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Nordic Journal of Freshwater Research is a modern version of the Report of the Institute of Freshwater Research, DROTTNINGHOLM. The journal is concerned with all aspects of freshwater research in the northern hemisphere including anadromous and catadromous species. Specific topics covered in the journal include: ecology, ethology, evoulution, genetics, limnology, physiology and systematics. The main emphasis of the journal lies both in descriptive and experimental works as well as theoretical models within the field of ecology. Descriptive and monitoring studies will be acceptable if they demonstrate biological principles. Papers describing new techniques, methods and apparatus will also be considered.

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Workshop on the Postsmolt Biology of Salmonids in Ranching Systems

November 10-12 1992, Umeå, Sweden

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Introduction

TORLEIF ERIKSSON

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At the NJF-seminar "the role of Aquaculture in fisheries", in Reykjavik, Iceland 1990, it was proposed that a meeting summarizing the knowledge concerning postsmolt biology among salmonids would be of major importance. Two years later we were able to arrange this workshop (NJF-seminar nr. 220) focusing on the postsmolt period among salmonids.

The postsmolt period is one of the most critical periods in the life-cycle of anadromous salmonids. It is defined as the period from that the migrating fish has reached the marine environment to the end of its first season in the sea. A number of behavioural (feeding behaviour, antipredator behaviour etc.) and physiological (sea water adaptability etc.) mechanisms have to be adopted for a successful exploitation of the new environment.

At present the knowledge regarding the biology of the fishes during the postsmolt period is still scarce. Therefore, it is an important task to increase the knowledge of factors, which are important for a successful shift into the new habitat (food, feeding and growth, predation, environmental factors etc.). A better understanding of the postsmolt period will be the basis for an appropriate management of our anadromous salmonid stocks.

The seminar was divided in three main sessions. During the first day the main topic was the smolt and postsmolt behaviour, focusing on food and feeding. The second session focused on postsmolt survival and the importance of environmental factors, while the third session took into acount information of importance in connection to ranching strategies in salmonids.

The meeting has been organized by a steering committee including; Lena Söderholm-Tana (Finland), Tor G. Heggberget (Norway), Vigfus Johannsson (Iceland), Gorm Rasmussen (Denmark) and Torleif Eriksson (Sweden). We were very pleased that the seminar received such a strong response among the Nordic scientists working with salmonid biology. After the meeting, we concluded that the oral presentations and discussions had contributed to a fruitful meeting. We would like to thank our invited key note speekers Dr. B. Hargreaves (Nanaimo, Canada), Dr. C. Levings (Vancouver, Canada) and Dr. A. Isaksson (Reykjavik, Iceland) for giving us superb overviews of the main topics. In this proceedings 8 full papers and 16 abstracts are included, reflecting the contents of the workshop.

The seminar was possible to arrange thanks to generous support from; NJF section of aquaculture, NORFA (Nordisk Forskerutdanningsakademi), the Directorate for nature management in Norway and the Fisheries Board of Sweden.

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Feeding Behaviour of Juvenile Salmon and Significance of Habitat during Estuary and Early Sea Phase

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Abstract

The transition from fresh water to marine habitats is one of the most life-threatening events for anadromous salmonids. Smolting is accompanied by an elevation in metabolic rate which increases the energy requirements of juvenile salmon. At the same time, the smolt must adapt to a new fish community, with possible increases in predation and competition. This paper provides a review of feeding habits of juvenile Pacific and Atlantic salmon in estuarine, coastal, and ocean habitats. The acquisition of food by the young salmon is related to food availability and ecosystem productivity or carrying capacity of particular habitats. Food webs for postsmolts in inshore habitats are based on detritus while coastal and offshore systems are driven by pico/phytoplankton. Biological factors other than availability affecting use of particular prey include prey size, previous experience by the predator, prey visibility and colour, prey behaviour, and nutritional aspects such as protein and fatty acid content. Some of the important biophysical factors which affect use are temperature and structural features such as sheer zones, pycnoclines, and fronts. Postsmolts must obtain sufficient food to enable migration and predator avoidance, but growth cannot be compromised, and therefore feeding is a key factor for the survival of young salmon in the sea.

Keywords: Pacific salmon, Atlantic salmon, feeding, estuaries, coastal zone.

Introduction

The transition from fresh water to marine habitats is one of the most life-threatening events for anadromous salmonids. Smolting is accompanied by an elevation in metabolic rate (Hoar 1988), which increases the energy requirements of juvenile salmon. At the same time, the postsmolt must adapt to a new fish community, with possible increases in predation and competition. Escape responses in open water may require burst swimming and energy demands higher than those needed in rivers and streams where cover can provide protection. General physiological principles suggest the scope for growth is much higher in small salmonids (Brett and Groves 1979) such as postsmolts, with corresponding larger food needs per unit body weight. Acquisition of food is clearly one of the key factors that affect survival of salmon after their arrival in the sea, and the rate at which salmon obtain food can determine the carrying capacity of particular marine habitats.

In this paper I provide an overview of our knowledge of the feeding behaviour and ecology of Pacific (*Oncorhynchus* spp.) and Atlantic (*Salmo* spp.) salmon postsmolts in estuarine, coastal, and offshore habitats. I describe the ecosystems that generate the food for young salmon, the biological and biophysical factors influencing which food species are used, and summarize current knowledge of the significance of food supply for critical life processes of salmon in their first few months in the sea.

Limitations of the review

Young salmon grow from smolts to postsmolts and then to immature adults in the sea, but usually researchers sampling in the ocean do not distinguish between the latter two life stages. Therefore some of the data included in the review may pertain to fish older than the postsmolt stage. There is a vast literature available which describes the feeding habits of young salmon in the sea, but the majority of the work has been in the Pacific. Higgs et al. (1994) found over 100 reports dealing with feeding of Pacific salmon in the marine phase. Although only chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), sockeye (*O. nerka*), Atlantic salmon (*Salmo salar*) and sea trout (*S. trutta*) have well-defined smolt stages (Hoar 1988) I included the early sea life stages of pink *(O. gorbuscha)* and chum (*O. keta*) salmon for completeness. I organized the ecological material on feeding habits into three major habitat types, namely estuarine, coastal, and offshore. Estuary habitats are those characterized by reduced surface salinities and are generally in the vicinity of river mouths. Coastal habitats are areas remote from river mouths, but in enclosed waters such as embayments and straits between islands. Offshore habitats are those outside the coast line, with sampling typically over five km from shore, over deep water. For the purposes of this review I have categorized data from the Baltic Sea in coastal and offshore habitats, even though the upper layer of this sea is dominated by brackish and fresh water.

Production systems and food habits

The general availability of food for postsmolt salmon is influenced by the productivity regime of the marine region where the fish are rearing. The following section gives a brief overview of the sources of food in the major marine ecosystems and diets of postsmolts in these areas.

Estuaries

Secondary and tertiary production in estuaries and other shallow and brackish and stratified areas are detrital based (e.g., Levings et al. 1983 for Strait of Georgia, British Columbia). In estuaries, detritus originating from a variety of autochthonus (e.g. sea grass beds, algae, phytoplankton) and allochthonous (e.g., phytoplankton, riparian input from rivers) is typically colonized by heterotrophic bacteria. The organic carbon in the detrital complex is then used by epibenthic organisms, mainly crustaceans and insects, which in turn are eaten by fish. Food organisms such as calanoid copepods from phytoplankton based ecosystems, usually located off the river mouth, can also become available via the salt wedge, and drift insects can become available via river runoff (Macdonald et al. 1987). Postsmolt salmon rearing or migrating through estuaries thus have food available from a variety of habitats.

Of Pacific salmon, juvenile chum and chinook salmon are thought to be most estuarine dependent (e.g., Simenstad et al. 1982), although all species must pass through estuaries as juveniles. Chinook salmon show three life history strategies for use of estuaries, with the juveniles of "ocean type" life history stocks showing more extensive use relative to other species of Pacific salmon. For example at the Campbell River estuary in British Columbia, chinook fry of 35-40 mm length enter the very brackish habitats (salinity <5 ‰) of the upper estuary in April. By June or July the juveniles have grown to 60-70 mm and have migrated into more saline areas closer to the sea (salinity 15 to 25 ‰) (Levings et al. 1986). When caught in the latter habitats the fish are silvered and may be considered postsmolts. While rearing in the estuary, juvenile chinook use shallow shoreline habitats (<1 m) extensively and as they grow use deeper water. During their stay or migration in the estuary, juvenile chinook feed on wide variety of organisms, including adult insects, intertidal gammarid amphipods, harpacticoid copepods, and calanoid copepods (e.g., Kask et al. 1988).

The use of estuarine habitats by juvenile wild Atlantic salmon may vary between the northwest and northeast Atlantic ocean, however even within those geographic areas there appear to be stock-specific or genetic differences. In the Nabisipi River estuary in Quebec, Power and Shooner (1966), found that juvenile Atlantic (age 3) salmon resided in the brackish estuary and were caught nearshore using beach seines. During this rearing phase their dominant foods were gammarid amphipods, capelin eggs, and insect larvae. Atlantic salmon postsmolts caught in the main estuary of the St. Lawrence River using gillnets showed a somewhat similar diet (Dutil and Coutu 1988). Atlantic salmon in the Koksoak River in northern Quebec demonstrate the most intensive use of an estuary by this species, as some members of this stock reach reproductive maturity without leaving the estuary (Robitaille et al. 1986). Fewer data on feeding are available from estuaries in the northeast Atlantic. In the estuary of the Orkla River in Norway, tagged Atlantic salmon smolts moved to sea within a few hours of leaving the river (Hvidsten et al. 1993). The fish did not appear to be shoreline oriented, but those caught by two boat trawl had been eating estuarine gammarid amphipods that are typically found in shallow estuarine areas (Levings et al. 1994). Sea trout appear to use estuarine areas extensively and feed on shoreline habitats as postsmolts. A number of studies in Scotland showed this species ate estuarine food organisms such as intertidal insects and gammarid amphipods (Pemberton 1976).

Coastal areas

Production in the coastal zone is usually based on pico and phytoplankton (e.g., Fenchel 1988) so organic carbon used in these areas is mainly of autochthonous origin. In these areas oceanographic features such as nutrient upwelling and sheer zones, which affect local primary productivity, can influence zooplankton production and hence salmon food supply. In addition, advection of zooplankton from ocean areas into enclosed areas such as fjords (e.g., Aksnes et al. 1989) can be an important mechanism to provide salmon food, but this has not investigated for salmon migrating through fjords. Food organisms available to postsmolt salmon in these regions are zooplankton and larval fish, although as explained below epibenthic organisms are eaten in certain coastal habitats.

General food availability may be affected by the morphology and oceanography of the coastal zone. For example juvenile salmon migrating northwards out of the Strait of Georgia through Discovery Passage to the Pacific Ocean must pass through constrained channels (<1 km wide) characterized by strong tidal mixing (e.g., Levings and Kotyk 1983). In Discovery Passage the food of postsmolt chinook salmon was a mixture of plankton copepods originating from the pelagic zone together with epibenthic amphipods (Kask et al. 1988). The latter probably were eaten when the fish were feeding along shoreline habitats and kelp beds in the narrow channels. Some fjords in British Columbia are characterized by reduced tidal mixing and in these areas significant zooplankton populations develop which are eaten by migrating pink salmon (Parker et al. 1971).

Very little information is available on feeding of postsmolt Atlantic salmon in the coastal zone. Off the Kintyre Peninsula in Scotland, Morgan et al. (1986) reported that postsmolt salmon caught in June were feeding mainly on sand eels (*Ammodytes* spp.). In the coastal zone of the Baltic Sea, postsmolts fed extensively on adult insects which had blown from land (Jutila and Toivonen 1985). Adult insects also dominated the diet of juvenile Atlantic salmon smolts in the outer Trondheimsfjord in Norway in (Levings et al. 1994) and in fjords of the Faeroe Islands (Fjallstein 1987).

Offshore and oceanic

As in the coastal zone, production of salmon food organisms in oceanic regions is strongly controlled by autochthonous pico- and phytoplankton productivity which in turn is influenced by nutrient supply, temperature and light intensity. Annual peak zooplankton biomass in the offshore regions where salmon feed in the North Pacific and North Atlantic Oceans is about the same. Timing of the peak is later in the Atlantic (Parsons and Lalli 1988) and the Baltic (Kankaala 1987).

Information from the Pacific Ocean showed that sockeye postsmolts in the Sea of Okhotsk ate hyperiid amphipods in areas over 96 km offshore while larval fish predominated in stomach contents closer to shore (Andrievskaya 1970). Diets of postsmolt chinook and coho off Oregon were also dominated by hyperiid amphipods and larval fish, in addition to euphausiids (Peterson et al. 1982). In the Gulf of Alaska, squid were eaten by larger postsmolt sockeye (mean length est 37 cm) and postsmolt chum of about the same length ate the pelagic larvae of a polychaete (Pearcy et al. 1988). Very few data are available on the feeding ecology of postsmolt Atlantic salmon in oceanic regions. In the southern Baltic, Atlantic salmon postsmolt over about 25 cm in length were piscivorous and ate herring (Mitans 1970). Euphausiids, hyperiid amphipods, and fish were eaten by Atlantic salmon (>50 cm length) off the coast of Norway (Hansen and Pethon 1985) and similar findings were reported from the northwest Atlantic (e.g., Lear 1972).

Feeding success and feeding intensity in habitats

Field experiments are required to realistically estimate the feeding rate of fish, but very little of this type of work has been done with postsmolt salmonids. Researchers have attempted to estimate the amount of food used by indirect methods. One of the commonest methods to estimate feeding success is to determine the ratio of the weight of the food in stomach at a particular time to the weight of the fish - the so-called "forage ratio" (FR). Indirect methods have been frequently used to estimate feeding intensity or food consumption by: a. determining food intake needed to maintain measured growth rates, using change in weight data, temperature, and information on respiration and oxycalorific equivalents (bioenergetic method); b. estimating food consumption by gastric evacuation rate models and data on stomach contents over 24 h periods (gastric evacuation method).

Both forage ratios and food consumption have been found to vary between habitats and with environmental conditions. Postsmolt chum salmon in British Columbia showed the higher forage ratios in estuarine habitats (FR=1.84) compared to offshore areas (FR=1.48) in the Strait of Georgia. The same trend was shown by postsmolt chinook salmon in the same area (Healey 1982). Using the bioenergetics method, consumption rates of chum salmon were estimated between 4.2-6.8% body weight d^{-1} in the Sea of Okhotsk (fish 20-24 cm at 7 °C) (Gorbatenko and Chuchukalo 1989) compared to 2.9 to 3.8% body weight d^{-1} in Hecate Strait, British Columbia (fish 11-14 cm at 12 °C) (Healey 1991). Brodeur et al. (1992) found that postsmolt chinook and coho off the Oregon coast consumed between 0.05 and 0.10% d^{-1} of maximum total plankton biomass available (as estimated by bongo nets) but some taxa such as larval fish were consumed at higher rates (2.7-6.7% d^{-1} of maximum biomass). Both the bioenergetic and gastric evacuation models were used and there was substantial agreement between the two approaches. During years of reduced upwelling (Fisher and Pearcy 1988) reduced planktonic and larval fish abundance has been documented and it was suggested that postsmolt chinook and coho could encounter food limitations in those periods (Brodeur et al. 1992).

Fewer data are available for both FR and food consumption rates for postsmolt Atlantic salmon. Levings et al. (1994) found that FR for Atlantic salmon in Trondheimsfjord decreased with distance from the estuary, possibly in response to temperature changes or food availability. FR from fish caught ≤5 km from the estuary was 0.32, decreasing to 0.01 in postsmolts taken about 20 km further seaward.

Specific factors affecting food acquisition

Tables 1 and 2 give a summary of some of the major biological and habitat factors which vari-

Table 1. Selected examples of proximate biological factors affecting use of particular food species by post-smolt salmonids.

Biological Factor	Examples	References
Prey size	chum salmon show marked shift in prey size at 60 mm;	Okada and Taniguchi 1971
	Atlantic salmon show increased feeding response to oblong shaped food which is 2.2-2.6 % of body length	Jobling 1989
Previous experience of predator	hatchery reared coho salmon switched to natural food in <24 h in the laboratory;	Paszkowski and Olla 1985
	hatchery reared coho postsmolts using channel habitats in an Oregon estuary ate more larval fish relative to wild coho	Myers 1978
Temporal abundance of prey species	diurnal migration of zooplankton affects timing of feeding for coho;	Pearcy et al. 1984
	seasonal peak in zooplankton abundance matches chinook migration into Strait of Georgia	Healey 1980
Prey visibility, colour and contrast	large black eyes of hyperiid amphipods enhance their visibility to coho	Peterson et al. 1982
Biochemical and nutritional aspects	requirements for protein, amino acids, and fatty acid composition may be specific for the post-smolt stage	literature summarized in Higgs et al. (1994)
Perceived risk by predator on post-smolt	chinook avoided surface feeding, when predator threat perceived	Gregory 1990
Risk avoidance by schooling with other fish affects habitat where food obtained	Chum fed on surface food when schooling with sticklebacks, even though predator present	Tompkins and Levings 1991

ous authors suggested influence the "choice" of certain food species from the variety of invertebrate and fish species which postsmolts encounter in estuarine and marine habitats. These proximate or near-field factors are in addition to the broad scale ecosystem and oceanographic influences, described above, which determine the general availability of food in the sea. Biological factors affecting use of particular prey include prey size, previous experience by the predator, prey visibility and colour, prey behaviour, and biochemical aspects such as protein and fatty acid content. Particular nutritional factors provided by prey species may be important for the survival of postsmolt salmonids, but very few data are available on this topic. Laboratory studies with postsmolt chinook salmon showed that the digestible energy needs for good growth were between 18-19 MJ kg^{-1} dry matter. For wild prey, the only sparse information available on the lipid content of insects, for example, indicates major differences compared to crustaceans such as hyperiid amphipods or fish (data summarized in Higgs et al. 1994). For larger postsmolts, the energy required to obtain sufficient adult insects from the surface of the sea for maintenance and growth requirements must be substantial relative to single large prey items such as fish.

Table 2. Selected examples of proximate habitat factors affecting use of specific food by postsmolt salmon.

Habitat Factor	Examples	References
Refuge for prey	Rainbow trout consumption of pink fry influenced by lack of cover and shallow water in an estuary	Dobrynina et al. 1988
Habitat and vegetation structure	chum consumption of harpacticoids facilitated by vertical architecture of eel grass at high tide;	Webb 1991
	chum use vegetation as refuge in the presence of a predator	Tompkins and Levings 1991
Temperature	Atlantic salmon migrated through Labrador Current to warmer North Atlantic water, even though capelin abundant in former water mass;	Reddin 1985
	Atlantic salmon restricted to warmer surface layers in Bothnian Sea, insects eaten;	Jutila and Toivonen 1985
	squids dominated diet of salmon rearing in Subarctic Current compared to crustaceans in colder Alaska Current	Pearcy et al. 1988
Salinity	marine zooplankton eaten by chinook and coho in salt wedge of Campbell River estuary	Macdonald et al. 1987
Sheer zones and fronts	chinook more abundant in frontal zone of Fraser River plume, possibly in response to food aggregations;	St. John et al. 1992
	Fronts may have accumulated zooplankton and neuston off the Oregon coast	Brodeur 1989

Some salmon hatcheries produce smolts which move to the sea within a few days and transform to postsmolts quickly. Therefore processes such as behavioural conditioning and chemical composition of the food in the hatchery probably have an influence on feeding performance once the fish arrive in estuarine and marine habitats. There is some evidence that the feeding behaviour of postsmolt hatchery reared salmon differs from wild salmon, but the effect may be specific to certain habitats. Laboratory work suggests hatchery fish can adapt to live food in <24 h (Paszkowski and Olla 1985). In the Yaquina River estuary in Oregon, Myers (1978) found that the diets of hatchery and wild coho postsmolts were similar in beach habitats but diverged when fish were sampled from open water, channel areas. In the latter habitats, wild fish ate epibenthic crustaceans, whereas hatchery fish fed on larval osmerids. For chum salmon in Japan, fish that were fed in the hatchery survived better than those were not fed (Mayama 1985). Since hatchery fish have a different nutritional background relative to wild fish, the artificially-fed fish probably entered the sea with an "unnatural" biochemical profile, but chum salmon were not negatively influenced. There is almost no detailed information concerning the influence of such physiological differences relative to wild salmon. Because of the variability in formulated diets in salmon hatcheries around the world it is difficult to characterize the typical biochemical profile of hatchery food for comparison with the food of wild fish. As an example, wild Atlantic salmon postsmolts (Ackman and Takeuchi 1986 cited in Higgs et al. 1994) and wild chinook salmon postsmolts (Plotnikoff et al. cited in Higgs et al. 1994) showed higher percentage of specific fatty acids (C20:4(n-6)) relative to hatchery fish. These particular fatty acids are known to be important for the proper function of gill phospholipids (Higgs et al. 1992), possibly a vital function when salmonids change from living in fresh to salt water.

Some of the habitat factors affecting food use by postsmolt salmon include temperature, availability of refuges for prey species, and food concentrating mechanisms such as salt wedges in estuaries and sheer zones (Table 2). The role of temperature may be particularly important. For example in the northern Gulf of Bothnia in the Baltic Sea, postsmolt Atlantic salmon may be required to use surface layers because deeper water is colder (12 °C vs 5 °C) when the fish move out of the estuaries. While living in surface layers, adult insects were the primary food of the postsmolts (Jutila and Toivonen 1985), even though forage fish may have been potentially available in the deep colder layers.

Significance of feeding in various habitats

Over and above needs for routine levels of metabolism, it is likely that osmoregulatory changes, swimming, growth, and food acquisition are some of the main energetic demands on postsmolt salmon. As an example, coho postsmolts rearing in the Chehalis River estuary needed to use 66% of their energy output for swimming to maintain position on an ebb tide (Moser et al. 1991). The smoltification process is accompanied by an increase in lipid utilization in Atlantic salmon at the time of smolting (Hoar 1988; Blake et al. 1984). For pink and chum salmon on the coast of Kamchatka, growth rates in the littoral zone were reduced compared to those observed in embayments (Karpenko 1990). Rapid growth in the coastal zone might be an advantage if predators seek out smaller fish from the population, but the partitioning of energy into various life processes by postsmolts has received very little attention in field studies. Although many authors have stated that larger postsmolts survive better relative to smaller individuals, and have related this to predation (e.g., Fisher and Pearcy 1988), others have found that interactions between time and size are important (e.g., Bilton et al. 1982). More recently, Holtby et al. (1990) found that growth of postsmolt coho salmon in the coastal zone was correlated with survival, but only for the faster-growing 1+ fish, and the authors speculated that food could affect growth of this age class. Similar speculations were raised by Brodeur et al. (1992) who concluded that food limitations for postsmolt chinook and coho salmon would be particularly significant in years of reduced upwelling and ocean productivity. Fewer data are available on Atlantic salmon postsmolt energy relations or possible food limitations. Erkamo et al. (1992) showed that Atlantic salmon (Neva River stock) rearing in the Bothnian Sea showed poorer survival rates relative to those using the Gulf of Finland. In the latter area, the size of available food (herring) matched the foraging needs of the postsmolts. In the Bothnian Sea, young-of-the-year herring were too small and yearling herring too large to be used as food by the salmon.

Evidence for competition for food between salmon species and non-salmonids in coastal and ocean areas is equivocal because it is difficult to determine if the carrying capacity of marine areas have been exceeded. Assessing carrying capacity of relatively enclosed areas such as the Baltic Sea might be easier, however. Healey (1991) found little evidence for feeding interference among juvenile salmon in Hecate Strait, British Columbia based on food overlap considerations. Gorbatenko and Chuchukalo (1989) speculated that juvenile pink and chum salmon move off the continental shelf in the Sea of Okhotsk because of interactions with juvenile walleye pollock (*Theragra chalcogramma*). Juvenile salmon and walleye pollock use the same suite of zooplankton for food in this are.

Many of the proximate factors given in Tables 1 and 2 influence rates of physiological and/or behavioural processes (e.g., handling time) and have been described as important by specialists working on optimal foraging theory with fish from other ecosystems (reviewed in Calow 1985). Most of the research on optimal foraging, where fitness has an evolutionary significance, has been in fresh water, often with non-salmonids. The fitness of anadromous salmonids in relation to optimal foraging theory was considered very briefly in a theoretical treatment by Calow (1985) but the postsmolt stage was not examined specifically. This is an area of research which clearly requires further investigation. However there are obvious difficulties in assessing the reproductive contribution of individual salmon with particular feeding behaviours and food utilization patterns.

Only a few experiments have been conducted to determine feeding strategies of postsmolt salmonids. Much of the work has dealt with feeding in relation to prey abundance and has been conducted in aquaria (e.g., Parsons and LeBrasseur 1970; Wissmar and Simenstad 1988) or cages (English 1983; Hargreaves and LeBrasseur 1986) and results may not be applicable to natural habitats because of scaling problems. Given the complex life history of salmonids and the variety of food used, research on feeding strategies in the early marine phase of salmon presents major difficulties. However because feeding at the postsmolt phase of salmon presents a major life stage challenge to the species, work in this area may give important insights to factors affecting survival of salmon in the sea.

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Ocean Ranching Strategies, with a Special Focus on Private Salmon Ranching in Iceland

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Abstract

The success of salmon ranching depends on many factors, primarily stock selection, smolt quality and release techniques as well as the ranching potential, fisheries policies and laws. Harvesting strategies can have profound effects on wild salmon populations, e.g., if harvest takes place in mixed stock fisheries, and wild stocks may furthermore be affected by large scale straying of ranched salmon. The paper discusses ocean ranching strategies in various areas in relation to the above factors, comparing public ranching in the Baltic, semiprivate ranching in Alaska and private ranching in Iceland, which provide contrasting scenarios.

Introduction

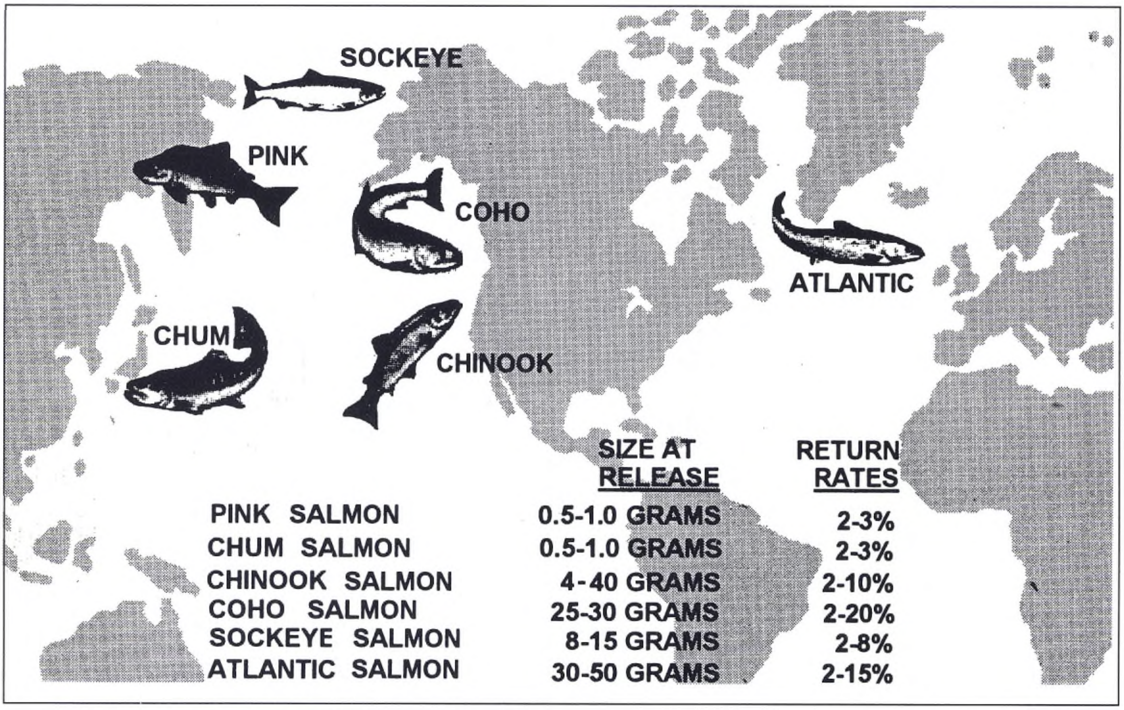
Salmon ranching strategies are the tactical plans and decisions made before and during the ranching process. These decisions include the selection of a species for ranching and site selection as well as the development of rearing, release and recapture techniques. As we can see these strategies are primarily dictated by the life history of the salmon species, e.g. the length of rearing required and smolt size. Species selection is also closely linked to natural habitat of the species, latitude and the environmental conditions in the area, both geographic and oceanographic. Political and socioeconomic climate, on the other hand, dictates whether ranching can develop as a private enterprise. Finally the economic value and marketing potential of the salmon species in question must be carefully scrutinized.

In this paper I will discuss some of these basic ranching principles, give examples of different strategies in Alaska, the Baltic and Iceland. My major emphasis, however, will be on the strategies used in the private ranching operations in Iceland. I will discuss case histories and describe the recapture techniques developed at some of the major ranching operations. Finally I will discuss some of the stray information and the possible effects on wild salmon stocks.

Strategic principles

Rearing aspects

Lets first look at the lenght of rearing prior to release for some of the major salmon species. Fig. 1 shows the major salmon species used for ranching in the Pacific and the Atlantic along with expected return rates and smolt size. Pink and chum salmon are supporting large scale ranching programs in the Pacific; chum have been the primary species in Japan but pink salmon in Alaska. The basis for the successful ranching of these species are the relatively high return rates of 2-3% (Suda 1991), relative to the small smolt size and limited pre-release rearing. The other three Pacific species, although more valuable in the marketplace require more extensive rearing and have not shown the return rates necessary for commercial ranching. The Atlantic salmon have a large smolt size, require extensive rearing for 1-2 years depending on location and must thus enjoy high return rates in



	SIZE AT RELEASE	RETURN RATES
PINK SALMON	0.5-1.0 GRAMS	2-3%
CHUM SALMON	0.5-1.0 GRAMS	2-3%
CHINOOK SALMON	4-40 GRAMS	2-10%
COHO SALMON	25-30 GRAMS	2-20%
SOCKEYE SALMON	8-15 GRAMS	2-8%
ATLANTIC SALMON	30-50 GRAMS	2-15%

Fig. 1. Major salmon species used for ranching in the Pacific and the Atlantic showing the smolt sizes and common return rates in ranching operations (Graphics by S. Óskarsson).

commercial rearing operations. Sockey salmon have been disease prone and difficult to rear but recent breakthroughs might make it the prime competitor of ranched Atlantic salmon within a few years (Kron and Suzumoto 1989).

Fig. 2 shows the contribution of ranching in the salmon catches in the Pacific and the Atlantic. We can see that the total catches of Atlantic salmon are minute compared with the Pacific salmon catches amounting to almost 700 thousand tonnes. Pink and chum salmon catches of 500 thousand tonnes make up the bulk of the Pacific catches with a ranching contribution of 50%. The large contribution of these species demonstrates vividly the limitation that the long freshwater cycle puts on the other Pacific species and Atlantic salmon. The ranching contribution to coho, chinook and Atlantic salmon catches is sizeable, although the total catches are lower, but these are primarily the results of enhancement and mitigation efforts rather than commercial ranching. It must be stressed that the Atlantic salmon figures are rough averages and include the Baltic salmon catches.

Ecological and political constraints

Ranching is constrained by various ecological as well as political factors, which would affect the ranching strategies in various countries and areas.

Ecological constraints

The major ecological constraints are the carrying capacity of the marine environment, conflicts between ranched and wild stocks and the effects of pollution. It has been suggested that the northern Pacific has in some years been overstocked with salmon (Peterman 1984, Eggers et al. 1992, Ida 1992, Rogers and Tuggerson 1992). The carrying capacity of the marine environment fluctuates in short and long term cycles depending on upwelling and the flow of warm and cold oceanic currents. It is known that a domination of

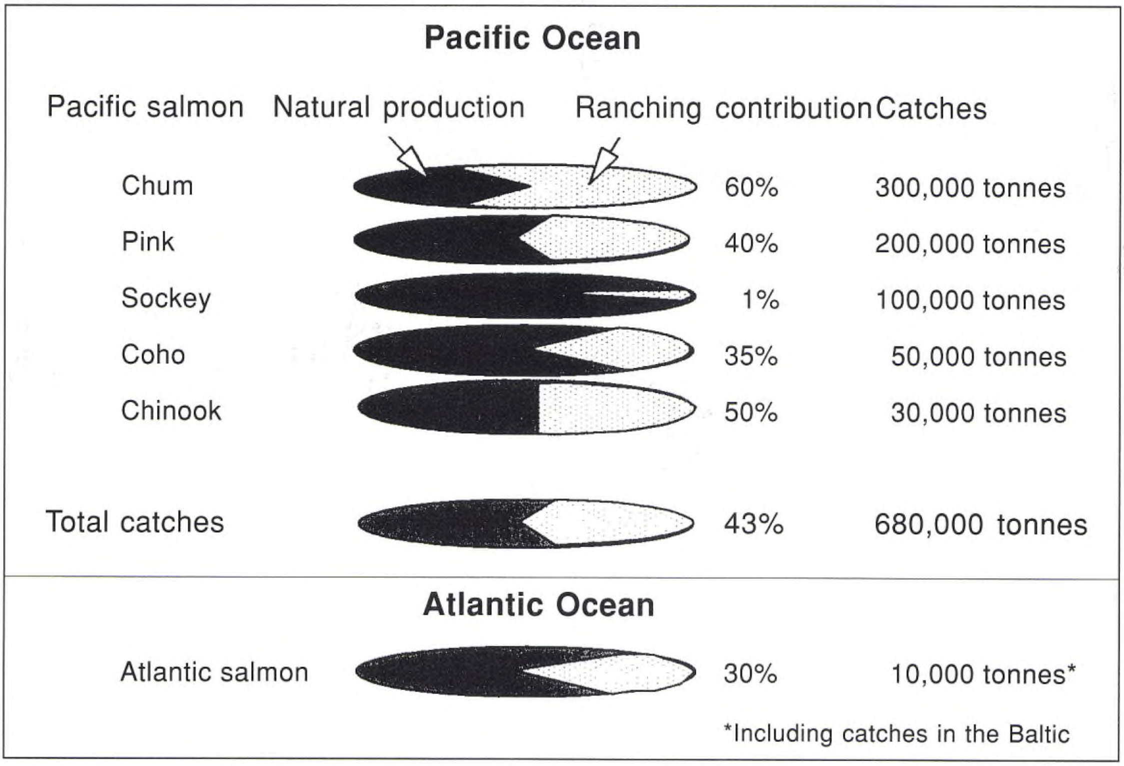


Fig. 2. Ranching contribution in the catches of various salmon species in the Pacific and the Atlantic in 1988 (Assembled from FAO 1990).

warm currents off the west coast of North America called "El Nino" has seriously affected the survival and growth of salmon stocks in some years. Similar effects of cold polar currents have been noted in northern Iceland (Ísaksson 1991).

Ranched salmon can affect wild stocks in several ways. Large amount of straying can possibly result in undesirable genetic mixing or transmittance of diseases. The most serious effect, however, has usually been an overharvest of the small wild stocks, if the two groups are harvested on their spawning migration in a mixed stock fishery. This has been a pronounced problem in many Pacific salmon fisheries as well as in the Baltic.

Pollution is probably primarily a problem in relatively enclosed areas with little water circulation, such as the Baltic and the American Great Lakes. It would in most cases express itself in the contamination of the salmon's flesh, making it less or not fit for human consumption.

Pollutants, which are not a direct health hazard for fish, can indirectly affect the survival of the species. A prime example is the M-74 disease, which has caused massive alevin mortalities in the offspring of hatchery salmon in the Baltic. The M-74 syndrome was first observed in hatchery populations at the Swedish Salmon Research Institute, Älvkarleby, in the early 1970s. It is thought to be pollution related, probably as a result of an uptake of a poisonous substance by the adults through the food chain. Similar effects on wild populations are suspected and large scale research projects are being launched (Johansson et al. 1993).

Political constraints

The political environment and the existing laws dictate the ranching strategy that must be used in that particular country. In some countries such as Iceland all rivers are privately owned and can be leased for private ranching operations. This is unthinkable in a country like the US, where all rivers are publicly owned. Private ranching is also impractical in a country, where major salmon fisheries are operating along the coastline as well as in the international sea areas. Poorly managed mixed stock salmon fisheries are common in most countries of the world and have had detrimental effects on wild stocks even where no ranching activity is occurring.

Most biologists and managers realize that terminal fisheries are the most sensible method of harvesting salmon. In most countries, however, there is a political resistance to such a solution due to a heritage in traditional salmon fisheries and for employment purposes. Alaska e.g., which has a long tradition in salmon fisheries and a 20 year history in semi-private ranching, has prohibited terminal trapping of salmon for cost recovery at public hatcheries and limited the quantity to be trapped at semiprivate hatcheries to 30% of total catch by each hatchery. The remainder has to be caught by conventional fishing methods such as purse seining, using expensive boats (Holland and McKean 1991, Orth et al. 1981). In some areas of the world the commercial fishermen, which in many respects reap the benefits of ranching programs, have been strongly opposing private salmon ranching driven by a fear of price reduction and competition on the market.

Due to the extensive migrations of most salmon species, the salmon rancher can be seriously affected by salmon fisheries in nearby countries and must take this into account, when devising his strategies.

Improvement in ranching performance

Ranching success can be dramatically affected by changes in rearing and release strategies. Unfortunately these strategies are highly local as well as species specific and can in many cases not be transferred between countries or areas, even for the same species. It should be pointed out that no chain is stronger than its weakest link and any mistakes in the smolt rearing and release strategies can have disastrous effects, although natural conditions are otherwise favourable.

Husbandry methods can have great effects on the economic success of ranching operations. It is clear that one-year smolts are cheaper to produce than two-year smolts and the development of usable zero- or half-year smolts would be a major breakthrough. It has been theorized that a reduction in the size of released smolts could provide economic benefits (Ísaksson 1980, Jóhannsson et al. 1991). This, however, is highly dependent on the relationship between smolt size and the resulting return rates as well as the size and age of returning salmon. Some evidence on these aspects has been gathered in Icelandic ranching operations.

Ísaksson (1980) suggested, that the increase in return rates with smolt size in many ranching programs using external tags was partly an artifact of the tag used as these differences were less pronounced when microtags were used. He proposed that an increase in smolt size from 20 to 40 g would only increase return rate by one fifth. It was also suggested that these differences were even less important if return rates were measured in kilograms of grilse per kilogram of released smolts. Jóhannsson et al. (1991) suggested that there was no increase in return rates for smolt larger than 20 g at release time.

The relationship between smolt size and the weight of returning grilse is highly important in ranching operations as the average weight of Icelandic salmon grilse (2.6 kg) is below the weight in greatest demand in the marketplace (3.0 kg). Any reduction in this size is thus highly critical. This relationship is dependent on various external factors in addition to genetic traits. Jóhannsson et al. (1992) showed that the weight of grilse of the Kollafjörður ranching strain was highly correlated to the size of smolts released. Jóhannsson et al. (1991) concluded that an increase in smolt size from 15 to 40 g would increase the size of returning male grilse by 0.9 kg; a very significant fraction of the average weight. This difference was less pronounced for females. The mean weight of grilse is also highly dependent on sea conditions (Ísaksson 1991).

A minor delay in release time has also been shown to affect grilse size. Ísaksson and Bergman (1978) showed that smolts released in late May were 0.3 kilograms heavier as grilse, than smolts released in late June, a difference of 12.5%. Less information is available on the relationship between smolt size and age of maturity, which is also known to be related to oceanic conditions (Ísaksson 1991).

It is also clear that the cost of facilities needed for ranching operation is highly variable between countries depending on economic parameters such as material and labour costs as well as environmental factors such as latitude and climate.

Release techniques often hold the key to success in ranching operations. Smolts are most commonly released from freshwater facilities, but salt-water adaption before release is getting common in private ranching operations and delayed release techniques have been highly successful in Pacific and Baltic ranching operations (Novotny 1980, Eriksson 1991). Beneficial side effects of delayed release, at least in some areas, seem to be a shorter migration, localized feeding and thus avoidance of distant fisheries (Novotny 1980).

Through selective breeding it is possible to affect numerous biological parameters of salmon. This was first demonstrated with respect to Pacific salmon ranching by Dr. Lauren Donaldson at the University of Washington in Seattle (Hines 1976), but more spectacular results have been obtained in the Norwegian salmon rearing programs, where growth rates have been progressively increased and maturity delayed (Gjerde 1984). Icelandic ranching experiments during the last 25 years have demonstrated a development of a ranching strain and a recent co-nordic program in ranching has demonstrated a genetic component in freshwater survival and growth rate (Jónasson 1993). Preliminary results indicate that survival and growth rate in the sea can be genetically manipulated (Jónasson J. pers. comm.).

Examples of different strategies

The ranching strategies are highly variable in differents parts of the world depending on the local customs and laws, the species used and the environmental conditions. I will now give some examples of ranching programs, going from semi-private pink salmon ranching in Alaska to the public ranching programs in the Baltic. Finally I will focus on the private ranching programs in Iceland, which have grown dramatically in recent years relative to the production of wild salmon.

Semi-private ranching in Alaska

Salmon ranching started in Alaska in the early 1970s as a response to low salmon catches as a result of adverse climatic and oceanographic conditions (Peltz 1989). A large scale ranching program with pink salmon is now in operation in the Prince William Sound area, where 40 million pinks are harvested annually, mostly by purse seine. Several ranching programs are using chum salmon but the major interest is in developing the ranching of sockeye salmon, which is a very valuable food species.

The Alaskan ranching programs are considered semi-private as they are not run for profit and operated by fishermens cooperatives (McNeil 1980). The fishermen harvest the returning fish by purse seine in the inshore areas in a heavily regulated fishery to protect wild pink salmon runs. As a consequence a sizeable portion of the run returns to the hatchery, where the salmon are harvested with a purse seine, either for broodstock or to recover the costs of the hatchery operation.

The Alaskan ranching programs are mostly based on pink and chum salmon, which require no freshwater rearing. This means that the hatcheries are large with large incubators as the output of fry is frequently measured in hundreds of millions. The freshwater cycle is simple, the newly hatched fry being transferred immediately after yolk sac absorbtion into sea-water floating pens, where they are frequently fed for a month or two until release. Zooplankton indices, commonly called plankton watch, are frequently used to determine proper release time for the salmon (Hauser 1981, Cooney and Willette 1991).

The ranching strategy is thus simple. The human hand never touches the fry, rearing costs are minimal and return rates of 2-4 percent are common. The biological strategy is thus in good order. The same is not true for the economics. The salmon are harvested by expensive gear and return during a very short period. This creates a great surplus of salmon during this short time, which lowers the price of the salmon dramatically. Most of the pink salmon have been going to canneries for a very low price and fresh fish markets have been neglected (Orth et al. 1981). The pink salmon programs may not pay for heavy investment in hatcheries but the sockeye salmon programs, if successful, might offer real competition to Atlantic salmon ranching.

Public ranching in the Baltic

Smolt rearing started in Sweden in the early 1950s under the leadership of Dr. Carlin. Most of the hatcheries were built by the Swedish hydroelectric companies to compensate for the loss of spawning and rearing areas due to hydroelectric development. The use of river water in the hatcheries dictated that two years were required for the rearing of smolts, the first year indoors and the second year in outdoor ponds. This rearing strategy is still dominating in Sweden and Finland, which are the prime contributors in the Baltic ranching programs.

A unique characteristic of the Baltic ranching programs is the fact, that much of the harvest takes place on the feeding grounds although a sizeable fraction is taken in trapnets along the Finnish coast during the spawning migration (Kuikka 1992). The fishery is primarily sustained by smolt releases from Sweden and Finland but other nations around the Baltic take a large share of the catches in the main basin. As the harvest rates in the fishery are quite high the strategy of restocking underseeded salmon rivers has fallen short of expectations and many wild stocks are seriously threatened (Jutila 1992).

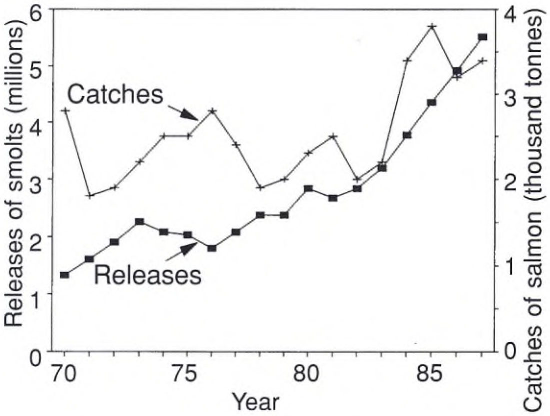


Fig. 3. Releases and catches of Atlantic salmon in the Baltic 1970-87 (Adapted from Ackefors et al. 1991).

Fig. 3 shows the releases by Sweden and Finland into the Baltic since the early 1970s and the development in the sea catches of salmon (Ackefors et al. 1991). The catches have clearly responded to the increased releases, but might have been even higher if the salmon markets had not deteriorated and the fishing effort fallen in the last three years due to a drop in prices. The fishing effort is also restricted by catch quotas and gear restrictions in order to protect the remaining wild populations, which are only a few percent of their original abundance.

