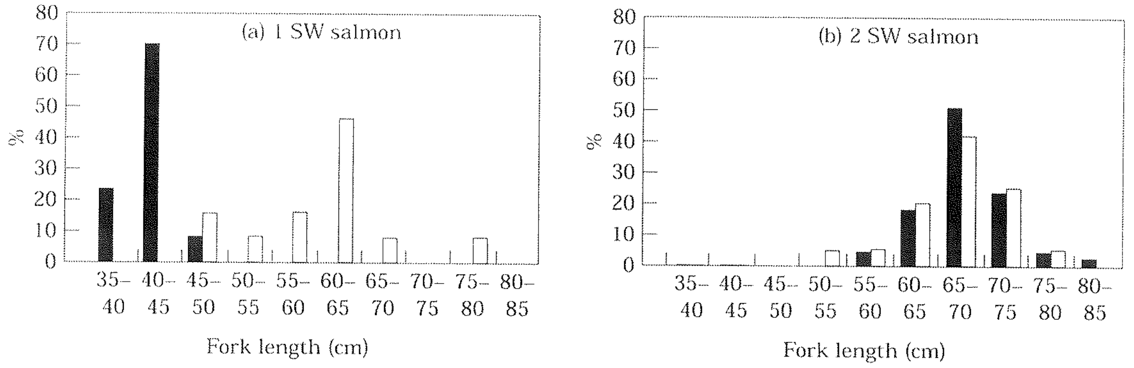

Figure 2. Length distribution of wild and escaped farmed salmon, (a) 1 sea winter (■ Wild, n=13; □ Farmed, n=13) and (b) 2 sea winter fish (■ Wild, n=56 □ Farmed, n=24). Data from November 1994 to March 1995.

Salmon were examined under a magnifying glass and a dissecting microscope, and all sea lice were removed and stored in 70% ethanol. Species and developmental stages were identified according to Johnson and Albright (1991a) for *L. salmonis* and Piasecki (1996) for *C. elongatus*. Fork lengths, total lengths, and weights were obtained for all salmon caught. In addition, for the 112 fish caught in the 1994/1995 season, smolt age, sea age, and origin (wild or escaped farmed fish) were determined from scale samples following the procedure of Lund *et al.* (1989). The age reading of 2SW farmed fish might have been overestimated due to the inclusion of false zones on the scales, however, less than 8% are expected to be incorrectly classified (Lund *et al.*, 1989). The body surface area of the salmon was calculated according to the formula $S=9.5864\ W^{0.629}$, where S is the body surface area (cm^2) and W is the wet weight (g) (Jaworski and Holm, 1992).

Mann–Whitney U-tests were used to test for differences in abundance and density between sea ages and between wild and farmed salmon. Three sea winter fish were excluded from this analysis due to inadequate samples (five salmon).

The terms prevalence, mean intensity, and abundance are defined by Margolis *et al.* (1982). Density is defined as "the number of parasites per unit area of all hosts examined". Salmon in the first winter in the sea, i.e. from May the first year to August the following year, are referred to as one sea winter (1SW) salmon, and fish caught from September in the second year to August in the third year at sea are referred to as two sea winter (2SW) salmon.

Results

Mean sea-surface temperature (SST ± s.d.) at the sampling locations was 7°C (± 1.6°C) in November–December and 3°C (± 1.3°C) in February–March. Fork lengths of salmon caught during the 1994/1995 season ranged from 38 to 85 cm (Fig. 2). The mean fork length of 1SW escaped farmed salmon was significantly greater than that of 1SW wild salmon (Mann–Whitney U-test; $p<0.001$). There was no significant difference in the mean fork length of 2SW escaped farmed and wild salmon.

The overall prevalence of *L. salmonis* was 99.2%, the mean intensity was 29.7 lice per salmon, and the abundance was 29.5 lice per salmon with a range of 0–187. The prevalence of *C. elongatus* was very low (5.5%) with a mean intensity of 17 lice per salmon and an abundance of 0.9 lice per salmon with a range of 0–112.

One escaped farmed fish (sea age 0+, river age 1) was found to carry 299 lice in all, 187 *L. salmonis* and 112 *C. elongatus* (94% of all *C. elongatus* observed). This individual differed significantly from the other fish with regard to the abundance of chalimus stages of both *L. salmonis* and *C. elongatus* and was excluded from further analysis.