Return rates in the Baltic are normally very high, being over 10% for river released smolts. The recoveries of the external tags (Carlin tags) primarily occur in the commercial sea fisheries and freshwater returns are minimal. Non-river based delayed releases of 200-300 g post-smolts along the Swedish coast in the autumn have resulted in 20-30% return rates from the commercial fishery (Eriksson 1991). Upon maturation the salmon home to the area of release, creating an opportunity for fishing. Considering the high survival rates, these public ranching operations are nationally profitable for Sweden. Similar release strategies have been tried in various areas around the Atlantic with limited or variable success.

Private ranching in Iceland

In Iceland, all rivers and lakes have been privately owned since the country was settled a thousand years ago. This means that all salmon and trout fishing rights are controlled by the owners of the nearby land and the law actually forbids that those rights are separated from the land. This political situation has paved the way for private salmon ranching in Iceland.

One of the main arguments for the development of private ranching in Iceland is the absence of a sea fishery within the Icelandic 200 mile economic zone. Other factors include favourable ground water resources for smolt production, suitable ranching locations away from major salmon producing areas and relatively small catches of wild salmon populations, possibly indicating that the feeding areas close to Iceland are not overstocked with salmon.

Ranching strategies and potential

Fig. 4 shows the ocean ranching potential in Iceland, the location of the main commercial ranching stations as well as releases and total returns in 1991. Experience has shown that return rates to ranching stations are highest on the south and west coasts, which are affected by the Gulf stream, but much inferior on the north and east coasts, which are frequently affected by cold polar currents from east Greenland. Most of the ranching stations are located on the west coast and released about 5.5 million smolts in 1991, mostly from Hraunsfjörður and Vogavík.

Return rates during the last three years have been low, mostly below 4%, due to unfavourable oceanic conditions around Iceland, which also have affected the cod and capelin stocks in the area (Malmberg and Kristmannsson 1992). A definite improvement was noted in 1992, both

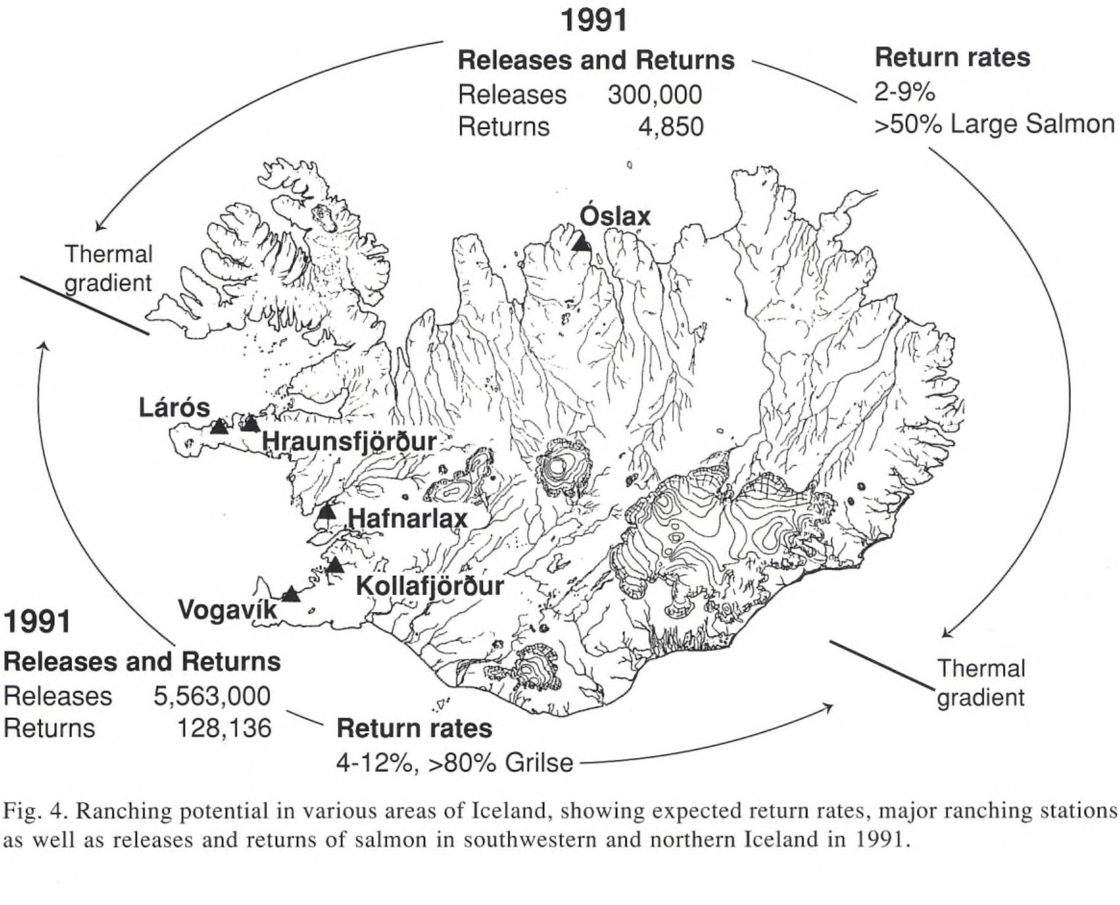


Fig. 4. Ranching potential in various areas of Iceland, showing expected return rates, major ranching stations as well as releases and returns of salmon in southwestern and northern Iceland in 1991.

in return rates and general condition of returning salmon. Some of the larger stations, however, still seem to have problems, probably related to smolt quality and release techniques possibly as a result of the enormous size of the release programs.

All Icelandic ranching programs are almost exclusively using one-year smolts and the Kollafjörður ranching stock is gaining acceptance as the most suitable strain for the west coast operations. Grilse or one-sea-winter salmon, which average 2.6 kg in size are considered most suitable for ranching and current selection programs aim at increasing the return rates and average weight of that year-class.

Salmon ranching, release and recapture strategies have been highly variable between ranching stations, depending on environmental conditions and water resources in the area. Initially ranching was only conducted from rearing stations located close to the coast. It was soon clear that expansion of ranching would depend on the use of release sites. Experiments at Lárós in the early 1980s demonstrated that return rates to release sites matched and sometimes exceeded those to the site of rearing (Ísaksson and Óskarsson 1986). Currently a large part of the ranching production occurs at release sites.

Release sites are normally using coastal lagoons or small streams for ranching and are highly dependent on rainfall and the resulting water discharge for the recapture of ranched salmon. Due to the reluctance of the salmon to enter during low water flows many of the facilities have had to devise estuarine traps to procure bright salmon. The operations at Lárós and Hraunsfjörður are typical release site facilities, although limited rearing is now occurring at Hraunsfjörður.

Ranching from rearing stations can be broken into two categories, those using stream water for ranching and those using pumped well water. Kollafjörður Fish Farm is a typical stream water facility, although mostly well water is used for rearing. Vogavík, on the other hand, only uses the hatchery run-off for ranching, which does not increase during rainy periods. The salmon do not enter such an outflow to any extent and the facility is highly dependent on estuarine trapping of returning salmon.

Major ranching stations

The location of the main salmon ranching facilities in Iceland is shown in Fig. 4. Kollafjörður Fish Farm is a government run experimental station, which has been conducting salmon ranching experiments since the early 1960s (Guðjónsson 1973). It was a pioneer in the development of one year smolts for ranching using geothermal resources. Its major task at the present time is to determine if selective breeding can be used to improve performance in ranching and continue to study smolt quality and release techniques.

Vogavík ranching station was established as a commercial ranching station in the early 1980s. It has been the second largest operation in Iceland with close to 1.5 million smolts released. Being located on lava bedrock far away from any natural streams, the station has designed efficient estuarine traps shown in Fig. 5 for harvesting returning salmon. The outflow from the station, which is very small can be seen in the upper right hand corner of the figure. The operation at Vogavík is entirely based on pumped fresh or salt water from geothermal boreholes and smolts are thus adapted to seawater before release. The returning salmon enter this bay on high tide and are guided into a metal trap by the two fences, when the tide recedes.

Fig. 6 shows an overview of the Hraunsfjörður ranching site operated by Silfurlax. Silfurlax is the largest ranching company in Iceland, releasing over 2.5 million smolts annually. Ranching on this scale has no precedent in Iceland and must be considered a large developmental project, both in technological and economic terms.

The figure shows the dam, which created a large fresh water lake upstream of the bridge. Smolts are transported from the smolt station located on Icelands south coast for overwintering in the floating pens throughout the winter, which allows the company to increase the rate of turnover in their smolt rearing facilities. The advantages of this rearing cycle are, however, partly

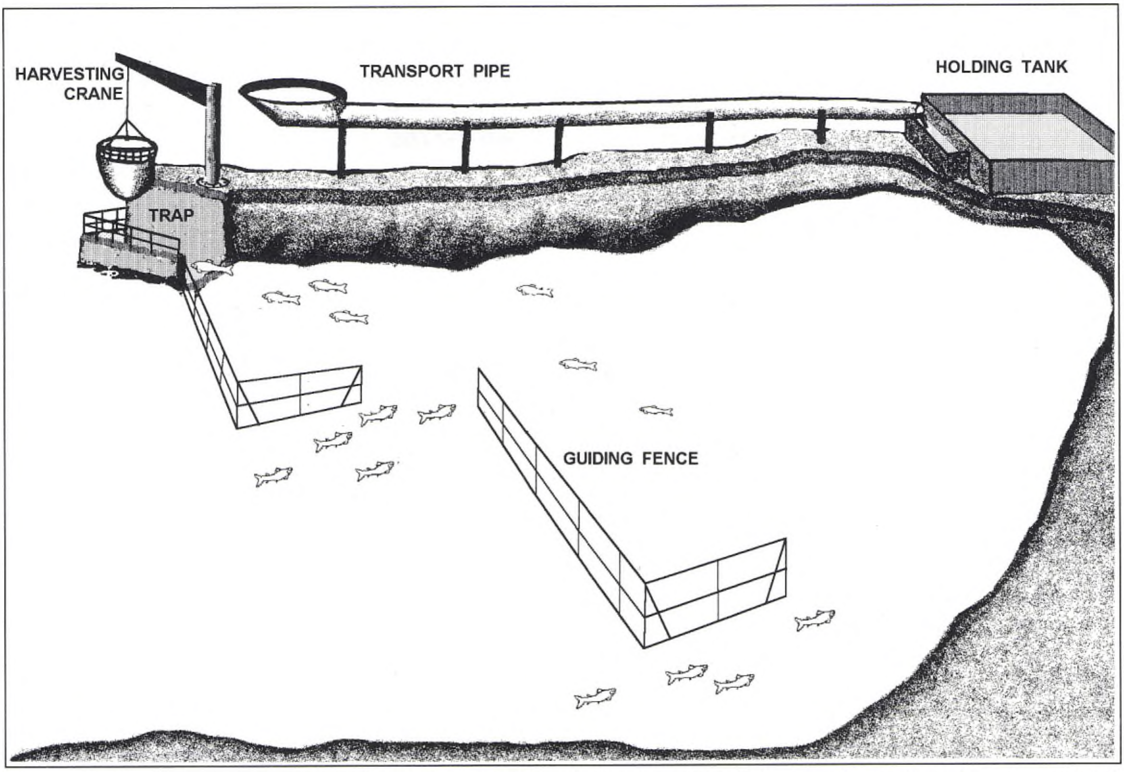


Fig. 5. Estuarine trap at the Vogavík ranching facility during low tide. Salmon migrate into the area on high tide and are guided into the trap by the metal fences during the receding tide (Drawing by S. Óskarsson).

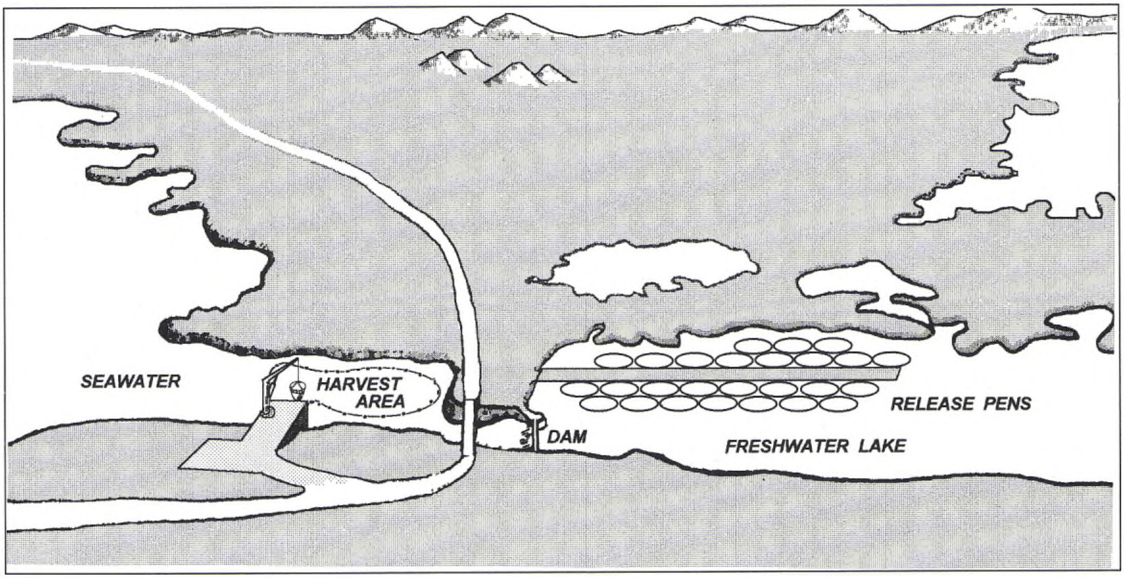


Fig. 6. Overview of the Hraunsfjörður ranching facility, showing the smolt rearing cages and the dam, which creates the freshwater lake. The trapping of adults is conducted within 100 meters downstream of the highway bridge (Drawing by S. Óskarsson).

offset by the vulnerability of the floating pens to adverse weather and ice conditions in the wintertime and smolt have occasionally escaped prematurely from the pens. In the spring smolts are moved from the freshwater pens into saltwater pens below the bridge and moved into deeper water, where they may be reared for considerable period before release.

The returning salmon are trapped through an ingenious seining operation between the bridge and the pier situated in the estuary. The operation is swift and treats the salmon well, which are in stored in netcages until slaughtering. The trap is actually a large net lying on the bottom with an underlying cork line which lifts the net during the seining operation.

Other major ranching stations are Lárós, which has been in operation on a small scale since the late 1960s (Fig. 4), Hafnarlax, a small facility in the Borgarfjörður area and Óslax, the only facility on the north coast.

Oceanographic variations

The last decade has demonstrated the great fluctuations that one can expect in return rates in Icelandic ranching operations. I have previously described the difference in ranching potential between the southwest and the north coasts, which primarily reflects the dominant oceanic currents in the areas.

Fig. 7 shows a model constructed from data obtained at the Kollafjörður Experimental Fish Farm during the last ten years. The figure shows, that, when the Gulf stream is strong around Iceland and oceanic conditions relatively good, as reflected in the left side of the picture, the return rates are higher, the ranched fish larger and most of the fish return after one year in the sea, having a fairly even ratio of males and females in the grilse population.

Conversely, if the Gulf stream is weak and oceanic conditions relatively poor, as reflected in the right side of the picture, the return rates

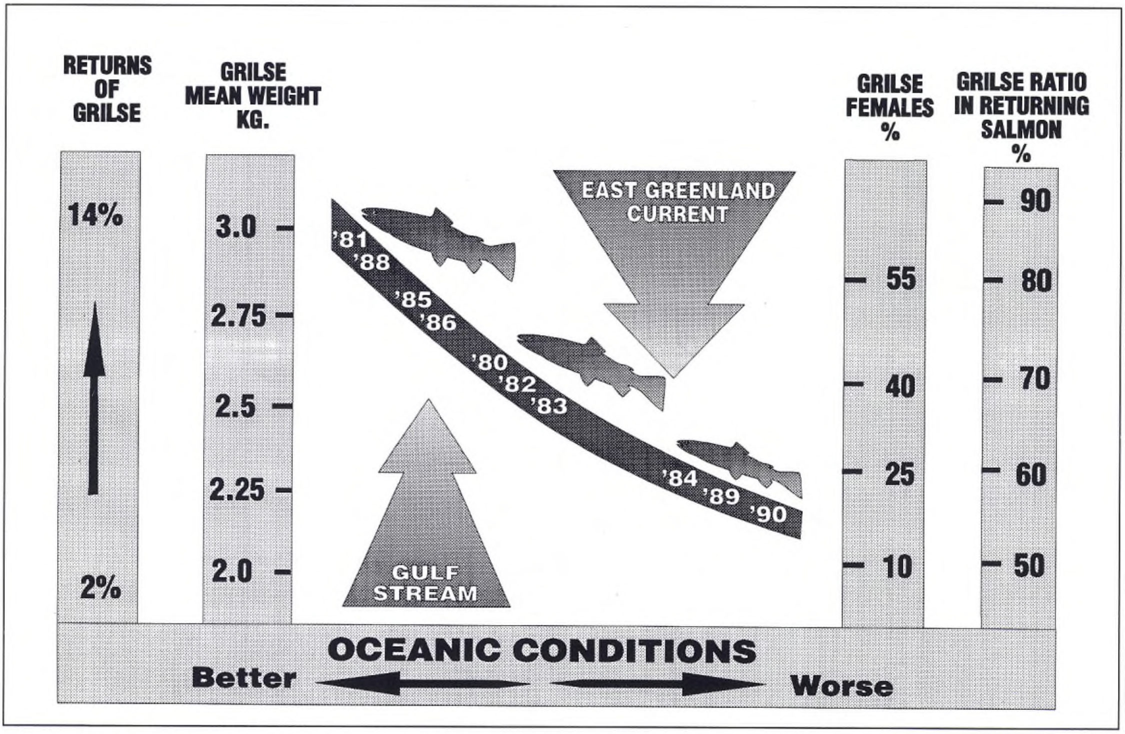


Fig. 7. A model showing the effects of oceanographic factors on return rates and various population parameters of Icelandic ranched Atlantic salmon (Drawing by S. Óskarsson).

are low, the grilse are small in size, there is a delay in maturation over to the second year and there is a dominant male ratio in the returning grilse. These fluctuations have been especially noticable in Iceland during the 1980s and one must probably go back to the late 1960s to find similar periods. Periods of low salmon abundance have been experienced by most countries bordering the Atlantic during the last three years and low abundance of cod and capelin around Iceland can also partly be traced to reduced productivity of the marine environment (Malmberg et al. 1992, Jakobsson 1992).

Straying of ranched salmon

It is of considerable concern to the Icelandic salmon ranchers, that straying between stations has increased with a growing number of stations. In 1991 over 100,000 ranched salmon were harvested but the harvest in the home traps based on microtag recaptures ranged from 84% to 98%. The four major ranching stations and the proportion straying between stations is shown in Fig. 8. As we can see the lowest straying rates occur at Vogavík, which gets over 98% of its returns to their facility. Lárós has intermediate strays but Hraunsfjörður and Kollafjörður only get 84% of their returns to their facilities but the remaining 16% go mostly to Vogavík.

The distribution of these strays probably reflects a very effective trapping mechanism and a strategic location of Vogavík on Reykjanes peninsula. It is located close to the ocean and traps the salmon in the estuary soon after arrival. Salmon migrating along the coast bound for other stations and possibly exploring the Vogavík facility are likely to be trapped.

This stray information is for the 1991 salmon season, which seemed to be high in strays of ranched salmon. Strays have turned out to be much lower for the 1992 salmon season and in general appear to be highly variable between years.

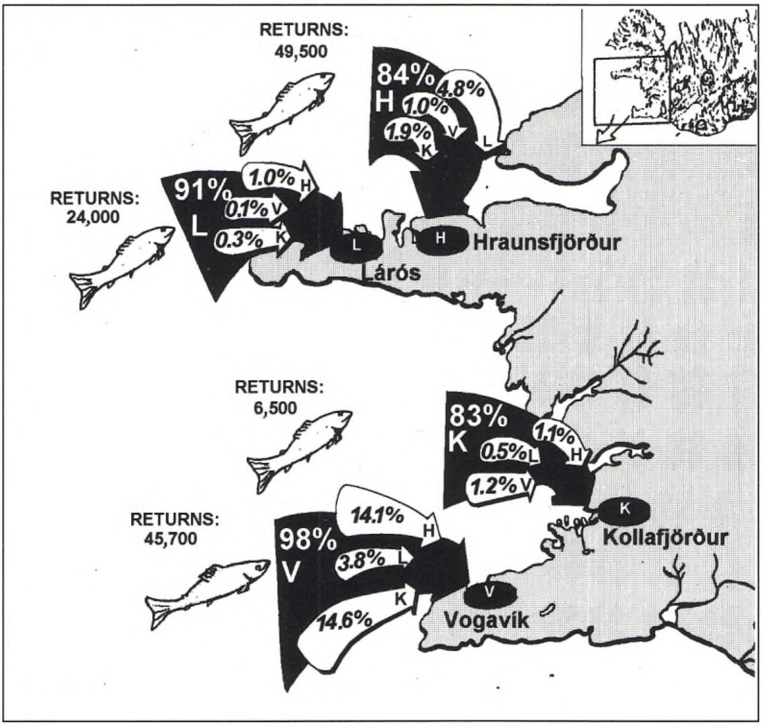


Fig. 8. Straying of salmon between the major ranching stations in 1991, showing the absolute return numbers to each station as well as the relative proportions returning to the home station and other stations. Especially noticeable are the larger strays from stations located further inland, possibly indicative of active trapping of their salmon at the stations located closer to the ocean (Drawing by S. Óskarsson).

Stock selection and straying

There is no doubt that salmon stocks are highly variable in their suitability for ranching. Wild stocks in general are often poorly adapted to hatchery life, which is often reflected in low return rates after release. The ranching stock used at Kollafjörður Fish Farm has demonstrated exceptional survival and growth during rearing and relatively high return rates in ranching experiments. This is the result of inadvertent as well as planned selection during the last 25 years. There are also indications that its homing ability has improved through a selection process.

Fig. 9 shows the strays of several stocks released at Kollafjörður Fish Farm in 1990 to the Vogavík facility in 1991 (Jóhannsson 1993, unpublished). These experiments compared the straying rates of microtagged smolts of Kollafjörður stock to those of two wild stocks as well as hybrids between the ranching stock and the wild stocks. As seen in the figure the Kollafjörður stock has the lowest straying rate to Vogavík, the wild stocks have the highest rates and the hybrids are intermediate. Further studies have confirmed that these findings seem to demonstrate an adaption of the Kollafjörður stock to ranching conditions (Jónasson J. pers. comm.).

Effects on wild stocks

Many scientists are concerned about the effects of ranched salmon on wild populations. This of course is a major problem in countries, where the two groups are harvested in a mixed stock fishery, as the ranched populations can tolerate much higher exploitation rates than the wild stocks. In Iceland the primary concerns have been regarding the genetic effects and transmission of diseases if strays are high.

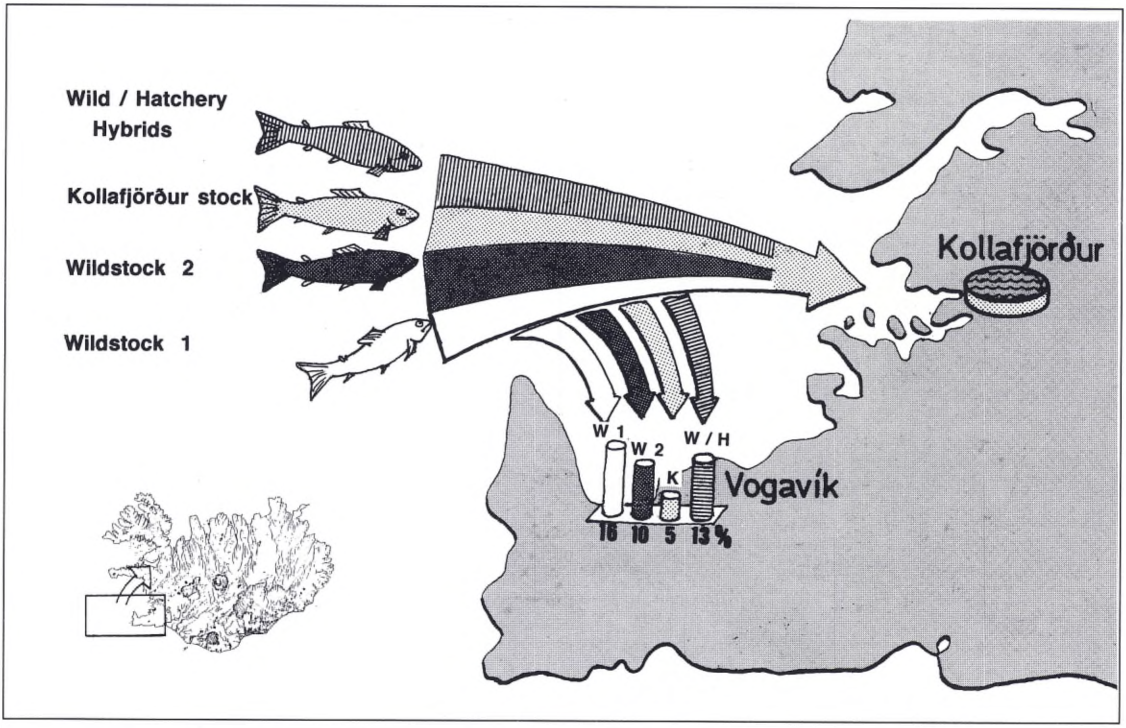


Fig. 9. Straying of different stocks released at Kollafjörður to the Vogavík ranching facility in 1991. The low strays of the Kollafjörður ranching stock as opposed to wild stocks and wild/ranched hybrids are especially noticeable (Drawing by S. Óskarsson).

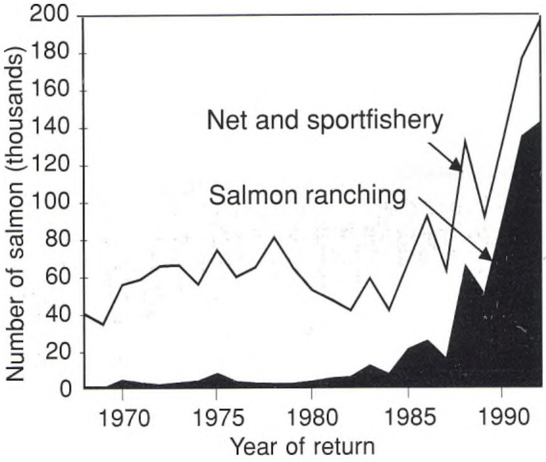


Fig. 10. Contribution of salmon ranching to the total Icelandic salmon catch during the last 25 years (Ísaksson 1993).

Fig. 10 shows the current contribution of ranching to the total Icelandic salmon catch. With the expansion of ranching the total salmon catch rose rapidly, reaching 600 tonnes in the 1992 season. The contribution of ranching in the total Icelandic catch has been close to 75% in recent years but over 80% on the west coast, where most of the ranching takes place.

Despite the fact, that all the salmon are caught in a terminal fishery, there has been considerable concern that the increase in ranching might be detrimental for the wild stocks, especially through straying and subsequent genetic mixing. Fortunately the largest ranching stations are located a fair distance from the major salmon streams and straying mostly occurs into nearby stream and is highly variable from year to year.

Examination of microtags from rivers surveyed for tags throughout the sport fishing season has indicated that strays of ranched salmon into rivers varies from 1-5% of total returns, being highest in rivers close to the ranching stations (Jónasson J. pers. comm.). Incidence of straying seems to be even less pronounced in large complex river systems such as the Hvítá river on Icelands west coast.

The relatively low straying rate into salmon rivers probably reflects the effective recapture methods developed by most ranching operations. The recapture methods, however, which mostly are used in brackish water, have generated considerable unrest among river owners inland from the ranching facilities, which claim that wild salmon are being trapped by the salmon ranchers. No proof exists on this matter and solutions to the problem are not apparent without considerable research effort. This problem now stands out as the greatest problem facing the Icelandic freshwater management system and is a high priority research project.

In 1988 a regulatory measure was set to minimize the effects of ranching and rearing on wild stocks. It specified the distance between major salmon rivers and the rearing and ranching operations as well as the distance between ranching operations. It further prohibited the rearing of imported stocks in sea-cages and specified that ranching stations should microtag at least 10% of their releases up to a 10,000 smolt minimum. Most stations have microtagged many times that number annually.

Concluding remarks

Salmon ranching tends to be a high risk business, especially in those species requiring substantial rearing prior to release. The most successful ranching ventures, at least in socioeconomic terms, are those using chum and pink salmon in Japan and Alaska, which require little or no rearing prior to release. These operations, however, are used to enhance sea fisheries for salmon and could be detrimental to wild stocks through mixed stock harvest, e.g. in Alaska. Atlantic salmon ranching operations in Iceland are the only ranching operations which rely on an estuarine terminal fishery and pose thus minimal threats to wild salmon stocks with respect to harvesting techniques as well as straying.

Substantial rearing of salmon prior to release enables the salmon rancher to perform genetic selection of his stock and Icelandic experience indicates that selective breeeding of ranched salmon may be an important tool to increase size as well as freshwater and marine survival of the salmon. Salmon can furthermore be selected at one locality and released at number of localities within a certain geographic region, which increases the efficiency of the selection process.

At this time private ranching of Atlantic salmon is not profitable and the large scale ranching stations operating in Iceland must be considered long term developmental ventures. This is a logical consequence of the scaling up of releases from a few hundred thousand smolts to releases in excess of three million smolts.

The public ranching of Baltic salmon seems to be technically and economically sound venture using delayed release techniques but current harvest strategies have been considered detrimental to the wild salmon populations in the area and complex political issues prevent just allocation of the resource to those responsible for the ranching effort.

Fair sharing of ranched salmon will be of growing concern in the Atlantic in the years to come. Icelandic ranched salmon move across international boundaries and have been caught in oceanic fisheries, both in the Faroes and West Greenland. The quotas for those fisheries, as negotiated by NASCO (North Atlantic Salmon Conservation Organization) have recently been bought by private sport fishing interests. This will benefit salmon ranchers as well as river owners in the countries of origin. These transactions, however, do not prevent salmon fisheries in the vast oceanic areas outside national jurisdictions by vessels with flags of convenience. It is to be hoped, however, that such unfavourable developments can be stopped through diplomatic negotiations.

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Divergence in the Feeding Migration of Baltic Salmon (*Salmo salar* L.); the Significance of Smolt Size

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Abstract

Around 2.50 million reared and 0.16 million wild salmon smolts enter the northern part of the Gulf of Bothnia annually. Their main feeding area is the Baltic Main Basin, but a small and highly variable proportion stays and feeds in the southern part of the Gulf, the Bothnian Sea. The main factors regulating this divergence are probably environmental. For example, a positive correlation has been demonstrated between offshore salmon catches and the abundance of herring in the Bothnian Sea.

Most smolts released in the north in May-June pass through the Bothnian Sea in August-September. By this time, they exceed the median size of 25-26 cm. Interestingly, this appears to be very near the threshold size for the shift in the diet of post-smolts from invertebrates to fish in the Bothnian Sea. Taking these factors into account, we formulated a hypothesis connecting the shift in diet with the option of staying in the Bothnian Sea instead of migrating a greater distance. This implies that the proportion of fish remaining in the Bothnian Sea should be higher among large smolts than among small ones.

According to our analysis of tagging (Carlin tag) data on River Iijoki salmon, the percentage of fish feeding in the Bothnian Sea increased by 7.1 (from 1.6% to 8.7%) for a 10 cm increase in smolt size (from 15 to 25 cm), lending circumstantial evidence to support our hypothesis. The significance of smolt age and the role of selective fishing as a potential source of bias are discussed.

Keywords: Baltic salmon, smolt size, post-smolt migration, growth rate, diet.

Introduction

The mechanisms of orientation and goal recognition during the spawning migration of anadromous salmonids are quite well documented (Wisby and Hasler 1954, Hasler 1960, 1966, 1980, Toft 1975, Nordeng 1977, Quinn and Groot 1984, Döving et al. 1985, Hart and Dell 1986). Local orientation and homing seem to depend mainly on the olfactory system of the fish. The key word is imprinting. Smolts have the ability to remember a sequence of sensory cues in the correct order when migrating down a river or along a coast. As mature adults, they find their way back to their natal river by following these cues in reverse order.

When leaving the river as smolts, young salmon encounter an open, unknown habitat - the sea. Our understanding of the mechanisms of orientation and goal recognition during this phase of migration is limited. In order to find a suitable feeding area, the fish must possess some kind of pre-programmed ability to recognize appropriate environmental stimuli characteris-

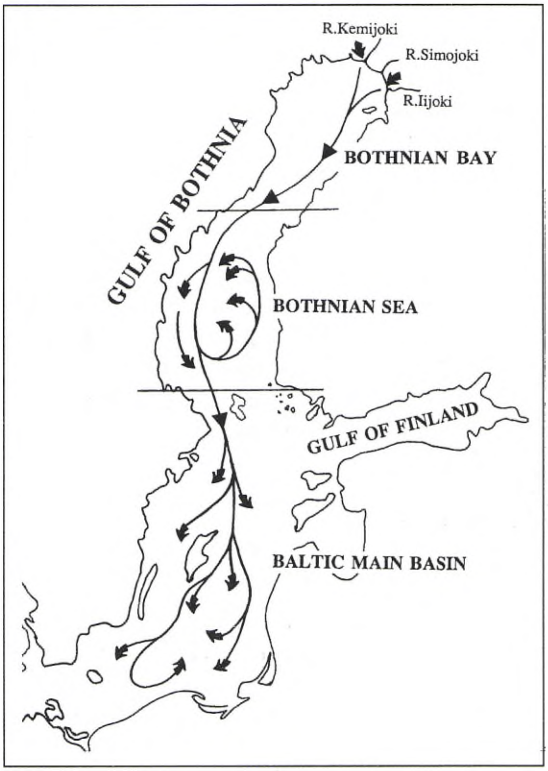

Fig. 1. Release sites and feeding migration routes of River Iijoki salmon in the Baltic Sea.

tic to the goal area, or some kind of biological clock capable of timing the different phases of the migration (McKeown 1984, Eriksson 1988).

The most important stocks of Baltic salmon originate from the large rivers draining into the northern part of the Gulf of Bothnia, the Bothnian Sea (Fig. 1). At present, around 2.50 million reared and 0.16 million wild salmon smolts enter this area annually (Anon. 1992). Their main feeding grounds are in the southern part of the Baltic Main Basin (Christensen and Larsson 1979), but a small and varying proportion of the fish stay and feed in the southern part of the Gulf, the Bothnian Sea (Fig. 1). The pattern of migration through a system of three successive basins offers a good opportunity to study the mechanisms of goal recognition in Baltic salmon.

The variation in the migratory behaviour of the northern stocks of salmon is reflected in offshore catches of salmon in the Bothnian Sea, which tend to fluctuate within wide limits. In a recent study, Ikonen and Parmanne (1991) considered the possible dependency of salmon catches in this area on certain hydrographical and biological factors. According to their analysis, the factors best explaining the between-year variation of offshore catches in the Bothnian Sea were total herring biomass and smolt production in the previous year.

Indeed, there seems to be a plausible correlation between the abundance of feeding salmon and the availability of their main food item, the herring. But what is the mechanism? Could the abundance of prey fish act as a direct "environmental cue" that stimulates the salmon to end their migration? To find the answer, we have to examine the migratory phase at which the

Table 1. Geographical distribution of post-smolt recoveries. Percent of total catch given. Stock: River Iijoki. Year-classes 1981-91.

Month	Bothnian Bay		Bothnian Sea		Main Basin		Total
	No.	%	No.	%	No.	%	No.
May	17	100.0	0	0.0	0	0.0	17
Jun	226	98.7	3	1.3	0	0.0	229
Jul	58	75.3	19	24.7	0	0.0	77
Aug	15	20.0	59	78.7	1	1.3	75
Sep	12	30.0	25	62.5	3	7.5	40
Oct	3	16.7	8	44.4	7	38.9	18
Nov	2	13.3	8	53.3	5	33.3	15
Dec	1	5.9	2	11.8	14	82.4	17

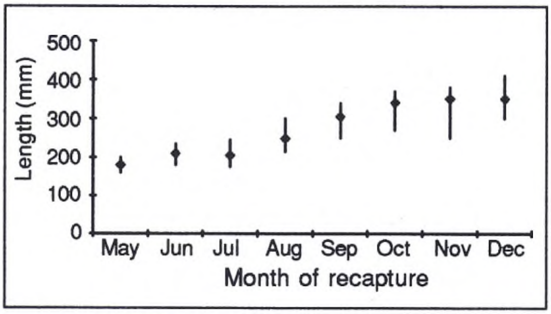

Fig. 2. Monthly median lengths of River Iijoki salmon captured during their first year in the sea. Vertical bars indicate 75% and 25% quartiles.

salmon that migrate farther split away from the rest of the group, i.e. the first months of post-smolt migration.

Most smolts released in the north from early May to early June migrate through the Bothnian Sea in August and September (Table 1). By this time, their median size exceeds 25 cm (Fig. 2). Interestingly, this appears to be near the threshold size of salmon post-smolts when they shift from an invertebrate diet to piscivory in the Bothnian Sea (Fig. 3).

It seems reasonable to assume that the abundance of herring can act as an environmental cue only for fish-eating individuals. On this basis we formulated a hypothesis connecting the shift in diet with the option of staying in the Bothnian Sea instead of migrating farther. The proportion remaining in the Bothnian Sea should therefore be higher among the larger smolts than the smaller ones.

The aim of this study was to assess the effect of smolt size on the migration pattern of the salmon stocks originating from the northern part of the Gulf of Bothnia.

Material and methods

From 1981 to 1988, 114,243 1+, 2+ and 3+ smolts from the River Iijoki stock of salmon were individually tagged with Carlin tags (Carlin 1955) and released into the estuaries of the rivers Kemijoki and Iijoki (Fig. 1). The 1+ smolts were reared in the warm water effluents of the Olkiluoto nuclear power plant, and the 2+ and 3+ smolts at a number of conventional fish farms. All releases were made during the natural smolt run from early May to early June.

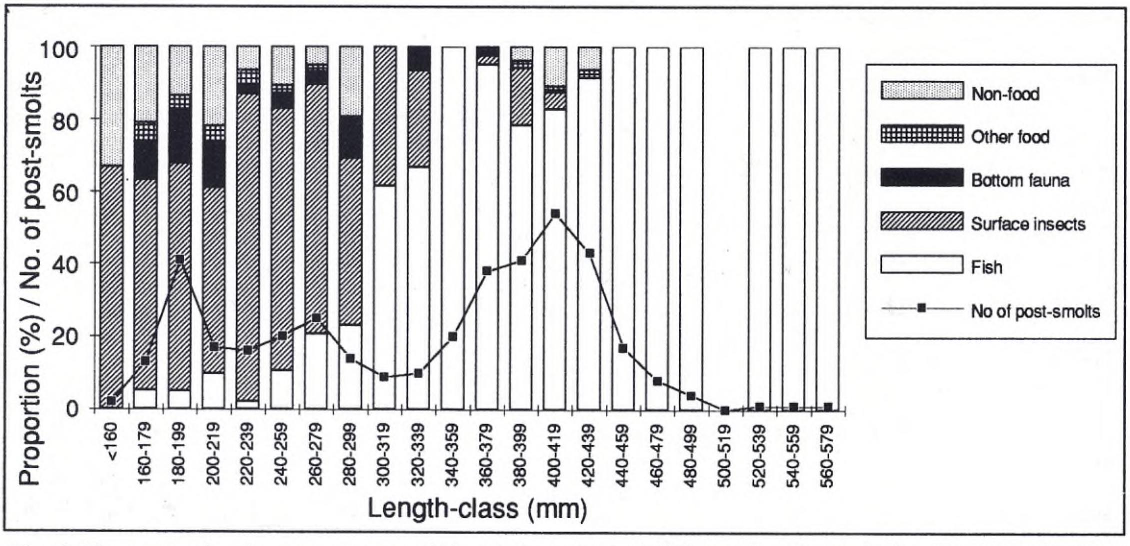

Fig. 3. The proportion (as a percentage of the total number) of different food items in the stomachs of salmon post-smolts by size classes in the Bothnian Sea (Erkamo et al. 1992, manuscript). The data consist of 336 post-smolts sampled in conjunction with professional fishery in the summer and autumn of 1990.

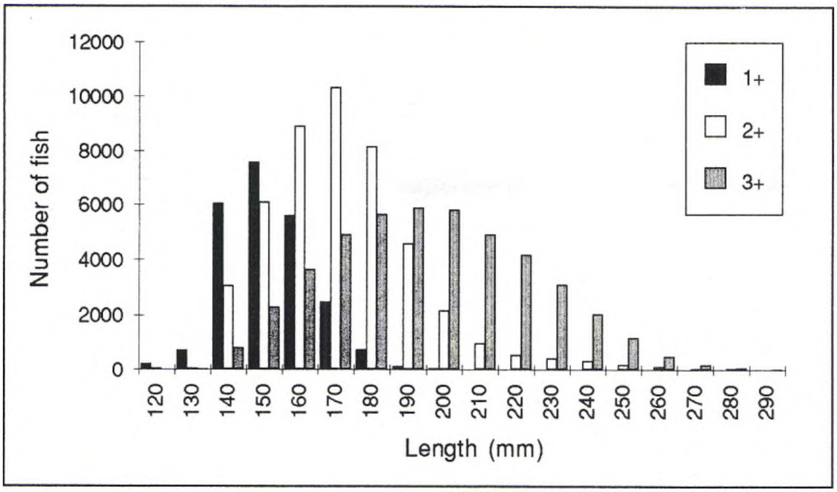

Fig. 4. The length distributions of Carlin-tagged 1+, 2+ and 3+ smolts released in the estuaries of the rivers Kemijoki and Iijoki in 1981-88.

When tagged, all fish were measured to the nearest millimetre in total length. Most groups were tagged a couple of days or weeks before release, but some had already been tagged in autumn or winter. Because the rearing temperatures are very low (near 0 °C) in the north, even in late May, the post-tagging growth of the latter groups was assumed to be minimal. Our analysis was accordingly based on the assumption that tagging length was equal to length at release. The length distribution of the released smolts is given in Fig. 4.

Table 2. The classification of tag recoveries into "sea years" and migratory phases.

Time of recapture Year	Month	Sea-year	Gear* used	Migratory phase
Year of release	all	1st	all	Post-smolts
2nd year	=<IV			
2nd year	>IV	2nd	2	Spawning**
3rd year	=<IV		1	Feeding
3rd year	>IV	3rd	2	Spawning
4th year	=<IV		1	Feeding
and so on				

* Gear 1 = drift net or long line, Gear 2 = other gear
** (grilse)

Until May 1991, 7956 tag recoveries were reported from the experiments. We classified the recoveries into "sea years" and migratory phases according to the time of capture and gear used as recorded in Table 2.

The mean smolt length of feeders caught in the Bothnian Sea was compared with that of feeders caught in the Main Basin. The comparison was made separately for eight year-classes (1981-88) and two age groups (2nd sea-year feeders; >2nd sea-year feeders). The Kolmogorov-Smirnov two-sample statistic was used to test for differences in length distributions.

From the pooled data, we calculated the proportion of feeders caught in the Bothnian Sea for every two-cm-class among smolts ranging from 14 to 26 cm in total length. The proportion was calculated separately for all three smolt age-groups (1+, 2+ and 3+). Length-classes for which fewer than 100 observations were recorded were omitted from the data. The chi-square-test was used to test for differences between smolts of the same size but of different ages, and linear regression was used to test the overall dependency of the proportion remaining in the Bothnian Sea on smolt size.

To compare the feeding conditions of salmon in the Bothnian Sea and the Main Basin, we analysed the growth rates of feeding salmon in these areas. For the growth analysis, all second sea-year feeders caught from November to April were extracted from the data. The individual length of these fish at recapture was used as "growth-rate". The Mann-Whitney U-test was used to test the statistical significance of the difference between the length distributions in each year-class.

Results

For every year-class (1981-88), the mean smolt length of feeders caught in the Bothnian Sea was higher than that of those caught in the Main Basin (Table 3). For younger feeders (2nd sea-

Table 3. Mean smolt length of recaptured salmon by migratory phases. Asterisks indicate the statistical significance of the differences between the smolt length distributions of feeders captured in different areas (Kolmogorov-Smirnov two-sample statistics, *** = $P<0.001$, ** = $P<0.01$, *=$P<0.05$).

		2nd sea-year			>2nd sea-year			All recoveries		
Year-class		Spawn.	Feeding B-Sea	Feeding Main-B	Spawn.	Feeding B-Sea	Feeding Main-B	Spawn.	Feeding B-Sea	Feeding Main-B
1981	Mean	19.7	21.9	21.0	19.7	21.0	20.1	19.7	21.5	20.6
	S.D.	2.3	1.7	2.3	2.7	2.3	2.5	2.6	2.0	2.4
	n	22	7	114	51	6	101	73	13	215
1982	Mean	17.9	21.3***	18.0	17.9	19.1	17.9	17.9	19.7***	17.9
	S.D.	2.5	2.5	2.5	2.8	3.0	2.5	2.6	3.0	2.5
	n	109	14	270	99	39	229	208	53	499
1983	Mean	19.8	22.5***	20.0	19.3	20.8	19.6	19.6	21.9***	19.8
	S.D.	3.3	2.6	3.1	3.2	2.0	3.3	3.3	2.5	3.2
	n	64	36	337	35	17	183	99	53	520
1984	Mean	17.5	19.3	18.0	17.8	17.9	17.8	17.6	18.5	18.0
	S.D.	2.1	2.7	2.2	2.3	1.9	2.1	2.2	2.3	2.2
	n	148	18	983	126	29	434	274	47	1417
1985	Mean	19.5	22.4***	20.2	19.3	21.5	19.7	19.4	22.0***	20.0
	S.D.	2.2	1.6	2.3	2.5	2.8	2.4	2.3	2.2	2.3
	n	126	13	601	85	9	366	211	22	967
1986	Mean	20.2	26.5	20.1	19.4	25.0	19.7	19.8	25.5	20.0
	S.D.	3.0		3.1	2.7	0.7	3.0	2.9	1.0	3.1
	n	37	1	406	48	2	129	85	3	535
1987	Mean	20.3	22.0	21.0	20.4	21.8	20.6	20.4	21.9	20.9
	S.D.	2.9	3.5	3.0	3.3	3.1	2.8	3.0	3.0	2.9
	n	124	2	367	57	6	135	181	8	502
1988	Mean	20.1	21.6	20.6	20.4	20.9	19.4	20.2	21.3	20.3
	S.D.	3.3	3.2	3.3	3.5	2.8	3.4	3.4	3.0	3.3
	n	368	33	564	156	23	140	524	56	704
Total	Mean	19.4	21.6***	19.6	19.2	19.9*	19.0	19.3	20.7***	19.4
	S.D.	3.0	2.8	2.9	3.1	2.9	2.8	3.1	3.0	2.9
	n	998	124	3642	657	131	1717	1655	255	5359

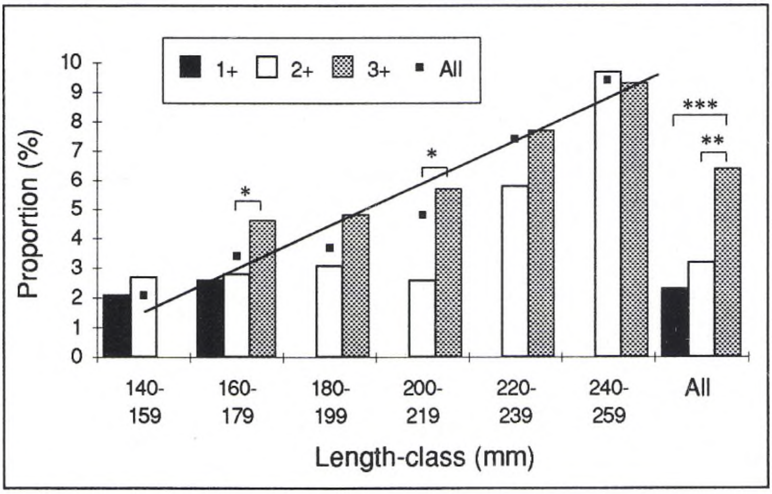

Fig. 5. The proportion (%) of feeding salmon captured in the Bothnian Sea by smolt age-groups and length-classes. Asterisks indicate the statistical significance of the differences between smolts of the same size but of different ages (chi-square; *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$). The line indicates the overall (all age groups) dependancy of the proportion of fish remaining in the Bothnian Sea on smolt length. The equation of the regression line is $y=0.709x-9.038$ ($F=54.7$, $P<0.01$).

year) as well as in the pooled data, the difference between the length distributions was statistically significant in three year-classes out of eight.

The overall percentage of feeders caught in the Bothnian Sea increased by 7.1 for a 10 cm increase in smolt size (from 15 to 25 cm, Fig. 5). The regression was statistically significant ($F=54.7$, $P<0.01$). The pattern seems to be about the same irrespective of smolt age, although there were statistically significant differences between 2+ and 3+ smolts in two size-classes (Fig. 5). Taken together, 3+ smolts yielded a significantly higher proportion of feeders (6.4%) to the Bothnian Sea than either 2+ (3.2%) or 1+ (2.3%) smolts (chi-square 17.1 and 25.8, $P<0.001$, respectively).

Feeding salmon grow better in the Main Basin than in the Bothnian Sea. The difference between the mean lengths of feeding salmon after two seasons in the sea (71.5 and 62.6 cm, respectively) was highly significant (Fig. 6).

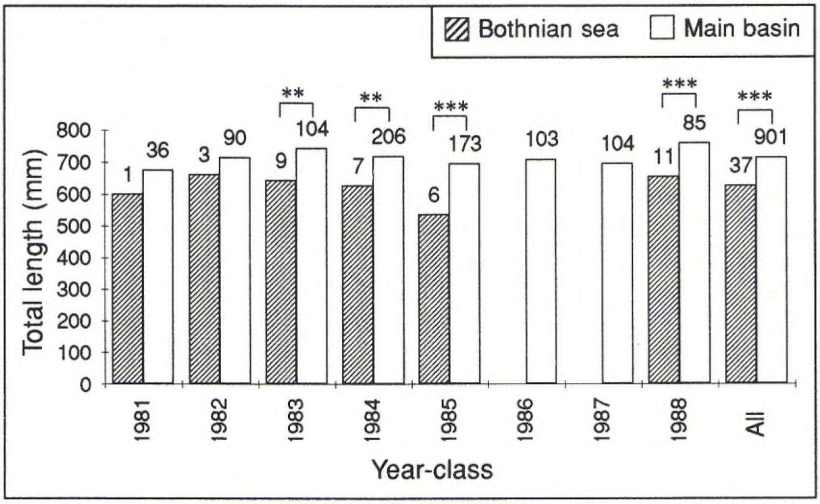

Fig. 6. The mean length of the feeders in the Bothnian Sea and in the Main Basin after two seasons in the sea. The number of observations is given above the columns. Asterisks indicate the statistical significance of the differences between the means (the Mann-Whitney U-test; *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$).

Discussion

Evaluation of the data and statistical tests

Our analyses suggest a close relationship between smolt size and the segregation of River Iijoki salmon into two groups feeding in separate areas. As far as the tagging data are concerned, the link seems to be clear, but before any biological conclusions can be drawn, we should consider some potential sources of methodological bias.

First, the sampling of feeding fish is not random. At present, some 80% of the total offshore catch of salmon is caught in 160-mm drift nets, which are highly size selective, and 20% by long lines, which are probably somewhat less selective. The ratio is, however, by no means constant from year to year or even from one sea area to another. Even if the composition of the fishery were the same in the Main Basin and in the Bothnian Sea the differences in the growth rates of salmon in these areas would generate a differential selection for smolt size. The combination of different growth rates and intensive size selection may partly explain the observed relation between smolt size and feeding area. This is especially true of the youngest feeders (2nd sea-year), which, in the Bothnian Sea, hardly exceed the 60-cm minimum catch limit and thus remain well below the peak of the selection curve for drift nets. However, the possibility of a pure artefact is excluded by the fact that the relation between smolt size and migration is the same for older feeders, too. Differences in the willingness of the fishermen of the Main Basin and the Bothnian Sea to report their tag recoveries is another possible source of error. As far as the variation is concerned, however, catch and tagging data seem to be in agreement (Fig. 7).

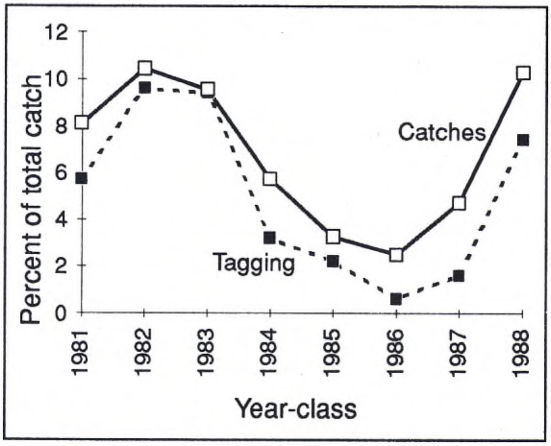

Fig. 7. The annual variation in offshore salmon catches in the Bothnian Sea according to tagging and catch data. Tagging: the number of feeding River Iijoki salmon caught in the Bothnian Sea as a percentage of all recaptures during the feeding migration by year-classes. Catches: the offshore catch of salmon in the Bothnian Sea (Anon. 1992) as a percentage of total nominal offshore landings in the Bothnian Sea and in the Main Basin as a moving average for the two following years.

The Carlin tag is known to have an adverse effect on the growth rate and survival of fish (Saunders and Allen 1967, Isaksson and Bergman 1978, Berg and Berg 1987). Small individuals seem to suffer the most. This effect may well be magnified in the poor growth conditions of the Bothnian Sea. A different size-specific mortality for salmon post-smolts, whether tagged or not, in the Bothnian Sea and the Main Basin may also have important bearing on our results.

In the statistical tests we chose not to adjust the *P*-values according to the number of the comparisons. This decision was based on the fact that, in almost every case, all differences in mean values supported the results of the statistical tests. Thus, the statistical reliability of the results is actually higher than indicated by individual tests.

Goal recognition vs. biological clock

Eriksson (1988) suggested that the distance covered in the sea is the result of a migratory activity sequence, i.e. a biological clock, rather than definite goal orientation. Delayed-release smolts migrated a shorter distance than fish released at the normal time of smolt run. The distance was inversely related to the period of delay before release. To adapt our results to Eriksson's theory, we must assume a negative correlation between fish size and the duration of the migratory activity sequence. This would also be consistent with the results of Eriksson's experiment. The fish were fed throughout the delay period and, evidently, attained a larger size than fish released in the spring.

Our original hypothesis was based on the goal recognition concept. We assumed that the abundance of herring could act as a direct environmental cue that stimulates the fish-eating post-smolts to end their migration in the Bothnian Sea. However, the connection between herring abundance and salmon migration may also be adapted to the biological clock theory, assuming that the end of the active migratory sequence of post-smolts coincides with the shift in diet. In this case, an abundance of herring means that a higher proportion of post-smolts start eating fish, thereby removing any stimulus to migrate farther.

Physical environment and salmon catch

The spatial distribution of feeding Atlantic salmon is influenced by water temperature (May 1973). Salmon in the northwest Atlantic were found in 3-6 °C surface waters in the spring, with very few caught at temperatures of 2 °C or lower. The surface temperatures of the Bothnian Sea are highly variable, sometimes falling below 2 °C as early as the end of November, sometimes not before mid-February (Anon. 1987). Furthermore, the duration of the ice period varies, e.g. in 1980-89 from 0 to as much as 125 days (Kalliosaari and Seinä 1987, Seinä and Kalliosaari 1991). Because the ice prevents all fishing operations, no data are available on the coldest winters. On the other hand, Ikonen and Parmanne (1991) found no correlation between the duration of the ice period and the annual offshore catch of salmon.

Inherited mechanisms

Tagging experiments suggest some kind of genetic segregation between Baltic salmon stocks from different rivers with respect to migratory behaviour (Christensen and Larsson 1979, Kallio-Nyberg and Ikonen 1992). Releases of River Neva salmon into the Bothnian Sea have demonstrated that this stock tends to migrate shorter distances than River Iijoki salmon released in the same area (Kallio-Nyberg and Ikonen 1992). In the year-classes of 1978-82, about 95% of the River Neva salmon were caught in the Gulf of Bothnia, whereas the majority of the River Iijoki salmon (68%) were caught in the Main Basin (Ikonen and Auvinen 1984).

According to the tagging experiments, the yields of River Neva salmon releases have generally been lower and more variable in the Gulf of Bothnia than in the native area of this stock, the Gulf of Finland (Erkamo et al. 1992, manuscript.). The poorest results were obtained for the year classes with the lowest proportion of northern salmon feeding in the Gulf. In this respect, the limited migration, that is, the absence of the "Main Basin option", of River Neva salmon could be regarded as a weakness with regard to survival in the variable conditions of the Bothnian Sea.

If migration is to be adaptively beneficial, the benefits must generally outweigh the costs (Baker 1978, McDowall 1988). For anadromous salmonids, the trade-off is between increased mortality and enhanced growth followed by higher fecundity. One might assume that with natural selection, the divergent pattern of migration of River Iijoki salmon would be able to persist only if the poor growth in the Bothnian Sea were outweighed by lower mortality due to a shorter distance of migration.

However, we do not know the extent of the divergence under natural conditions. Perhaps this arises from hatchery practices. In the year-classes of 1978-82 the proportion of feeders caught in the Bothnian Sea was 27% for reared smolts from the River Simojoki stock (Fig. 1) and only 1.6% for wild smolts from the same river (Ikonen and Auvinen 1984). This may be because wild smolts are usually smaller than reared ones (Toivonen 1977, Christensen and Larsson 1979).

The significance of smolt age, sex and maturity

According to Hansen and Jonsson (1991), smolt age influenced the migratory pattern of the River Neva salmon transplanted to the rivers Imsa and the Akerselv in Norway. A large proportion of the 2+ smolts remained in the fjord during the summer and autumn after release, whereas the 1+ smolts left the fjord and migrated to the feeding areas in the Norwegian Sea. Hansen and Jonsson (1991) proposed that the observed difference was caused by the higher developmental rate of the larger 2+ smolts leading to earlier maturity.

According to our analysis, 3+ smolts yielded proportionally more feeding migrants to the Bothnian Sea than did 2+ or 1+ smolts. Even though age group has some effect on the results, this difference seemed to be more readily attributable to size than age. Nevertheless, we cannot reject the possibility that the divergent pattern of feeding migration is influenced by both smolt size and age-dependent differences in the attainment of maturity. The first group of spawners (grilse) would have left for spawning grounds before our first group of feeders (2nd sea-year feeders) could be "sampled" in the open sea; older feeders would have gone through this selection process several times.

Our data suggest a relation between smolt size and maturity, but contrary to expectations (Hansen and Jonsson 1991) the relation is negative: the grilse seem to have been among the smallest individuals at the time of release (Table 3). We assume that this is because almost all grilse in the Baltic are males and, on the other hand, males seem to have been in the majority in the smallest size-groups of smolts (Fig. 8). Some of the males attain maturity already in the hatchery (precociousness) and, consequently, fall behind in growth.

According to Ahvonen et al. (1991), the migration of male salmon is, in general, shorter in time and distance than that of females. However, the observed divergence in the feeding migration cannot be attributed to behavioural differences between the sexes. In both groups of feeders the sex-ratio is about the same (Table 4), with a clear female domination.

Management

For the manager, the observed connection between smolt size and migration seems to offer a promising tool for manipulating the distribution of salmon catches in the Baltic Sea. Larger smolt sizes would lead to higher, and possibly less variable, offshore catches of salmon in the Bothnian Sea. Most of all, this would benefit

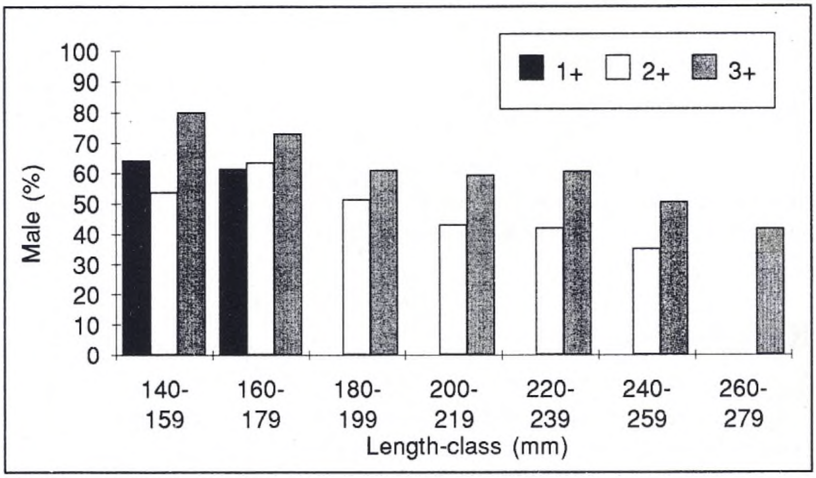

Fig. 8. The proportion (%) of males among recaptured and sexed River Iijoki salmon by smolt length-classes and age-groups.

Table 4. Sex-ratio of tagged Iijoki salmon recaptured as feeding migrants in the Bothnian Sea and the Main Basin (sexed by the fishermen).

Time of recapture Area of recapture	Sex Males No	%	Females No	%	Total No.	χ^2	*P*
2nd sea-year							
Bothnian Sea	6	20.0	24	80.0	30		
Main Basin	88	27.3	234	72.7	322	0.75	>0.05
>2nd sea-year							
Bothnian Sea	8	17.4	38	82.6	46		
Main Basin	56	29.3	135	70.7	191	2.68	>0.05
All feeders							
Bothnian Sea	14	18.4	62	81.6	76		
Main Basin	144	28.1	369	71.9	513	3.14	>0.05

fishermen in the area, who have invested large sums of money in offshore fishing gear in recent years. It would also be consistent with the principles of salmon management in the entire Baltic region. The managers (International Baltic Sea Fishery Commission) have decided that the main objective of fishery management is the protection of the few remaining wild stocks of Baltic salmon. The most difficult problems encountered are related to the mixed fishery of wild and reared stocks in the Main Basin. In this respect, the enhancement of the offshore fishery of the Bothnian Sea, with its low proportion of wild fish (Anon. 1992), can be seen as a reasonable goal.

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Food of Ranched Atlantic Salmon (*Salmo salar* L.) Postsmolts in Coastal Waters, West Iceland

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Abstract

Atlantic salmon (*Salmo salar* L.) postsmolts of hatchery origin were caught in floating gill nets (0-3m) in coastal waters West Iceland in 1989 and 1990. The smolts had been released from net pens out in the fjord, by a ranching station. The postsmolts started migration to the ocean soon after being released and partly migrated along the shore of the fjord. A small proportion of the released smolts were abnormal in behaviour as shown by the migration of males preparing for maturation the coming autumn back towards freshwater. The postsmolts fed heavily on pelagic prey that were primarily planktonic; mainly larvae of crabs (*Hyas* spp. and *Pagurus bernhardus*), crustaceans of the order cyclopoida and dipteras were also eaten in considerable amounts. The postsmolts also found food near the bottom. Benthic amphipods together with gastropods and polychaets made up a considerable part of the stomach volume. Nektonic prey were found as sticklebacks (*Gasterosteus aculeatus* L.). The postsmolts consumed prey of width ranging from 0.3-4.7% of their fork lenght.

Keywords: *Salmo salar*, postsmolts, food, maturing males, ranching.

Introduction

Recently, considerable effort has been directed towards the development of sea ranching of Atlantic salmon (*Salmo salar* L.) in Iceland. The number of released smolts has increased from about one million in 1988 to nearly six million in 1991 (Stefánsson and Sturlaugsson 1992). The first part of the ocean migration of Atlantic salmon is of special interest for sea ranching projects due to indications of high mortalities during early sea life, either due to predation on postsmolts (Larson 1985, Valle 1985, Hvidsten and Møkkelgjerd 1987, Hvidsten and Lund 1988, Montevecchi 1988) or the influence of adverse sea condition in the beginning of feeding migration (Scarnecchia 1984a, b, Scarnecchia et al. 1989). Considering the large number of salmon smolts that leave rivers and sea ranching stations, the infrequent capture of postsmolts in inshore areas along with small catches, indicate that they move fairly rapidly away from the fresh water and disperse to feeding areas in the open ocean (Reddin 1988, Hvidsten et al. 1993).

The literature on the diet of Atlantic salmon postsmolts is sparse (Anon. 1983, Morgan et al. 1986, Dutil and Coutu 1988, Hvidsten et al. 1992, 1993). The food of salmon at later stages has been studied in the North Atlantic (Templeman 1967, Jensen 1967, 1974, Lear 1972, 1980, Anon. 1983, Hislop and Youngston 1984, Hansen and Pethon 1985, Reddin 1985). These studies showed that the salmon is largely piscivorous but pelagic invertebrates are also important prey. Main prey items were capelin (*Mallotus villosus* Müller), launce (*Hyperoplus lanceolatus* Le Sauvage), sand eels (Ammodytidae), herring (*Clupea harengus harengus* L.), *Paralepis* spp., lantern fish (Myctophidae), squids, amphipods and euphausiids.

The aim of this project was to obtain information on the food of Atlantic salmon postsmolts during the beginning of their sea migration.

Material and methods

Study area

Experimental fisheries were carried out in Hraunsfjordur and Kolgrafarfjordur on the Snæfellsnes peninsula, West Iceland (Fig. 1).

Topography

Kolgrafarfjordur is about 28 km^2 with a maximum depth of 41 m. The bottom of the fjord is mainly covered with stones and gravel but proportion of finer sediments increases towards the inner part, with mudflats at the head of the fjord. Algae characterize most of the littoral and sublittoral in Kolgrafarfjordur.

Before 1987 Hraunsfjordur was divided into two main parts by a lava constriction and a highway bridge, but when the salmon ranching operation started, the upper part of the fjord was dammed and the inner part is now a 1.7 km^2 freshwater lake. The actual Hraunsfjordur (2.3 km^2) is shallow with large intertidal zones, mainly mudflats. The maximum depth of Hraunsfjordur at high tide is 3-6 m in the inner part and 4-9 m in the outer part. Due to the shallowness and high amplitudes of tides there is a strong inn- or outward water current dependent on the tidal cycle, resulting in replacement of the water in Hraunsfjordur during tides. During sampling the maximum difference between low and high tide was ranging from 3.3-3.7 m in 1989 and between 2.3-4.2 m in 1990. Sigurðsson (1974) and Jónsson (1974) have shown large number of species and individuals in the littoral community in Hraunsfjordur.

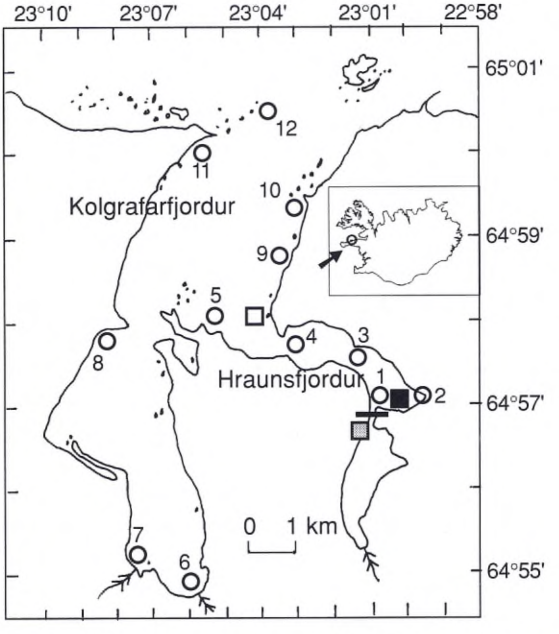

Fig. 1. The catchment area and the location of sampling stations (○); 1-3 in 1989 and 4-12 in 1990. The symbols indicate: ▬ = dam, ▨ = winter rearing of parrs in the lake, ■ = rearing in sea, □ = rearing and releasing, $\overset{\wedge}{\wedge}$ = outlets of rivers.

Salinity and temperature

Relatively little input of freshwater in the catchment area is reflected in available salinity data based on measurements in late June (Institute of Marine Research, unpubl. data). This data showed that salinity changed very little from the mouth of Hraunsfjordur were the mean salinity in the uppermost meter was 33.7‰ and 33.9‰ at depth of 8 m, to the mouth of Kolgrafarfjordur were the salinity was 34.5‰ at both these depths.

Water temperature in Hraunsfjordur during the study periods was approximately 9 °C in 1989 and 9.5-11.8 °C in 1990. In Kolgrafarfjordur in 1990 the water temperature in the uppermost three meters fluctated around 10 °C between the fishing stations. A seaward decrease in water temperature was observed in 1990 and continued into regions few kilometers off the Kolgrafarfjordur mouth where colder water (down to 8.0 °C) was observed.

Releases

The rearing process in Hraunsfjordur ranching station, in 1989 and 1990, started when parrs were transported to net cages in the freshwater lake (Fig. 1). There they were reared for 3-11 month prior to release, but early in the summer after the majority of fish in each net cage had shown smolt characteristics, the fish were transported from the lake into net pens that were placed in a sublittoral channel in the inner part of Hraunsfjordur. The smolts were reared in these cages, to adapt them to salt water and for maintainance of smoltification. After 6-14 days in seawater the smolts were transported out into Kolgrafarfjordur by towing the net pens. The smolts were subsequently reared for 4-6 days prior to release, wich always took place in the beginning of outgoing tide.

The smolts caught in Hraunsfjordur in 1989, were released on June 26. This first release of that year, was composed of approximately 73,000 two years old (2+) smolts in two size groups (measured in late May 1989). One group consisted of 55,000 slow growing fish of mean length 14.8 cm (SD=2.0). The other group released consisted of 22,000 larger smolts (mean L=20.1cm, SD=3.3), that were fast growing, but were held back as one-year smolts.

Releases in 1990 consisted of nearly 440,000 smolts, that were released on four dates, from June 18 to 28. The smolts released in 1990 were 1+ smolts apart from the first releasing that consisted of 9,000 2+ smolts. The size distribution of released 1+ smolts reflected the size interval found among this hatchery reared 1+ smolts (approximately 11-20 cm).

Sampling

The definitions of postsmolt and other life-history phases of Atlantic salmon used here are according to Allan and Ritter (1977). This means that the postsmolt phase starts when the fish start feeding in the sea. The fish are thus called postsmolts after being reared in salt water pens in Hraunsfjordur, although the actual postsmolt phase of these fish starts when they start their seaward migration.

The postsmolts examined in this investigation were collected in Hraunsfjordur on July 3-4, 1989 and in Kolgrafarfjordur on June 22-29, 1990. The fishing was done both during day and night, but at this latitude the sun only sets for approximately three hours at this time of the year.

Samples of smolts were taken using series of 30 m long floating monofilament gillnets of bar mesh sizes of 12.5, 16.0, 18.0 and 22.0 mm and once with a extra 8.0 mm net. The net series were laid perpendicular to the shore both years; the mesh size gradually increasing along the serie, ranging from 12.5 (8.0) mm nearest to the shore to 22 mm farthest from the shore. The mean interval between visitation of net series was approximately 12 hours in 1989 and 6.7 hours (SD=4.4) in 1990.

In 1989, experimental fisheries took place at high tide above intertidal areas of Hraunsfjordur at stations 1-3 (Fig. 1), to detect possible migration of postsmolts in the area inside the release site. The net series were laid over drained intertidal areas at low tide from little above the tide line and when the tide came in they floated up.

In 1990 the effort was directed towards outward migrating postsmolts in Kolgrafarfjordur, but fishing took also place in the inner regions (station no. 4, 6, 7 and 8) to detect other migration routes (Fig. 1). The shore located net series were laid out from the tide line with two exception (stations no. 5 and 7) when the landward end was approximately 50 meters from tide line. Test fisheries in areas farther from the shore were done once in the beginning of the fishery with one net series in the mouth of Kolgrafarfjordur (station no. 12).

Measurements

The fish caught were weighed to the nearest gramme and forklength was measured to the nearest millimeter. The coloration as criteria of smolting was estimated according to modification of the procedures of Johnston and Eales (1967) and Birt and Green (1986). The state of maturity was estimated according to Dahl (1917).

Stomachs (pharynx-pyloric spinchter) from salmonid fishes were frozen and subsequently thawed in the laboratory. Stomachs of trout (*Salmo trutta* L.), Arctic char (*Salvelinus alpinus* L.) and of bycatches of sea fishes (The Institute of Marine Research, Unpubl. data) were examined in order to dectect predation on postsmolts. The stomachs of postsmolts were cut open and fullness estimated as percentage of stomach volume (5% intervals). Empty stomachs and those that contained traces of food (<5%) were grouped as empty. Food composition of the stomachs along with 30 subsamples of intestines in 1990 were examined in relation to placement of prey types in them. The total amount of food from the stomachs were blotted and weighed (wet weight) with slime in both years and without slime in 1990. The food was weighed to 1/10 of a gram in 1989 and to the nearest 1/100 of a gram in 1990.

Prey items were then spread in a shallow dish and visually analyzed under a binocular microscope. The stomach contents, were sorted to taxonomic groups and an estimation of the volume of prey was carried out using glass cylinders.

To detect the interval of the prey width/fish fork lenght ratio (PFR), the largest and smallest prey were sorted visually out from 26 smolts stomachs and their maximum width measured to the nearest 1/10 of millimeter.

Statistical analysis

t-test were used for pairwise comparisons of mean lenghts of smolts with and without stomach content. Regression analysis was performed to estimate if there was linear relationship between log-length and stomach fullness. For fish that had ≥5% stomach fullness, linear regression analysis was used to get the relationship between lenght (cm) of fishes (log L) and weight (g) of the food (log W): mean$W = aL^b \cdot 100$.

Index of body shape for salmonids is commonly obtained from Fultons condition factor (K) formula: $K = 100W \cdot L^{-3}$ (Bagenal and Tesch 1978). The fish weight is given in g, and lenght is given in cm. Here the regression coefficient b was not equal to 3 (allometric growth) This deviation of b would result in a biased K according to fish lenght. This is prevented here since the equation for the lenght-weight relationship: $W = aL^b$ (Bagenal and Tesch 1978) is added to the Fultons condition formula and the fish weight (W) divided into the formula (Jensen 1977). Then we get relative condition factor: $K_{rel} = 100aL^b \cdot L^{-3}$ also shown as: $K_{rel} = 100aL^{(b-3)}$ that enabled comparison of the different groups observed (Jensen 1977, Bagenal and Tesch 1978). The coefficients a and b were retained from linear regression analysis on fish lenght (log L) versus fish weight (log W): $\log W = \log a + b \log L$. The statistical analysis were performed using SAS computer package.

Results and discussion

Catch

During the experimental fisheries in 1989, a total of 39 postsmolts (18-408 g) were caught in Hraunsfjordur, compared with 65 postsmolts (12-356 g) caught in Kolgrafarfjordur in 1990. Additionally some grilse (5) and multi sea winter salmon (11) were caught.

In 1989 the rate of recapture in the fishing in Hraunsfjordur was 0.05% of the number of released fish and the catch per unit effort was from 0.03-0.72 salmon postsmolts/net/hour. In 1990 the recapture rate in Kolgrafarfjordur was ranging from 0.015-0.021% of the number of released fish and the catch per unit effort was from 0-2.0 salmon postsmolts/net/hour.

Other fish species caught during the experimental fisheries in 1989-90 were: saithe (*Pollachius virens* L.), launce, cod (*Gadus morhua* L.), plaice (*Pleuronectes platessa* L.), lumpsucker (*Cyclopterus lumpus* L.), sea trout, Arctic charr and sticklebacks.

Sex and sexual maturation

The postsmolts caught in Hraunsfjordur in 1989 showed bimodal length distribution (Fig. 2) reflecting the variation in smolts size between the two groups released in 1989. Nearly all fish in the upper lenght mode of captured fish were maturing males and they were also dominant in the upper part of the lower mode. There were 3.9 times more males than females in the catches of postsmolts in Hraunsfjordur in 1989. This is explained by aggregation of maturing males in Hraunsfjordur were they were 76% of the males.

In the catches in Kolgrafarfjordur in 1990 the postsmolts reflected the size interval of released smolts (Fig. 2). In Kolgrafarfjordur there were more females than males in the catches of

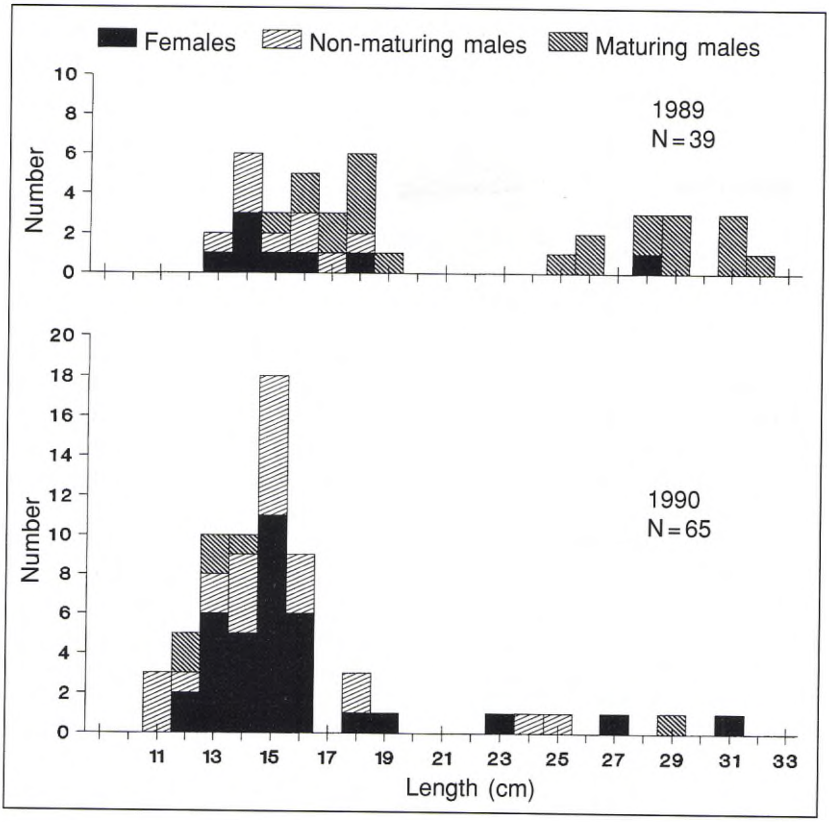

Fig. 2. Lenght distribution of caught salmon postsmolts in Hraunsfjordur (1989) and Kolgrafarfjordur (1990), in relation to their sex and maturation.

postsmolts (sex ratio =0.9), which was possibly reflecting aggregation of maturing males in Hraunsfjordur as the year before. Maturing males were caught at the fishing stations nearest to the release site.

The maturation stage among maturing males, ranged from stage 3 in instances of the bigger males (25-32 cm) to stage 5 that were general among the smaller (12-19 cm) maturing males. The postsmolt caught, apart from majority of the smaller maturing males, had final smolt dress of brightly silvered scales and black edges of fins. Mature males had higher condition factor than non-maturing fish in both years (Table 1). The observed difference between the groups, may reflect better smoltification of non-maturing fish than maturing males, but due to difference in rearing process and life history the comparison has to be cautious (Järvi et al. 1992). The maturation stage together with other characteristics

Table 1. The regression coefficients *a* and *b* for the formula of relative condition factor; $K_{rel} = aL^{(b-3)} \cdot 100$. Both for non-maturing smolts and maturing males in 1989 and 1990. The correlation factor (r), number (N) of fishes and their K_{rel} interval are also shown.

Year	N	Non-maturing males and females				N	Maturing males			
		a	b	r	K_{rel}		a	b	r	K_{rel}
1989	16	$6.11 \cdot 10^{-3}$	3.14	0.99	0.87-0.97	22	$3.21 \cdot 10^{-3}$	3.38	0.99	0.88-1.19
1990	59	$11.92 \cdot 10^{-3}$	2.92	0.98	0.91-0.99	6	$5.44 \cdot 10^{-3}$	3.22	0.99	0.93-1.14

indicates that the smaller maturing males were pseudo smolts, but because of former life history of the bigger maturing males, their appearance may have stand for postsmolt maturing.

Migration

The salmon ranching in Hraunsfjordur is based on releases from net pens in the sea. As a result smolting status of the smolts and the resulting migration are not at an optimum level for all the fish when released. Each release group therefore consist of normal outward migrating postsmolts that usully are a large majority of the releases and atypical postsmolts migrating towards freshwater that in terms of their status may be defined as pseudo postsmolts. The atypical postsmolts are here divided into three groups. Two of them consisted of sexually maturing males and the third group consisted of sexually non-maturing fish that are found in Hraunsfjordur when they would expected to be on their way to open ocean.

Location in the nets

The smolts were in both years caught along the net series but the innermost nets of the series gave often the best capture. This was prominent in Hraunsfjordur where most of the postsmolts of all size were caught from tide line up to approximately 10 meters from tide line, showing that most of the fish was only captivated for approximately half of the time between visitations and indicating that their migration was most active along the shore when the tide was rising highest. Out in Kolgrafarfjordur the postsmolts were more scattered troughout the nets although patches of 4-6 postsmolts in 1-2 m^2 area of the nets were observed, perhaps indicating schools of postsmolts. Large majority of the postsmolts caught in Kolgrafarfjordur in 1990 occurred in the upper part of the nets (surface - 2 m). In Hraunsfjordur where all net series lay above intertidal areas where sea level was variable, little conclusion can be drawn from the vertical location of captured fish.

Feeding migration towards the ocean

The catches in Kolgrafarfjordur in 1990 indicated that a part of the postsmolts migrate near to shore on their way to the ocean as best indicated by capture of 16 postsmolts in the mouth of Kolgrafarfjordur (station no. 11). The fishing in areas farther from the shore (station no. 12) gave no recapture of postsmolts, possibly because rough weather resulted in quick entanglement of the net series. As a result fishing in outer areas was not continued.

The low catches of postsmolts in 1990 in relation to amount released and the fishing effort, along with scattered catches of postsmolts along and out from the shoreline in Kolgrafarfjordur suggests that released fish dispersed rapidly across the fjord, commencing their oceanic migration. Instance of catch of postsmolt in the mouth of Kolgrafarfjordur (station no. 11) two days after last release, indicate that a fraction of the postsmolts spent some time in the fjord before migrating to ocean.

Migration towards freshwater

The migration of postsmolts from the release in 1989 back into Hraunsfjordur was indicated by catch of non-maturing and maturing postsmolts a week after release over the intertidal area on all stations, showing their littoral migration (McKeown 1984). The number of postsmolts in the area has probably been underestimated because the nets used were not efficient in catching the biggest postsmolts (e.g. Jensen 1990). Their sexual maturation status together with capture of 2 microtagged maturing males from the release, confirmed that a part of the releases were atypical postsmolts that migrated into the less saline water of Hraunsfjordur after release. The postsmolts feeding in Hraunsfjordur were mostly non migrants as indicated by the dominance of maturing males in the catches, although they may partly be questionable with respect to their migrating behaviour (Berglund et al. 1992, Eriksson et al. 1987). The non-maturing postsmolts aggregating in Hraunsfjordur after release may in time reach a smolt status that triggers their migration to the ocean.

Predation by salmonids

Observation on stomachs of the littoral migrating chars (12.4-42.5 cm) and the trouts (15.9-37.5cm) showed that sea trout preyed upon salmon postsmolts in Hraunsfjordur. The biggest trout had eaten three small smolts (11-13 cm).

Food and feeding

Consumption

Information about the fullness of fishes is valuable when considering their forage status. Postsmolts were not caught in large numbers and therefore medians were used along with means to describe the fullness according to Amundsen and Klemetsen (1986). The fishing gear used altered the fullness distribution because fish had been in the nets for various time intervals. Despite this the visitation of nets in 1989 and 1990 along with information about digestion rate of salmonids shortly after release (Brodeur and Pearcy 1987, Johnsen and Ugeldal 1988), indicate that these medians (Fig. 3) should be showing approximately the average fullness of postsmolts in the sampling area.

When feeding postsmolts were analysed separately, the relationship between the length of fish and the weight of their food were significant, both in Hraunsfjordur in 1989 ($P<0.01$) and the year after in Kolgrafarfjordur ($P<0.001$) (Table 2). But although amount of food generally increased with increased size of fish among these fish, their stomach fullness and length were not

Table 2. The regression coefficients *a* and *b* for the formula of mean food weight (g) of fishes with $\geq 5\%$ stomach fullness in relation to their lenghts (cm): mean $W = aL^b \cdot 100$ for both 1989 and 1990. The correlation factors (*r*) and number of fishes (*N*) are shown.

		Prey and slime			Prey		
Year	*N*	*a*	*b*	*r*	*a*	*b*	*r*
1989	21	$59.6 \cdot 10^{-5}$	2.18	0.58			
1990	46	$9.7 \cdot 10^{-5}$	2.64	0.66	$1.0 \cdot 10^{-5}$	3.08	0.56

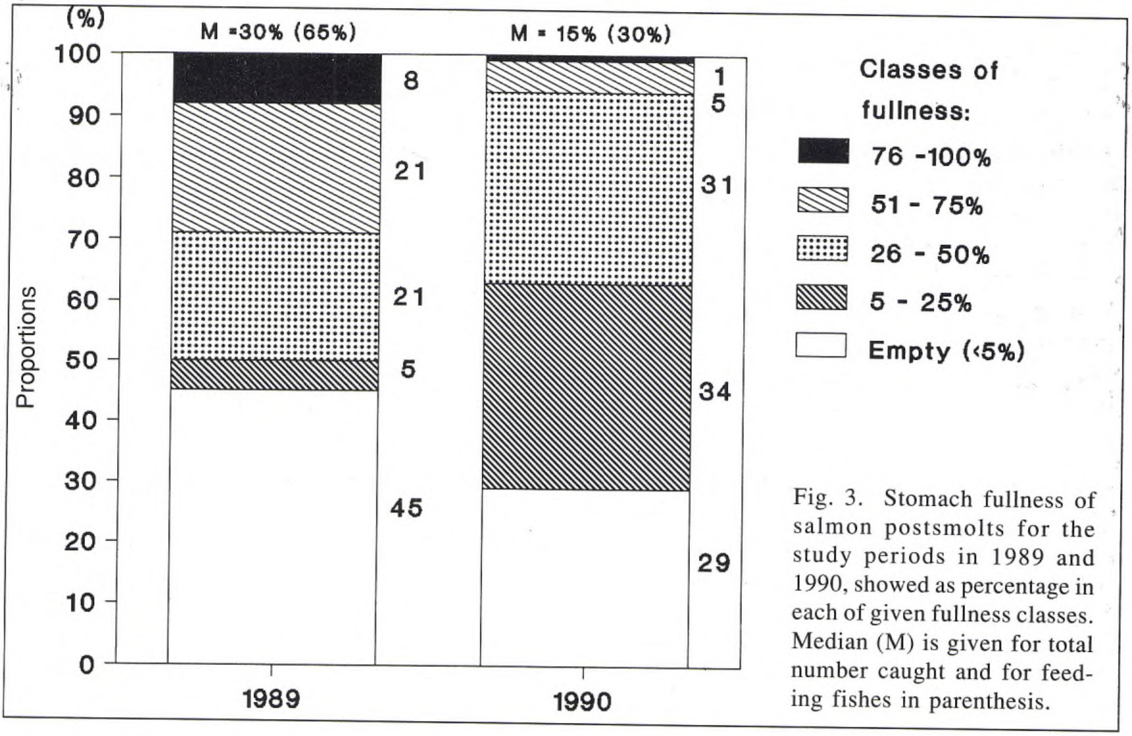

Fig. 3. Stomach fullness of salmon postsmolts for the study periods in 1989 and 1990, showed as percentage in each of given fullness classes. Median (M) is given for total number caught and for feeding fishes in parenthesis.

Table 3. Comparison of stomach content of salmon postsmolts categories in Hraunsfjordur (1989) and Kolgrafarfjordur (1990). Distribution of fish within these groups are given (i.e. number of feeding fish and empty fish, together with means, medians, minimum and maximum values of stomach fullness of feeding fish).

	All samples		Non-maturing males and females		Maturing males	
	1989	1990	1989	1990	1989	1990
Number (no.)	39	65	16	59	23	6
(%)	100	100	41	91	59	9
Number (%)						
Feeding	54	71	75	75	39	59
Empty	46	29	25	25	61	50
Fullness (%)						
Mean (SD)	55 (24)	28 (18)	58 (28)	28 (19)	51 (18)	17 (13)
Median	65	30	60	30	50	15
Min	25	5	25	5	30	5
Max	100	80	100	80	75	30

significantly related, for both years, showing the similarity in amount of food as proportion of fish size.

Feeding postsmolts (stomach fullness ≥5%) were significantly smaller (*P*<0.001) in Hraunsfjordur in 1989 than fish with empty stomachs but this was not the case in Kolgrafarfjordur in 1990. Fewer foraging postsmolts among the largest fish in Hraunsfjordur may be explained by the high ratio of maturing males among these postsmolts, suggesting that their large size and/or maturity stage may have been prohibitive factors concerning feeding (Fig. 2). The maturing males however that were feeding showed in both year fullness that was little less at average than observed with non-maturing fish. (Table 3).

In Hraunsfjordur in 1989, high ratio (46%) of the postsmolts had empty stomachs (Fig. 3) but the average weight of food per kg of feeding postsmolts was 6.0 g but was 1.7 g/kg when all postsmolts captured are included. In Kolgrafarfjordur in 1990, a large part (29%) of the postsmolts had empty stomachs and average weight of food per kg of feeding postsmolts was 1.9 g but was 1.5 g/kg when all postsmolts caught are included. It is suggested that the low fullness among majority of the postsmolts in Kolgrafarfjordur can partly been explained by their rapid outward migration trough the fjord leading to suppression of feeding at that time.

The observed forage efficiency of the postsmolts is low at average compared to the general intensive feeding of grilse and multi sea winter salmon in the feeding areas (e.g. Lear 1972, 1980). Similar forage status of postsmolts in the beginning of postsmolt migration was observed by Hvidsten et al. (1992, 1993). But low forage efficiency has also been found among postsmolts after staying 2-4 months in nearshore area (Dutil and Coutu 1988).