The distribution of the different developmental stages of *L. salmonis* on the salmon is shown in Figure 3. The age distribution of lice within the host infrapopulations is characterized by a very low abundance of young stages and a predominance of adult stages, with most of the adult females being ovigerous (Fig. 3). The abundance and the density of lice on 1SW salmon were significantly higher on escaped farmed fish than on wild salmon ($p=0.001$ and 0.009, respectively) (Tables 1 and 2). In particular, the chalimus and pre-adult stages occurred in much higher numbers on the escaped farmed salmon than on the wild salmon (Table 1). No significant difference was observed in abundance ($p=0.663$) or in density ($p=0.941$) between 2SW wild and farmed salmon (Tables 1 and 2). Abundance and density increased with the sea age of the wild salmon ($p<0.001$ for both measures), but not for farmed salmon ($p=0.916$ and 0.861, respectively) (Tables 1 and 2).

On the basis of external examination, the average abundance of about 30 lice did not cause damage to the

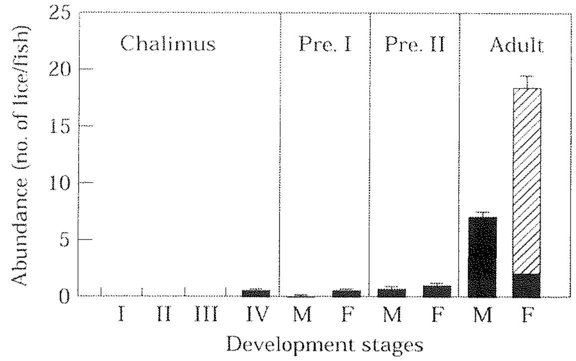

Figure 3. Abundance (+standard error) of *Lepeophtheirus salmonis* on 127 salmon, from March 1993 (3 salmon), February–March 1994 (13 salmon), and from November 1994 to March 1995 (111 salmon). Excluding one farmed salmon with an atypically high burden of lice. Notation: Pre.=preadult, M=male, and F=female. Hatched bar represents ovigerous females.

host, even though 90% of the lice were adults and 72% of the adults were females (Fig. 3).

The positively skewed frequency distribution of *L. salmonis* among the 1SW fish is evident from Figure 4. The information presented in Figures 4(b) and (c) for 2SW fish indicates a dome-shaped distribution. The frequency distribution for 1SW wild salmon is skewed compared to the distribution for 2SW wild salmon (Fig. 4a and b). The 1SW farmed salmon also differ from the 2SW farmed fish, but with a less pronounced difference (Fig. 4c and d).

Discussion

The presence of both chalimus and pre-adult stages of *L. salmonis* on wild salmon throughout the winter months and the increasing abundance and density of lice with sea age indicate that infestation occurs in the open-ocean. Infestation on the high seas is common for other caligid copepods (Boxshall, 1974; Neilson *et al.*, 1987). However, the difference between 1SW and 2SW salmon could be explained in part by differences in lice levels experienced by salmon in coastal areas in 1993 and 1994.

The observation of the high abundance of adult lice compared with the number of the younger stages on the hosts indicates an accumulation of adult stages in the oceanic phase. The significant increase in density of lice with sea age suggests this. The less positively skewed frequency distribution of lice on 2SW salmon, as compared with 1SW fish, also indicates a "stabilizing tendency" (Anderson and Gordon, 1982). Furthermore, the similar density of adult lice stages of about 0.02 cm^{-2} on 2SW wild and farmed salmon and 1SW farmed salmon compared to the lower density on 1SW wild salmon may indicate a regulatory mechanism in the open-ocean, e.g. death of heavily infected fish or lice mortality. High abundance of juvenile lice (more than 30 chalimus) becomes lethal to smolts when the lice develop into the first pre-adult stage (Grimnes and Jakobsen, 1996).

The significantly higher lice burden observed on 1SW escaped farmed fish than on 1SW wild salmon suggests that the escapees might carry lice from the coastal areas in higher abundance than wild smolts. An alternative explanation could be that the escaped farmed salmon are more susceptible to infestation on the high seas. We expected, however, that the escaped farmed fish would carry higher lice burdens than the wild salmon when they migrated to the high seas for the following reasons. Wild smolts are observed to migrate directly out into the open sea (Jonsson *et al.*, 1993; Lacroix and McCurdy, 1996), and thus spend a shorter time in areas where there is a high probability of being infected, while escaped farmed fish have been observed to stay in the vicinity of the site of escape for up to 3 weeks (Hansen and Lund, 1992). The significantly higher number of the internal parasite *Anisakis simplex* observed in escaped farmed salmon, compared with wild salmon (B. Berland, University of Bergen, Bergen, Norway, pers. comm.) indirectly supports the idea of residence in coastal areas prior to seaward migration. Furthermore, the highly skewed frequency distribution of lice on 1SW wild salmon as compared with the less positively skewed distribution for 1SW farmed salmon, a typical difference in dispersion patterns between wild and farmed fish (Costello, 1993), supports the view that the initial parasitic load on farmed fish is higher when they leave coastal waters. Wild smolts are only in coastal areas long enough for the infective copepodid stage to develop to the chalimus stages (Finstad *et al.*, 1994) while escaped farmed salmon are more likely to carry all stages. The greater size of 1SW escaped farmed salmon than of 1SW wild salmon in the sea suggests that most of the farmed fish were of a larger size when they escaped compared to the size of wild smolts when they migrate to the sea (Fig. 2). Thus it is possible that the farmed fish experience lower mortality from the louse burden than wild salmon smolts.