In some instances prey were eaten in high numbers (Fig. 4, Table 4) showing how effective feeders postsmolts can be and also that there must have been considerable density of prey available (Rimmer and Power 1978). This indication of high abundance of prey and its contrast to the low average of feeding, supports that the forage intensity could be explained partly by different states of the individuals with respect to their physiological status and migration routes. Studies on reared Atlantic salmon juveniles regarding acceptability of wild prey indi-

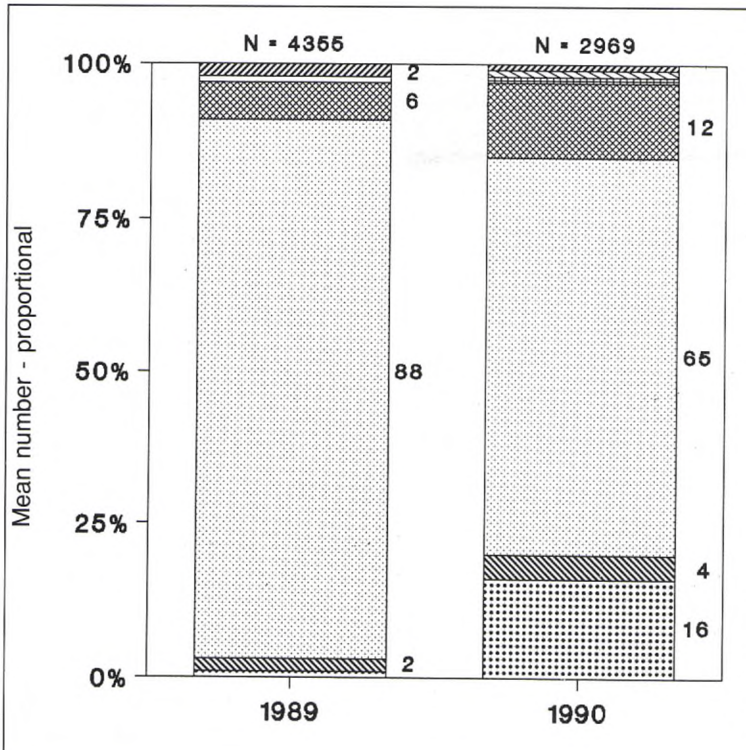

Fig. 4. The proportion (%) of prey types eaten by salmon postsmolts in Hraunsfjordur (1989) and Kolgrafarfjordur (1990). Total number of prey is given (N).

Table 4. The size of prey types eaten by smolts in Hraunsfjordur (1989) and Kolgrafarfjordur (1990). The size range of smolts that predated on each prey type is given along with the size range of smolts that were subsampled for measurements of prey in paranthesis and calculations of PFR. The maximum number of prey per stomach are given.

Prey		Predatory smolts	PFR	Max no. of
Max width (mm)	Type	Fork length (mm)	%	prey/stomach
0.5-1.0	Cyclopoida	129-279 (142-279)	0.4-0.6	1176
1.0-1.6	Calanoida	130-145 (143)	0.7-1.1	9
2.0-3.0	Decapoda larvae	115-308 (115-124)	1.7-2.4	184
0.8-6.0	Amphipoda	114-312 (140-312)	0.4-3.6	16
2.6	Mysidacea	130-193 (193)	1.3	1
2.0-2.5	Polychaeta	124-284 (124)	1.6-2.0	2
1.2-3.4	Gastropoda	142-160 (155-160)	0.8-2.1	15
2.9-5.0	Mytilus edulis	160-312 (160-312)	1.6-1.8	1
0.5	Invertebrata eggs	132-145 (132-145)	0.3-0.4	32
13.0	Gasterosteus	279-318 (279)	4.7	1
0.9	Ammodytidae larvae	114-308 (161)	0.6	5
0.6	Hydracarina	142-151 (143)	0.4	2
1.0-3.0	Diptera imago	145-279 (145-279)	0.4-1.8	326

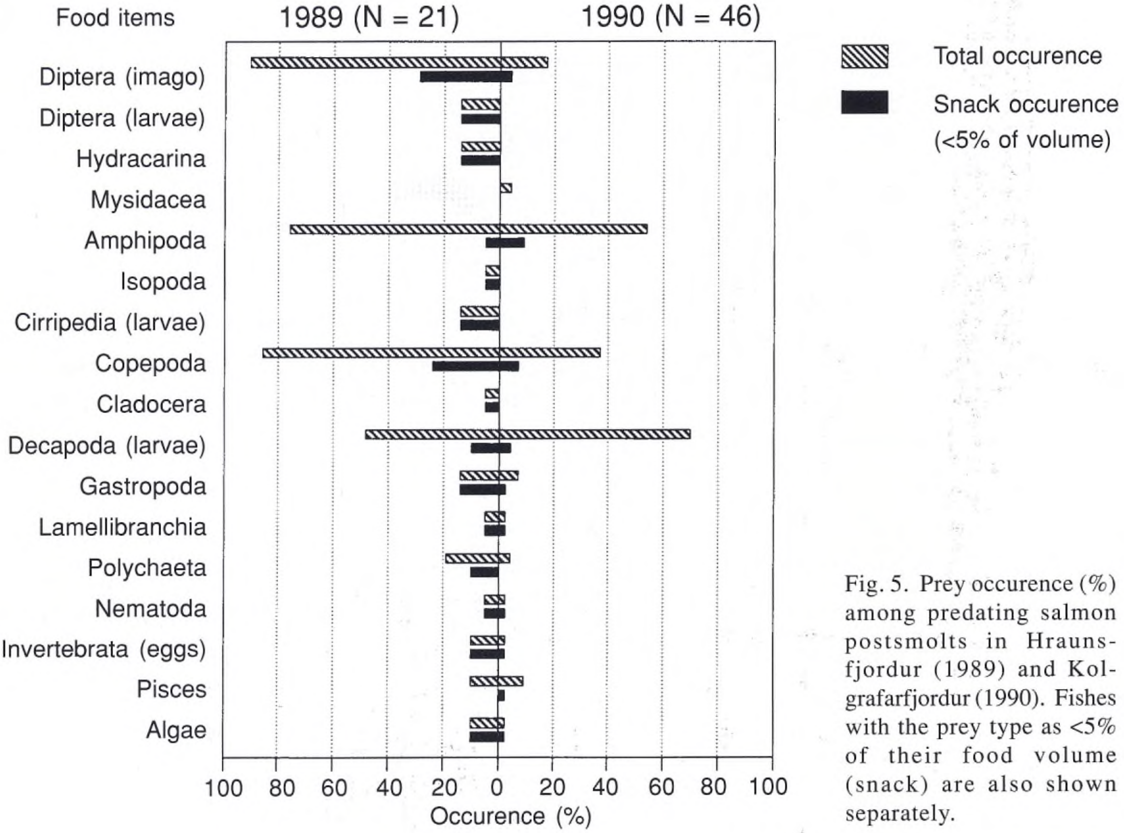

Fig. 5. Prey occurence (%) among predating salmon postsmolts in Hraunsfjordur (1989) and Kolgrafarfjordur (1990). Fishes with the prey type as <5% of their food volume (snack) are also shown separately.

cate that the rearing phase should not limit their performance after release into the wild (Stradmeyer and Thorpe 1987b, Paszkowski and Olla 1985). Field investigations on the other hand on feeding of hatchery reared salmonids released into freshwater (Johnsen and Ugeldal 1988, Marcotte and Browman 1986, for review) and into sea water (Fjallstein 1987), have shown that the adaptation to the environment including learning to feed successfully on living prey can delay the forage efficiency for considerable time, most commonly from a few days up to a couple of weeks but instances up to two months are known.

Prey and prey importance

Many taxa contributed to the diet of the postsmolts (Fig. 5) but when the mean food composition is compared between sampling stations and years (areas), it shows that few taxa constituted the bulk of the diet in all instances (Fig. 6).

In Hraunsfjordur 1989, the most important prey types in all stations, in relation to volume, numbers and occurrence were copepods, amphipods and terrestrial originated flies (imago stage) of the order diptera (Fig. 4, 5, 6), both among non-maturing and maturing fish. In addition to this, sticklebacks (in 28-32 cm long smolts) and megalopa larvae of the order decapoda (*Hyas* spp. and *Pagurus bernhardus*) were found to be of some importance, both in terms of occurence and volume estimates.

The most important prey types of postsmolts from the inner area of Kolgrafarfjordur (1990) were the same as those found in post smolts caught in the outer area of Kolgrafarfjordur (station 10 and 11). This fact, together with the low number of fish caught at each of the stations, led to pooling of data for the whole study area

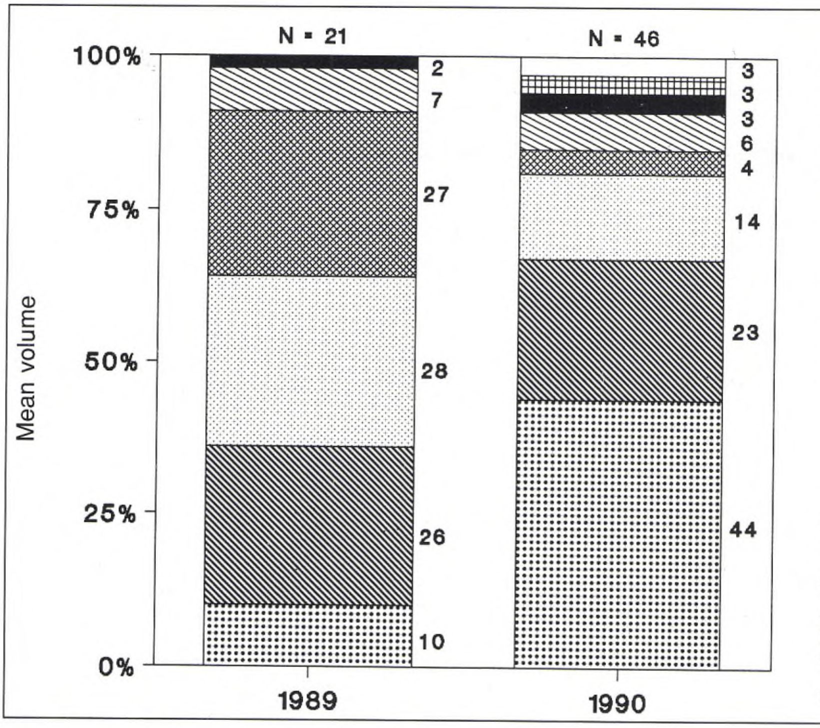

Fig. 6. The mean volume of prey (%) in predating salmon postsmolts in Hraunsfjordur (1989) and Kolgrafarfjordur (1990). Total number of feeding fishes is given (N).

in 1990. The most important food items in Kolgrafarfjordur were megalopa larvae of *Hyas* spp. and *Pagurus bernhardus* crabs, amphipods and copepods (Fig. 4, 5 and 6). Other important prey types were larvaes (0+) of sand eels (Ammodytidae), insects (Diptera), gastropods and polychaets.

In general the crustaceans were the most important food of postsmolts in these coastal waters in West Iceland. The class Malacostraca was the main bulk of crustacea in the food; mainly composed of the order Decapoda and of the order Amhipoda, but animals from the orders Mysidacea and Isopoda were also eaten. The mysids eaten in Kolgrafarfjordur, did not belong to the semibenthic species known from Hraunsfjordur (Sigurðsson 1974, Jónsson 1974) and were probably pelagic species. Isopods were eaten in Hraunsfjordur in 1989, but like so many other littoral animals they were not found in postsmolts in Kolgrafarfjordur in 1990 (Fig. 6). The smallest crustacean prey were of the class cirripedia, eggs of crustacea, suborder cladocera and of the order cyclopoida. Cyclopoids were common as prey in Hraunsfjordur in 1989 and were also found the following year in migrating postsmolts in Kolgrafarfjordur. In Kolgrafarfjordur the larger copepods of the order calanoida appeared in the food.

An ectoparasite of the order caligoida was observed on one postsmolt in Kolgrafarfjordur. Diet related parasites of the class cestoidea were found in three postsmolts as adults together with oncosphere and larvae that also were found in intermediate hosts (Amphipoda).

Individual feeding in Hraunsfjordur was characterized (in 95% of instances) of a mixture of 2-8 prey types. In Kolgrafarfjordur, the postsmolts most often (65%) had eaten 2-5 prey types. Those fishes that contained only one type of prey, generally had eaten larvae of decapods. When the food composition was examined in relation to placement of prey types in the stomachs and as subsamples from the total alimentary canal, mixed food was observed but it was also common to see a continuous bulk of one prey type followed by a bulk of another prey. The opportunistic forage of the postsmolts reflects vital quality of fishes that are feeding *en route* (McKeown 1984), ranging here from eating many prey types from a multi species patch, to be eating the same prey for variable time due to patchiness and/or selective foraging behaviour.

Optimum PFR was 0.4-3.6 according to the main prey types; Cyclopoids, decapods, amphipods and dipteras (Table 4). The main prey types except for amphipods were very uniform in size (Table 4). The observed highly effective predation on the main prey types as shown by their occurrence in intensively feeding fish (Table 4), emphasize that the smolt utilize these prey sizes easily. Notably, high occurrence of postsmolts preying heavily on prey of width lower than 0.8% of their fork lenght showed that the postsmolts can utilize very small prey proportional to their size. Observed optimum PFR is similar to the most common PFR (0.5 -1.0%) among feeding grilse and multi sea winter salmon in the Norwegian Sea (Anon. 1983). Observed optimal PFR is also largely corresponding to the optimal PFR of reared Atlantic salmon juveniles in freshwater, from first feeding to approximately 20 cm in lenght wich have been shown to be; 2.5% (Wankowski 1979), 2.2-2.6% (Wankowski and Thorpe 1979) and 1.9% (Stradmeyer and Thorpe 1987a).

Prey habitat

When prey types were ranked according to their habitat preference, the postsmolts were in both years feeding heavily on pelagic prey (71-72%); mainly zooplankton but winged flies of the family nematocera were also a considerable part of the food in Hraunsfjordur in 1989 (Fig. 7). These dipteras (imago stage) had drifted with wind and freshwater to Hraunsfjordur and Kolgrafarfjordur were they are likely to be caught mostly from the neuston layer. Nektonic food items were only found as mature sticklebacks (50-60 mm long) in Hraunsfjordur. Other fish prey were planktonic sand eel larvae (25-35 mm long) in Kolgrafarfjordur. The distribution of this age group of sandeels in Icelandic waters (Einarsson 1951) together with information on the feeding of nektonic 0+ sandeels in Scottish fjord (Morgan

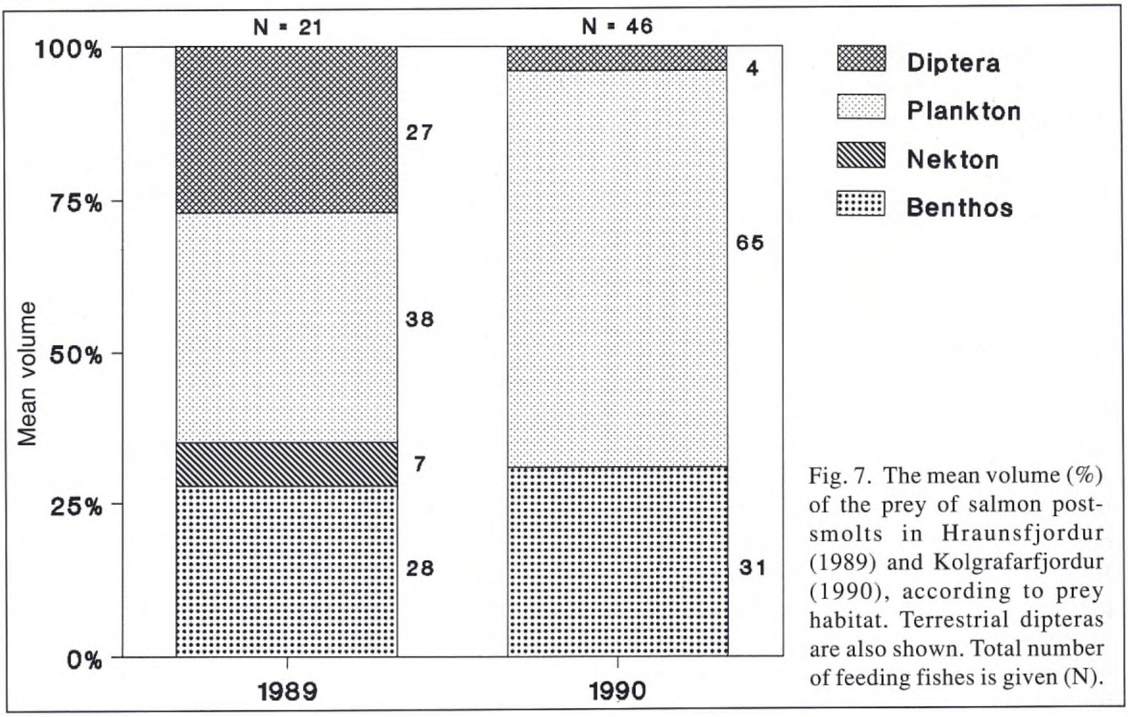

Fig. 7. The mean volume (%) of the prey of salmon postsmolts in Hraunsfjordur (1989) and Kolgrafarfjordur (1990), according to prey habitat. Terrestrial dipteras are also shown. Total number of feeding fishes is given (N).

et al. 1986), suggest that observed occurrence of sand eels as food of postsmolts may continue when the sand eels switch from the plankton to the nektonic phase. Benthic animals were also important as food for the postsmolts, manly the substrate - associated amphipods which mainly consisted of gammarids (*Gammarus* spp.). The gammarids have the least connection to the bottom of the benthic prey found, because of their relatively high swimming ability. The lower occurence of prey of the classes; Gastropoda, Lamellibranchia and Polychaeta showed that the smolts were rather seldom eating prey types that are usually burrowing in the sediments or sessile, but this prey types have been shown to be dominating the littoral fauna in Hraunsfjordur both by number and weight (Sigurðsson 1974, Jónsson 1974). The identified polychaets were *Neires* spp, and the mussel (*Mytilus edulis*) was the most common species of Lamellibranchia. Predation on this prey types is not suprising when considering that Atlantic salmon parr have been shown to eat from the substrate in 25% of instances in the river environment (Stradmeyer and Thorpe 1987b) and that these smolts were migrating over shallow areas at the beginning of their feeding migration. Benthic prey types were eaten simultaneously with pelagic prey types, underlining the plasticity of the visually feeding postsmolts.

Concluding remarks

Postsmolts migrating from Hraunsfjordur preyed mainly on crustaceans that have also been observed as early food of postsmolts in the Norwegians fjord and also in the Gulf of St. Lawrence (Dutil and Coutu 1988, Hvidsten et al. 1993). The feeding on crustaceans is supplemental to predation on fishes if they are available (Morgan et al. 1986, Dutil and Coutu 1988). In the Baltic, early food of postsmolts consists mainly of aerial insects of terrestrial origin (Lindroth 1961, Thurow 1968, Jutila and Toivonen 1985, Anon. 1983). Baltic postsmolts are also piscivorous especially later in the ocean migration when they reach length of 25 cm that seems to be their threshold size for active piscivorous feeding (Thurow 1968).

High forage efficiency of postsmolts in the beginning of their feeding migration is expected to be of vital necessity to reduce mortality, especially considering that increased size reduces the risk of being eaten. The observed low forage efficiency of postsmolts migrating through Kolgrafarfjordur in the beginning of their feeding migration is not expected to have any perceptible effects on their survival because of the short time interval (few hours - few days).

The biology of the Atlantic salmon postsmolt stage has only partly been explained with respect to the first step in their migration towards the open Atlantic both in this study and by Hvidsten et al. (1992, 1993) and Morgan et al. (1986). The later steps of this migration have to be followed to get information about the importance of various feeding migration routes. It is a long term project to study the feeding activity of postsmolts farther out in the sea. This is a challenge that calls for reaction soon, if we want in the near future to be able to link the main factors of postsmolts mortality to fluctating recaptures of the Atlantic salmon populations.

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Growth of Anadromous and Resident Brown Trout with Different Life Histories in a Danish Lowland Stream

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Abstract

The sea trout population in the Simested River were studied during 8 years by electrofishing the breeding stock of the river annually. Growth and life history were estimated from scale readings and external measurements on these fish. The results were compared to less intensive studies from other Limfjord rivers. The growth rate in freshwater, the premature growth rate in sea water, and the growth rate of mature trout could be modelled using a simple model using constant length increments over time. Calibration was made separately for these three periods of life, but common values for freshwater growth could be used for all life histories investigated including resident brown trout, and common values could also be used considering sea-growth of all anadromous fish. For the population from The Simested River the calibration of the model yielded a growth rate in fresh water of 100 mm per year. For maiden sea trout a growth rate of 200 mm per year was found for all investigated populations. Mature fish have a decreased growth rate equivalent to a net loss from spawning related activities totalling 33% of the energy content, for all observed life stories. It could be deduced that the large variation of individual size observed within spawning Danish sea trout populations most likely originates from differences in life histories rather than from differences in growth rate.

Introduction

The Danish release program for native brown trout (*Salmo trutta* L.) was instigated in the beginning of this century (Larsen 1944). The aim of the program has been to provide a normal population of fishable trout despite problems with pollution and channelization of rivers (Hermansen et al. 1982, Iversen et al. 1983). Today the program virtually covers all streams in the country, and provides detailed instructions on the amount of trout at different life stages to be released (Rasmussen 1984). At present this release programme is being evaluated by several projects which consider different aspects of the physiology and ecology of trout in lowland streams.

The following report considers growth in relation to different life cycle stages of both stationary and anadromous trout populations of the Simested River, northern Jutland. It includes the development and application of a linear growth model.

Models for growth of salmonid fishes have been proposed by a wide variety of authors throughout this century (see From and Rasmussen 1984). The most elaborate ones are derivations of the original Pütter concept (Pütter 1920), also used by von Berthalanffy (Berthalanffy 1957) and Beverton-Holt (Beverton and Holt 1957), where growth is considered to be the result of a balance between anabolic and catabolic processes in the organism. The From-Rasmussen model (From and Rasmussen 1984) represents a specific elaborate version of this concept, implemented with rainbow trout *(Oncorhynchus mykiss)*. Incorporation of this type of growth model in population dynamics simulations are often difficult due to lack of sufficient environmental data.

Because it is desirable to be able to make comparisons between growth of different populations and different releases, it is tempting to try to use a simple linear growth model, which describes the growth as addition of a constant amount of length over time. This kind of description makes comparison between growth of different sized fish straightforward, because the size dependence of growth are eliminated by the dimension shift from weight to length.

Inclusion of different growth rates for the presmolt, the postsmolt and the mature part of the life cycle, as well as differentiation between growth of the stationary and the anadromous subpopulations needs specific calibration in both types of model mentioned, and although the numerical difficulties involved are very different, there are no basic differences between the two types of models in this context.

The present account attempts to show whether a simple linear growth model can estimate the measured growth data with adequate accuracy after inclusion of simple adjustments due to life history differences.

Materials and methods

The major part of this work took place in a midsized Danish stream called The Simested River situated in northern Jutland. The Simested River emties into The Limfjord (Fig. 1). The river drains approximately 200 km^2 of land and has a medium flow of about 2 m^3/s at the estuary. Although pollution and chanelization of the Simested River have resulted in a decline in population size, it still retains a fair population of trout consisting of approximately 350 annual spawners of sea trout, and several thousand mature brown trout. The population of anadromous trout has diminished because damming has prevented the use of a major part of the potential breeding area (Fig. 1).

The fish population of the river are characterized by unusually large average sizes, representing a variety of different life histories. This occurrence permits investigation of growth on almost all life histories of trout. The trout, being a repeating spawner also provides extraordinary possibilities for investigating post-spawning growth in salmonids.

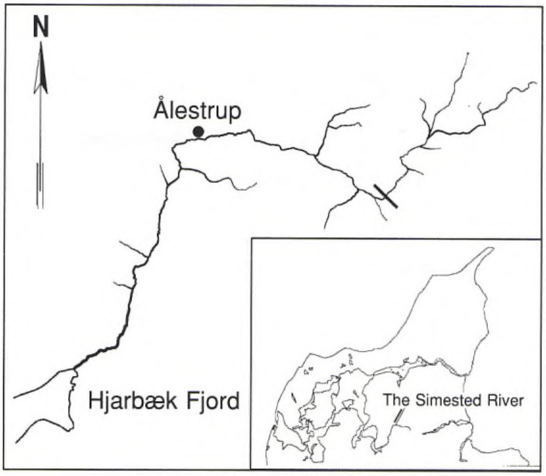


Fig. 1. Map showing the couse of the Simested River. The bar across the rivers marks an impassable obstacle for migrating fish.

Most data described in this investigation apertain to measurements of length, weight, age, and spawning type during regular annual electrofishing of the stream during the period 1982 to 1989. Electrofishing was undertaken using two sets of DC equipment placed in the same boat. The stream was fished downstream from the inpassable dam at Hannerup (Fig. 1) to its estuary. Some minor stretches were avoided due to lack of permission from the owners.

The efficiency of electrofishing was calculated using the capture mark recapture method (Krebs 1978, Manly 1970). The stream was fished twice with an interval of one week. The fish caught on the first trip were marked by a cut in the adipose fin. The efficiency of the elctrofishing on this first trip was given by the proportion of marked fish recaptured on the second trip; migration being eliminated by the impassable dam and the sea. The efficiencies varied little from year to year, always being between 20 and 30%.

Length was measured as total length. Fork length was measured for two years but gave no methodological improvements. Weight was

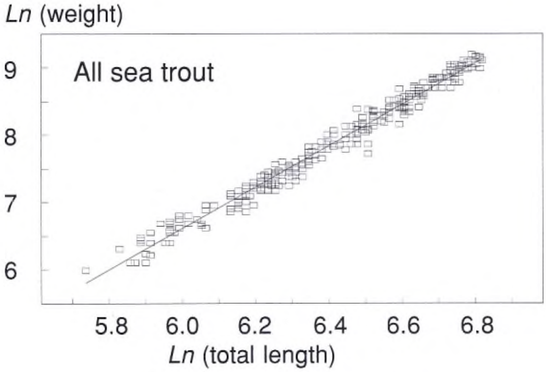


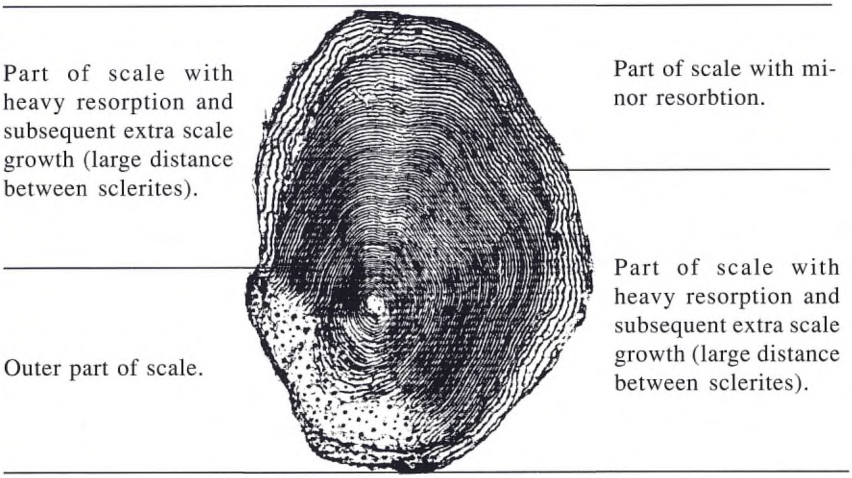
Fig. 2. Length - weight relation for sea trout in the Simested River. The relation can be expressed numerically as: $W=L^{3.07} \cdot 135084^{-1}$, where W is the weight in g and L is the length in mm.

measured during the first four years. After that period the length-weight relation was used ($W=L^{3.07} \cdot 135084^{-1}$; length in mm, weight in g). Fig. 2 shows this length-weight relation for all sea trout measured during the study period.

A sample of more than ten scales were taken from immediately below the dorsal fin from each animal sampled. These scales were examined and life history events, such as overwintering and spawning were deduced from the sample as a whole. Length measurements were only made on one selected scale from each fish.

The freshwater period in the scale was represented by dense annuli forming a closed circle. In contrast the saltwater period was represented by widely spaced annuli only showing in the protected inner part of the scale (Fig. 3). In both the freshwater and the saltwater part of the scale, winter periods could be deduced by the reduction in the distance between the annuli, while summer periods resulted in wider spacing. Spawning resulted in resorption of scale material from the scale edge which was most clearly seen at the point where the outer and inner part of the scale met (Fig. 3). This resorption could either be seen directly on the edge of scales from spawning fishes or indirectly on the subsequent repair of scales from postspawners (Fig. 3).

Trout scales are generally more difficult to read than those of salmon partly because of the more elaborate life story and partly because winters do not always show as clearly as in salmon. Maiden sea trout that overwinter in rivers make "false" spawning marks, making differentiation between group 0 sea-winter spawners and group 1 sea-winter spawners difficult to establish. Sea trout that do not spawn every year following first spawning also gave problems because their first spawning mark was often hard to detect. Consequently such fish are easily confused with regular three or four group sea-winter fish. This phenomenon is undoubtly rare with only 22 sus-



Part of scale with heavy resorption and subsequent extra scale growth (large distance between sclerites).

Outer part of scale.

Part of scale with minor resorbtion.

Part of scale with heavy resorption and subsequent extra scale growth (large distance between sclerites).

Fig. 3. Scale from 880 mm sea trout with repeated spawning, showing the the difference between the inner and outer part of the scale, and the repairment of spawning resorption along the edge of the scale.

pected specimens in the present material. These specimens were discarded from the analysis.

The length of trout at different life stages was measured on scales using a start length at scale formation of 2.7 cm, found as Y-intercept of a regression between scale radius and fish length in this population. Apart from this starting length, the rest of the fish length was considered proportional to scale radius. Care was taken to use a measuring radius from each scale which has been touched as little as possible by scale resorption (Fig. 3).

The linear growth model used postulates that trout add a fixed length every month, one value for freshwater and another for saltwater. Two further complications are introduced into the model. First the growth of the fish is set to 0 during the winter period, where the sea trout are trapped in cold coastal waters (average around 0 °C). Second, an extra energy cost of breeding is introduced. This cost consists of loss of energy during the prespawning starvation period, actual energy loss with spawning products, minus compensative growth during the post-spawning period. Numerically this results in delayed spring growth.

The model was calibrated to the specific data using the pooled averages of length increments on data from the freshwater period (for presmolts and stationary trout) and the premature saltwater period. No distinction between spawning types were made in this context. For mature trout a common net cost of spawning was introduced and the same value fitted to the data for all five spawning types (stationary trout plus four types of sea trout). The calibration thus resulted in three values common to all trout of the population: Growth rate in fresh water (mm per month), growth rate in sea water (mm per month) and net cost of spawning (percent weight per spawning). To improve the fit of the model to the actual data, different times for spawning migrations, and thereby growth termination, were introduced for each spawning type. This was allowed only for the first spawning migration, while a common value for repeating spawners was used.

Results

The life cycle of the brown trout in the Simested River is shown in Fig. 4. Spawning takes place from mid-November, at which time the first kelts are taken by electrofishing. Spawning commences in December, where the proportion of kelts to total mature fish increases to 80%. The fry emerge from the gravel of riffles during early spring after the usual temperature dependent developemental period (Frost and Brown 1967). Following emergence the fish spend one or two years in the stream as fry and parr (Table 1), at the end of which their length ranges from 100 mm to 150 mm or 170 mm to 240 mm respectively (Table 1). Almost one third of the fish smoltify during the first year, while the majority of the remainder smoltify after two years (Table 1). Most fish leave the river in April as has been reported from other Danish rivers (Rasmussen 1986). A minority of individuals stay in the stream for the rest of their lives.

The anadromous forms spend one to four "summers" at sea before returning to spawn. Anadromous fish are classified in this paper according to the numbers of winters spent at sea before first spawning, irrespective of their later spawnings. The 0-sea-winter fish is termed "spawning type I" fish, the 1-sea-winter fish is

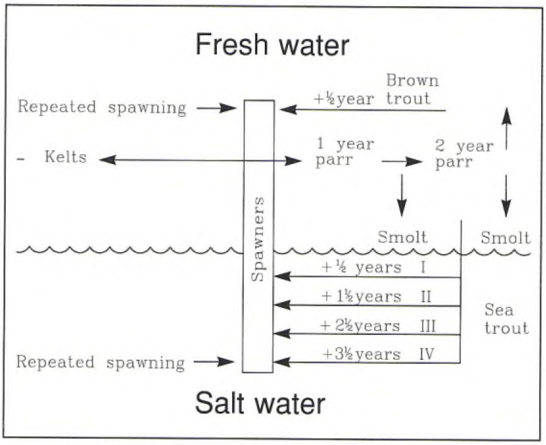


Fig. 4. Life cycles of the different breeding types of brown trout and sea trout in the Simested River.

Table 1. Size of smolt and parr in the Simested River during the first three years of trout life. The data are related to spawning types. In the upper part of the table the smoltificating fish are marked with grey shadows while parr are with white background.

	No. smolts	Distribution (%)	1 year	2 year	3 year
TypeI 1-year smolt	32	14	150		
TypeI 2-year smolt	192	81	119	228	
TypeI 3-year smolt	13	5	121	221	323
TypeII 1-year-smolt	79	38	146		
TypeII 2-year smolt	120	58	114	218	
TypeII 3-year smolt	9	4	127	227	322
TypeIII 1-year smolt	42	25	148		
TypeIII 2-year smolt	124	73	118	227	
TypeIII 3-year smolt	4	2	111	195	292
TypeIV 1-year smolt	13	25	159		
TypeIV 2-year smolt	40	75	112	212	
TypeIV 3-year smolt	0				▨
Smolt length in mm			148	223	318
S.D., (%)			13.5	14.5	18.1
S.D.			20.1	31.9	57.5
Min. lenght			101	137	238
Max. length			199	345	438
No. smolts of each age group			164	476	26

"spawning type II" fish, the 2-sea-winters fish is "spawning type III" fish, and the 3-sea-winter fish is "spawning type IV" fish. Generally the spawning type I fish migrate to the river during late fall, while spawning type IV fish migrate during late spring (personal observations during electrofishing in summer and winter). This occurrence thus makes classification on the basis of summers spent at sea misleading. In the period following spawning in November-December the kelts leave the river. In the middle of April, at the same time as the smolts migrate downstream, the last kelts go to sea (Jensen 1988, Kristiansen 1991). The kelts commence feeding in fresh water (personal observation), and normally rapidly build up a healthy condition during the following period at sea. Such fish are usually ready to spawn after the summer, and will return to the stream during autumn. However some fish (judged on the few scales with signs of sea winters between repeated spawnings) undoubtly require an extra year for recovery and thus over-winter at sea before they spawn again the following year. Repeat spawners make up approximately 25% of the total number of spawners in the river.

The premature growth of all seatrouts is shown in Fig. 5. No significant differences could be detected between the three sets of values from spawning type II and III as well as between the three sets of values from spawning type IV. Pooling the above sets of values in the two groups mentioned yielded a significant difference between the pooled data from type II and III and the pooled data from type IV. Spawning type IV fish grew significantly slower than the others.

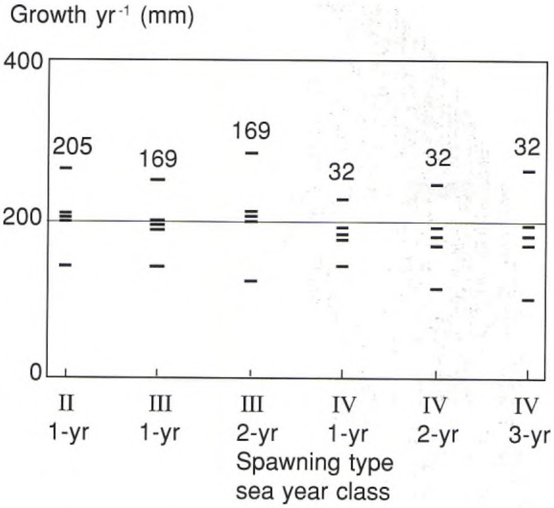


Fig. 5. Premature growth in sea of spawning types II, III, and IV (type I cannot be measured through a full season). The crosses mark the mean values. The inner pair of small horizontal bars mark the standard error of the mean, and the outer pair marks the standard deviation. Above each set of measurements the number of observation are indicated.

However the differences found were too small to justify further elaboration of the model, and a common value of 200 mm per year used. Including the stagnation period in winter (4 month) this implies a growth of 25 mm per month during the growth season.

The stationary trout grew approximately 100 mm per year for three full years before spawning (Table 1). Including the stagnation period in winter (4 month) this implies a growth of 12.5mm per month during the growth season. The sea trout grew at the same rate as the stationary trout during the freshwater part of their life, with the exception of one year smolts of anadromous spawners, which grew at an elevated rate during their single year in freshwater (Table 1). This elevated growth rate of one year smolts could also be detected in the sea (Table 2).

The observable (Figs. 8-11 and Table 2) lowering of growth during the year of first spawning has been calibrated using different dates of river return for each spawning group. First spawning migration was calibrated to 1 December for stationary trout, 14 October for type I, 1 September for type II, 14 July for type III, and 1 June for type IV sea trout.

Postmature growth of all seatrouts are evaluated in Fig. 6, where all the observed values of yearly postmature length increments were plotted against length of kelts. No obvious difference between males and females were observed, and the results from both sexes were pooled. The pooled data are fitted by linear regression. The model predictions for postmature growth, using a common net growth cost of 33%, yields a linear relationship in the same kind of plot. The

Table 2. Size at first spawning and growth for maiden sea trout from the Simested River including standard deviations of the numbers. N gives the number of observations, L is length at spawning, G is growth, and y is growth per year. The trout are related to spawning type and smoltification type. The average values are averages for each of the four sea trout spawning types. Total values includes 1, 2, and 3 year old smolt.

	Total				Smolt age 1				Smolt age 2			
	N	L mm	G mm	y mm	N	L mm	G mm	y mm	N	L mm	G mm	y mm
Resident trout	395	299±58	297±61	90								
Type I	239	391±49	169±48	169	32	357±36	209±36	209	192	389±40	163±45	163
Type II	209	528±70	331±58	166	79	497±55	350±49	175	120	538±64	320±61	160
Type III	170	705±75	499±84	166	42	700±59	552±57	184	124	706±81	482±84	161
Type IV	53	804±73	605±72	151	13	783±64	624±58	156	40	811±74	599±74	150
Average				166				188				160

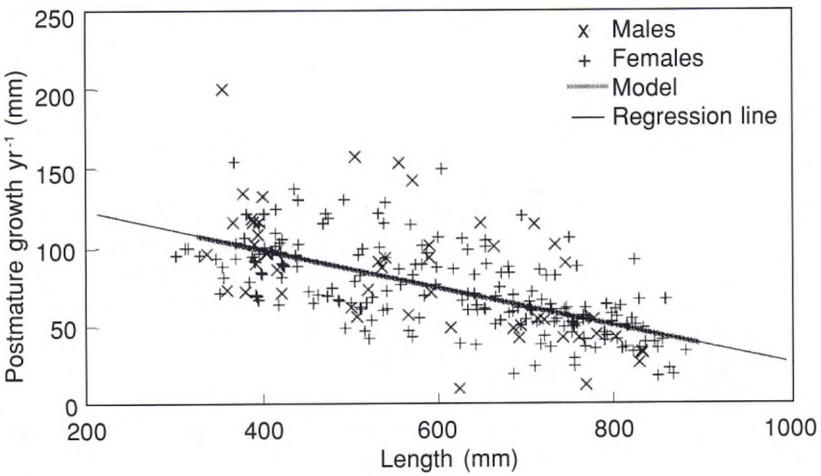


Fig. 6. Post smolt length increments for different sized spawners of all sea trout groups. Males and females are indicated separately. The "model" line indicates the result of a calibration with 33% costs of spawning. The regression line is based on both females and males.

model predictions including these values are shown together with the regression line on Fig. 6. For the purpose of estimating growth with reasonable accurancy for trout in the Simested River the above mentioned net cost of 33% was used.

For all repeating spawners except resident brown trout migration time (or growth stop) used has been 14 September. For the resident brown trout 14 November has been used.

The final numerical description of length according to the linear model are:

$$L_t = L_i + (\Delta L_{mf} \cdot M_{gf}) + (\Delta L_{ms} \cdot M_{gs}) - \sum_{i=1}^{n} L_{sci}$$

Where:

L_i	is initial length
ΔL_{mf}	is growth in length per growing month in fresh water
M_{gs}	is the number of growing months in sea water (i.e. minus winter months or months spent in fresh water during spawning)
L_{sci}	is the length equivalent of the common energy costs from spawning activities for the ith spawning.

L_{sci} is calculated converting the spawning length to weight using the length-weight relation, subtracting the common energy cost (here 33%), and converting back to length again. This conversion is size dependent and thus yields a different length value for different sizes.

Including the calibration values this gives for the four spawning types of sea trout:

$$L_t = 27 + (12.5 \cdot M_{gf}) + (25 \cdot M_{gs}) - \sum_{i=1}^{n} L_{33i}$$

Figs. 7-11 show actual measured sizes during the different life stages of the five different spawning types studied. The freshwater period is only shown for the stationary trout, but data for the remaining types can be found in Table 2. In all the figures mentioned model estimates are shown using the calibration parameters found. The actual measured data does not differ considerably from the model value in any set of mesurements in type I, II, and III fish, but premature growth of spawning type IV are overestimated by the model.

Fig. 12 shows the premature sea growth of carlin-tagged trout released in three Limfjord rivers as smolts, and recaptured at sea by various fisheries. The model estimate of premature sea growth is shown as a line. The model estimate depicted uses the same growth rate estimate as used for the Simested trout population.

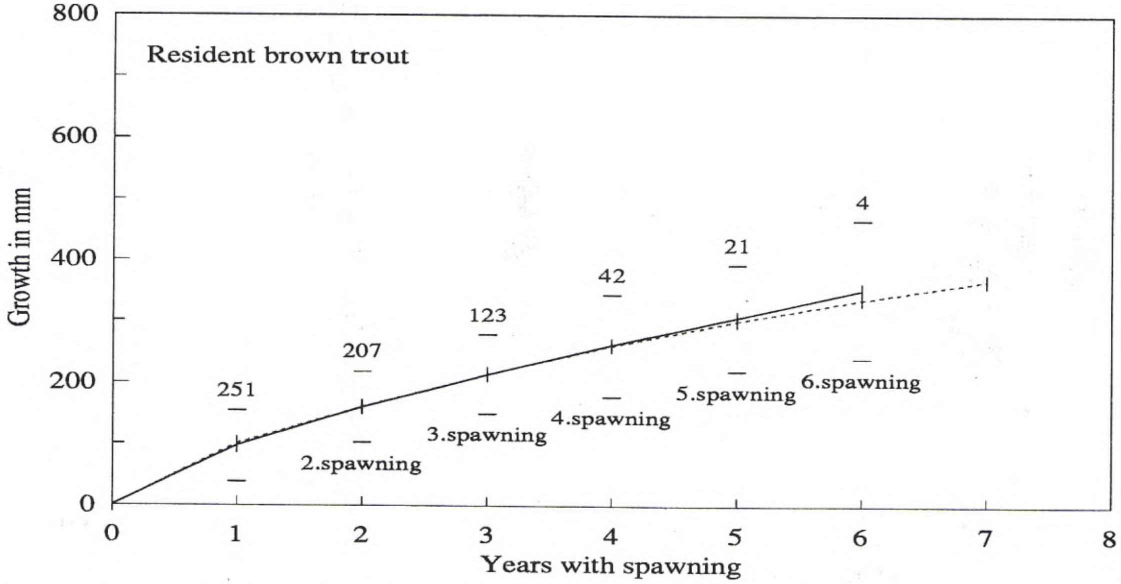


Fig. 7. Growth of resident brown trout in the Simested River. The full line connects the average values for the datasets. The stipled line shows the values calculated using the linear growth model. The sets of short horizontal lines delimits the standard deviation of the length data for each age group. Over every set of data the number of observations are indicated.

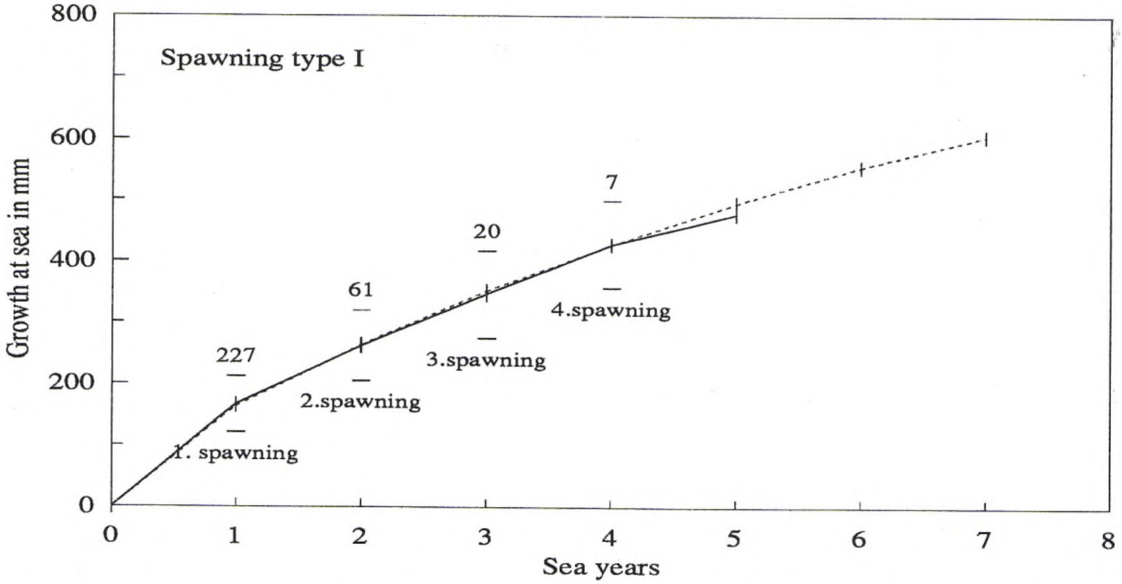


Fig. 8. Growth of sea trout of spawning type I in the Simested River. The full line connects the average values for the datasets. The stipled line shows the values calculated using the linear growth model. The sets of short horizontal lines delimits the standard deviation of the length data for each age group. Over every set of data the number of observations are indicated.

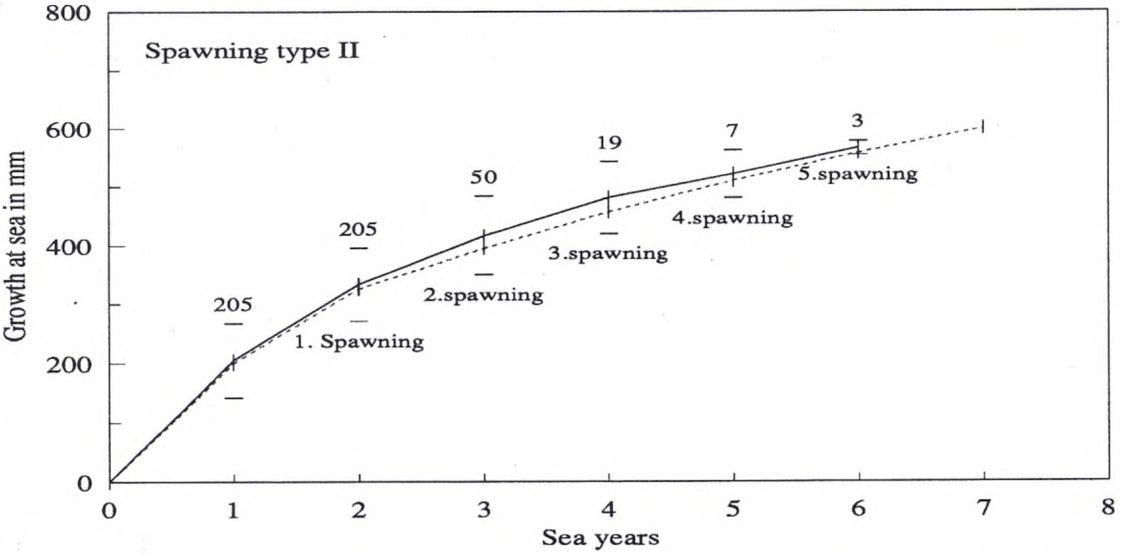


Fig. 9. Growth of sea trout of spawning type II in the Simested River. The full line connects the average values for the datasets. The stipled line shows the values calculated using the linear growth model. The sets of short horizontal lines delimits the standard deviation of the length data for each age group. Over every set of data the number of observations are indicated.

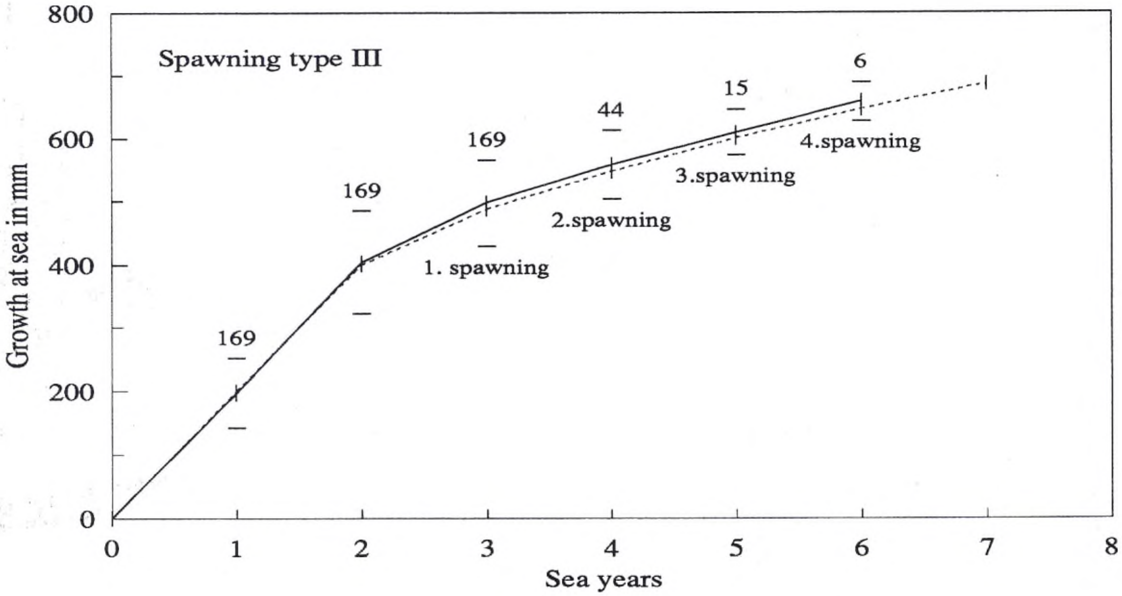


Fig. 10. Growth of sea trout of spawning type III in the Simested River. The full line connects the average values for the datasets. The stipled line shows the values calculated using the linear growth model. The sets of short horizontal lines delimits the standard deviation of the length data for each age group. Over every set of data the number of observations are indicated.

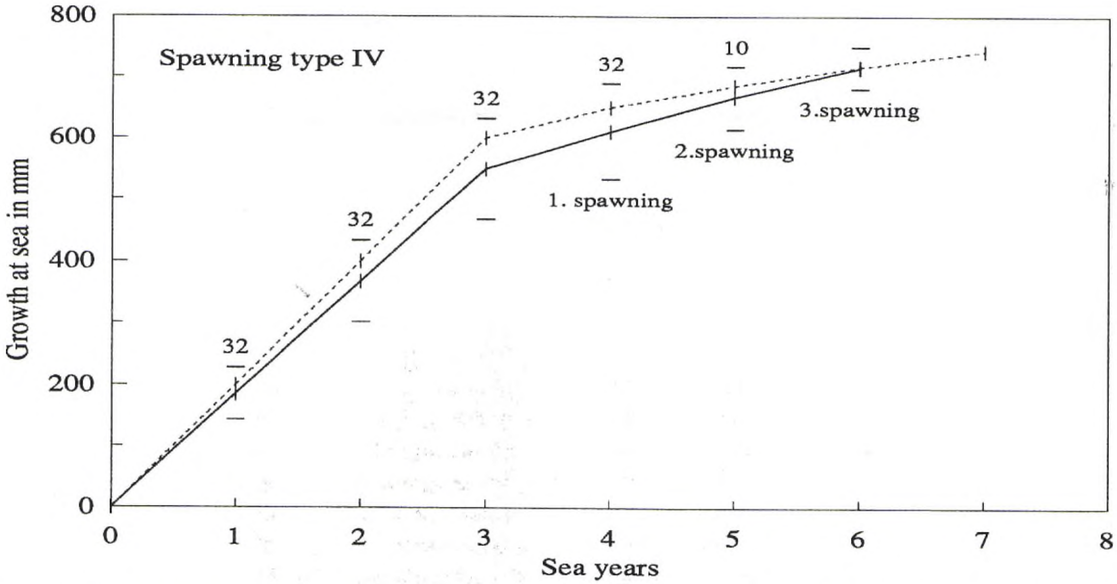


Fig. 11. Growth of sea trout of spawning type IV in the Simested River. The full line connects the average values for the datasets. The stipled line shows the values calculated using the linear growth model. The sets of short horizontal lines delimits the standard deviation of the length data for each age group. Over every set of data the number of observations are indicated.

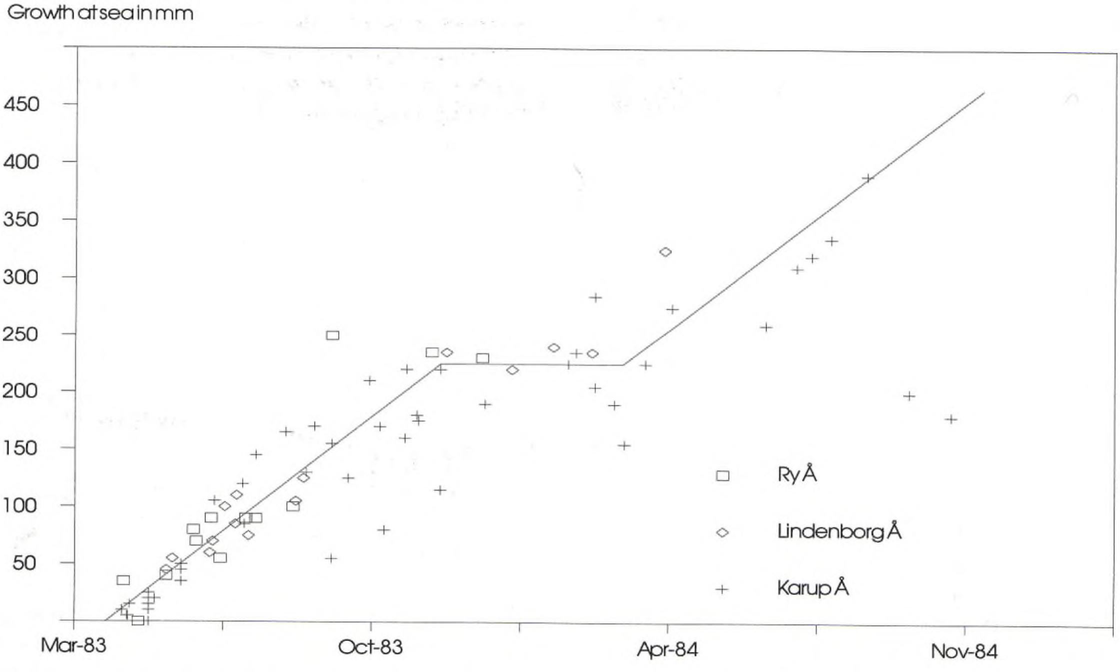


Fig. 12. Comparison of the linear model and data obtained from carlin tagged fish released in the Limfjord area.

Discussion

Scale readings or other measurements of meristic characters (i.e. otoliths or fin-rays) (Beall and Dovaine 1978, Hubert et al. 1987, Shirvell 1981) are the only methods of measuring growth of fish with a known life history with the exception of experimental studies where an entire population may be tagged, counted, and measured each year. The advantage of the method applied herein accordingly lies in the possibility of measuring growth of natural populations retrospectively.

Scale readings as a basis for growth measurements are normally considered a fairly inaccurate method , although considerable evidence for the validity and limitation of the method has been presented (Davies and Sloane 1986, Flain and Glova 1988, Newmann and Fleisberg 1987). This has especially been the case when dealing with repeating spawners, because resorption at the scale edges makes the observed halt in growth appear nearer the center of the scale than it otherwise would be. Using the proportional method (Frost and Brown 1967, Kipling 1962), as in this paper, thus leads to a slight underestimate of length at first spawning. Looking carefully for scales with a minimum of resorption and using the length radius of the scale for measurements minimizes this error.

If the resorptions made are of any significance addition of these errors could be of considerable importance in repeat spawners. If scale resorptions are additive and the original size is not restored immediately following spawning, the scale length - fish length ratio will decrease with repeated spawnings for the same fish. The average scale length - fish length ratio for the whole population would accordingly also decrease with number of spawnings. There are no indications from the present study of such a decrease. Accordingly the simple assumption is made (Fig. 3), that the fish reestablishes its original scale size after spawning, thereby keeping a constant proportion between scale size and fish size for the whole life span.

As fish repair the scales after each spawning, reestablishing original scale size, the scale edge, during subsequent spawnings, will be displaced with the same distance. Growth of mature fish are conclusively slightly overestimated because the distance between spawning rings, being measured correctly, are divided by the total scale radius being diminished by scale resorption. Growth during the freshwater phase is also slightly overestimated because measured scale radii is divided by the total radius being slightly diminished by resorption. The quatitative underestimate of sea-growth for maiden fish of course equals the sum of overestimates from the freshwater phase and from mature fish.

It is possible from the material presented herein to compare growth measurements from scales with the smaller number of actual length measurements for fish of the same spawning class and age group. Indeed this was accomplished without detecting significant differences. It is concluded that this reflects the selection of scales where resorptions were as small as possible.

The major purpose of this paper has been to show how a linear growth model satisfactorily describes the growth of trout and probably also other salmonid fishes. Using this kind of model does not demand any environmental input data. The model merely relies on the growth measurements which can be obtained from scales or direct measurement of tagged fish. On the other hand the model makes it possible to include fairly complicated life history events, because of its basic simplicity.

The simplicity of the growth model is based on three assumptions:

- Growth of all four different spawning classes and both types of smolt is the same in fresh water
- Growth of all four different spawning classes and both types of smolt is the same in sea water before spawning.
- Total costs of spawning are a fixed percentage of the energy content of the fish for all four spawning groups.

Assumption one was evaluated using the results presented in Fig. 7 and Table 1, where all the different measured rates of freshwater growth from the first three years were compared. A clearcut difference between the length of the one-year-old smolts and the parr of the same cohort existed. This difference was not significant for the two-year trout or the three-year trout. The above phenomenon has already been thoroughly described and investigated experimentally for salmon (Thorpe et al. 1982).

Assumption two was evaluated using the results presented in Fig. 5 and Table 2. Also here a considerable difference between growth at sea for the one-year smolts and the two- and three-year smolts was observed. However the growth rates measured for all four spawning types were reasonably uniform (see comparison with model in Figs. 5, 8-11). Including the year of first spawning (as in Table 2) differentiates the four spawning groups, with the group I trout showing much more growth during the spawning year than the group IV fish. It is assumed that this correlated with the different spawning groups appearing in the river and accordingly terminating growth at different times. In the model the growth of the year of first spawning is described separately for each spawning group, and calibrated on the measured data for each of these. Therefore the model describes the growth for each group correctly independantly of the actual reasons for the different growth rates observed.

Assumption three was evaluated using the results in Fig. 6. Growth after maturation can be adequately described using a common value (33%) for all spawning groups for total energy loss during the spawning migration. The linear growth model was not suitable for differentiating between the different spawning related losses and gains (i.e. starvation, egg and sperm production, and compensatory growth), and physiological allocation of the net loss cannot be made. Using a modified version of the From-Rasmussen model (From and Rasmussen 1984) on the present data, it can be deduced that a considerable part of the energy loss would be caused by the starvation period preceeding spawning. This is further evaluated by fact that females and males have the same postmature growth although the females evidently loose much more energy with the eggs than the males with the sperm (Fig. 6).

The relative late spawning run (and growth stop) of repeating spawners (14 September) used in model predictions could be substituted by equivalent compensatory growth at sea during spring, but no evidence from the existing data on brown trout and sea trout seem to justify this complication at present.

The purpose of Figs. 7-11 is first of all to show the fit of the simple growth model to the actual date from the Simested River. The figures thus provides and integrated test of the model, evaluating basically the three assumptions mentioned above.

Fig. 12 shows the fit of the model to measured growth in a release experiment in three rivers using Carlin-tagged smolts recaptured during the following two years. Using the same calibrated values as for the Simested River trout population these growth data show good agreement with the model. The above experiment was conducted in the same sea area and thus presumably at the same feeding grounds as used by the Simested River population, which underlies why the same calibration values of growth could be used. Surely growth of sea trout are very different in other areas of the sea, and although the basic structure and concepts from the linear growth models could be applied to these areas, the constants would naturally have to be recalibrated.

In the Limfjord area the shown uniformity of linear growth rate is striking and it must be concluded that differences in life histories and not growth are responsible for the major part of the size differences observed among spawning populations.

The primary advantage of the linear growth model is the possibility of straightforward comparison of different batches of fishes. The model could be used in physiological experiments in place of percent weight gain because length increment is independant of size. The model might also be useful in population dynamics models, where numerical describtions of life history dependencies are often essential. Comparison of different smolt releases and their subsequent growth rates are a third field of application. For instance where growth at sea from one year and two year smolts have to be compared, smolt length could be subtracted and the sea growth compared directly. This could not be reasonably accomplished with weight over time data because adding absolute weight for a small fish takes longer time than for larger individual (i.e. weight over time curves are not linear). Correlating freshwater and saltwater growth is another straightforward example where the problem lies in making freshwater size and final size stochastically independent. Subtracting freshwater growth in length from final length according to the model makes it possible to correlate growth instead of sizes for both the freshwater period and the saltwater period.

For conclusion it can be argued that there is a need for a more feasible growth concept than the simple percent weight gain method, which must also be less complicated than energetic growth models for purposes where size independence would be an advantage and quantitative description of relations to abiotic parameters not a must.

The application of the present model to the natural population of trout in the Simested River appears to meet such needs, because the growth of the different stages and spawning types are described adequately with the use of a minimal number of calibration parameters.

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Exposure of Sea-Trout Smolt, *Salmo trutta* L., to Avian Predation, Mediated by Capture in Commercial Pound Nets

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Abstract

In the shallow Danish estuary, the Ringkøbing Fjord, an experiment was conducted to show the extent of bird predation on sea-trout smolt, *Salmo trutta* L. The pot (last enclosure) of a commercial pound net was closed by lifting the throat (i.e., the entrance). The pot was stocked with sea-trout smolts and an amount and composition of other fish comparable to a normal catch. The number of survivors was counted daily during the following five-day period. The bird activity at the pound net was observed each morning. Direct observations revealed that the main predator was herring gull, *Larus argentatus*. At a similarly accomplished control experiment, where birds were excluded by using a cover-net, no fish disappeared from the pound net. The mortality of the sea-trout smolts was estimated to 59% when captured, handled and discarded. Total smolt predation rate by gulls during the estuary passage was estimated to 60-100% of the number of smolts entering the estuary.

Keywords: Sea-trout smolt, mortality, gulls, predation, pound net fishery.

Introduction

In Denmark, most streams are routinely stocked with trout, *Salmo trutta* L., according to specific compensatory stocking schemes as described by Rasmussen (1984). When releasing one-year-old smolts in the lower reaches of the streams, the returns of sea-trout are generally good. However, large differences in the return-rates between different watercourses has focused attention on commercial pound net fisheries in the estuaries.

While passing the shallow Danish estuaries, bays, and fjords, many smolts are captured in commercial pound nets. The pound net fishery for eel, *Anguilla anguilla* (L.), typically begins in March-April, simultaneously with the commencement of the smolt migration. Pound nets of a special type, with no fyke nets attached, are from April to June employed to catch immigrating herring, *Clupea harengus* L. Both kinds of pound nets are highly effective for catching smolts.

Releases of sea-trout smolts in the River Skjern Å have for more than a decade failed to produce adequate returns of mature fish. According to investigations in the estuary of the River Skjern Å, the total pound net bycatches were estimated to 50,000-60,000 sea-trout smolts during March-June in 1990 and 1991 (Dieperink 1990, 1993). Most of these fishes were, however, released alive. Except for some scale loss due to the handling, the smolts did not suffer any apparent injury.

The loss of scales might cause osmoregulatory malfunction and/or infectious diseases. Therefore, a simple experiment was set up to assess the survival of smolts as a function of scale-loss. Four degrees of scale-loss were inflicted on a batch of sea-trout smolts. Soon after release in large net pens in the estuary, the fish disappeared. Apparently, they were caught and eaten by the omnipresent sea-gulls. The uninjured null-trial group of smolts was also eaten. This bird-imposed mortality showed potential of being an important factor for the smolt survival. A new experiment was set up to study the sea bird predation on trout smolts, held captive in commercial pound nets.

Materials and methods

Study site

The Ringkøbing Fjord is the estuary of the largest Danish river, the River Skjern Å. A 1-2 km wide tongue of marine deposits separates the 325 km^2 estuary from the North Sea. The estuary is quite shallow with a maximum depth of 4.8 m. Salinity varies between 5-12 ppm.

In the mid 1970s the ecosystem collapsed. The submersed macrophytes disappeared from large areas, and increased resuspension maintained the environmental deterioration. Within a couple of years, the summer Secchi depth decreased from 2.0 m to 0.4 m.

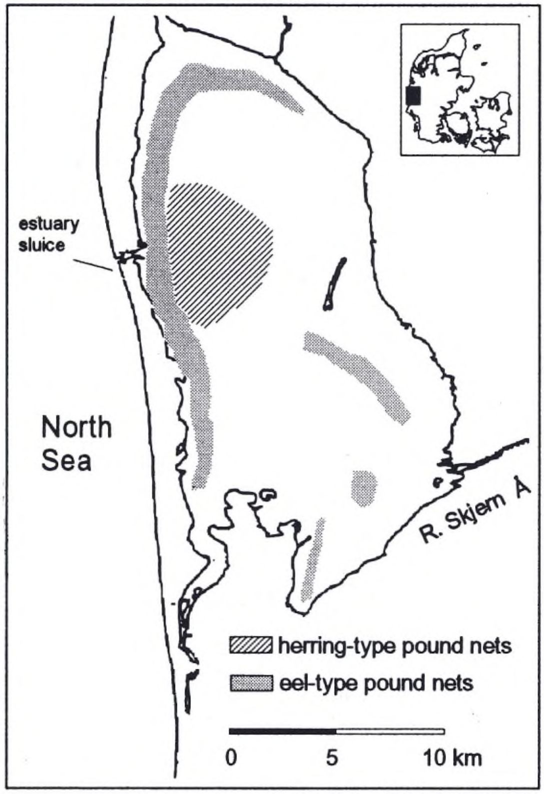

Fig. 1. The River Skjern Å estuary. The concentration of the pound net fishery during April-May is indicated.

In the estuary the commercial fishery is intensive during all seasons. The trout smolts pass the estuary in April and May, during which period eel-type pound netting increases from 20 to 100 nets. Typically, 30 to 50 herring-type pound nets are used throughout this period, mainly in the vicinity of the estuary sluice (Fig. 1). Eel-type pound net fishery is more evenly spread at submerged slopes alongside the margins of the estuary.

Pound net practise

An eel-type pound net was rented from a local fisherman in the central period of smolt migration. The pound net had been actively fishing since the beginning of April. The pound net (Fig. 2), consisted of a 100 m long lead, 200 m from the coast. The pot net, with a circumference of 45 m, consisted of a 16 mm (knot to knot) mesh width twisted nylon net. A fyke net was attached to the bottom of the pot net at a depth of 2 m.

The open pot trial was started on April 26 The throat (entrance to the pot) was lifted out of the water, making the pot net completely closed except from above. All fish were thoroughly removed from the pot net and the fyke net. Thereafter, 98 sea-trout smolts and a mixture of fish species, normally caught in the estuary (Table 1), were released into the pot.

The covered pot trial was started on May 3. Again, the pot was stocked with 98 sea-trout smolts and a mixture of other fish (Table 1). This time, the pot was covered totally with a net to prevent avian predation on the fish. The cover net was actually a separate pot net, that was hauled over and tied to the poles. The cover-net was so large, that the edges reached to the bottom on the outer side of the poles. With a mesh width of 16 mm knot to knot no fish was able to escape through the meshes. The cover-net hung from the poles as a roof over the pot net in at least one meters distance from the water surface. Birds were now effectively excluded from getting to the fish.

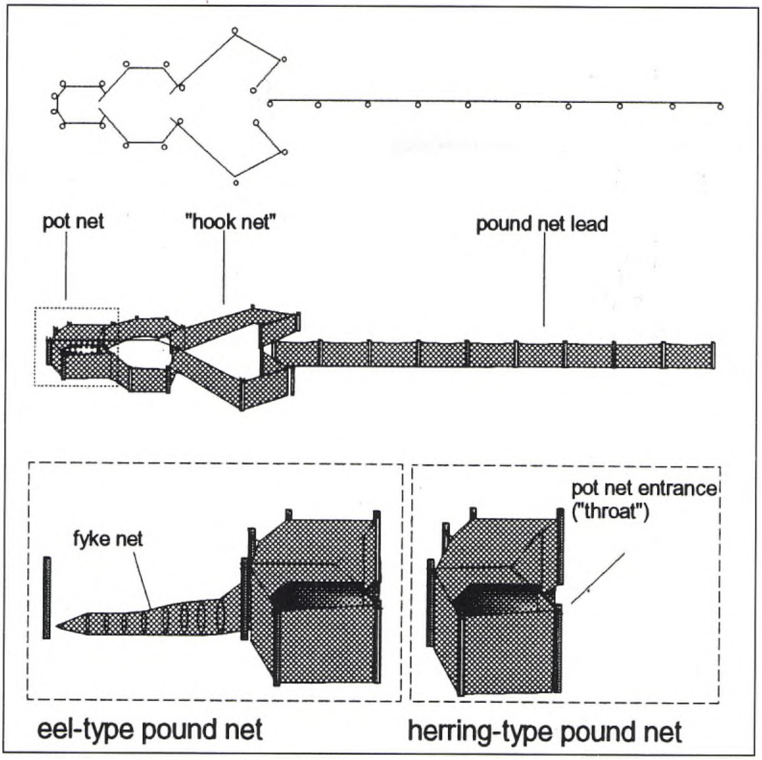

Fig. 2. Schematic diagram of typical commercial pound nets.

Table 1. The fish species, the length groups and the number released into the pound net in the two trials.

Species	Av. length (cm)	Range (cm)	Open trial No. released	Open trial Survivors after 4 d	Open trial No. found dead	Trial with cover net No. released	Trial with cover net Survivors after 4 d	Trial with cover net No. found dead
Sea-trout smolt, *Salmo trutta* L.	18.5	16-22	98	25	0	98	89	9[1]
Eel, *Anguilla anguilla* (L.)	70	60-80	6	5	0	6	5	1
Flounder, *Platichthys flesus* (L.)	20	12-26	25	0	25	19	2	17
Viviparous eelpout, *Zoarces viviparus* (L.)	26	20-30	25	5	20	3	2	1
Whitefish, *Coregonus lavaretus* (L.)	17	15-25	20	17	0	1	1	0
Perch, *Perca fluviatilis* L.	21	13-28	40	40	0	25	23	2
Roach, *Rutilus rutilus* (L.)	22	13-28	25	23	1	25	24	1

[1]) Includes the 4 smolts that were accidentally lost.

In both trials, the fishes were released into the net pot at approximately 23:00 (i.e. 2 hours after sunset), to avoid predation until sunrise. In this way the smolts were given at least five hours to recover from transport, handling and release.

During the following five days the pound net was routinely emptied each morning at 07:00. The catch from the pot net and the fyke net was counted separately, and then again released into the pot net. Handling of the fish was kept at an absolute minimum. After release of the fish the boat was kept at the side of the pound net in 15 minutes to keep gulls at distance, and to give the fish time to recover. At 08:00 the boat left.

Each morning the pound net was observed for bird activity from 05:00 to 07:00, when the net was emptied. After the boat left the pound net at approximately 08:00, observations continued until 09:30. The number of birds was counted once every 15 minutes. For each species present, counting included:

1. The total number of individuals;
2. The number swimming;
3. The number sitting on net or on poles;
4. The number flying or hovering.

As an indicator of foraging activity in the pot, the total number of attacks in two minutes was counted for each bird species present.

Results

Smolt mortality

The general result of the experiment is, that without cover net a severe loss of trout smolts occurs already after the first day (Fig. 3). When placing a cover net over the pot net, no smolts disappear.

Without cover net, the first night showed only a minor loss from the pound net. The 98 smolts were released into the net at 23:00 , but at emptying the net the first morning, only two individuals were missing. In the following morning, however, a very large proportion of the smolts was missing. On April 27, 57 of the 96 smolts restocked into the net had disappeared (59%). This high rate of disappearance did not hold for the following days. The next days, the rate of disappearance was 21%, 19% and 47 % per day, respectively. The average daily disappearance rate was 37%. On May 1,which was planned to be the last day of experiment, it was too windy to attempt checking the pot net, and only the fyke net was checked. In the fyke net 13 smolts were caught. During the five days of open net trial, no smolts were found dead.

On May 3 the cover net was set, and the pound net was restocked with fish at 23:00. In the fol-

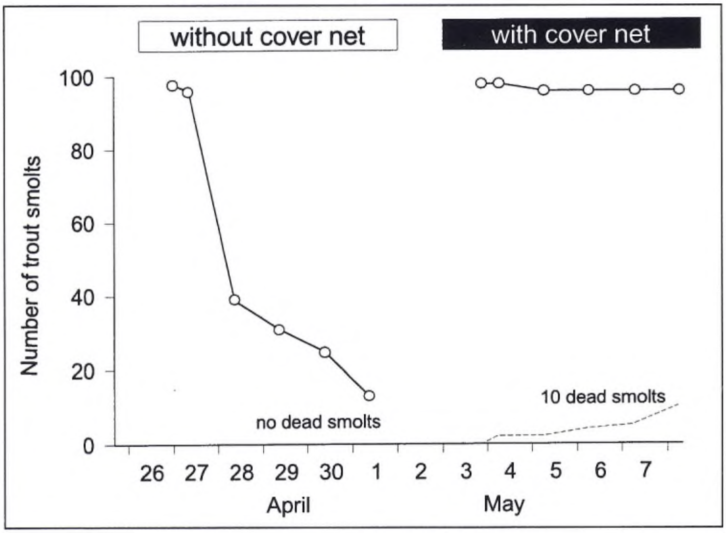

Fig. 3. Daily counts of sea-trout smolts during the two trials. During the open trial no dead smolts were included in the daily counts, but in the trial with cover net, a total of ten dead smolts were observed.

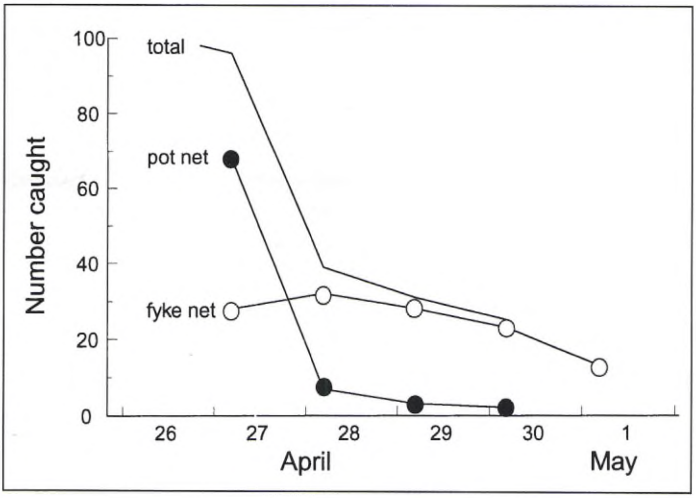

Fig. 4. Number of sea-trout smolt as captured from either the pot net or from the fyke net during the open trial.

lowing morning, two smolts were found dead, but none were missing. In the second morning, a large wave unfortunately sweept over the pound net, as the fisherman was about to take the fish into the boat. In this way four fish were accidentally lost. No further losses occurred for the last days of closed pot net trial. During all five days of closed pot net trial, a total of ten smolts were found dead in the pot net and in the fyke net.

An interesting pattern emerges, when the catch in the open net trial is separated into the fyke net catch and the pot net catch (Fig. 4). The first morning, 68 of 96 smolts caught (71%) are taken from the pot net. The remainder 28 smolts had entered the fyke net. This pot net contra fyke net distribution did not hold during the following days. The second morning, most of the survivors (82%) had entered the fyke net. During the following days, the percentages of fish in the fyke net were 90% and 92%, respectively. The daily number of fish to enter the fyke net was thereby quite stable during the experiment. In contrary to this, the number of fish caught in the pot net decreased drastically after the first day.

Bird activity

The bird species at the pound net during the morning observations were, in order of decreasing abundance: herring gull *(Larus argentatus)*, common gull *(Larus canus)*, great blackbacked gull *(Larus marinus)*; blackheaded gull *(Larus ridibundus)*; cormorant *(Phalacrocorax carbo)*, and tern *(Sterna* sp.) Gulls, in particular the herring gulls, were dominating the bird community at the pound net, especially when the net was being emptied.

The number of herring gulls and blackheaded gulls increased, as the fisherman's boat arrived at 07:00 (Fig. 5). At human presence, blackheaded gulls were somewhat more imprudent than herring gulls and common gulls. The great blackbacked gulls were repelled by human presence. Cormorants and terns were observed only once during the entire observation period.

During the short period of human presence, most gulls maintained swimming position at a distance of 50-100 m from the boat. When the boat left, the gulls took off to approach the net. The most active gulls were hovering 1-3 m above the net pot, looking out for a fish to get near the surface. Others were sitting on the poles with their wings spread out, ready to perform a sudden attack. Whenever a fish was caught, the successful gull hurried away trying to swallow the prey, before the tail of conspecifics succeeded in depredation. Herring gulls, great blackbacked gulls, and common gulls were much more successful than blackheaded gulls at depredation. However, due to its audacity, the blackheaded gull was the most successful during the first moments when the boat was leaving.

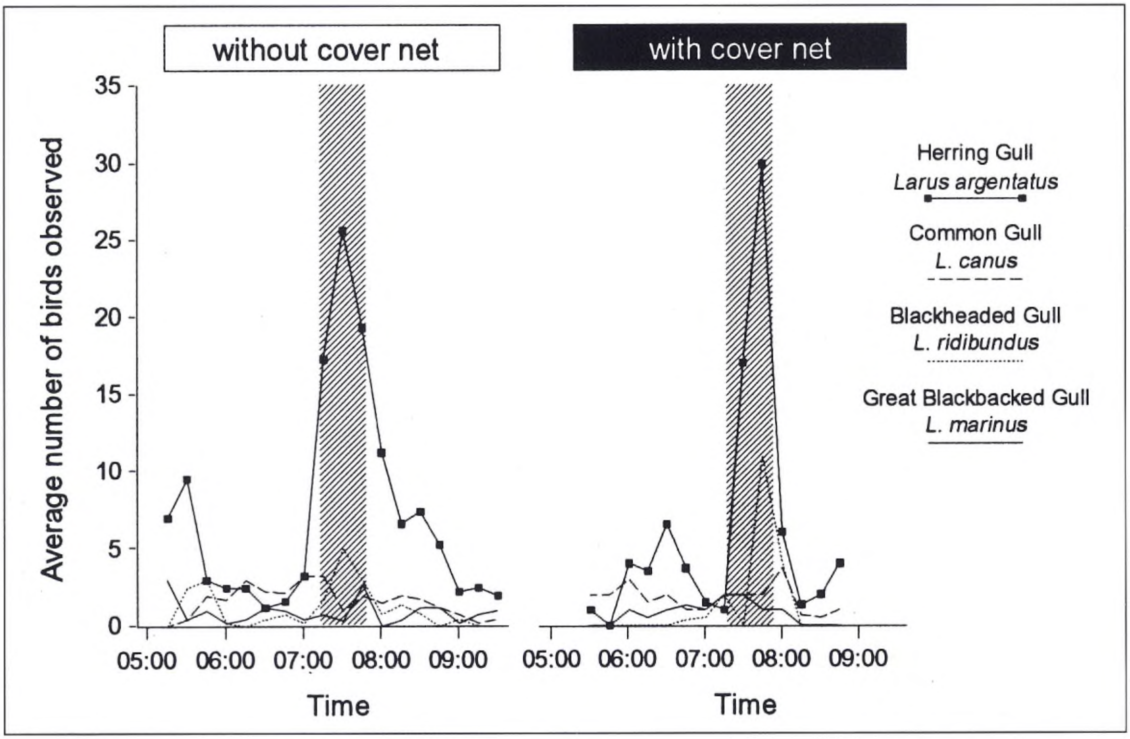

Fig. 5. Average number of gulls present during the early morning hours. The crosshatch indicates when the pound net was being checked.

The first morning without cover net, when fish density was highest in the pot net, only few herring gulls left with the boat. At 07:45, as the boat had just left, 48 herring gulls were counted actively fishing at the pot net. During a two-minute count, these gulls made 30 well recognized attacks (sudden dives from a sitting or hovering position), in which they removed 11 fish. Only in the first morning, successful attacks were observed during the two-minute counts. At 08:45, one hour after the boat had left, nine herring gulls were still present, well above the normal "background" level of 2-4 birds.

The general pattern of sea-bird abundance at the pound net did not alter much after the pot was covered with a bird-exclusion net (Fig. 5). The birds were able to see the fish below the cover net, as they performed several impulsive attacks where only a fast reaction saved them from a collision with the cover net. A significant difference from the open net trail, however, was that the herring gull-peak at the covered pound net endured less time; only about half an hour. The pound net was sooner left by the gulls as food was not accessible.

Discussion

Although several potential predators of salmonid smolts have been reported in the literature, nothing has been reported regarding gull predation on sea-trout smolt. Kennedy and Greer (1988) investigated predation by cormorants in an Irish river, and reported that brown trout formed a major proportion of cormorant diet. Gulls, and especially common gulls have been reported as important predators on salmon, *Salmo salar* L., smolts in the Norwegian River Eira (Reitan et al. 1987).

The presence and the activity of the gulls in the present study suggests that the major part of the smolt mortality occurs in a very limited period immediately after the boat leaves the pound net. Handling and subsequent release of the fish causes a stress situation resulting in severe mortality in the presence of gulls. When gulls are unable to catch the stressed smolts due to an exclusion cover net, the resulting mortality is much lower. The ten smolts found dead during the covered pot net trial can be attributed to stress imposed by repeated handling and release. That no smolts were found dead during the open pot net trial was probably due to the fact that stressed fishes are more susceptible to predation than unstressed. Accordingly, Järvi (1989, 1990) reported a synergistically increased mortality rate of predator-stressed salmon smolts, when suscepted to a seawater challenge test. Mortality due to predation is highest within the first days after release (Hvidsten and Hansen 1988). Smolt mortality attributed to the adverse effects of handling at a counting fence was reported by Ward and Slaney (1990), working with steelhead trout, (anadromous rainbow trout, *(Oncorhynchus mykiss* Walbaum).

The relatively constant daily number of fish to enter the fyke net in the open pot net trial may result on selection acting on predator avoidance behavior. When threatened by a predator from above, the natural response would be to escape downwards, where the fishes are more susceptible to become trapped in the fyke net. In the present experiment, the fyke net was functionally a safe retreat for the fish during captivity. If the smolts had been individually tagged, the question as to whether it was the same individuals that repeatedly entered the fyke net, could have been answered. However, the survival value of the downwards flight reaction as opposed to the fatal alternative of ignoring the predators is evident.

In comparison with wild smolts, hatchery reared smolts may not be as well accustomed to predators. There is some evidence, that cormorants show food preference for hatchery released salmon smolts over that of wild ones (Kennedy and Greer 1988). The authors estimate an overall predation rate of 51-66% of the salmon smolt run. However, Hvidsten and Lund (1988) investigating predation by cod *Gadus morhua* (L.) and saithe *Pollachius virens* (L.) found no difference between mortality rates of wild and hatchery reared salmon smolts.

When attempting to estimate the mortality of smolts during (and after) their first captivity in a pound net, the smolt mortality on the first full day (59%) is probably the most correct value, as it comes closest to the typical discard situation of the commercial pound netting practise. This is probably a low estimate, as the smolts were treated much more careful during the experiment than is normally the procedure.

As earlier described, the total pound net bycatch (discard fish) in the Ringkøbing Fjord was in 1990-91 estimated at approximately 50,000-60,000 sea-trout smolts (Dieperink 1990, 1993). In 1991, the total sea-trout smolt input to the Ringkøbing Fjord was estimated at 40,424 with 0.95 confidence limits of 33,511-49,765 (Dieperink 1994), and some individuals must thus have been caught in pound nets more than once. Using the 59% mortality rate, gull-predation on discard fish may account for the death of 30,000-35,000 sea-trout smolts. The total smolt predation rate by gulls concerning discard catch can in this way be estimated at 60-100% of the initial number of smolt.

Large mortality rates due to predation on the smolts have been reported for both the freshwater and for the marine phase of the migration. In the estuary of the Norwegian River Eira, predation from birds on hatchery-reared salmon smolts was evaluated by recoveries of tags from bird pellets (Reitan et al. 1987). Recoveries varied between 0-11%, which must be considered as minimum estimates of predation. Reporting on mainly fish predators on salmon smolts from three different Swedish rivers, Larsson (1985) concluded that the predation rates in the freshwater phase alone reached 50%.

A prerequisite for obtaining an increased smolt survival and thereby an augmented return of mature fish is that the smolts killed off by gulls would otherwise survive to adulthood. This may not generally be true, as many potential vectors of smolt mortalities can be listed among birds, mammals, other fish species (Meacham and Clark 1979, Larsson 1985, Shearer et al. 1987) and of course; man.

In the River Skjern Å estuary, the observed high predation rate and the intensive pound net fishery makes the present sea-trout smolt stocking practice seem wasteful. The smolt stocking strategy, the early spring pound net fishery, and perhaps the legislative status of the gulls, are all items to be reconsidered. At present, two main lines are being pursued. Primarily, experiments with the eel-type pound nets have been initiated to reduce their ability to capture sea-trout smolts. Secondly, it has been recommended to initiate transportation of hatchery reared smolts in large net pens through the estuary to the open sea. Compared to releases in the river, open sea releases has been shown by Gunnerød et al. (1988) to give higher total recaptures.

If sea-bird predation on smolts in pound nets is the primary cause for the low returns of mature sea-trout to the River Skjern Å, why was this not the case during the period 1960-70? Then, the spring time fishery in the estuary was even more intensive than today. At present, there is no indication of increased catch or bycatch of sea-trout in the North Sea. Ornithological observations show no increased abundance of sea gulls during the intervening period.

An interesting hypothesis explains the reduced return rate by the increased turbidity of the estuarine water. Even a large gull species, such as the herring gull, is not able to reach more than about 30-40 cm below the water surface. Smolts are therefore only vulnerable to predation by gulls when in close vicinity of the water surface. Allthough turbidity may also decrease the visibility of the gull, turbidity reduces the distance at which the smolt first sees the predator. When the water is very turbid, the fish is within reach of the predator (less than 40 cm below surface) before the predator is to be seen. In this way, the increased turbidity may be responsible for reducing the time available to respond to the sight of a predator. Increased turbidity thus mediates a delayed flight-reaction.

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Ocean Mortality of Ranched Atlantic Salmon during the Second Year in the Sea

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Abstract

Atlantic salmon in salmon ranching in Southwest Iceland mature and return one or two years after release as salmon smolts. A formula is presented to calculate mortalities at second year at sea before returning as two sea winter salmon. The calculations depend on knowing the sex ratio (males/females) of migrating salmon smolts, the fraction of males and females returning as grilse (one year at sea) and salmon (two years at sea). Mortalities during the second year at sea for three year-classes are presented. Mortalities were estimated to the maximum of 65±10.8% for two sea winter salmon in salmon ranching in Southwest Iceland.

Keywords: Ranching, smolt, salmon, mortality, stock.

Introduction

Survival rate of salmon during the second year at sea depends on many factors such as predation and fishing. Miller (1989) suggested that squid could be a serious predator of adult salmon and they have been observed in high numbers in the salmon feeding grounds north of the Faroes in some years. He also reports that porpoises and dolphins could be predators of salmon. Rae (1960) describes the distribution of both grey (*Halichoerus grypus*) and common seals (*Phoca vitulina*) and their association with the Scottish fisheries. It was found that there was considerable damage to fish, nets and fishing power and probably the seals also diverted fish from nets. Rae and Shearer (1965), on the basis of the number of seals seen by fishermen in the vicinity of their nets, estimated that about 148,000 salmonids had been killed by seals on the Scottish east coast from 1959 to 1963.

In the report of the working group on North Atlantic Salmon (ICES, 1991), natural mortality rate of two-sea-winter salmon is estimated 12% per year in the West Greenland sea.

The purpose of the following estimations of mortality in the second year is to evaluate whether one should use two-sea-winter salmon stocks for ranching instead of grilse stock. At the same time the results can also give some indication of mortality of wild stocks during the second year in the sea.

The returns of microtagged salmon are quite well documented in ocean ranching programs in Iceland as almost all returning salmon return to the site of release. Most tags from salmon straying to other ranching sites or to rivers are retrieved.

Methods

Survival rate during the second year at sea was calculated according to Murphy's method (Ricker 1975, p. 200-202). Murphy used the method to estimate survival during the last year of sea life. In his experiments, coho salmon (*Oncorhynchus kisutch*) mature at age two and three; among mature age-two salmon males are in excess, whereas females are usually in excess at age three. This is similar for Atlantic salmon in sea ranching in the southwestern part of Iceland where salmon return as one-sea-winter salmon (grilse) and two-sea-winter salmon. Three-sea-winter salmon are seldom found. Males frequently dominate among the grilse whereas two-sea-winter fish are mostly females.