One escaped farmed fish (excluded from the analysis) with an atypically high number of lice (299 lice) was caught in an area far to the north of the traditional fishing areas in November (Fig. 1). This fish is thought to have left coastal areas shortly before capture, either directly from a fish farm or from an inshore area with high levels of infection.

Our findings suggest that adult female lice survive on salmon during the winter period in the sea, since they were found on wild salmon in our spring samples. They also survive on farmed salmon over the winter in northern Norway (A. Nylund, University of Bergen,

Table 1. Abundance of *Lepeophtheirus salmonis* on Atlantic salmon by sea age (SW) and origin. Lice stages grouped into chalimus (stages III and IV), pre-adult, and adult lice. Data from November 1994 to March 1995, excluding one farmed salmon with an atypically high number of lice. Abundance is defined as the total number of parasites divided by the total number of hosts examined (Margolis *et al.*, 1982).

	Wild salmon			Farmed salmon			
Stages	1 SW	2 SW	1+2 SW	1 SW	2 SW[a]	1+2 SW	Total
Chalimus III–IV	0.1	0.6	0.5	0.6	0.5	0.6	0.5
Pre-adult I–II	0.1	2.9	2.3	4.4	2.0	2.8	2.5
Juveniles	0.2	3.5	2.9	5.0	2.5	3.4	3.1
Adult males	2.3	7.6	6.6	5.5	10.3	8.6	7.3
Adult females[b]	3.5	22.4	18.8	16.5	20.0	18.8	18.8
Adults both sexes	5.8	30.0	25.4	21.9	30.3	27.4	26.1
All stages	5.9	33.5	28.3	26.9	32.9	30.8	29.2
No. of fish	13	56	69	13	24	37	106

[a]The sea age of farmed fish may be biased upwards because of inclusion of false zones in the age reading.

[b]About 90% of the females were ovigerous.

Bergen, Norway, pers. comm.). Boxshall (1974) estimated the total lifespan of *L. pectoralis* (Müller, 1776) to be 10 months on plaice (*Pleuronectes platessa* L.), with an overwintering population of adult lice ready to shed their eggs in early spring when the sea temperature increases. Hogans and Trudeau (1989) found overwintering *C. elongatus* on salmon at temperatures below 5°C in Canada.

Laboratory investigations of *L. salmonis* indicate that the generation time of lice is between 1 and 4 months, and is inversely related to temperature (Johannesen, 1978; Johnson and Albright, 1991b; Tully, 1992). However, no growth experiments of the entire life cycle of *L. salmonis* at temperatures below 7°C have been reported in the literature and the longevity of ovigerous females is not known.

By using a combination of the reported temperature relationships we estimate the generation time from chalimus to adult to be about 3 mo in the autumn (7°C ambient temperature) and 4–6 mo in the early spring (3°C), thus the infestation rate in the sea during the winter months is likely to be low. The average abundance of 30 adult lice on 2SW wild salmon compared to the average abundance of only 6 lice on 1SW wild salmon (Table 1) is higher than we would have expected from the assumed low infestation rate during the winter period. The infestation rate might be higher in late spring and summer as compared to the winter months at sea and the ambient temperature in the sea is unknown for the period other than November–March. An increase in infestation rates through the late spring and early fall is recognized for farmed fish (see e.g. Tully

Table 2. Density of *Lepeophtheirus salmonis* on Atlantic salmon by sea age (SW) and origin. Lice stages grouped into chalimus (stages III and IV), pre-adult, and adult lice. Data from November 1994 to March 1995, excluding one farmed salmon with an atypically high number of lice. Density is expressed as number of lice × 10^3 per surface area of fish (cm^2).