Let there be M' males and F' females approaching the end of their first year in sea (approaching grilse). Let x be the fraction of one-sea-winter males which matures, y the fraction of one-sea-winter females that mature, and S the survival rate of non-maturing 1+ sea-winter salmon of both sexes up to the time they approach maturity as two-sea-winter salmon. Then the expected numbers in each category are as below, and can be equated to observed numbers A, B, C, D:

	1-sea-winter salmon		2-sea-winter salmon
Total	Matur.	Not matur.	Maturing
Males M'	$M'x$=A	$M'(1-x)$	$SM'(1-x)$=C
Females F'	$F'y$ =B	$F'(1-y)$	$SF'(1-y)$ =D

For one-sea-winter matures (grilse), males exceed females and the difference is:

$$A-B=M'x-F'y$$

For two-sea-winter matures, females usually exceed males and the difference is:

$$D-C=S(M'x-F'y+F'-M')$$

If we know the ratio of the two sexes before any mature as 1-sea-winter salmon then:

$$M'/F'=a$$

The best approach to 'a' is killing a random sample of outgoing smolts in a ranching program and study their sex ratio, and assume that mortality of sexes is the same before they reach maturity as one-sea-winter fish. The expressions can be developed algebraically into estimates of S (Survival).

$$S=\frac{a\cdot D-C}{A-a\cdot B} \qquad (1)$$

Where the numbers of females and males returning as two-sea-winter fish, corrected for sex ratio of outgoing smolts are in the numerator, and in the denominator, grilse counted one year earlier and also corrected for sex ratio. Mortality is then calculated as $1-S$. Standard deviation of the quotients for S is calculated to find the precision of the estimates.

If a fishery attacks two-sea-winter salmon near the end of the life span, the method can still be used if the two sexes are equally vulnerable or if the catch of each sex can be added to C and D. In that event fishing mortality is included in the estimate of total mortality ($1-S$). If a significant number of one-sea-winter salmon are caught in the sea, the method will fail unless estimates of number and sex of these removals are obtained and brought into the equations. In Iceland all fishing for salmon in the sea is illegal so fishing mortality would be expected negligible.

Material

Microtagging

The material used is from three year-classes of smolts reared at the Experimental Fishfarm in Kollafjordur SW Iceland in connection with selective breeding work, where families are produced of different salmon stocks (Jonasson 1993). Families were reared in separate trays/tanks from fertilization to tagging. Micro-tags were used. Tagging took place during September-December each year and smolts were released as 1+ smolts. At tagging families were graded in the way that only fingerlings larger than 10 cm. were tagged. Premature males with running milt were not tagged. After tagging all families were put together in an outdoor pond, until released by the end of May the year after. The smolts migrate to sea during June/July the same summer.

In 1988 year-class 11,276 smolts were released of Kollafjordur ranching stock and in 1989 year-class 54,437 smolts from the same stock were released. In 1990 two salmon stocks were used, 33,413 smolts of the Kollafjordur ranching stock and 5,561 smolts of the Isno ranching stock. The Kollafjordur stock is a grilse stock form West Iceland and the Isno stock is a multi-sea winter stock from northern part of Iceland.

Sex ratio and size

Before releases of 1988 year-class, 210 microtagged smolts were killed to study the sex ratio and 465 microctagged smolts for year-class 1989. For year-class 1990, a total of 1,094 smolts of the Kollafjordur stock and 280 smolts of the Isno stock were estimated. At tagging for year-class 1990 premature males with running milt were not tagged but the proportion estimated for both stocks. The proportion of premature males with running milt for the Kollafjordur stock was 2% compared to 0.7% for the Isno stock. From 15 June to 27 July all smolts were killed of year-class 1990. Tags, sex and length were recorded. Returning fish was slaughtered at returning site. Strayers were also reported and included in the sample.

Data analysis

Length values of smolts of both stocks were analyzed separately using two way analysis of variance (SAS-GLM) using the SAS-statistical packege (SAS-Institute,1988) including fixed effects of sex and date at slaughter. The interaction between sex and date was not significant and excluded from the analysis. Least-squares means were computed for each sex in each stock as adjusted treatment means for dates. Chi-square test were used for comparison of proportions of sex ratios.

Table 1. Number of males and females and sex ratio of outgoing smolts released in 1988, 1989 and 1990.

Stock	Year	Males	Females	Sex ratio
Kollafjordur	1988	105	105	1.0
Kollafjordur	1989	215	250	0.86
Kollafjordur	1990	537	557	0.96
Isno	1990	126	154	0.82

Table 2. Numbers (n) of smolts and Least square means (LSM) of length for sexes used for each salmon stock, 1990 year-class.

Stock	n	LSM (cm)	n	LSM (cm)
Kollafjordur	537	15.52	557	15.49
Isno	126	14.85	154	14.54

Results

There was no significant difference between the three year-classes in sex ratio (Table 1) (χ^2=1.291; P=0.52). These sex ratios however were the best point estimates for each year-class for sex ratio and will be used in the calculations for mortalities.

The data on length analysis between sexes (Table 2) are not significant for the Kollafjordur stock ($F_{(1.1089)}$=0,15; P=0.696) and also between sexes in the Isno stock ($F_{(1.275)}$=0.64; P=0.426)

The total returns were quite low during the three years or 1.28% for 1988 year-class, and 1.1% for 1989 year-class, 3.2% for the Kollafjordur stock and 1.2% for the Isno stock in 1990 year-class.

Mortality was estimated to a maximum of 65% (Table 3), for year-class 1988 and the standard deviations of the mortality estimate is ranging from 8.8-66.5%.

Table 3. Number of returning salmon as grilse and two-sea-winter salmon grouped by sex, percent returning as grilse and percent returning as two-sea winter (2SW) salmon and calculated second year mortality with standard deviation for mortality estimates.

Stock	Release Year	Grilse		2SW		Grilse %	2SW %	Mortality %
		male	female	male	female			
Kollafjordur	1988	87	13	9	35	69.4	30.6	65±10.8
Kollafjordur	1989	255	31	92	220	48.8	52.2	57± 8.8
Kollafjordur	1990	491	432	23	134	85.5	14.5	(-42)±66.5
Isno	1990	22	7	13	25	43.3	56.7	54±37.7

Table 4. Changes in sex ratio (male/female) over time from smolt stage to the end of the life cycle of Atlantic salmon released from the Kollafjordur Experimental Fishfarm in 1989-90 ($***=P<0.001$, $**=P<0.01$, $*=P<0.05$, $NS=P>0.05$).

Stock	Release year	Smolt	Grilse	2SW	Total
Kollafjordur	1988	1.0	6.7^{***}	0.26^{***}	2.0^{***}
Kollafjordur	1989	0.86	8.2^{***}	0.42^{***}	1.38^{***}
Kollafjordur	1990	0.96	1.1^{NS}	0.17^{**}	0.91^{NS}
Isno	1990	0.82	3.1^{**}	0.52^{**}	1.1^{NS}

The proportion of grilse is highest for the Kollafjordur stock in 1990 year-class and for two-sea-winter salmon in 1989 for the same stock. The sex ratio between smolts (Table 4) and returning grilse changes significantly for all years except for the Kollafjordur stock in 1990 year-class. Sex ratio for two-sea-winter stage changes significantly in all years. But the overall sex ratio changes in the 1988 year-classes and 1989 but not in 1990 year-class.

Discussions

Females were always in excess in the sex ratio of migrating smolts, except in 1988 year-class where they were in equal number with males. This is not unexpected as premature males are sorted away at tagging. Prematurity of male parr was only estimated in year-class 1990 to 0.7% for the Isno stock and 2% for the Kollafjordur stock. These proportions can only to a certain extent explain the larger number of females in the two smolt samples.

The estimation of mortality during the second year at sea assumes that mortality of the two sexes is the same before they reach maturity as grilse. Equal sizes between the two sexes of smolts in 1990 year-class indicate that mortality during the first weeks of migration is not sex dependant as they are of the same size. This can further be argued in the case of the Kollafjordur stock in 1990, which were 87% returning as grilse, the sex ratio did not change significantly from the time the smolts migrated to sea until the time when the salmon returned as grilse.

Return rate (%) was quite low for these three years. Similar results were observed for the Kollafjordur stock in Kollafjordur Experimental Fish Farm in the 1983 year-class (Isaksson 1990), where the return rate was only about 2.1%. The year-class gave about 50% of returning fish as grilse as in 1989 year-class. But in the years 1979 to 1988 with the exception of 1983 year-class return rate was always higher ranging from 5.1 to 11% (average 7.2%). The proportion of grilse was always higher than for 1988 and 1989 year-classes as reported here. Lower return rate during 1988-89 has been explained by poor conditions in the sea around Iceland (Isaksson 1990). During years with lower return rates, the males predominate in the one-sea-winter returns and females in the two-sea-winter return. This gives an opportunity to calculate the mortalities demonstrated here. When looking at the changes in the sex ratio from smolt stage to the end of the life cycle, mortalities of females is higher in the first two year-classes. Fewer females are returning as grilse compared to males, indicating higher mortalities for females at second year at sea, given the mortality is the same in the first year. This can only be demonstrated in 1990 year-class where the sex ratio at the grilse stage changes less for both stocks than in previous year-classes and is not significant for the Kollafjordur stock, indicating that mortalities until returning as grilse are not sex dependent in 1990 year-class.

The data of the returning fish satisfy the assumptions of the equation for calculating mortality. Large variation is in estimation of mortalities between year-classes and in year-class 1990. The estimate for the Kollafjordur stock in 1990 is a negative number and cannot be an estimate of mortality. In year-classes 1988 and 1989 the standard deviation is significant from zero indicating a relative good precision in the estimates of mortalities for these two year-classes. The estimated standard deviation of the quotients of mortality estimates is a measure of the precision.

A closer look at formula (1) shows that when the outcome of $A\text{-}a*B$ is close to zero (as in year-class 1990), S becomes very inaccurate, and the variation of the estimate high. The result will be imprecise estimate of the mortality.

Tomasson et al. (1987) estimated mortality during the second year in sea to be more than 40-50%, given that the estimated sex ratio of outgoing smolts was 1.0. They concluded that the mortalities were mainly of natural causes, because there were no indications of salmon from ranching programs in Iceland being caught in the high seas fisheries.

It is known that only two-sea-winter salmon from Iceland migrate outside of the jurisdictional limits around Iceland to the coast of Greenland and to the area around the Faroe Islands (Guðjonsson 1989). Until recently fishing for salmon was common in these areas and may have resulted in lower survival during these years, but it is very difficult to estimate the mortalities due to fishing alone.

The method of calculating the mortalities at second year at sea has many assumptions. One is the assumption that mortalities are the same for sexes in the first year and the second assumption is that one- and two-sea-winter fish travel to the same feeding arias during the first year in sea. At present there are little or no information about feeding areas of Icelandic salmon during the first year in sea.

In this study, two of three year-classes show high mortality estimates during the second year at sea and the same two year-classes show a reasonably good precision of the mortalities estimates.

Further studies on the mortality of salmon in the sea will be carried out in connection with sea ranching operations in Iceland. Information on survival rate of salmon during the second year in sea are of great importance when it comes to choosing a salmon stock for ranching or making decisions on selective breeding strategies for sea ranching.

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A New Release System for Coastal Ranching of Atlantic Salmon (*Salmo salar*) and Behavioural Patterns of Released Smolts

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Abstract

A tarpaulin barrier was used to accumulate a surface freshwater layer of about one meter depth in a small marine bay. The source of freshwater was the effluent from the hatchery where the smolts were held before they were transferred to net pens in the bay inside the barrier. The behaviour of the smolts after release from the net pens was monitored by underwater video cameras and divers. After release, several distinct behavioural patterns related to differences in salt water preference and migration motivation were observed and are described. The release system may be a promising way to handle smolt releases in marine environments.

Keywords: Freshwater layer, tarpaulin barrier, smolt, migration motivation, sea ranching.

Introduction

Sea ranching of Atlantic salmon (*Salmo salar*) has been developed in the Baltic sea, in Ireland and in Iceland (Ísaksson, 1988). In the Baltic sea most of the adult salmon are harvested in the feeding areas while they are caught at the release site in Iceland when they return. In Norway, studies of the potential for sea ranching is organized in the "Programme for Development and Encouragement of Sea Ranching" (PUSH in Norwegian). Coastal Salmon Ranching (CSR) is one of the new approaches within this programme. It is mainly based on utilization of small freshwater sources in coastal regimes (Holm et al. 1991), and some of the goals are to avoid the predation in the fjords and to maximize the distance between the release site and natural stocks. An evaluation of this release model must also include information on the imprinting and the straying rates of the returning adults.

Juveniles of Atlantic salmon smoltify under increasing day length in spring, but it is difficult to assure that all individuals in a group develop full salinity tolerance and preferance at the same time. The transfer from fresh water to sea water may therefore be critical. If the fish are offspring from different river strains it is also possible that the time of smoltification differ due to local adaptations. For rearing in net-pens the optimal time of transfer is important for survival and growth rates under farming conditions. In sea ranching, and especially in this new approach, the optimal time of release may be even more critical. The anti-predator behaviour of the released fish (Järvi 1989a) and imprinting which enables the fish to return to the release site are probably dependent on the parr-smolt transformation.

One possible solution to these problems is to construct systems that allow the fish to leave on their own when they are motivated to migrate to sea. Generally, we have little knowledge on key stimuli for ocean migration behaviour, which are fundamental for developing a successfull release strategy. In addition, handling problems in large scale releases should be diminished to reduce stressors and to guarantee that fish are being treated according to their stage of parr-smolt transformation. For these reasons, there is need to develop new release designs.

In natural rivers, it has been observed that the migrating smolts often stay in the estuary for a short time before leaving (Calderwood 1906, Hvidsten and Møkkelgjerd 1987). The estuary salinity gradient from the freshwater in the surface to higher salinity in deeper waters may be one reason for the stay, if the smolt need to gradually acclimate to sea water. The goal of the present work was to develop a new releasing facility that utilize small coastal water sources. An artificial freshwater layer was accumulated in a marine bay and the effect of retaining and releasing the fish in this system were studied.

Materials and Methods

The study was performed in the Selstø bay on Sotra Island, a 600 m long bay west of Bergen, Norway (Fig. 1). The difference in water line between ebb and flood tide is normally 0.5-1.0 m. A small water course of 1.5 km^2 basin drains to the bay. The operation of Selstø hatchery located close to the inner bay depends on a dam in the main water reservoir of this water course to secure the water supply during dry weather in spring and summer. The brook was dry during the experiment when the freshwater was delivered directly to the hatchery trough pipe lines. This freshwater source, about 3000 L min^{-1} during the study, was the only effluent into the bay. To accumulate freshwater in the bay, a 55 m long, 3 m deep barrier (Fig. 1 and 2) made of reinforced PVC tarpaulin was attached in to iron pins on each side of the bay on May 20, 1992. One of the pins on each side was cemented in to the rock above tide while the other was below ebb. On the south side, the uppermost end of the tarpaulin was secured more firmly to the rock by sacks of sand. This was not possible on the steep

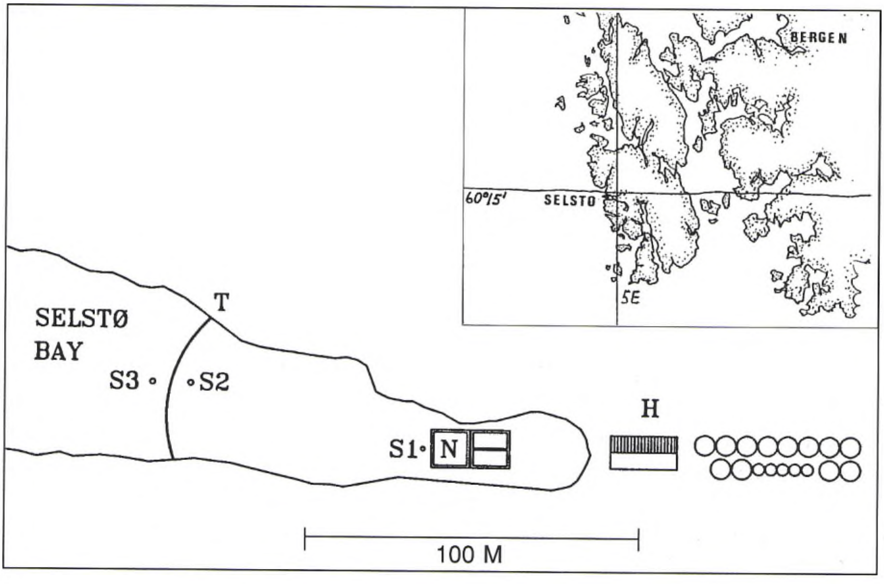

Fig. 1. Maps showing area and the release site in the Selstø bay. The location of the tarpaulin (T), the net pens (N), the Selstø hatchery (H) and the locations of the salinity profiles on the inside (S1 and S2) and the outside (S3) of the tarpaulin are included.

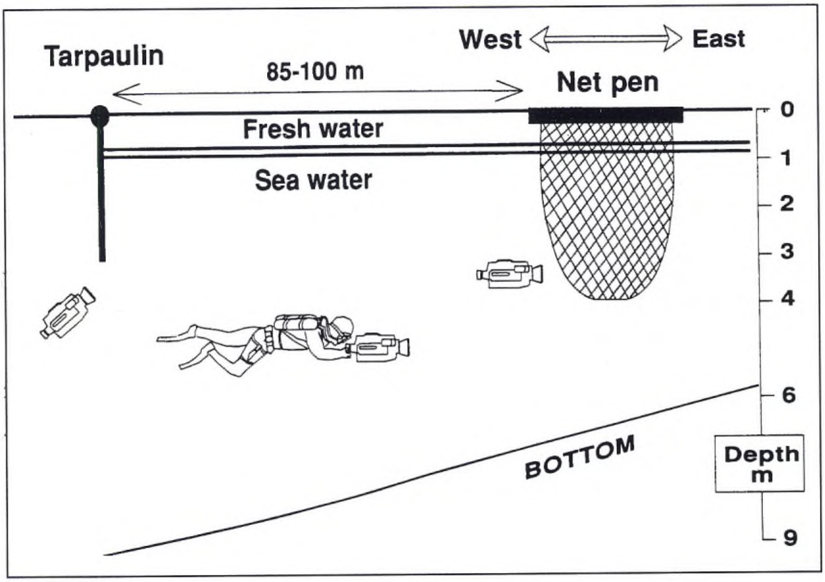

Fig. 2. Principal diagram of the release system, showing net pen, tarpaulin, surface freshwater layer, and observation methods.

rock on the north side of the bay. Weights, about 250 kg in total, were distributed along the bottom line of the tarpaulin. Net pens were located in the inner part of the bay (Fig. 1 and 2).

The fish were offspring from wild parents from four regional rivers; the Dale river, the Vosso river, the Lone river and the Onarheim river. They were reared at the commercial hatchery Sagen Settefisk. During December 1991 and January 1992, potential two-year smolts (based on size difference between lower and upper mode fish, (Thorpe et al. 1980)) were removed from the hatchery tanks and the release groups consisted of a total of 41,361 one-year smolts that were distributed into six tanks of 6,100-7,500 fish per tank (Table 1). Each of the six tanks contained comparable numbers of fish of each strain. The fish in tank 1, 3 and 5 were given lower water current speed than those in tank 2, 4 and 6. These differences did not effect the results of the present study and will be reported elsewhere. Carlin tags were used to tag appoximately 7% of the fish, 500 from each tank in early April. The six groups were transferred to six tanks at the Selstø hatchery in mid-April and supplied with freshwater.

On May 20, 60 fish from release group 1 (tank 1 and 2, Table 1) were transferred to the Institute of Marine Research in Bergen and distributed into two tanks (32 and 28 individuals in tank 1 and 2, respectively) supplied with running freshwater. On May 21 a seawater tolerance test (40‰ salinity, starting at 9 °C, 96 h) was conducted. The test water was made by dissolving sea salt in laboratory salt water and was continuously aerated throughout the test. Mortality recorded on May 24 and 25. During the night to May 25 the aeration stopped in tank 2

Table 1. Dates for transfer from hatchery to net pen, dates and times for release groups and numbers in each tank in January.

Tank	Transfer Date	Release			Numbers
		Date	Time	Group	
1[1]	23.5	26.5	13:10	1	7,499
2[1]	23.5	26.5	13:10	1	6,512
3	27.5	2.6	12:28	2	7,058
4	27.5	2.6	18:41	3	6,092
5	27.5	3.6	09:34	4	7,336
6	27.5	3.6	14:30	5	6,864

[1] Fish from both tanks were kept in one net pen of double size, separated by dividing the net pen into two parts by a rope, and released simultaneously.

and all fish died. A random sample of 97 fish were taken from release group 1 on May 22 to measure size.

The fish were transferred from hatchery outdoor tanks to net pens in the Selstø Bay, through a pipe line on May 23 or on May 27 where they were held 3-6 days before release (Table 1). Fish from two pens were released on each of the three release dates (May 26, June 2 and June 3), but fish from two pens were released simultaneously, giving five release groups (Table 1). To release the fish from the net pens, the ropes attaching the westward part of the net pen to the floating framework were untied. Weights had been fastened to the upper line of this part of the net pen so that the fish could swim freely out of the 4 m deep net pen after about 10-20 s.

Three video cameras were used to observe the behaviour of the fish before and after the five first releases (Fig. 2). One camera (Seametrix) was installed up to the net pen at 3.5 m depth. It was connected to a monitor and operated by the use of a joy stick: with scope of 360 degree horizontal and vertical movement relative to its fixed position. One camera (Sony HI8) was operated by a diver. The diver held position close to the tarpaulin for 30 min from time of release. Another diver made visual or video (Osprey camera, release 1 and 2) observations close to the barrier. For the next hour, after the release from the net pen, both divers searched the bay inside the barrier. The same area were also surveyed the day after release, except on June 4. During the first release one of the divers followed smolt migration from the net pen to the tarpaulin barrier using the Sony HI8 camera. The divers did not use cameras during the last release. There were visual observations of the bay (from land and boat) on day 3, 4, 5 and 7 after release 1. Because of good water clarity the bottom was visible down to appoximately 7 m depth when using water glass.

The numbers of fish in schools during escapement under the tarpaulin barrier were estimated from the video tapes. Slow motion, stop action and playback were used to count the numbers of individuals in isolated schools. The distance between the members of the schools was long enough to see the individuals, but it is still possible that the estimated numbers are minimum numbers because of shading. The distance from the camera to one large school was too long to count each fish. A conservative minimum number ($N>1000$; Table 2) was estimated from the passing time (30 s) and an estimate of 50 fish passing per second.

After release of group 1, on May 27 (12:00-13:00 p.m.), two samples of non-migrating fish were caught with gillnets close to the tarpaulin (sample 1) and in the inner part of the bay (sample 2). To catch the fish a diver chased the fish towards the net. Carlin tagged individuals were more easily caught than untagged or were more abundant in the two samples compared with the release group, 25% (5 out of 20 in sample 1) and 31% (14 out of 44 in sample 2). Data from the tagging in April was used to statistically compare the length of non-migratory individuals with the release group. All fish from the two samples were checked for salmon lice (*Lepeophtheirus salmonis*), six fish from each group were examined carefully using a binocular microscope.

Results

When freshwater accumulated on the inside of the barrier, the tarpaulin stretched in a tight bow due to the pressure of freshwater, and some freshwater flowed out where the barrier was secured. The outflow of freshwater past the barrier was largest when a strong ebb tide managed to lift under side of the mid part of the barrier towards the surface. This was observed several times. On May 26, 27 and on June 2 there was a distinct thermocline (from 17.5-18.5 to 14.0-14.5 °C) and halocline (from 10-14‰ to 25-28‰) varying from 0.7-1.0 m depth (location S2-S1, Fig. 1) depending on location of measurement and direction of wind. On the surface (5 cm depth) the salinity was 0-4‰. The salinity on the surface outside the tarpaulin (location S3) was above 30‰, but a thin freshwater layer of a few cm was visible during western winds. On the afternoon June 2,

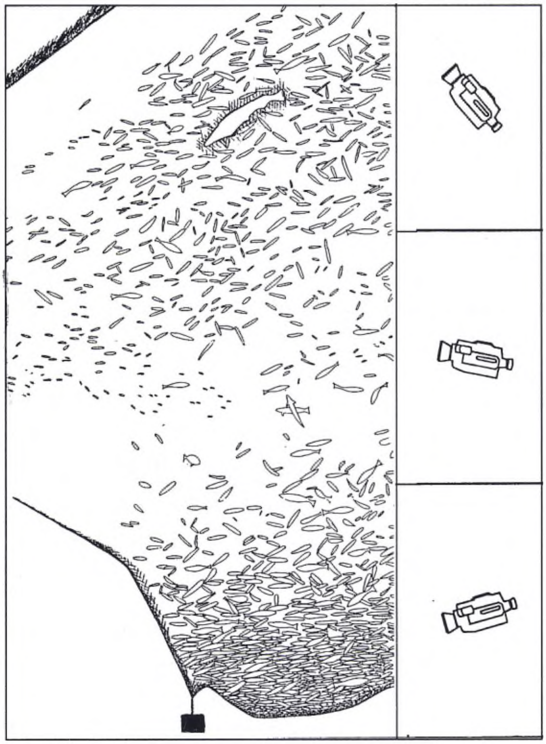

Fig. 3. Spatial distribution of fish in a net pen. Drawn from three single pictures of a video sequence. The contribution from each picture, and the angel of the camera, is indicated by the three squares to the right. The Seametrix camera was turned vertically relative to its fixed position, viewing from the bottom of the net pen towards surface. A part of the floating framework is seen in the upper left corner of the figure. The "smaller" fish in the mid figure was father away and probably was not deeper than the fish in the upper figure. The large fish, indicated by a shadow, is a pollach outside the net pen.

at low tide, a strong wind lifted the tarpaulin, starting with the northern part of it. To prevent it from being damaged it was detached from land and the sand sacks had to be removed, allowing an opening of about three m between land and the tarpaulin. Most of the freshwater flowed out of the bay. When the tarpaulin was reinstalled after some hours the leakage of freshwater was larger than before. The next day the layer of freshwater was about 20-30 cm thick, but because of turbulence the halocline varied from 0.1-0.4 m within minutes.

All fish had not developed full seawater tolerance before the first release on May 26. The fish tested on May 21 at the Institute of Marine Research demonstrated that after 72 h exposure to 40 ppt. salinity the mortality was 28% (tank 1) and 18% (tank 2). Mortality increased to 37% in tank 1 after 96 h. The mean length of release group 1 was 15.3 cm (SD=1.6, n=98).

There were spatial differences in the distribution of fish in all net pens (Fig. 3). One part (roughly estimated to be 10-30% of the fish) was distributed close to surface, while most of the smolts crowded in the lower part of the net pen. From video tapes it was demonstrated that the fish in the surface did not stay mainly in freshwater, but were very close to the halocline in seawater. They frequently passed through the freshwater to jump. A few (5-15) pollacks (*Gadus pollachius*) outside the pens were attracted by the smolts in the pens. They were swimming close to the deeper part of the net pens. They sometimes tried to bite through the netting to catch smolts that were temporarily fastened to the net because of their Carlin tags.

Release 1

After release 1, several behavioural patterns were observed by combining all video and visual observations (Fig. 4). These are described in more details below.

A) Fast migrating schools

After release, the first fish to leave the net pen swam rapidly downwards in a western direction, towards the tarpaulin barrier. The schools that were observed by one of the divers between the net pen and the tarpaulin barrier swam close to the bottom. The fish that reached the barrier within a few min after release were moving in separate schools (Table 2; Fig. 5). The first schools moved close to the bottom, six m below the lower part of the tarpaulin. Most rapid swimming schools approached the barrier in water shallower than the bottom of the tarpaulin and made a turn under the barrier and disappeared.

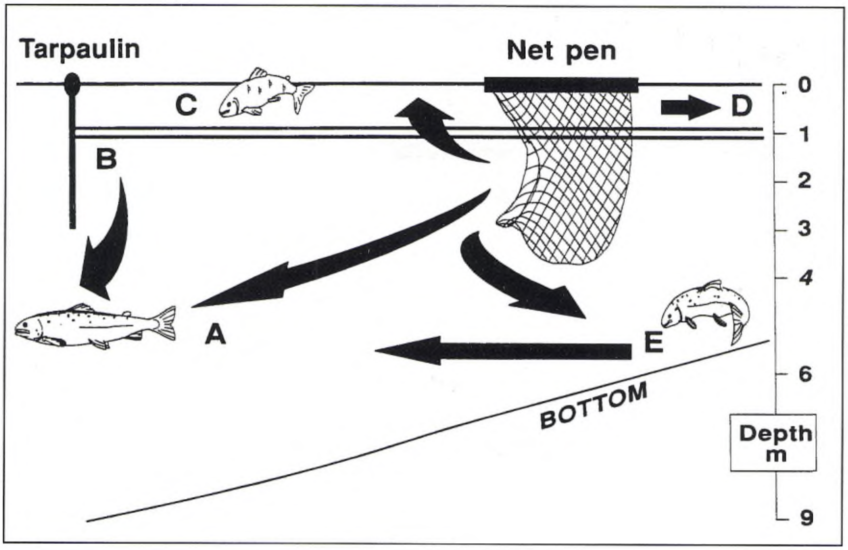

Fig. 4. Principal diagram of main behavioural patterns after release. The fish passed the tarpaulin quickly after release (**A**), segregated on the inside of the tarpaulin and migrated during one hour (**B**) or after longer time (**C**), moved to the inner part of the bay where they stayed in the surface layers for days (**D**) or stayed at bottom for days before leaving the bay (**E**). See text for further explanation.

B) School formation behind barrier and migration

These fish moved more slowly from the net pen to the barrier and started to segregate inside the barrier. The first school to stop swimming seaward when reaching the barrier was observed 3 min 50 s after the passing of the first fast-migrating school (Pattern **A**). The fish showing pattern **B** were swimming in large shoals along the barrier, mainly in seawater. It was, however, frequently seen (and recorded on videotape) that smaller schools separated from the larger shoals and moved seaward under the tarpaulin and dissappeared. Because of the formation of new schools which moved seaward, the numbers of fish inside the barrier were gradually reduced. After being obstructed by the tarpaulin barrier, the fish swimming along the barrier in deeper water left first, but fish swimming in freshwater or transition zone to seawater did not move. One half hour after release most of the temporarily «trapped» fish moved close to surface. The divers estimated the numbers to be about 1000-1500 individuals. One hour later the number close to surface was low (see **C**).

Table 2. Numbers in schools (Pattern **A** and **B**) passing under the tarpaulin.

Release Group	Numbers in separate Schools						Mean Number
1	37	100	50	150	72	105	86
2	135	92	90				106
3	80	195	91	110			118
4	80	>1000[1]	100	80	156		104

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[1] Excluded in calculation of mean number.

C) Longer stay in freshwater close to tarpaulin barrier

One hour after release of group 1 several shoals of approximately 200 individuals each were still swimming in the area inside the barrier. Similar numbers were also observed the two next days. The Carlin tagged individuals caught by gillnet on May 27 were significantly smaller at tagging than the main group (*t*-test, $P<0.05$; mean length: 13.4 cm, $N=5$, versus 15.1 cm, $N=1000$). No individuals in sample 1 ($N=20$) were larger than 17 cm, compared to 16% over that size in the sample on May 22 ($N=97$). There were no salmon lice found on the gillnet caught fish.

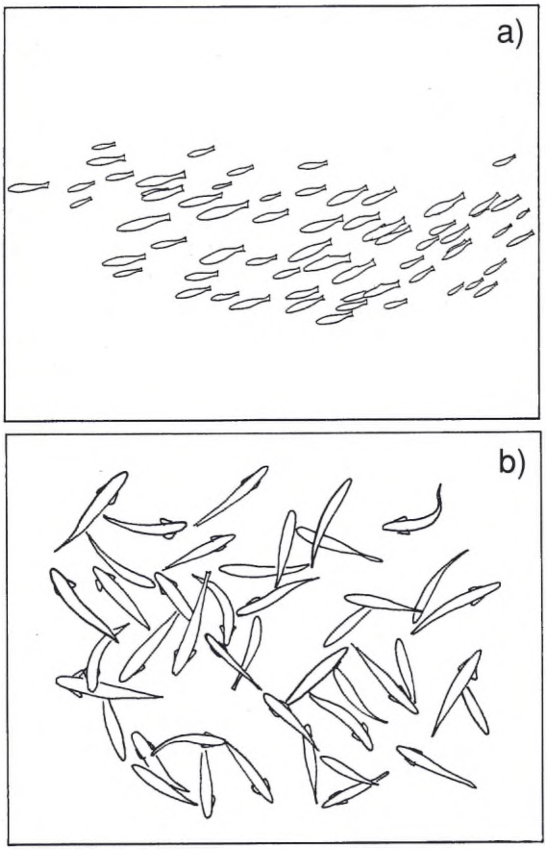

Fig. 5. a) Typical migrating smolt school (of pattern **A** and **B**) and b) part of shoal at bottom (Pattern **E**). Drawn from video recordings. Scale is different in a) and b).

D) Immobile fish in freshwater

On the first release day (May 26), the divers observed smaller groups of approximately 20-30 individuals remaining in the upper freshwater in the littoral zone in the inner part of the bay. These groups held positions close by seaweed and from video recordings they had a brownish color and parr marks were visible on the smaller fish. The smaller parr-like schools in the inner part of the bay were still seen on June 2, when about 30 individuals were observed.

E) Immobile fish at bottom

After being released from the net pens a large proportion of the fish did not leave the release site, they swam more slowly out of the net pen towards the bottom. Many fish followed the route of the fish swimming in a western direction (Pattern **A**), but some turned downward, resulting in a shoal of fish building up close to the bottom under the net pen at 6-7 m depth. After 5 min they drifted slowly away and one hour later these fish accumulated about 30 m east of the net pen, towards the inner part of the bay. They formed a dense shoal very close to bottom over 30-50 m^2 at 3-5 m depth (see fig. 5). The number in the shoal was estimated to about 2,000 individuals. The shoal held position, but the individuals were mowing slowly within it.

The gillnetting on May 27 showed that the Carlin tagged salmon were significantly smaller at tagging than the average for the Carlin tagged fish (t-test, $P<0.05$; mean length: 14.1 cm, $N=14$, versus 15.1 cm, $N=1000$) and only 7% of the sample (3 out of 44) were larger than 17 cm compared to 16% in the size sample on May 22 (16 out of 97). One copepodite of salmon lice was found in this group of fish.

The main shoal was observed on the same spot for the next three days. On the third day, parts of the fish were observed to form seperate schools which moved around in a larger area close to bottom. On day four, the shoal was reduced in size and on day six all the fish had migrated out of the bay.

Release 2-5

During subsequent releases (2-5) the overall migration speed was higher compared to the first release, the tendency to prolonged stay in freshwater or seawater was not observed, and only the behaviours described by patterns **A** and **B** were seen. In addition, there was a shift from the **B** to the **A** behaviour from June 2 (release 2 and 3) to June 3 (release 4 and 5). After releases 2 and 3 the numbers of pattern **B** fish amounted to some hundred fish after 30 min, compared to a few individuals after release 4 and 5. In addition, the fish of release 4 and 5 passed the tarpaulin so quickly (5-10 min) that it was difficult to distinguish between behaviour pattern **A** and **B**. The main part of the smolts left the net pen within 1 min after the releases, and all fish had moved in a western direction after 2-3 min. However, the sizes of the schools that passed the tarpaulin were relatively similar to those observed during the first release. With one exception, the average numbers were close to 100 individuals (Table 2).

Discussion

The installation of the tarpaulin, as a barrier, was an effective way to accumulate freshwater within the bay. The salinity profile in the Selstø bay resembled the estuary of some large rivers, with a relatively thick freshwater layer and a distinct halocline. A river estuary differs, however, from this seminatural system because of the freshwater current in the surface (Macdonald et al. 1987) and the free access from the freshwater layer to the fjord or sea. It was also experienced that an effective barrier must withstand strong tidal forces and the windaction. When combined with the pressure of accumulated freshwater, these forces may become critical. These problems suggest that further improvements have to be developed, especially for the attachment of the barrier and the control of leakage of freshwater.

The reported release system may affect the infestation of marine parasites such as salmon lice. During late May and June 1993 premature returns of sea trout (*Salmo trutta*) with extreme high intensities of salmon lice were observed in other water courses in the Sotra region (Per Jakobsen, Institute of Zoology, University of Bergen, pers. comm.). Infested sea trouts were also seen in the surface layer in the Selstø bay during the same period. In a cooperative experiment during and after the reported releases Grimnes (1993) found very low numbers (0-7 per smolt, release group 4 and 5) of salmon lice when the freshwater layer was thick on June 2, but high numbers (43-301) on June 9, one week after the reduction of the freshwater layer.

Estuaries are transition zones where migrating fishes can adjust their physiology during the fresh water/salt water transition (McDowall 1988). In amphihaline species, the ability to migrate between fresh water and sea water is periodic and the fish must migrate at specific, often limited, times (Fontaine 1975). If we assume that it takes time to accomplish the parr-smolt transformation, all migrating fish may not have reached optimal sea water tolerance when they reach the estuary. It has been shown that Atlantic salmon smolts may stay in the estuary for some time (Calderwood 1906, Hvidsten and Møkkelgjerd 1987), but there are also observations that salinity increases do not represent a significant barrier to the migration of smolts (Tytler et al. 1978).

Establishment of an artificial freshwater layer permit the smolting fish to move free in water layers as required by their physiological status. The present observations clearly indicate that the fish responded to salinity differences. The preference for freshwater for some groups of fish and their delay in surface layers before outward migration suggest that the fish in the first release group (especially the pattern **D** fish) had not completed their parr-smolt transformation and not developed seawater preference. The time difference from the first to the last release and the difference in acclimatization time in seawater may therefore have contributed to the change in overall migration speed. The difference in size between fast migrating smolts (Pattern **A**) and those that remained at the surface (Pattern **C**) during the first release, may also indicate that the stay was due to delayed smoltification. As salmonids grow and move seaward, a decreased dependence on the estuary surface layer is reflected in occupation of deeper, more saline environments by larger fish (Macdonald et al. 1987), and larger coho smolts (*Oncorhynchus kisutch*) migrate earlier than smaller coho (Durkin, 1982).

The introduction of a physical barrier may be one reason for the delayed migration of fish staying close to surface. It may be an advantage in sea ranching that smaller parr-like fish are held back, thereby being better protected against predators when they are "waiting" for sea water preference. The performance of the fish is reduced under the action of stressors such as variation in osmotic pressure (Eddy 1981) and fear caused by presence of predators (Bradley and Schreck 1987, Järvi 1989a,b, Järvi 1990). Because of the possible individual differences in optimal time for migration and the need to migrate during the "smolt-window" (Larsson 1977, Hansen and Jonsson 1989), it may be important that the fish can make their own choice when to migrate. Common treatment of all the fish in release groups may give variable results, as the survival of hatchery smolts have been increased (Jensen 1979) or decreased (Hansen and Jonsson 1986) after sea water adaptation before release.

Smolt undergoes behavioural changes to prepare it for migration during the parr-smolt transformation (Hoar 1976). The chronology of these events may however be complex or vary between individuals. The prolonged stay of one group on the bottom of the bay in sea water (Pattern **E**), showing low migration motivation, indicates that these fish had obtained a high degree of sea water adaptation, but that the motivation for migration was low. Similar to the present results, Huntsman and Hoar (1939) observed smolts lying completely inactive for a time after entering the sea, and tank experiments on several Pacific salmon species (*O.* spp.) has shown reduced activity after entry into sea water (Hourston 1957). Hourston (1957) proposed that the positive response of coho smolts to concentrated sea water is an integral part of the behaviour that leads migrants from freshwater into the sea, but osmotic stress may reduce the swimming performance of smolts (Järvi 1989a) and the stay at the bottom may reduce predation risk (Jacobson and Järvi 1976). In the Selstø bay, predators were seen in the middle of the shoal on the bottom and it was also observed that the fish formed a vacuole when a large cod (*Gadus morhua*) penetrated the shoal (Jørstad pers. comm.). Several other fish predators were also attracted by the shoal, but we do not know the probabilities of being attacked in a 'bottom shoal' versus the dangers of migration.

In the present study, most of the fish stayed in sea water in the net pen and migrated quickly out of the inner bay after being released. It is unclear whether they may have been influenced by the freshwater layer or not. If they perform vertical movements, the freshwater may, for example, play a role in imprinting and have implications for return rate and straying. During migration, the shifts towards the pattern **A** behaviour, and also the shorter duration of the **B** behaviour during the last releases, may imply that the migration motivation increased during the experimental period. The rapid movements of the fish past the outer bay and towards the open sea was observed by echo sounders (unpublished data). The formation of actively migrating schools, i. e. synchronized and polarised swimming groups (Pitcher 1986), may be typical for sea water adapted smolts during daytime in late spring and similar observations were also made during the releases from the Selstø bay in 1991 (Holm et al. 1991). While the migration through lakes has been reported to be very slow (Hansen and Jonsson 1985, Thorpe et al. 1981), the smolts tend to move faster than the currents in the fjords (Holm et al. 1982, 1986), and the migration speed is believed to be high in the sea (Reddin 1988). Observations suggest that the migration takes place during night in early spring and basically during daytime in late spring in the river (Munro 1965), and also for Pacific salmon in the estuary (Durkin 1982).

When considering the large number of smolts released, and the short distance from the net pen to the tarpaulin barrier, the school sizes were relatively similar. Fish school to reduce predation risks (Pitcher 1986), but the advantage afforded by being in a school appears to increase with the size of the school (Patridge 1982) as the probability of being attacked is reduced with the school size (Pitcher 1986). Fish in smaller groups are more timid, nervous and have higher respiratory rates (Itazawa et al. 1978). Larger schools locate patchy food faster (Pitcher et al. 1982), but the intraspecific competition for food also increase (Bertram 1978). In theory, there should exist some intercept between the benefits and costs of increasing the school size, thus pointing to the optimal school size. According to the conclusion of Pulliam and Caraco (1984) the optimal group size may not exist in realistic situations, and even if it does, equilibrium group sizes may not be of optimal size. The present results do not enlighten the complex process of school formation and structure, but demonstrated the ability of cultured smolts to form schools rapidly after release and indicate that the school size may not be at random.

Concluding remarks

By simple technology it was possible to create a freshwater surface layer in a marine bay. The different behavioural patterns of the smolts, after being released from the net pens, suggest that the smolts behaved according to their physiological demands and preferences. When releasing smolts in a marine environment, the salt water preference and migration motivation may influence whether the fish are being temporarily obstructed by the tarpaulin barrier and the salinity gradient or if they form fast migrating schools. By keeping the fish in a seminatural system like this the possible deleterious effects due to stress by handling and transport (Schreck et al. 1989) may also be reduced. In sea ranching, the "quality" of the smolt during release is very important for the subsequent performance in sea. It is therefore a goal to reduce the influence of environmental stressors to increase post-smolt survival, and hopefully to obtain low straying rates and high returns to the release site.

Acknowledgement

We are grateful to Vidar Wennevik, Harald Næss and Ole I. Paulsen for practical assistance during the field work and to Oskar Selstø who took care of the fish. The financial support were provided by the "Programme for Development and Encouragement of Sea Ranching" (PUSH) and by the Department of Aquaculture, Institute of Marine Research.

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Feeding, Food Quality, and Nutritional State of Salmon Postsmolts in the Finnish Coast of the Bothnian Sea

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Abstract

According to tagging experiments stockings of river Neva strain salmon have given poor and highly variable results in the Bothnian Sea. In the original habitat of this strain, the Gulf of Finland, the rate of recapture has been much higher and less variable in the same year classes. We started 1990 a research program to find out main causes for low recapture rates. Our main hypotheses were: 1) Mortality of stocked smolts is high during their first year in the sea. 2) Mortality is caused mainly by starvation and indirect effects of food shortage.

More than 1,000 postsmolts were sampled in 1990 and more than 300 in 1991 from the Finnish coast of the Bothnian sea. Stomach contents and fullness, condition factor, growth and in some cases also energy reserves of postsmolts were determined.

This paper describes nutrition of postsmolts in 1990 and 1991 in the Bothnian sea. The effects of smolt size on nutrition, growth and survival are discussed and preliminary results from our stocking experiments concerning optimal smolt size are presented.

The Effect of Starvation on the Physiological Condition and Migratory Status of Baltic Salmon Smolts

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Abstract

In relation to the Finnish research program to find the main reasons for the low recapture rates of the releases in the Bothnian sea, effects of starvation on the smolts were tested.

In the spring after smolt release, Baltic salmon smolts were kept in cages outside Reposaari, in the Bothnian sea, for two months. Two groups, 1- and 2-year old fishes, were starved and two groups of the same ages, were fed. Control groups of the same fishes were reared at the inland fish farm.

The condition and the migratory status of the fish were estimated in May before transport to sea, and in June and July.

Forage of Anadromous Arctic Charr (*Salvelinus alpinus* L.) in an Estuary area in West Iceland

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Abstract

Food composition of Arctic charr was studied throughout the summer of 1987 in the Langárós esturay in Borgafjördur, west Iceland.

The length interval of chars was 9-37 cm with small charr dominating. Age ranged from one years old fish (1+) to four years old fish (4+), but two year old fish dominated the catches.

Forage of charr was active through summer but declined in June. Condition of fish improved during the study period with the exception of larger fish that showed decline in condition in late June.

Food of charr was mainly benthic. Planktonic prey types were in greatest abundance as diptera Imago in late May and at the end of July. The only nektonic prey type were sticklebacks (*Gasterosteus aculeatus* L.). Amphipods were most important prey type, but the charr also preyed on polychaets, dipteras and mysids in consideeerable quantities.

The Effect of Timing of Anadromous Arctic Char and Sea Trout Migration on Growth and Sea Stay in Finnmark, Northern Norway

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Abstract

The annual seaward migration of Arctic char and sea trout occurs in spring and the fish reside in coastal waters for a few weeks before returning to freshwater. During the sea stay the fish exhibit a rapid growth. The annual cycle of anadromous char and trout is therefore divided into two distinct periods, one of extremely rapid growth in summer and one of weight loss in winter.

This study were performed to compare the effect of timing of wild Arctic char and sea trout migration in two different size groups (first-time migrants and repeat migrants) from 1987 to 1991. The size groups were divided in groups of a ten days period on ascent from 1 May until 8 August. Growth and length of sea stay were calculated and growth were related to the sea temperature for both groups.

Processes Controlling Behaviour and Mortality of Salmonids during the Early Sea Life Period in the Ocean

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Abstract

Post-smolt mortality of salmon is highly variable and remains largely unexplained. Numerous correlations have been derived which relate physical conditions (water salinity, temperature, sea level, upwelling, winds, etc.) to subsequent marine survival rates of salmon. These patterns have proven useful for the important task of forecasting the annual production of adult salmon. However typically there is little consistency in these patterns between salmon stocks, and these patterns provide little insight into the mechanisms which actually control marine survival.

A more biologically-based approach has generally been more useful in probing the mechanisms of marine mortality. Direct experimentation (e.g. size, time or duration of smolt releases), and investigation of large scale patterns in marine growth and mortality can assist in identifying the timing, location, and possible causes of marine mortality. However these studies also typically show little consistency between stocks, or even between years for the same stock, and do not resolve the many possible explanations for the observerd patterns.

I belive that further progress now requires more focused research, directed at formulating and testing specific marine mortality hypotheses. One of the two main hypotheses currently proposed is that variability in ocean conditions affects the survival of salmon primarily by altering the intensity of predation, via changes in the distribution, species composition, or size of predators and/or prey.

During the past six years I have conducted two major field studies to investigate the "predation-intensity" hypothesis. The first study was designed to investigate predation of juvenile salmon in Barkley Sound, a large inlet on the west coast of British Columbia. The results have confirmed that there is substantial interannual and seasonal variation in the abundance and distribution of predators, and intensity of predation on juvenile salmon. The variation in predation intensity in Barkley Sound resulted primarily from much larger scale changes in ocean conditions.

The second study was designed to extend the near-shore work onto the continental shelf. To facilitate this work I developed a new paired beam trawl which consists of two large nets (112 m^2 mouth openings) which are towed simultaneously and continuously at 3-4 knots, 24 hours a day, to sample juvenile salmon and other fish species in the surface waters of the open ocean. The results obtained to date provide the first evidence of substantial interannual variation in distribution and migration routes of juvenile salmon, and composition of predator-prey complexes, in B.C. coastal waters. These variations also appear to be a direct response of juvenile salmon and other species to variations in ocean conditions. The next stage of this study will use this new sampling gear to test specific hypotheses concerning the mechanisms which control variations in growth and mortality of salmon in the open ocean.

Migratory Behaviour of Individuals and Schools of Atlantic Salmon Postsmolts Observed by Hydroacoustic Methods

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Abstract

The migratory behaviour of Atlantic salmon postsmolts has been studied with two different hydroacoustic methods. Individual smolt behaviour has been studied with the aid of hydroacoustic transmitters attached to fish migrating from the river Imsa in SW-Norway, while a SIMRAD EK-500 split beam echo sounder was used to observe the behaviour of smolt schools and individual fish on migration from a marine release site in a small bay on the west coast of Sotra Island, SW-Norway. The relationship between the observed behaviour and hydrographic conditions in the release area is discussed.

Selection Experiments in Salmon Ranching: Genetic and Phenotypic Family Correlation between Freshwater and Seawater Growth Rate and Postsmolt Survival of three Year-classes of Salmon Returning as Grilse

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Abstract

The Nordic project "Selection Experiments in Salmon Ranching" started in Iceland 1987 and is scheduled to finish in 1993. The aim of the project is to study the possibility for breeding and selection in sea ranching of Atlantic salmon.The results shown are from three year-classes of salmon returning after one year at sea (grilse). Mean weight and mean length from swim-up stage to 190 days of age in freshwater as well as size of smolts at tagging, mean weight of returning grilse and return rate of grilse is used to estimate the genetic- and phenotypic correlations between these life stages in a ranching program of Atlantic salmon. Results of three yearclasses will be used, data from about 350 families.

Individual Swimming Speed and Time Allocation during Smolt Migration in Salmon

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Abstract

The downstream swimming behaviour of two-summer-old salmon from the Umeälven hatchery stock was monitored throughout the natural smolting period. The experiment was performed in an artificial stream tank (area - 95 m^2) equipped with a PIT-tag monitoring system. About 200 individually PIT-tagged immature and previously mature young of salmon were analysed on the individual swimming speed in relation to water velocity and the proportion of time an individual fish show active versus passive displacement.

At peak migration the fish swam with more than double the water velocity, indicating active downstream migration. There were no difference in downstream swimming speed between migrating and nonmigrating fish independent of previous sexual maturity. But they used considerably different proportions of total time actually swimming faster than the water current. The main impression was however a small active part of the migration, never exceeding 10% of total time.

It has long been discussed if the downstream migration is active or passive. This study indicate that the salmon smolts deliberately use the water flow to reach the sea and, when necessary, swim actively downstream.

Dependency of Stocking Result on the Size of the Released Salmon Smolts (*Salmo salar L.*) in the Northern Part of the Baltic Sea

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Abstract

This paper describes the effects of smolt size on the stocking results of salmon in the northern part of the Baltic Sea. Expected stocking results and the variability of the stocking result are analysed in respect to the size of the smolts. Proportional uncertainty in the results in respect to environmental changes is analysed and the risk attitude of the managers is included to the decision analysis of salmon management. Negative effects of the uncertainty are discussed and some new basis for releasing programs are suggested.

Mortality Risks of Baltic Salmon during Downstream Migration and Early Sea-phase: Effects of Body Size and Season

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Abstract

Mortality risks in Baltic salmon during early migration was estimated through a sequential release experiment. Effects of fish size and time of release on survival rate were studied.

Already a protected transfer to the sea and acclimatization prior to release increased the recapture rates by 1.6 to 2.0 times compared to fish released in the river. Furthermore, fish that were delayed released had a 2.8 to 5.0 times higher recapture rate than smolts released in the river.

There were a strong positive correlation between size of the fish and recapture rates during all experimental years.

Mortality rates peaked during the downstream migration and entry to the sea. The weekly risk of mortality during the two first weeks was estimated to be 27.8%. Thereafter the mortality risk declined rapidly, and was found to be 6.1% per week during the following 8-9 weeks. From mid September until the end of November the mortality rate estimated was only 3.5% per week.

The mortality curve obtained by the release experiments stresses the high mortality risk for Baltic salmon during their downstream migration and first weeks in the sea. Althought Baltic salmon appears to migrate at a sub-optimal size with respect to survival during migration, the gain in migration survival due to larger size is considered be outweighted by an accelerated growth in the sea. The importance of a seasonal timing of transfer to sea and the effects of an endogenous circannually governed smoltification/desmoltification cycle, is discussed.

Migration and Nutrition in Wild and Hatchery Reared Salmon Postsmolt

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Abstract

A two-boat trawl was used to catch migrating wild and hatchery reared smolts in the Trondheim and Foldfjord in Norway. Stomachs of wild salmon smolts from the outer part of Trondheim fjord contained little food, adult diptera were most common and marine food items to less extend. Near the outlet of the river Orkla the stomachs were mainly full, insects originating from the river were most common. Hatchery reared smolts released in the Foldfjord had mainly empty stomachs, except for adult diptera and different food items of marine origin. Acoustic tagged smolts were migrating in the top layer following the currents.

Consequences of Parr Maturity in Salmon Stocking Programmes

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Abstract

This paper summarises our findings on smoltification in previously mature male parr from the Umeälven and the Skellefteälven stocks. Previously mature males were not as likely as immature fish to develop high hypoosmoregulatory ability and to show intensive downstream migratory behaviour. Instead, many early mature males started to remature sexually during the smoltification period and retained fresh water adaptations. Previously mature males released into the river Umeälven showed lower adult recapture rate compared to released immature fish. Recaptured individuals from the two categories had, however, the same growth pattern in the sea.

The smolting success of previously mature males seem to be related to body size and conditions for growth during the winter following sexual maturation. There was a positive effect of length at tagging on recapture rate among both immature fish and previously mature males, but the effect differed between the two categories. Our findings are discussed in relation to alternative smolt management strategies.

Effect of Different Photoperiod and Water Temperature on Smoltification in Atlantic Salmon (*Salmo salar*) and Arctic Charr (*Salvelinus alpinus*)

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Abstract

Development of smoltification and degree of sea water tolerance were measured in Atlantic salmon and Arctic char exposed to following experimental conditions:

Group 1: Natural photoperiod (NP) and ambient water temperature. Group 2: Simulated natural photoperiod (SNP) and ambient water temperature. Group 3: SNP and heated water (12C). Group 4: 24 hours light and heated water.

Fish from each group were sampled repeatedly from December until July measuring growth, seawater tolerance, activity of gill Na-K-ATPase and sexual maturation. Results will be presented and discussed.

Video-Documentation of Salmon Smolt Behaviour Comparison between Releases from a River and from a Small Coastal Bay

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Abstract

Salmon smolt behaviour after release at two different sites was studied in May/June 1992 by divers, and recorded with three underwater video cameras. At one site, 3,000 genetically tagged smolt were released into the River Öyreselv from a acclimatisation pond about 100 m from the river mouth. The downstream movements of the smolts to the estuary and the estuarine migration are described by video recordings. At the coastal site, Sotra Island, 39,000 smolts originating from the same rivers as the genetically tagged ones, were released in five batches. At this site, where the only freshwater source is the hatchery effluent collected in the bay behind an oil barrier, several distinct behaviour patterns were observed. The differences in behaviour of the smolts at the two sites are discussed in relation to temperature, geographic location and release strategy.

Effect of Smolt Size and Time of Release on Recapture of Atlantic Salmon (*Salmo salar*) in Sea Ranching, Southwest Iceland

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Abstract

Smolts were produced and released from the salmon ranching station Vogavík, in SW-Iceland. One- and two-year old smolts were kept in sea water in land-based tanks and released into the sea after a varying period of delay. Delayed releases were demonstrated to improve return rates in the Vogavík-experiment.

The effect of time of release and size of smolts on return rate, growth in sea, age at maturity and homing precision of adults are discussed.

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Workshop on the Population Ecology of the Nordic Crayfish Species

April 19-21, 1993, Älvkarleby Research Station, Sweden

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Introduction

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Interest in crayfish goes back centuries in several of the Nordic countries. This may be why there are a large number of research scientists and research teams dealing with a variety of aspects of crayfish biology in the Nordic countries. Having similar climates and the same species, we share several problems and questions of common interest concerning the ecology of long-lived crayfish species in temperate lakes.

There have been two previous Nordic crayfish meetings. The first was held at Erken, Sweden in 1977 and the second at Lammi in Finland 1979. There have also been two EIFAC (European Inland Fisheries Advisory Committee) meetings, focusing on aspects of the aquaculture and management of crayfish, in Trondheim in 1987 and in Kuopio, Finland in 1991.

In the spring of 1992 the research on freshwater crayfish in Sweden was evaluated by an international committee at the request of the Swedish Council for Forestry and Agricultural Research. The committee emphasized the importance of good communication within and between the groups working in the field of crayfish biology and management and they strongly recommended that intra-Nordic exchange should be continued and expanded. They suggested that this could best be accomplished by annual or biannual meetings at which information could be exchanged and cooperation and coordination could be achieved. They also suggested the development of a Nordic crayfish association and/or a network of scientists at universities and research institutes. Apart from promoting the exchange of ideas and results, such an open system would work to counter too much "inbreeding" in research and the approach to research.

The Institute of Freshwater Research therefore organized a Nordic crayfish meeting at Älvkarleby Research Station April 19-21, 1993. Initial contact had been made between Norway, Finland and Sweden and scientists working on crayfish in the Baltic countries, where the situation is much the same and where they face the same problems with their crayfish as we do. It was considered mutually beneficial to have participants from the Baltic countries as well and consequently they were invited to attend the meeting.

It was thought that the meeting would be most productive if it concentrated on a central theme. Moreover, the main part consisted of group discussions and only a minor part was devoted to ordinary talks. Although the two freshwater crayfish species, the noble crayfish (*Astacus astacus*) and the signal crayfish (*Pacifastacus leniusculus*) have been the focus of research in most Nordic countries for a long time, joint projects between the countries are still rare.

The purpose of the meeting was to further personal contact between researchers in the Nordic countries, to identify subjects and issues of common interest to crayfish researchers in the Nordic countries and to initiate joint projects. It aimed to deal with factors important to the population dynamics of natural populations of long-lived crayfish species.

The meeting was organized as a workshop starting with an introductory talk by an invited speaker, entitled "Factors affecting crayfish populations and crayfish behaviour". The participants had submitted abstracts in advance, addressing central problems of crayfish ecology and management. A selection of those fitting into the themes of the workshop were then presented as short talks (10 min). The rest of the workshop consisted of group discussions on two major themes. The themes for the working groups were:

1. Interspecific and intraspecific interactions, including predation, parasites and diseases.
2. Managing natural populations, including fisheries, pollution, stocking, regulations, and methodology for estimating size and structure of crayfish populations;

The workshop ended with a presentation of the results from the working groups and a general discussion involving all participants. Conclusions and future cooperative work were also formulated.

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Factors Governing Species Composition, Population Size, and Productivity of Cool-water Crayfishes

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Abstract

To assess what factors most often limit population size and production of cool-water crayfishes (Astacidae and Cambaridae), we review the literature and unpublished data on the role of density-independent and density-dependent abiotic and biotic factors. The literature and our data suggest that the abiotic factors temperature, calcium, pH, dissolved oxygen, salinity, and substratum may all be important. Among biotic factors, competition (for refuges, thermal habitat, and food) and predation (by invertebrates and vertebrates) may often be important. Data from northern Wisconsin lakes demonstrate that crayfish abundance is positively correlated with refuge abundance and negatively associated with abundance of predatory fishes. With a conceptual, diagrammatic model we argue that when physicochemical factors are within acceptable ranges, the most important limiting factor is often the strong interaction of intraspecific competition for habitat (or food) with predation by visually feeding fishes. Crayfish that are small or inherently poor competitors are excluded from shelter and are therefore more vulnerable to predation by fishes. Interaction of competition and predation is the major mechanism driving the ongoing invasion of northern Wisconsin USA lakes by *O. rusticus* and the consequent local extinction of pre-existing populations of *O. virilis* and *O. propinquus*. Management strategies to increase yield of cool-water crayfishes may include lake liming to increase calcium and pH, aeration to prevent summerkill or winterkill, fertilization to increase food, refuge additions to reduce competition and predation, fish management to reduce predatory fishes, and strict regulation of introductions of exotic crayfishes (which have often been disease vectors). In addition, increased human harvest of mature crayfish may often result in increased crayfish yield.

Keywords: Crayfish, population regulation, competition, predation, management.

Cool-water crayfishes of commercial interest

The goal of this paper is to assess the state of knowledge about factors controlling the species composition, size, productivity, and yield of natural crayfish populations of north-temperate regions. Five (Holdich 1988) and >300 (Hobbs 1991) species of crayfishes are native in Europe and North America, respectively, with the number of species declining with increasing latitude in North America (France 1992). In this paper, we focus on the small fraction of those species that occur in cool waters and are of current or potential commercial interest. According to Momot (1991; see also Holdich and Lowery 1988), these species are *Orconectes immunis*, *O. virilis*, *O. limosus*, *O. rusticus*, *Cambarus robustus*, and *Pacifastacus leniusculus* in North America, and *Astacus astacus* and *Austropotamobius pallipes* in Europe. The large maximum size and relatively high density of populations that are susceptible to harvest with simple traps makes these species commercially attractive for human consumption. Some information on closely related species is included for the insight it may provide on commercially valuable congeners.

These species belong to two families, Cambaridae (*Orconectes*, *Cambarus*) and Astacidae (*Pacifastacus*, *Astacus*, *Austropotamobius*), which have somewhat different life history features (Hobbs 1991). Life spans are typically 2.5-4.0 years for cambarids (Hamr and Berrill 1985, Hobbs 1991) and up to eight years for astacids (Hobbs 1991). Sexual maturity occurs at three months-two years in cambarids (Hamr and Berrill 1985, Hobbs 1991), but not until 2-4 years in astacids (Söderbäck 1993). Cambarid females extrude eggs in spring or summer and carry them for a few weeks, whereas astacid females extrude eggs in the fall and carry them through the winter. Both groups are typically iteroparous (Hobbs 1991). Relative to warmwater cambarids (e.g., *Procambarus clarkii*), the coolwater cambarids and astacids grow and mature more slowly, making them poor candidates for intensive aquaculture. Thus, the major focus for human exploitation is on managing wild stocks (Westman and Westman 1992).

Sound management, however, requires a more complete understanding than currently exists of what controls natural populations. For example, in two recent reviews of crayfish population biology, contradictory conclusions about what limits crayfish populations emerged. Momot (1991, p. 18) concluded that cool-water crayfish populations were ". . . food limited systems," whereas Hobbs (1991, p. 846) concluded that in the "apparent absence of food limitation in most systems, the principal resource bottleneck may be crevice availability." In this paper, we synthesize published and some of our recent, unpublished studies to highlight what we do and do not know about what controls crayfish species composition, population size, and production. Based on this synthesis, we propose for further evaluation some ideas to increase crayfish production.

Conceptual approach to population limitation

One of the central, mid-century debates in population ecology was whether natural populations were controlled by density-dependent or density-independent factors. The answer for most species is "both" (Krebs 1994, p. 322-335). For crayfish, we explore the importance of both density-dependent and density-independent factors (Table 1). By density-dependent, we mean any

Table 1. Factors that may control natural population density of cool-water crayfishes, with tentative assignments of their density-dependence and density-independence.

	Density-Independent	Density-Dependent
Abiotic Factors		
Temperature	X	
Calcium concentration	X	
Water-column pH	X	
Dissolved oxygen	X	
Salinity	X	
Substratum (refuge abundance)	X	X
Biotic Factors		
Food quality	X	
quantity		X
Intraspecific competition		
For refuges		X
For thermal niche		X
For food		X
Interspecific competition		
For refuges		X
For food		X
For mates		X
Intraspecific predation		X
Interspecific predation		
By other crayfishes		X
By invertebrates		X
By fish		X
By other vertebrates		X
By humans		X
Parasitism and disease		X
Autogenous molting mortality	X	

factor that causes mortality rate to be positively related to crayfish population size (or recruitment rate to be negatively related to population size). The distinction between density-independent and density-dependent has important implications for management of wild stocks.

If a limiting factor is density-dependent, then the potential exists for compensatory population responses to manipulations. For example, if competition with adult crayfish reduces survival of YOY crayfish, then harvesting of adult crayfish will decrease mortality rates of YOY crayfish. All other things being equal, crayfish standing stock will be little changed and crayfish production increased. This sort of response is typical of many finfish populations, and its potential for crayfish populations will be explored in a later section. If, on the other hand, the major limiting factor is density-independent, e.g., temperature, harvesting adults may only decrease crayfish population standing stock and production. As we review the factors most important in affecting crayfish populations below, we assess where possible the degree of density-dependence of each and how manipulations of that factor might increase crayfish production.

Factors affecting crayfish populations

Abiotic factors

Abiotic factors that are of obvious importance to crayfish populations include temperature, calcium concentration, pH, dissolved oxygen, salinity, and substrate particle size. The first three of these factors are the best-studied for crayfish. For calcium and pH, ability to predict which lakes or streams can sustain crayfish is good for a few species. However, for temperature, data come primarily from short-term laboratory assays with a few life stages. Thus, on the basis of temperature, our ability to predict ranges under current or future climates is poor.

Because several of these factors may interact strongly in affecting crayfish, it is important to consider them jointly in attempting to predict or affect the distribution or abundance of crayfish. For example, both oxygen (Järvenpää et al. 1983) and calcium (Malley 1980) balance are easier for crayfish to maintain at circumneutral relative to lower pH. These interactions are especially germane to field conditions because, for example, low pH lakes are usually also low calcium lakes. Thus, crayfish populations in marginal habitats are often under multiple stresses. Unfortunately, laboratory explorations of the affects of individual factors are often very inadequate for extrapolation to the field (France 1986, Appelberg 1989), and important interactions between limiting factors have often not been quantitatively explored.

Temperature

Surprisingly few laboratory tests or field surveys of temperature tolerance and preference have been conducted for cool-water crayfishes (Table 2). Those that have been done must be interpreted with caution because each investigator has used different methods and endpoint criteria, different acclimation temperatures and duration, and different life stages and different crayfish populations (possibly locally adapted). Nevertheless, the available values suggest that for preferred and maximum temperatures, little difference exists between astacids and cambarids: all species tested have a preferred temperature at or slightly higher than 20 °C, and a thermal maximum near 36 °C (Table 2). Minimum lethal temperatures are unavailable. *Orconectes virilis*, at least, cannot tolerate freezing (Aiken 1968). Obviously the 1-4 °C that prevails under ice in winter is not acutely lethal to any cool-water species, but high winter mortality of *A. pallipes* in a northern England stream was attributed to the chronic stress of low temperature (and/or low food) (Brewis and Bowler 1983).

Minimum temperatures for reproduction and molting suggest that cambarids can thrive at lower temperatures than astacids (Table 2). Field observations on when females first extrude eggs suggest that *O. propinquus* and *O. rusticus* begin laying at a cooler temperature than *O. virilis*, and that *Orconectes* in general reproduce at

Table 2. Summary of abiotic factors that may limit cool-water crayfish distributions. When both correlative field data and laboratory experimental results were available, we reported the correlative data for minimum and maximum values (see text). MIN = minimum temperature or pH for reproduction or molting, or the lowest pH value observed in a lake with a sustaining population; PREF = preferred temperature as determined in laboratory temperature gradient choice experiments and/or temperature at which growth was maximal in laboratory; MAX = upper lethal temperature; NA = not available.

	Temperature (°C)			$[Ca^{+2}]$ MIN (mg/L)	pH MIN
	MIN	PREF	MAX		
Astacids					
Astacus astacus	10-15[1]	16-24[2]	NA	NA	5.5[3]
Astacus leptodactylus	9[4]	22[4]	36[4]	NA	NA
Austropotambius pallipes	8[4]	21[4]	34[4]	5.0[5]	6.5[5]
Pacifastacus leniusculus	8[4]	23[4]	38[4]	NA	NA
Cambarids					
Cambarus bartoni	NA	NA	NA	NA	<4.6[6]
Cambarus diogenes	NA	NA	NA	<1.8[7]	NA
Cambarus robustus	NA	NA	NA	NA	<4.0[6]
Orconectes immunis	NA	18-23[8]	36[9]	NA	NA
Orconectes propinquus	5[11]-6[10]	NA	36[9]	NA	6.1[6]
Orconectes rusticus	5[11]	22[12]	36[9]-40[12]	2.5[7]	6.1[6]
Orconectes virilis	<7[11]-10[13]	24[14]	36[9]	1.4[15]-2.5[7]	5.5[16]-5.8[17]

[1] Abrahamsson 1972, Pursianien and Erkamo 1991; [2] Söderbäck et al. 1988; [3] Appelberg 1992; [4] Firkins and Holdich 1993; [5] Jay and Holdich 1977, 1981; [6] Berrill et al. 1985; [7] Capelli and Magnuson 1983; [8] Crawshaw 1974; [9] Lippson 1976; [10] Capelli and Magnuson 1974; [11] Berrill 1978; [12] Mundahl and Benton 1990; [13] Aiken 1969; [14] Peck 1985; [15] Reid and David 1990; [16] France 1984; [17] Malley 1980, France 1993, and France and Collins 1993.

lower temperatures than astacids (Table 2). Abrahamsson (1972) concluded from the distribution of *A. astacus* that at least three months of temperatures in excess of 15 °C were necessary for adequate survival and growth of juveniles, but found self-sustaining populations in cooler climates. Comparable range-temperature correlations for *Orconectes* are unavailable, but, as for *Astacus*, they would likely be higher than the temperatures for initiation of egg-laying reported in Table 2. However, for *O. rusticus*, it is clear that low temperatures did not define the northern limit of the historical distribution, because the crayfish continues to spread northward into Wisconsin, southern Ontario, and Lake Superior (Olsen et al. 1991, W. Momot, personal communication). Thus, except for *Astacus*, available temperature data are inadequate to predict the sustainability of populations transplanted accidentally or purposefully to new temperature regimes.

Clearly, however, productivity declines with increasing latitude (Momot 1986), and concordant fluctuations of crayfish annual production in neighboring lakes implies climatic control of production (Momot 1993). Such climatic control could, however, be via changes in energy input into lakes and consequent changes in food resource (i.e., not a direct effect of temperature). However, quantitatively predicting the impact of changes in temperature on crayfish distribution or production is currently impossible. Such changes could occur with waste heat discharge from industry or may be occurring globally (Schindler et al. 1990).

Calcium

Crayfish are restricted to waters providing calcium adequate for recalcification of the exoskeleton after molting. The little information that is available for astacids suggests that the limiting calcium concentration is about 5.0 mg/L (Table 2). For cambarids, a field survey in northern Wisconsin found no *Orconectes* in lakes with calcium <2.6 mg/L, but *Cambarus diogenes* occurred in one lake with 1.8 mg/L calcium (Capelli and Magnuson 1983, Table 2). In south-central Ontario (on the low-calcium Canadian Shield), *O. virilis* occurred in lakes with as little as 1.4 mg/L calcium (Reid and David 1990, Table 2). Differences in minimum [Ca] among regions may result from local adaptation of crayfish stocks or differences in the net effect on crayfish of total chemical profiles that differ between regions. In any case, the effect of calcium approximates a threshold, i.e., below the critical concentration, no crayfish occur, whereas above the critical concentration, no relationship between crayfish abundance and calcium exists (Capelli and Magnuson 1983).

pH

Field experiments and surveys strongly suggest that in both Scandanavia (Appelberg and Odelström 1986) and North America (Davies 1989, France and Collins 1993), anthropogenic acidification has caused the local extinction of crayfish. The lower tolerance limits of most astacids and *Orconectes* appear to be similar, in the range of pH 5.5-6.1 (Table 2). *Cambarus* spp., however, sustain populations in lakes with pH at least as low as 4.0 (Table 2). The higher tolerance of *Cambarus* for low pH and low calcium might make *C. robustus* the only candidate for management in low alkalinity, low pH lakes. One management alternative practiced already in Sweden is liming, which increases both calcium concentrations and pH (Appelberg and Odelström 1986, Appelberg 1992).

Dissolved oxygen

During summer stratification in lakes with hypoxic hypolimnia, crayfish are excluded from the hypolimnion by low oxygen (Fast and Momot 1973). Thus, summer hypolimnetic aeration might increase crayfish productivity in such lakes by increasing available habitat and raising hypolimnetic temperature.

Because hypoxia under winter ice is common in moderately productive and productive lakes, the potential for winterkill to limit crayfish populations is strong, but completely untested. To our knowledge, laboratory studies on low oxygen tolerance have not been conducted. Lippson (1976) reported that for *O. virilis*, *O. immunis*, and *O. propinquus*, mortality began in laboratory chambers when oxygen concentration dropped to 1.5 ppm, but he did not provide information on water temperature or crayfish size (both of which may interact strongly with oxygen tolerance). It is possible that lakes exist that provide good summertime conditions for crayfish, but lack crayfish because of winterkill. If such lakes exist, wintertime aeration could be considered.

Salinity

For coastal streams and rivers, salinity is a potentially important distribution-limiting factor that is clearly understudied. Some *P. leniusculus* hatchlings survive at salinities up to 17ppt, but with lower survival and growth than in freshwater (Rundquist and Goldman 1978). This species supports a commercial fishery in the Sacramento-San Joaquin Delta, California, USA. The tolerance of other crayfishes for salinity is unknown.

Habitat

Associations between substrate type and crayfish abundance indicate that most temperate crayfishes prefer firm, refuge-providing substrates, with adult crayfish density increasing with increasing particle size (Table 3). For example, in northern Wisconsin (USA) lakes, 1+ and older *O. rusticus* occurred in local densities of 2-3/m^2 in scattered cobble, but were as abundant as 34-82/m^2 in dense cobble habitat (the highest densities occurring in the spring) (Lorman 1980). Typically though, mean summer

Table 3. Rank of habitat associations for adult and juvenile (YOY) crayfishes in lakes (lentic) and streams (lotic) (1=highest density). For Lentic: Rocky=gravel-boulder; Firm=non-rocky but can be easily walked on by crayfishes; Soft=organic-rich sediments that crayfish at least partly sink in; Veg=partial or complete coverage by macrophytes. For Lotic: Rocky=same as for Lentic; Fine Sed/Pools=soft substrates in depositional areas; Veg=same as for Lentic. Possible reasons for habitat preference are given when indicated by the author(s). *=burrowing.

		Lentic				Lotic			
Species	Size	Rocky	Firm	Soft	Veg	Rocky	Fine Sed /Pools	Veg	Possible reasons for pattern
Astacidae									
Astacus astacus[1]	YOY	1			1				shelter,food, excluded by adults
	adult	1	2	3		1	2		shelter, food
Austropotamobius[2] pallipes	?					1			shelter
Pacifastacus leniusculus[3]	YOY	1		2		1			shelter
	adult	1		2			1		shelter, food
Cambaridae									
Cambarus bartoni[4]	all					1	2		?
Cambarus hubbsi[5]	?					1			shelter
Cambarus robustus[6]	all	1				1			?
Cambarus tenebrosus[7]	all			1*	2				?
Orconectes immunis[8]	all	2		3*	1				shelter
Orconectes luteus[9]	YOY					1		1	shelter
	adult					1		2	shelter
Orconectes longidigitus[10]	?					1			shelter
Orconectes neglectus[11]	adult					1			shelter
Orconectes obscurus[12]	all	1							shelter
Orconectes propinquus[13]	YOY	1				1			shelter
	adult	1			2	1			shelter
Orconectes puntimanus[14]	YOY				1	2		1	shelter
	adult					1		2	shelter
Orconectes rusticus[15]	YOY	1				1		2	shelter
	adult	1	3		2	1	1		shelter
Orconectes sanborni[16]	YOY					2			prefer banks
	adult						2		prefer banks
Orconectes shoupi[17]	all	1		2		1	2		?
Orconectes virilis[18]	all	1		3	2	2	1*	3	shelter

---

[1]Rögle Ponds, Sweden (Abrahamsson 1966); River Pyhäjoki, Finland (Niemi 1977); Slickolampi and Vuorijärvie lakes, River Raudanjoki, Finland (Westman and Pursiainen 1982); Sweden (Appelberg and Odelström 1986); The Morvan, Burgundy, France (Lachat and Laurent 1988); L. Steinsfjorden, Finland (Skurdal and Qvenild 1988, Skurdal et al. 1988); [2]The Morvan, Burgundy, France (Lachat and Laurent 1988); [3]woodland stream, Oregon, USA (Mason 1975); Lake Tahoe, California-Nevada, USA (Flint and Goldman 1977); L. Slickolampi, Finland (Westman and Pursiainen 1979); southern Sweden pond (Blake and Hart 1993); [4]Kawartha Lakes Region (KLR), Ontario, Canada (Berrill 1978); [5]James River, Virginia, USA (Mitchell and Smock 1991); [6]N. Sylamore Creek, Ozark Mountains, Arkansas, USA (Payne 1986); [7]KLR (Berrill 1978); [8]Little Sioux River, Minnesota-Iowa, USA (Bovbjerg 1970); KLR (Berrill 1978); Wisconsin, USA (Rach and Bills 1989); [9]Current and Jacks Fork Rivers, Missouri, USA (Rabeni 1985); [10,11]N. Sylamore Creek, Ozark Mountains, Arkansas, USA (Payne 1986); [12]KLR (Berrill 1978); [13]Trout Lake, Wisconsin, USA (Capelli 1975); KLR (Berrill 1978); northern Wisconsin, USA (Capelli and Magnuson 1983); Lake Michigan, USA (Quinn and Janssen 1989); Wisconsin, USA (Hill and Lodge in press); [14]Current and Jacks Fork Rivers, Missouri, USA (Rabeni 1985); N. Sylamore Creek, Ozark Mountains, Arkansas, USA (Payne 1986); [15]Doe Run, Kentucky, USA (Prins 1968); KLR (Berrill 1978); Upper Sugarbush Lake, Wisconsin, USA (Lorman 1980); northern Wisconsin, USA (Capelli and Magnuson 1983); North Fork Creek, Ohio, USA (Butler and Stein 1985); Wisconsin, USA (Hill and Lodge in press); [16]North Fork Creek, Ohio, USA (Butler and Stein 1985); Ohio, USA (Mather and Stein 1993); [17]Mill Creek, Tennessee, USA (Miller and Hartfield 1987); [18]Massachusetts, USA (Camougis and Hichar 1959); small stream southeastern Michigan, USA (Hazlett et al. 1974); KLR (Berrill 1978); northern Wisconsin, USA (Capelli and Magnuson 1983); Lake Michigan, USA (Quinn and Janssen 1989); James River, Virginia, USA (Mitchell and Smock 1992); Wisconsin, USA (Hill and Lodge in press).

densities of 1+ and older *Orconectes* in rocky habitats range from about 1-15 crayfish/m^2 (Capelli 1975, Lorman 1980).

Among many of the possible parameters influencing crayfish habitat choice within a body of water are shelter and food availability (Table 3), temperature (Momot and Gowing 1972, Capelli and Magnuson 1975, Mundahl and Benton 1990), water velocity (Klosterman and Goldman 1981, Maude and Williams 1983, Mather 1990), and dissolved oxygen (Momot 1984, Skurdal et al. 1988).

Capelli and Magnuson (1983), in an extensive analysis relating Orconectid crayfishes' abundance in 67 northern Wisconsin (USA) lakes to various morphoedaphic and biogeographic factors, concluded "that substrate is the most important variable related to total crayfish abundance". Our analysis of data from a 1987 21-lake survey in the same region is consistent with this. We found a significant positive relationship (P=0.004) between abundance of cobble habitat and trap catches of crayfish (Fig. 1), suggesting that system-wide availability of preferred habitat strongly influences crayfish population size. The relationship suggests that lakes with less than 15-20% of the littoral zone occupied by rocky substrate can support only very low crayfish populations (Fig. 1). Above this threshold, average crayfish abundance is much higher. However, the range of residual variance in trap catches at higher cobble availability (Fig. 1) suggests that habitat or refuge availability establishes only the upper limit of potential crayfish abundance, while other factors interact with habitat availability to determine if that limit is reached.

Shelter limitation might be greater for juvenile than adult crayfish because juveniles are more susceptible to fish predators (DiDonato and Lodge 1993) and molt more frequently than adults (at which time they are susceptible to both fish predators and cannabalism). In an experiment with unlimited food and no predators, survival of YOY *Procambarus clarkii* increased with increased shelter (presumably because of reduced cannabalism) (Figiel et al. 1991). Large crayfish suffer less threat from fish predation, but if cannabalism at molting remains a major threat for adults, then shelter limitation for adults could have greater population consequences than that for juveniles because shelter size scales with crayfish size (Foster 1993), fewer large interstices exist (Caddy 1986), and the reproductive value of adults is far greater than for juveniles.

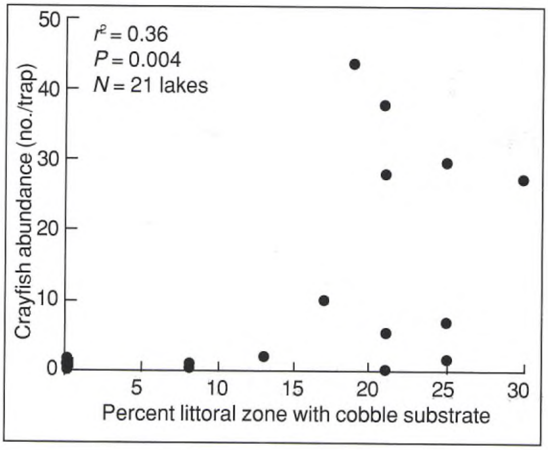

Fig. 1. Number of crayfish caught per trap in 21 lakes surveyed in 1987. For sampling, the shoreline of each lake was divided into 12-36 equal-length sectors, with the habitat in each sector categorized as rocky (cobble), vegetated, or open (non-rocky, unvegetated). One crayfish trap was set in each sector using methods described in Lodge et al. (1986). Percent littoral zone with cobble was determined in each lake by the number of cobble shoreline sectors/total number of sectors in the lake. From unpublished data of D.M. Lodge, R.A. Stein, K.M. Brown, and A.P. Covich.

In lakes or streams where habitat is limiting, addition of refuge-providing substrata (e.g. drain tiles, bricks, rocks) may be a viable management strategy to increase population densities and harvest (Fürst 1977, Hogger 1988, Westman 1991). Populations of several lobsters, including American (*Homarus americanus*) and spiny (*Panulirus argus*) lobsters, are thought to be shelter-limited (Addison 1986, Fogarty and Idoine 1986, Conan 1986, Eggleston and Lipcius 1992). If the most shelter-limited life stage for crayfish can be identified and shelters added for that size, crayfish production and yield may also be enhanced.

Biotic factors

Diet

All astacid and cambarid crayfishes are omnivorous (Table 4). Adult consumption of animal material falls below 10-30% by volume of their total diet (True 1990), while juvenile diets may consist of as much as 43-80% animal material (Westman et al. 1986, Tcherkashina 1977). Detritus is often a very abundant food source for adult crayfishes, but is generally thought to be low quality because nitrogen content of detrital leaves is low (usually about 2%) (Kaushik and Hynes 1971, Newman 1991). In contrast, actively growing crayfish require that about 30-35% of their diet consists of protein (D'Abramo and Robinson 1989). Thus, a super-abundance of low quality food, such as detritus, allows moderate to high survival, but little growth (Hill et al. 1993).

The greater consumption of animals by juvenile crayfish is consistent with the documented requirement by juvenile crayfish of calorie- and protein-rich food items such as insect larvae and gastropods in their diets for growth (Mason 1975, Huner and Romaire 1979, Odelström 1988, D'Abramo and Robinson 1989, Brown et al. 1990, Hill et al. 1993). When detrital diets of crayfish are supplemented with animal material, growth, but not survival, increases significantly (Odelström 1988, Hill et al. 1993). The paradox of why survival does not increase with high quality diets may be explained by the inherent risks of frequent molting with rapid growth. Many crayfish die while molting, perhaps because of the inherent physiological stresses (Hill et al. 1993) and because of increased vulnerability to predation or cannibalism as fresh molts (Capelli 1975).

Because they are not growing rapidly, larger crayfish apparently require less protein in their diets than juveniles, but they experience increased total energy requirements and compensate by simply consuming greater quantities of non-animal items such as detritus (Lorman 1975). In addition, because of their size, large crayfish may be less effective than juveniles as

Table 4. Diets of crayfish as determined by percent of materials in gut or ranked by abundance in gut (1=most abundant). The live plant category includes algae. With the exception of *O. propinquus*, rankings from different authors agreed.

	Juveniles			Adults		
	animal	live plant	detritus	animal	live plant	detritus
Astacidae						
Astacus astacus[1]	~20-43%	~21%	41-54%	6-29%	~80%	7-18%
Astacus leptodactylus[2]	(1)	?	?	?	?	?
Pacifastacus leniusculus[3]	(1)	(2)*	(2)*	(3)	(2)	(1)
Cambaridae						
Orconectes propinquus[4]	?	?	?	(2)	(1)	(3)
Orconectes propinquus[5]	?	?	?	6%	12%	27%
Orconectes rusticus[6]	(1)	(2)*	(2)*	(2)	(1)	(1)
Orconectes sanborni[7]	(1)	(2)*	(2)*	(2)	(1)	(1)
Orconectes virilis[8]	(1)	(2)*	(2)*	(3)	(2)	(1)

* detritus and live plant material were not distinguished.

[1]Appelberg 1990, Skurdal et al. 1988, Odelström 1988, Taugbøl et al. 1987, Hessen and Skurdal 1986, Westman et al. 1986, Abrahamsson 1966; [2]Tcherkashina 1977; [3]Mason 1975, Flint and Goldman 1975; [4]Capelli 1980; [5]Saffran and Barton 1993; [6]True 1990, Lorman 1975; [7]True 1990; [8]Momot et al. 1978.

predators on more abundant small invertebrates in smaller interstitial spaces (Abrahamsson 1966). Adult crayfish may, in effect, have less animal matter available to them for consumption than juveniles.

In laboratory choice experiments, adult *A. astacus* (Hessen and Skurdal 1988) and adult *O. rusticus* (Lorman 1980) both preferred animal over live plant material. However, for both *A. astacus* (Söderbäck et al. 1988) and *O. rusticus* (Lorman 1980), natural diets are largely detritus, whereas highest growth in laboratory experiments is on animal diets (Hill et al. 1993). These patterns suggest that protein is a limiting factor for individual growth (and perhaps population growth) in many populations. Size-specific diets of crayfish thus appear to be consistent with a trade-off between preferences for food and food availability, between less abundant high quality foods which would allow increased growth and reproduction and abundant lower quality foods which can be consumed in sufficient quantities to meet energy demands. Rapid growth in crayfish, and consequent larger size at a given age, is positively related to egg production (Abrahamsson 1971, Skurdal and Qvenild 1986, Corey 1987), success in competitive interactions (Bovbjerg 1956, Phillips 1984, Butler and Stein 1985, Rabeni 1985) and predator avoidance (Stein 1977, DiDonato and Lodge 1993, Garvey et al. 1994). Rapid growth is particularly important for juvenile crayfish because it enables them to more quickly pass through competitive bottlenecks and sizes of susceptibility to predation (Quinn and Janssen 1989). Competition and predation are more fully discussed in a later section.

Populations of crayfish, even recently established ones like *Orconectes rusticus* in many northern Wisconsin lakes, do not seem to show boom-bust cycles. Indeed, even northern Wisconsin populations that have almost eliminated macrophytes and snail prey (Weber and Lodge 1990, Lodge et al. 1994) show no strong declines in population. Detritus and periphyton, which are poor quality (Hill et al. 1993) but abundant, may sustain dense populations (but presumably in a state of low productivity). Thus, omnivory by crayfish may dampen resource-based fluctuations of populations, and maintain the long-term dominance of crayfish in food webs (Lodge et al. 1994).

Competition

There is a growing body of evidence that competition (intra- and interspecific) for habitat and food affects crayfish populations. Bovbjerg (1956) observed that larger size confers a competitive advantage and that male crayfish typically dominate female crayfish in intraspecific competitive encounters. Other researchers have suggested that interspecific competition for habitat results in competitive exclusion (Penn and Fitzpatrick 1963, Aiken 1965, Bovbjerg 1970, Berrill 1978, Capelli and Munjal 1982, Flynn and Hobbs 1984, Rabeni 1985, Lachat and Laurent 1988, Hazlett et al. 1992) and that competition for food may be more intense at higher latitudes due to decreased resource availability (France 1992). Laboratory evidence indicates crayfish interact aggressively when food or shelter is limiting (Capelli and Munjal 1982, Capelli and Hamilton 1984), suggesting that interference competition may be common.

Intraspecific competition

For habitat. Crayfish abundance increases with increasing availability of preferred habitat (cobble) on within-lake and between-lake scales (see above), suggesting that refuges may be a limiting resource. Some evidence suggests that refuges are the object of intraspecific competition. For many species, adults and juveniles prefer similar habitat, but adults may exclude juveniles from preferred habitat (Table 3). For example, adult female *O. virilis* in oligotrophic pothole lakes of Michigan (USA) are excluded from shallower littoral cobble habitats by male crayfish (Jones and Momot 1981). Large male *A. astacus* exclude juveniles and females from refuge- and food-rich rocky littoral areas, restricting the competitively inferior juveniles and females to the resource-poor lower littoral zone (Abrahamsson 1966). Success in competition for shelter is clearly related to both size and prior ownership (Ranta and Lindström 1993).

Exclusion of competitively inferior individuals from preferred habitats, at least in these examples, seems to have direct consequences for the reproductive potential of crayfish populations. Females relegated to poor habitats may experience increased vulnerability to predation and food limitation, resulting in reduced survival, growth, and fecundity.

For thermal niche. Adult and juvenile *O. rusticus* prefer habitats where water temperature approximates their joint thermal optimum for survival (Mundahl and Benton 1990). However, adults and juveniles are usually not found in the same habitat (Table 3), suggesting that adult crayfish competitively displace juvenile conspecifics into habitats which are shallower and warmer. In warmer habitats, juvenile survival is decreased but growth is increased (Mundahl and Benton 1990), which would increase their size-related success in competition, reproduction, and predator avoidance. The net impact on population growth is unclear.