	Wild salmon			Farmed salmon			
Stages	1 SW	2 SW	1+2 SW	1 SW	2 SW[a]	1+2 SW	Total
Chalimus III–IV	0.1	0.4	0.4	0.5	0.4	0.4	0.4
Pre-adult I–II	0.1	1.9	1.8	3.7	1.4	2.1	1.9
Juveniles	0.2	2.4	2.2	4.2	1.7	2.5	2.3
Adult males	3.7	5.1	5.0	4.6	7.1	6.3	5.5
Adult females[b]	5.6	15.1	14.2	13.8	13.7	13.8	14.1
Adults both sexes	9.3	20.2	19.2	18.4	20.9	20.1	19.5
All stages	9.5	22.6	21.4	22.5	22.6	22.6	21.8
No. of fish	13	56	69	13	24	37	106

[a]The sea age of farmed fish may be biased upwards because of inclusion of false zones in the age reading.

[b]About 90% of the females were ovigerous.

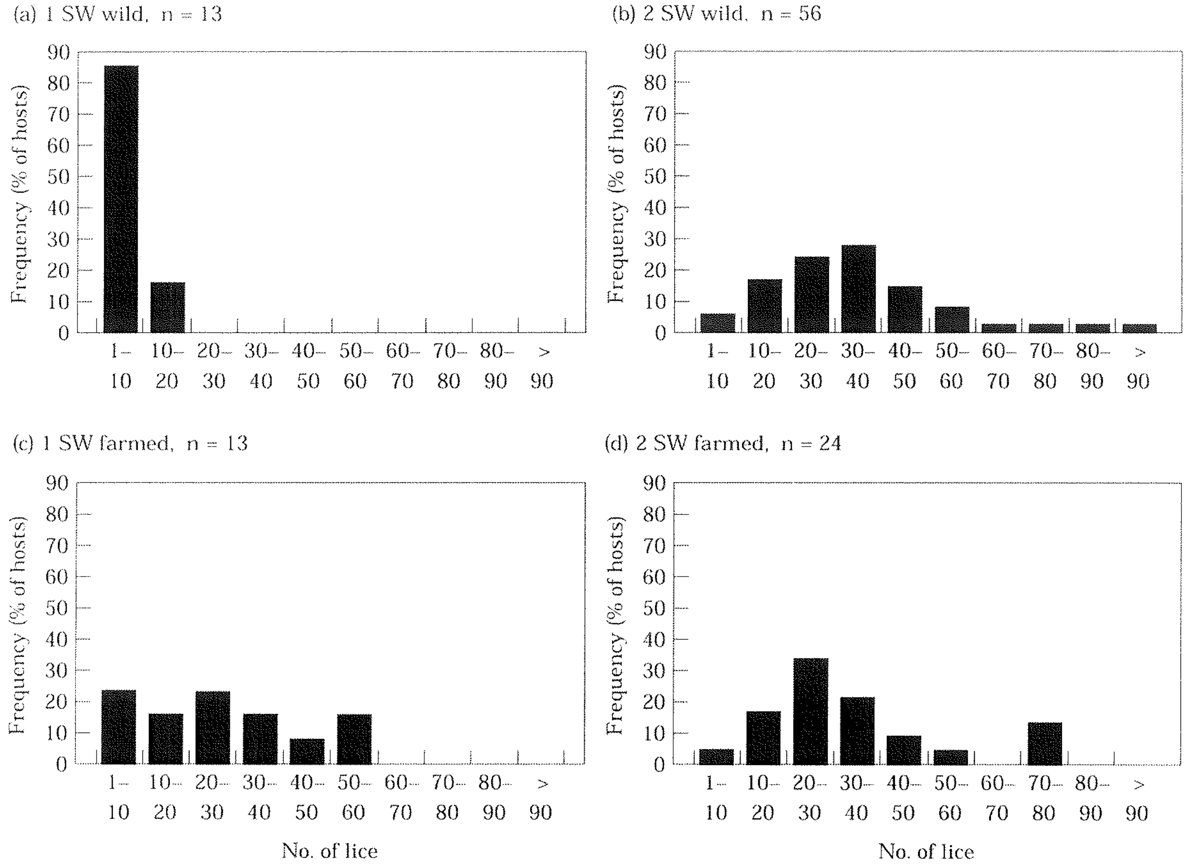

Figure 4. Frequency distribution of observed number of salmon with different numbers of *Lepeophtheirus salmonis*. (a) Wild 1 sea winter (1SW) salmon, (b) wild 2SW salmon, (c) escaped farmed 1SW salmon, excluding one farmed salmon with an atypically high burden of lice, and (d) escaped farmed 2SW salmon. Data from November 1994 to March 1995.

et al., 1993). Furthermore, the 1SW and 2SW fish might experience different environmental conditions due to spatial separation.

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