For food. Three lines of evidence suggest food limitation exists and that intraspecific competition for food occurs. First, growth of 1+ crayfish in *ad libitum* laboratory experiments is more rapid than that of conspecifics observed in lakes of similar latitude: *Orconectes rusticus* increases in carapace length by 0.4%/day with unlimited food (Hill et al. 1993), compared to 0.3%/day in Upper Sugarbush Lake (Wisconsin, USA), translating into about 43% and 32% increases in carapace length, respectively, over an assumed 108 day growing season (calculated from Lorman 1980 data). More strikingly, *O. virilis* gains weight at a rate of 2.1%/day with unlimited food in the laboratory (Hill et al. 1993) while weight gain is only about 0.5%/day in a Michigan lake (USA) (calculated from Momot and Gowing 1975 data).

Second, a positive relationship exists between mean annual primary productivity and growth of *O. virilis* in six oligotrophic Ontario lakes (France 1985). Because pelagic primary production probably correlates positively to availability of benthic food, the data suggest that crayfish growth is food limited.

Third, comparison of two similar oligotrophic Michigan (USA) lakes shows that the lake with more detrital material reaching habitats occupied by females (West Lost) produced about twice the density of breeding females relative to the other lake (North Twin) (Jones and Momot 1981).

Possible effects of increased intraspecific competition for food with increased population density include decreased survival of the more abundant age-classes (YOY and 1+ crayfish) decreased growth rates of surviving crayfish (Svärdson 1949), increased time until first reproduction, increased time between reproductive bouts (Huner et al. 1990), and decreased fecundity of surviving females.

Interspecific competition

Among crayfishes. At least partly as a result of interspecific competition, the introduced North American crayfish *P. leniusculus* is replacing the native species *A. astacus* in some European waters. Adult and juvenile, but not young-of-year, *P. leniusculus* are more successful than *A. astacus* in aggressive encounters such as might result from competition for food or refuge (Söderbäck 1991). *Pacifastacus leniusculus* also establish dominance hierarchies, reducing the energetically demanding activity of intense aggressive encounters, while *A. astacus* do not (Söderbäck 1991). *Pacifastacus leniusculus* may thus be able to invest more energy in growth and reproduction than *A. astacus*. Consistent with this idea, *P. leniusculus* grow more rapidly than *A. astacus*, reach maturity at an earlier age, and produce more eggs per female, all probably contributing to the greater success of *P. leniusculus* (Abrahamsson 1971). The growth rates of *A. astacus* stocked in low densities with abundant food and no interspecific competition (Gydemo and Westin 1988) match those measured for allopatric *P. leniusculus* (Abrahamsson 1971). This suggests that in sympatry, *A. astacus* suffer more than *P. leniusculus* from the effects of interspecific competition for food.

Another crayfish species replacement is occurring in northern Wisconsin, with *O. rusticus* replacing the native crayfish *O. virilis* and a previous invader *O. propinquus*. A variety of replacement mechanisms have been proposed including interspecific competition for both refuges and food (Hill and Lodge in press, Hill 1994). Interspecific competition for refuge leads to exclusion of *O. virilis* and *O. propinquus* from preferred cobble habitat (Hill and Lodge in press). Competition with *O. rusticus* for food reduces growth of *O. virilis* and increases mortality of *O. propinquus* (Hill 1994). Thus, strong evidence suggests that interspecific competition is an important mechanism by which *O. rusticus* replaces *O. virilis* and *O. propinquus* (see also later section).

With other organisms. Not only do crayfish compete with other species of crayfish, but they also compete with other organisms that experience resource overlap with the crayfish. Predation rates by *O. virilis* on fish eggs declined by 50% in the presence of competing slimy sculpin (*Cottus cognatus*), while sculpin feeding rates were unaffected by the presence of crayfish (Miller et al. 1992). The interactions of crayfish with non-crayfish competitors and their consequences for crayfish require futher study.

Predation

Earlier sections of this paper have established that many north temperate crayfishes prefer cobble substrates. In this section, we argue that crayfish habitat choice is strongly influenced by predation. Cobble habitats containing dense populations of crayfish probably cannot, in the long term, supply crayfish in these depleted habitats with abundant high quality food (see Abrahamsson 1966, Flint and Goldman 1977, Söderbäck et al. 1988). When crayfish abundances are high, aquatic invertebrates and macrophytes are depleted (Abrahamsson 1966, Avault et al. 1975, Saiki and Tash 1979, Lodge and Lorman 1987, Chambers et al. 1990, Hanson et al. 1990, Weber and Lodge 1990, Lodge et al. 1994). Thus, the observed preference by crayfish for cobble habitat is probably due to other factors, especially the need for shelter from predation (Stein and Magnuson 1976, Appelberg and Odelström 1986, Quinn and Janssen 1989) and cannibalism (Mason 1977, Gowing and Momot 1979). Given the diversity of terrestrial and aquatic predators that eat crayfish (Hobbs 1993), strong potential exists for predation to significantly affect crayfish species composition, abundance, and production.

Direct effects

By other crayfish. Crayfish exoskeleton parts are frequently found in crayfish guts (Lorman 1975, Mason 1975, Westman et al. 1986, Growns and Richardson 1988 cf. Momot 1993), but those parts could come from already dead crayfish or exuvia. In laboratory tanks, whether or not food supplements are available, adult male *P. leniusculus* and non-maternal female crayfish eat young crayfish (Mason 1977). *Orconectes rusticus* apparently kills *O. propinquus* in field cages (Hazlett et al. 1992). On the other hand, increased shelter availability in aquaria reduces cannibalism of YOY by adult *A. astacus* (Gydemo et al. 1990). Likewise, non-molting YOY *O. propinquus* (Capelli 1975) and *O. virilis* (Momot 1993) evade foraging adults in aquaria containing adequate shelter. The weight of available evidence suggests, then, that cannibalism is rare for non-molting individuals. Frequency of cannibalism on molting individuals and the importance of cannibalism in population regulation require testing (Dionne 1985).

By other invertebrates. In laboratory aquaria, Aeshnid dragonfly naiads have high feeding rates on YOY *Procambarus* (Witzig et al. 1986) and *Astacus* (Jonsson 1992). For example, without shelter, predation by one dragonfly larva (*Aeshna grandis*) eliminated 25 YOY *A. astacus* in seven days, and even with shelter, survival of YOY crayfish was low (Jonsson 1992). A single dragonfly larva had a greater impact on young crayfish than an adult crayfish. Similarly, in field cages, three Aeshnids/m^2 reduced abundance of *O. virilis* YOY (Dye and Jones 1975). The role of dragonfly larvae and other invertebrate predators in limiting crayfish populations requires further testing.

By vertebrates - terrestrial and amphibious. Many terrestrial and aquatic vertebrate predators use crayfish as a major food source (Penn 1950, Neill 1951, Hobbs 1983, Hogger 1988). In southern Florida (USA) cypress swamps, Everglade edge habitats, and lake colonies, crayfish comprise 60-70% of the diet of white ibis (*Eudocimus albus*) (Kushlan 1979). Other, more northerly wetland birds, reptiles, and amphibians (Penn 1950, Neill 1951) and terrestrial predators like muskrat and mink consume crayfish, perhaps to the point of population reduction (Westman 1991), but significant impacts on crayfish populations have not been rigorously documented. Like catfishes in central American streams (Power 1984), crayfish in lakes, larger streams and rivers may avoid shallower waters where they would be more susceptible to wading bird and mammalian predators, but no research has addressed this hypothesis.

By vertebrates - fish. Fishes often consume a large fraction of crayfish production (Rabeni 1992, Roell and Orth 1993), and considerable evidence suggests strongly that predation by fishes reduces crayfish populations (Table 5). A correlative analysis of historical information in Sweden showed that crayfish were more abundant in lakes with few to no eel and less abundant in lakes that yielded high eel catches (Svärdson 1972). Additionally, many crayfish populations rebounded after eels were excluded by dams, suggesting that eels substantially reduce crayfish populations. In Finnish lakes, crayfish populations increased dramatically when fish were removed by rotenone, suggesting a release of crayfish populations from predation pressure (Storberg 1980 cited in Westman 1991).

In North America, fish predators of crayfish include smallmouth bass (*Micropterus dolomieui*) (Penn 1950), largemouth bass (*Micropterus salmoides*) (Taub 1972, Saiki and Tash 1979, Rach and Bills 1989, Garvey et al. 1994), rock bass (*Ambloplites rupestris*) (Probst et al. 1984) and yellow perch (*Perca flavescens*) (Quinn and Janssen 1989). In Ohio (USA) streams, a significant inverse relationship exists between densities of predaceous fish and crayfish, suggesting fish predators reduce crayfish abundance in stream populations (Mather and Stein 1993).

Table 5. Effect of fish predators on adult crayfish population size in experimental (E) and correlative (C) field studies. - = negative impact; 0 = no impact.

Crayfish species	Predator species	Type of Study	Impact	Reference
Astacus astacus	Eel (*Anguilla anguilla*)	C	-	Svärdson 1972
Orconectes rusticus, *O. sanborni*	Smallmouth (*Micropterus dolomieui*) and rock bass (*Ambloplites rupestris*)	C	-	Mather and Stein 1993
O. rusticus, *O. propinquus*, *O. virilis*	Largemouth bass (*Micropterus salmoides*) and Yellow Perch (*Perca flavescens*)	C	-	this paper
Orconectes nais	Largemouth bass	E	-	Rickett 1974
Orconectes virilis	Largemouth bass	E	-	Saiki and Tash 1979
Orconectes immunis	Largemouth bass	E	-	Rach and Bills 1989
Orconectes virilis	Brook trout (*Salvelinus fontinalis*)	E	0	Gowing and Momot 1979

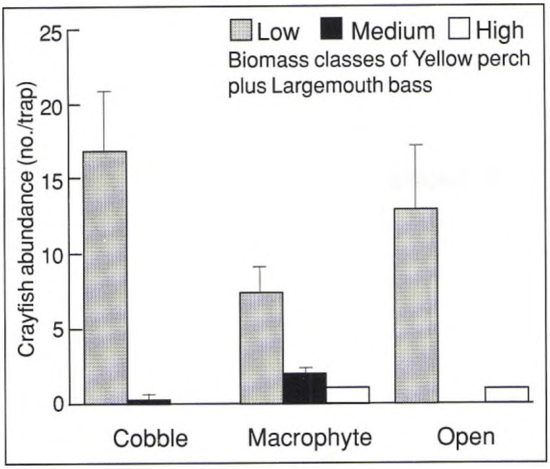

Fig. 2. Crayfish abundance in 21 northern Wisconsin lakes as a function of substrate type and abundance of two species of predatory fishes, yellow perch (*Perca flavescens*) and largemouth bass (*Micropterus salmoides*). Fishes were sampled with a boom electroshocking boat. Crayfishes, predominantly *Orconectes rusticus* but including *O. propinquus* and *O. virilis*, were trapped with standard methods (Lodge et al. 1986). From unpublished data of R.A. Stein, D.M. Lodge, K.M. Brown, and A.P. Covich.

For 21 northern Wisconsin (USA) lakes, crayfish abundance does not correlate strongly with abundance of all fishes, but does correlate negatively with abundance of largemouth bass (*Micropterus salmoides*) and yellow perch (*Perca flavescens*), species known to be predators of crayfishes (Fig. 2).

Rickett (1974) stocked six experimental ponds with three densities of adult largemouth bass (0.015, 0.03, and 0.06/m^2) to determine their impact on densities of existing crayfish populations (n = 2 for each bass density). A negative relationship existed between bass abundance and the number of *O. nais* recovered from the ponds after one year. In an 11 ha. hatchery pond stocked with bass (1.8 bass/500 m^2), density of *O. immunis* declined 98% in one year from an initial density of 5.8/m^2 (Rach and Bills 1989). The second experiment was not replicated, and neither experiment was run long enough to detect the effects of year to year variation, nor very representative of what may happen in waters with much benthic structural complexity, but they are consistent with other evidence suggesting predation reduces crayfish population size.

In Parker Canyon Lake, Arizona (USA), crayfish abundance declined as predation by largemouth bass increased with decreasing abundance of water milfoil (*Myriophyllum exalbescens*) (Saiki and Tash 1979). Laboratory experiments confirmed that greater benthic structural complexity (more macrophytes) decreased predator impact on crayfish numbers (Saiki and Tash 1979), suggesting that in structurally complex lakes, such as those with abundant cobble or macrophytes, the impact of predators on crayfish populations may be less than in lakes with less structure.

In the only field study suggesting no fish effect (Table 5), Gowing and Momot (1979) stocked three lakes with three densities of brook trout (*Salvelinus fontinalis*) and monitored *O. virilis* populations for two years. Stocked trout were small (127-152 mm total length at stocking and 130-370 mm at end of period) and only able to consume juvenile crayfish. In lakes stocked with fewer trout, 1-2% of the juvenile crayfish were consumed. In the lake with high densities of trout, predation on juveniles was 40%. However, even at high trout densities, no impact on recruitment to age one existed because predatory mortality was compensatory, not additive (Gowing and Momot 1979). For other crayfishes, e.g., *A. astacus*, whether heavy fish predation on juveniles (Söderbäck 1992, Svennsson 1993) reduces adult populations is unknown. Results of all other studies, with larger and/or natural assemblages of fish predators, suggest that fish predation significantly reduces adult crayfish population size (Table 5). The potential exists that such predation by fishes could increase crayfish production (Rabeni 1992), even while decreasing standing stock, as predation by humans sometimes does (see below).

By humans. In northern Europe, crayfish are favored human food, with wild populations harvested by humans since the 16th century or before (Westman 1991). Anecdotal evidence suggests that some European populations were overfished to the point of dramatically decreased yield. However, recent, quantitative evidence suggests this is probably rare and, in fact, difficult to accomplish (Qvenild and Skurdal 1986, Momot et al. 1990, Svärdson et al. 1991, Westman 1991).

Populations of *O. virilis* can withstand exploitation rates of at least 60% of age 1+ and older crayfish (Momot 1993). Such high harvest rates increase production and yield (Morgan and Momot 1988, Westman 1991, Svärdson et al. 1991, Momot 1993), probably by decreasing interference competition between YOYs and older males (ages 1+ and 2+) (Morgan and Momot 1988, Momot 1993). Thus, for conventional trap harvesting methods, which are selective for individuals larger than the minimum size at maturity, unlimited harvest may be appropriate (Momot 1993).

Because astacids generally mature at older and larger sizes than *Orconectes*, however, size-limited fisheries like those practiced historically in Europe (Westman and Westman 1992) may still be appropriate. Work on exploited populations of both *O. virilis* (Momot 1993) and astacids (Huner et al. 1991, Erkamo et al. 1992, Skurdal et al. 1993) suggest the following criteria should be applied to maximize sustainable yield. Minimum size (whether resulting passively from trapping methods or from size sorting by fishermen) must be larger than the size at maturity and the fishing season must start after females release their young. These criteria might lead to absence of restrictions on North American *Orconectes*, and reductions in minimum size limits for some European populations of astacids (Huner et al. 1991, Erkamo et al. 1992).

Where individual crayfish size is important to the market, the impact of harvesting practices on individual size as well as on total yield is relevant. Exploitation-induced increases in growth (Momot 1993) can lead to an increase in mean size (Huner and Lindqvist 1988), but probably more typical for both astacids (Svärdson et al. 1991) and *Orconectes* (Fig. 3) is a reduction in mean size of crayfish because of the selective removal of large crayfish. Thus, maximizing yield may produce a smaller than desired mean individual size for human consumption. Smaller size may, however, be acceptable (or desired) for the fish bait market.

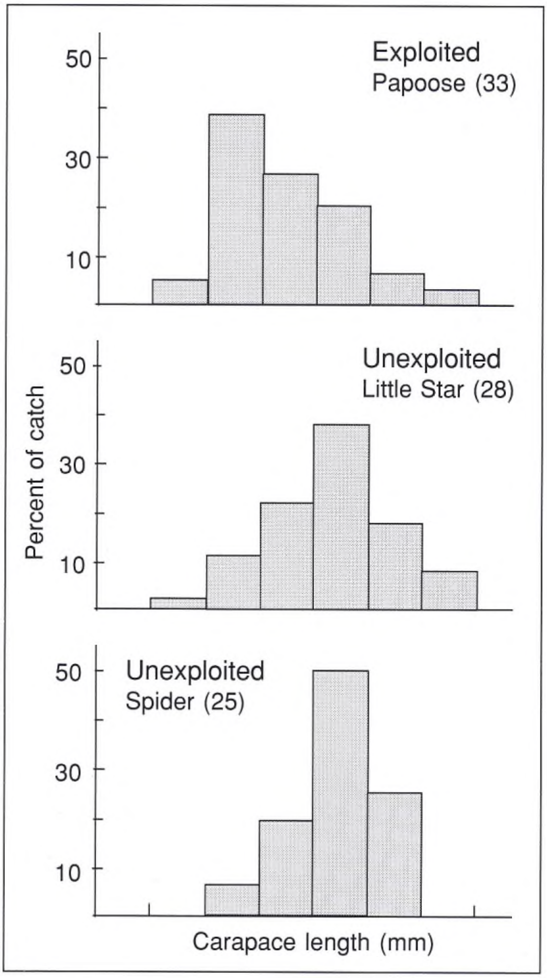

Fig. 3. Size distribution and mean catch per trap (in parentheses) of male *Orconectes rusticus* in one exploited (Papoose Lake) and two relatively unexploited Vilas County, WI (USA) lakes in August 1987. Note the smaller modal size (25-30 mm) in the exploited relative to the unexploited lakes (35-40 mm). For each lake, N=50 individuals. Previous to sampling, Papoose Lake had been heavily trapped by a commercial fisherman for at least seven years. Trap methods were as described in Lodge et al. (1986).

Indirect and sublethal effects

Fish predation not only causes significant mortality of crayfish, but it may also have long-term sublethal effects on surviving crayfish, including reduced growth, survival, and reproduction. Reductions in crayfish activity in response to predation risk from fishes have been well documented for astacids (Appelberg 1986, Hamrin 1987) and cambarids (Stein 1977, Garvey et al. 1994, Hill and Lodge in press). That reduced growth also results from predation risk is well documented for *P. leniusculus* (Appelberg and Odelström 1988) and *Orconectes* spp. (Hill 1994). Implications of reduced growth include greater length of time until first reproduction (Appelberg and Odelström 1988), reduced fecundity due to smaller size (Corey 1987), reduced success in aggressive encounters (Rabeni 1985, Söderbäck 1991, Hill 1994), longer period of time spent in predation-susceptible size range, and increased probability of predation by size-selective predators (DiDonato and Lodge 1993, Garvey et al. 1994). These sublethal effects of predation probably effect a much greater number of individuals than direct predation and may therefore be as important or more important to crayfish population size and production than direct predation.

Ectosymbionts and disease

Many species of protozoa are associated with crayfish (Sprague and Couch 1971), but, with the exception of *Thelohania* (see below), the impact of most on crayfish populations is unknown. Likewise, branchiobdellid annelids are non-host-specific ectosymbionts on many species of crayfish and other Crustacea (Holt 1975, Brinkhurst and Gelder 1990). About 100 species exist, all of which are typically described as "commensal." Of the few whose relationship to the crayfish has been rigorously examined, some are parasitic and some are not (Brinkhurst and Gelder 1990, Keller 1992). The impact of the parasitic species on crayfish populations is unknown.

Many helminths inhabit crayfish as intermediate and definitive hosts, but their impact on crayfish populations is unknown (Avault and Huner 1985).

Another organism (perhaps a protozoan or fungus), *Psorospermium haeckeli*, commonly occurs in both North American and European crayfishes (Henttonen et al. 1992), but its effect on individuals and populations is unknown (Svärdson et al. 1991, Westman 1991, Cerenius and Söderhäll 1993, Diéguez-Uribeondo et al. 1993). However, recent evidence suggests that *Psorospermium* challenges the immune system of *P. leniusculus* and *A. astacus* and increases mortality of *Pacifastacus* already infected with fungal plague (see below; Thörnquist and Söderhäll 1993).

Many diseases attack crayfish, but most are sublethal, and the consequences for the crayfish population are unknown (Smith and Söderhäll 1986, Gydemo 1992, Cerenius and Söderhäll 1992). The most common of the sublethal diseases include infections by microsporidian protozoa and fungi ("burn spot" and "brown abdomen" diseases). The microsporidian *Thelohania* spp. ("porcelain disease") has occasionally been blamed for population reductions (Carstairs 1978), but in the best documented case, was apparently an opportunistic parasite on *O. virilis* already stressed by low pH (France and Graham 1985, cf. Davies 1989).

The fungus *Aphanomyces astaci* ("plague") is endemic in North American crayfishes, but epidemic in European *Astacus astacus* and *Austropotamobius pallipes*, where it causes near 100% mortality in infected populations (Unestam 1973, Smith and Söderhäll 1986, Cerenius et al. 1988, Chinain and Vey 1988, Alderman 1993, Nylund et al. 1993). Crayfish plague has ruined many European and Scandanavian *Astacus* fisheries since its introduction (probably *via* North American crayfish) sometime in the late 19th or early 20th centuries (Unestam 1973, Holdich 1988), with commercial losses of many millions of dollars annually (Söderhäll et al. 1977). Plague was diagnosed in England in 1981 (Lowery et al. 1984, Alderman 1993) and Ireland in 1987 (Reynolds 1988), where local populations of *Austropotamobius pallipes* have been rapidly exterminated, sometimes with large ecological consequences (Matthews and Reynolds 1992, Matthews et al. 1993).

Only if stressed in other ways do North American crayfishes suffer acute plague (Svärdson et al. 1991). *Astacus* populations often rebound following plague outbreaks, but plague and high mortality recur. Some proposed methods for containing plague spread are promising (Söderhäll et al. 1977), but *P. leniusculus* appears to have permanently replaced *A. astacus* in many lakes (Svärdson et al. 1991). In a few lakes (e.g., Skillötsjön, Sweden), sympatric, plague-free populations of *A. astacus* and *P. leniusculus* exist (but even in these cases *Pacifastacus* appears to replace *Astacus via* other mechanisms [Svärdson et al. 1991, Söderbäck 1991, 1993]).

Mortality at molting

Molting is a very complex, endocrine-controlled process (Aiken and Waddy 1992). No quantitative data are know to us, but many authors believe that considerable "autogenous" mortality occurs at molting, i.e., not including increased predation and cannabalism on molting or newly molted individuals (Brewis and Bowler 1983, Mundahl and Benton 1990, Hobbs 1991, Hill et al. 1993). As Hobbs (1991, p. 827)) says, "molting . . . is a recurring crisis in the lives of . . . crayfishes." It seems likely that mortality at molting would be increased by other sublethal stresses like poor nutrition, parasites, and disease. Clearly, mortality at molting should be quantitatively investigated as a potential bottleneck in crayfish population growth.

Population limitation in cool-water crayfishes: a synthesis

From the review above, we propose the following hierarchical model of the factors controlling cool-water crayfish populations (Fig. 4). We will focus our discussion on among-lake differences in crayfish populations, but many of the same

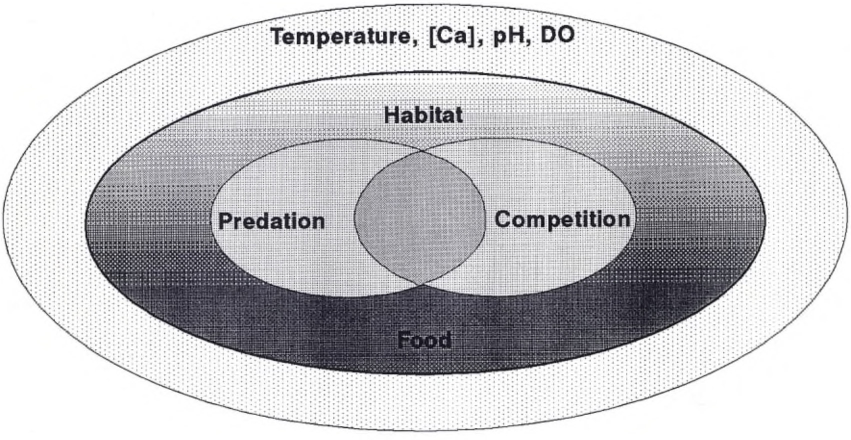

Fig. 4. Conceptual model of the interactions of physico-chemical factors, habitat availability, food availability, predation and competition in regulating crayfish species composition, population size, and production. Physicochemical parameters are the overriding factors and affect crayfishes based on physiological tolerances. Nested within the template of these parameters are habitat and food availability which interact to effect crayfish population size. Populations subject to habitat or food limitation experience competition for those items, resulting in exclusion and/or reduced growth and fecundity. Predation intensity varies with refuge availability and growth (size) of crayfishes. Competition and predation interact, with each affecting the outcome of the other. Too little is known about disease to place it in this framework.

factors restrict the horizontal and vertical distribution and abundance of crayfishes within lakes also. Effects of the density-independent abiotic factors temperature, calcium, pH, and dissolved oxygen approximate a threshold. That is, below a critical minimum, crayfish density is zero, whereas above the minimum, crayfish density is not strongly related to the level of these factors. In contrast to crayfish population size, crayfish production may be strongly related to some of these factors, especially temperature, even above the critical minimum. Interactive effects of these factors (e.g., temperature and dissolved oxygen; pH and calcium) are probably very important for crayfish populations and may blur the thresholds, but the effect of such interactions on crayfish populations has received little attention.

If density-independent abiotic factors do not limit crayfish density, habitat (refuge abundance) often does. Refuge from predation by fishes is required by small crayfishes, and refuge from cannabalism during molting is required by all sizes of crayfish. If available refuges are saturated by crayfish, population mortality rate from fishes and cannabalism is density-dependent.

Food quality is often limiting, as indicated most strongly by positive correlations of crayfish growth rate with lake productivity and comparisons of laboratory and field growth. Even if habitat is limiting, food may co-limit production such that food amendment would increase crayfish production (even if population density did not increase because of refuge limitation).

Interspecific competition for refuge and food may limit population density and productivity. Momot (1993) offers strong evidence that competition between adult and YOY *O. virilis* controls survival of YOY. Competition, in particular for shelter, interacts strongly with predation. Density-dependent mortality from direct predation is increased with increased competition for shelter (with more crayfish left without refuge), and sublethal effects (reductions in crayfish foraging and growth) are large regardless of shelter occupancy. Thus, competition for food and/or habitat strongly interacts with predation to limit population abundance and production. Therefore, Momot (1991), arguing food limitation, and Hobbs (1991), arguing refuge limitation, are both right. Trying to identify a single limiting factor is futile because of the strong interactions of multiple influences, as illustrated in Fig. 4 and the following section.

Interaction of factors: a Wisconsin (USA) example

As suggested in earlier sections, crayfish species composition, population abundance, and production are often limited by an interaction of factors rather than a single factor. Below, we focus on recent work that highlights multiple interacting mechanisms determining overall crayfish abundance and species composition in northern Wisconsin (USA) lakes. The only common crayfish in these lakes in the early 20th century was *O. virilis* (Lodge et al. 1986, Olsen et al. 1991). In the last 20-30 years, first *O. propinquus* and then *O. rusticus* were introduced in the bait buckets of fishermen. Observational and experimental evidence demonstrates that the establishment of *O. rusticus* has led to local extinction of congeneric *Orconectes* (Lodge et al. 1986, Olsen et al. 1991) and changes in the benthic community structure in many lakes (Lodge et al. 1985, Carpenter and Lodge 1986, Lodge and Lorman 1987, Lodge et al. 1987, Stahl and Lodge 1990, Weber and Lodge 1990, Lodge 1991, Olsen et al. 1991, Hill 1994, Lodge et al. 1994) and streams (Charlebois 1994), including reductions in macrophytes, invertebrates, and fishes. Like many invasions (Lodge 1993a), the *Orconectes* invasions provide a window throught which to examine abiotic and biotic interactions that govern population abundance and community structure.

The three *Orconectes* congeners respond similarly to important physicochemical variables including calcium, pH, and temperature (Table 2), and have similar life cycles (Berrill 1978). In lakes that provide appropriate levels of those variables, the overall abundance of *Orconectes* spp. is set largely by abundance of refuge providing habitat (Fig. 1; Kershner 1992, Lodge 1993b) and abundance of predatory fishes (Fig. 2; Kershner 1992). During the daylight (when most fish predators are active), all three species prefer cobble habitat over unvegetated sand/mud or vegetated sand, but both *O. virilis* and *O. propinquus* are excluded from such habitats by *O. rusticus* (Hill and Lodge in press). During darkness, all three species forage in more resource-rich habitats (Hill and Lodge in press).

When competition is for food (instead of refuges) and predators are absent, *O. rusticus* has an additional advantage over congeners: when co-occurring with *O. rusticus*, *O. virilis* suffers decreased growth and *O. propinquus* increased mortality relative to allopatric situations (Hill 1994). Competitive superiority of *O. rusticus* may partly result from its greater responsiveness to food odors (Willman et al. 1994) and its higher weight-specific consumption rates relative to both congeners (Olsen et al. 1991). Because cobble is important primarily as a refuge from fish predation, competition for habitat interacts strongly with fish predation (Fig. 4). Thus, the important consequence of congeners being excluded by *O. rusticus* from shelter is increased rates of predation by fishes.

Even if all three congeners were equal competitors for refuges, both *O. propinquus* and *O. virilis* would still suffer greater predation rates because of size and behavior, respectively. *Orconectes virilis* and *O. rusticus* have similar growth rates and maximum carapace lengths in the absence of competition and predation (Hill et al. 1993), but *O. rusticus* has larger chelae (Garvey and Stein 1993). *Orconectes propinquus* has a slower growth rate and smaller maximum carapace length (Hill et al. 1993). Because smaller crayfish are subject to much higher predation rates than larger crayfish, *O. propinquus* suffers disproportionately from predation (DiDonato and Lodge 1993, Garvey et al. 1994). Although *O. virilis* has no size disadvantage, it suffers more from fish predation because it engages in behavior (e.g., increased swimming) that puts it more at risk than congeners (DiDonato and Lodge 1993, Garvey et al. 1994). In addition to the advantage conferred on *O. rusticus* by direct predation, *O. rusticus* also suffers less growth reduction and mortality from the sublethal effects of predation risk (Hill 1994). Thus, not only is *O. rusticus* a superior competitor for both habitat and food, but it also suffers less than both congeners from both consumption by predators and the sublethal effects of predators. Increasing abundance of predatory fishes decreases absolute abundance of all crayfishes (Fig. 2), but increases relative abundance of *O. rusticus*.

Using the ratio of mortality:growth as an index of fitness (Werner and Gilliam 1984) is a useful way to synthesize the outcome of different combinations of competition and predation tested in different laboratory experiments (Hill 1994). Such calculations suggest that *O. rusticus* has higher fitness than both congeners under all combinations of interspecific competition and predation (Hill 1994). This is consistent with the unidirectional replacement in northern Wisconsin lakes of both congeners by *O. rusticus* (Lodge et al. 1986, Olsen et al. 1991). The relative fitness of *O. virilis* and *O. propinquus* differs only slightly, with *O. virilis* favored in the absence of predation and *O. propinquus* favored under most scenarios including predation (Hill 1994). The shifting relative fitness of the latter two congeners suggests that the direction of species replacement between them may change as resource and predator abundance changes in lakes. This is consistent with reverses in relative abundance of *O. virilis* and *O. propinquus* observed in Trout Lake, Wisconsin (Lodge et al. 1986).

Limited evidence suggests that hybridization among species may also favor the displacement of congeners by *O. rusticus*. For hybridization to play a role in species replacements, it must reduce fitness of one species more than the other, and the hybrids must be at a selective disadvantage.

Morphometric analyses suggest strongly that hybridization between *O. rusticus* and *O. propinquus* is common in invasion fronts in northern Wisconsin lakes, with putative hybrids comprising up to 27% of mixed-species populations (Capelli and Capelli 1980, Lodge et al. unpubl. data). Laboratory crosses have confirmed that viable offspring result from matings of *O. rusticus* and *O. propinquus*, but in numbers that are 60% fewer than in conspecific matings (Berrill 1985). No evidence of hybridization exists for *O. rusticus* and *O. virilis* (Capelli and Capelli 1980).

Matings of female *O. propinquus* and *O. virilis* with male *O. rusticus* are much more common than matings of female *O. rusticus* by male congeners, a pattern that appears to result from interspecific differences in response to pheromones (Tierney and Dunham 1984). Fertility of hybrids is unknown, but the disappearance of hybrids in lakes as an invasion drives local crayfish extinct suggests that reproductive success of hybrids is low at best (Capelli and Capelli 1980).

The apparent asymmetry of impact of interspecific matings and/or hybridization, with *O. virilis* and *O. propinquus* suffering a loss of fitness relative to *O. rusticus*, suggests that these interactions could contribute to the displacement of congeners by *O. rusticus*. However, parallel genetic analyses are required to rigorously define the prevalence and importance of hybridization.

Overall, the northern Wisconsin example is consistent with the proposed conceptual model (Fig. 4). Among northern Wisconsin lakes, only lakes with calcium concentrations >2.5 mg/L have *Orconectes*. Among those lakes with adequate calcium, crayfish abundance is positively related to abundance of cobble habitat (Fig. 1) and negatively related to abudance of predatory fishes (Fig. 2). Hybridization may contribute to the species replacements among *Orconectes*, but the interaction between competition and predation seems sufficient to explain the changes in crayfish species composition in northern Wisconsin lakes. In summary, within the template of adequate calcium, the interaction of intraspecific competition and predation establishes total crayfish abundance, while the interaction of interspecific competition and predation determines the relative abundance of *Orconectes* congeners.

Implications for managing wild crayfish stocks

Before any population of cool-water crayfish can be managed, the factors limiting its abundance, productivity, and yield must be understood. In the previous sections, we have provided a summary of what is known about limiting factors. In addition, we have synthesized the current understanding into a conceptual model (Fig. 4) emphasizing that crayfish populations may often be limited by a strong interaction of multiple factors like competition and predation. With this model in mind, several potential management strategies are obvious (Table 6), some of which have been successfully tested (see previous text sections) and others that to our knowledge have never been tried. Basing management decisions on a rigorous ecological understanding of what limits crayfish populations will increase sustainable yields of cool-water crayfishes.

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Reproductive Interference between two Co-occurring Crayfish Species, *Astacus astacus* L. and *Pacifastacus leniusculus* Dana

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Abstract

Reproductive interference between the native crayfish *Astacus astacus* and the introduced, North American crayfish *Pacifastacus leniusculus* was experimentally studied in outdoor pools with different relative densities of the two species. The mating periods of the two species were nearly synchronous, restricted to about three weeks in the beginning of October. Both species preferentially mated with conspecifics, but interspecific matings occurred, and were more common among *Astacus* females than among *Pacifastacus*. The proportion interspecifically mated females increased in the rarer species when the difference in relative abundance of the two species was increased. Interspecifically mated females spawned but lost all eggs before hatching, indicating that the two species cannot hybridize. The results suggest that interspecific matings should be unimportant for the dynamics of co-occurring populations when the two species are equally abundant, but reproductive interference may become increasingly important when the difference in relative abundance increases. *Astacus* is probably affected more by interspecific matings than *Pacifastacus*, and it seems likely that reproductive interference contributes to the observed in situ replacement of *Astacus* by *Pacifastacus*.

Keywords: Crayfish, *Astacus astacus*, *Pacifastacus leniusculus*, reproductive interference, species replacement.

Introduction

The introduction of an exotic crayfish species into new areas has frequently been accompanied by a reduction or elimination of native species (e.g., Bouchard 1978, Jezerinac 1986, Olsen et al. 1991). Several mechanisms have been proposed to explain observed species replacements among crayfish, including competitive exclusion (Bovbjerg 1970, Capelli and Magnuson 1983, Flynn and Hobbs 1984), differential susceptibility to fish predation (Butler and Stein 1985, Lodge et al. 1986, DiDonato and Lodge 1993, Mather and Stein 1993) and reproductive interference (Capelli and Capelli 1980, Berrill 1985, Butler and Stein 1985).

The native crayfish *Astacus astacus* and the introduced North American crayfish *Pacifastacus leniusculus* co-occur in several lakes in Sweden and Finland (Fjälling and Fürst 1988, Svärdson et al. 1991, Westman et al. in press). Observational studies indicate that *Pacifastacus* is gradually replacing *Astacus* in these lakes (Svärdson et al. 1991, Westman et al. in press). A combination of field and laboratory studies indicated that the replacement of *Astacus* by *Pacifastacus* is governed by a combination of several interacting mechanisms, of which interspecific competition and differential susceptibility to fish predation probably are the most important (Söderbäck 1991, 1992, 1993). Field studies in a lake where the two species have co-occurred for about 20 years documented a drastic recent decline in the relative abundance of *Astacus* (Söderbäck 1993). During the same period, the recruitment of young-of-the-year *Astacus* failed almost completely, suggesting that interspecific matings between the two species may also contribute to the replacement.

Astacus and *Pacifastacus* have seemingly synchronous breeding cycles. Mating occurs in autumn when the water temperature falls to about 10 °C (Lowery and Holdich 1988, Cukerzis 1988). Within a couple of weeks after mating, the females extrude their eggs and carry them under the abdomen until hatching in June-July the following year. The mating behaviour of the two species is similar to that described for a number of other crayfish species. Following an initial contact between the two sexes, the aggressive male attempts to mate with the female, while the female initially resists copulatory attempts from the male (Salmon 1982, Hogger 1988, Cukerzis 1988). The role females play in crayfish mate choice is unclear, although the initial resistance has been proposed to be a test of male strength (Berrill and Arsenault 1984). After male seizure of the female, he turns her over on her back, and copulation occurs. During copulation, the seminal fluid adheres under the female's abdomen and hardens to form cylindrical spermatophore strains (Cukerzis 1988).

In lakes with sympatric *Astacus* and *Pacifastacus* populations, the overlapping mating periods and similar mating behaviours may result in interspecific matings. Studies of reproductive interference between the two species are, however, lacking, and interspecific matings have to my knowledge not been documented. The purpose of this study was to experimentally evaluate the potential impact interspecific matings may have on co-occurring populations of *Astacus* and *Pacifastacus*. Specifically, I tried to answer the following questions; 1) Do interspecific matings between the two species occur?; 2) If so, are interspecific matings equally common among females of the two species?; and 3) Is the proportion of interspecifically mated females affected when the relative densities of the two species are changed? Additionally, to determine whether the two species can hybridize, survival of pleopodal eggs on interspecifically mated females was followed during the winter.

Materials and methods

Sexually mature *Astacus* and *Pacifastacus* of both sexes were collected from sympatric populations in Lake Skillötsjön, situated approximately 50 km SW of Stockholm, on September 25, 1990. More than 100 mature crayfish of each species and sex were collected during snorkelling and by capture in baited traps. Visual observation of the presence of spermatophores under the female's abdomen showed that only one female of each species were mated, indicating that the mating period in both species had just started. About 80 individuals of each species and sex, measuring between 40 and 65 mm carapace length (CL), were individually marked by cauterization (Abrahamsson 1965) and transported to the Lake Erken Laboratory of Uppsala University. Males and females of the two species were separated and placed in outdoor pools on September 26.

The mating experiment was performed in ten outdoor pools (1.5 x 1.2 m and 0.25 m deep), filled with water from the nearby Lake Erken. Pool substrate consisted of a one cm layer of sand, and each pool was provided with 30 brick shelters, each large enough to hold one crayfish. 24 crayfish (12 females and 12 males) were placed in each pool on October 1. Numbers of the two species were varied to give five different relative densities; 24:0, 20:4, 12:12, 4:20 and 0:24 (*Astacus:Pacifastacus*). Thus, each relative density was replicated twice. For each species and sex group, crayfish were divided into one large and one small CL group, and equal numbers of large and small crayfish were randomly assigned to the experimental pools. Total mean ±SD CL lengths for the different groups were: *Astacus* females 50.5 ±3.6 mm; *Astacus* males 56.2 ±5.8mm; *Pacifastacus* females 50.1 ±3.7 mm; and *Pacifastacus* males 56.1 ±5.8 mm. The size distribution did not differ between the two species, neither for males nor for females (Kolmogorov-Smirnov two-sample tests, $P>0.5$ for both sexes).

All females were checked for matings (presence of spermatophore strains under the abdomen) and pleopodal eggs on days 2, 3, 4, 5, 7, 9, 12, 15, 19, 23, and 28 after experiment start. For every new mating recorded, a small piece of a spermatophore strain was removed from the female. Spermatophore width differs between the two species (see below), and to determine from which species a spermatophore originated, spermatophore width was measured in a dissecting microscope. Multiple matings were recognized by noting form and position of the spermatophore strains on mated females for each new mating.

To examine whether the two species can hybridize, 10 *Astacus* and 10 *Pacifastacus* females were placed in separate pools together with males of the other species on October 1. All mated females from these pools and 20 females of each species, mated with conspecific males in the single-species groups, were placed indoors in two large plastic tanks with circulating water from Lake Erken at 5 °C, on November 1. Crayfish were provided an excess of brick shelters and were fed potatoes once a week. The number of pleopodal eggs on each female was counted in December 1990 and in May 1991. Four non-mated *Pacifastacus* females, which spawned in the outdoor pools, were included in the study to follow the development of non-fertilized eggs.

Results

Mating and spawning

The mating periods in *Astacus* and *Pacifastacus* in 1990 were almost completely synchronous (Fig. 1a). The first mated female of both species was observed on October 2, and by October 19 more than 90% of the females of both species were mated. Multiple matings were more common among *Astacus* females than among *Pacifastacus* (ANOVA, $P<0.001$), while there was no significant effect of relative density on the mean number of matings for either species. The number of matings per female (mean ±1SD, $N=60$) for *Astacus* and *Pacifastacus* were 2.5 ±1.36 and 1.4 ±0.68, respectively.

The time span between mating (the first of multiple matings) and spawning was considerably shorter for *Pacifastacus* females than for *Astacus* (Fig. 1b). The median time was 0 days for *Pacifastacus* (range 0-7 days, $N=56$), and 11.5 days for *Astacus* (range 0-25 days, $N=34$) (Mann-Whitney *U*-test, $P<0.001$).

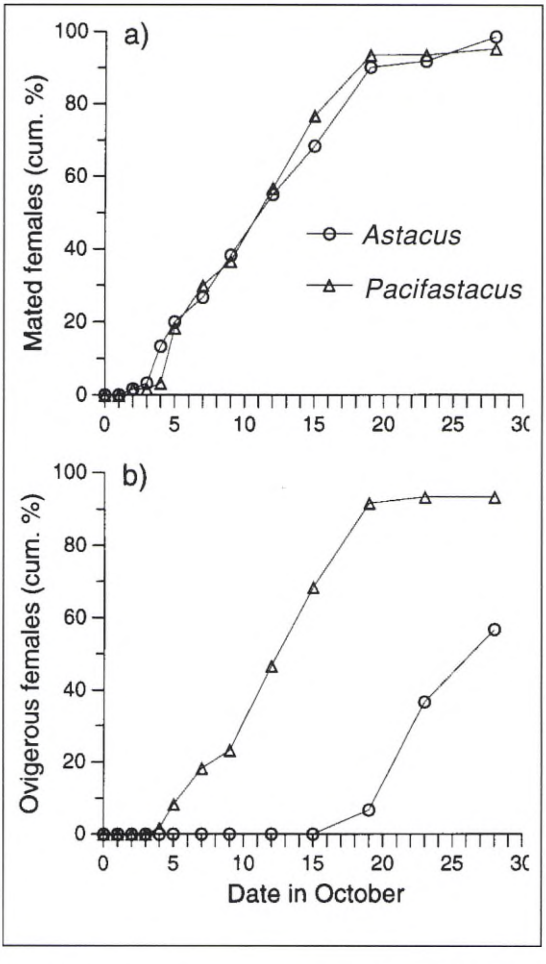

Fig. 1. Cumulative proportion of a) mated and b) ovigerous females of total numbers of *Astacus* and *Pacifastacus* females in the mating experiment ($N=60$ for both species).

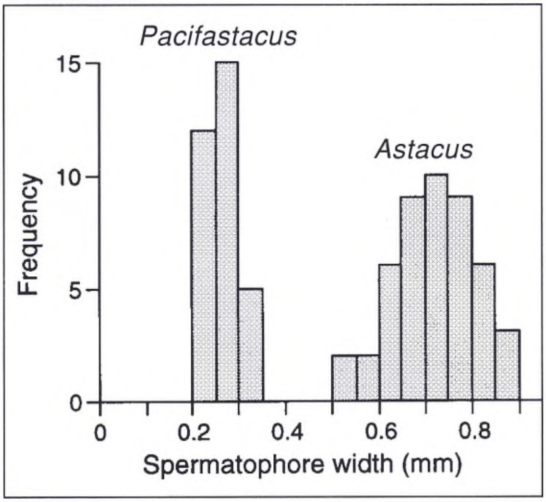

Fig. 2. Frequency distribution of width of spermatophores collected from mated females of *Astacus* and *Pacifastacus*, kept in single-species groups in the mating experiment.

Interspecific matings

Spermatophores from *Astacus* males were considerably wider than from *Pacifastacus* (Fig. 2). Since there was no overlap in spermatophore width between the two species, this measurement enables a reliable species determination of mating partner for mated females.

Both species mated interspecifically, although interspecific matings were more common among *Astacus* than among *Pacifastacus* females (Fig. 3). The total number of interspecific matings among *Astacus* females was 21 (20.2% of all *Astacus* matings in mixed-species groups), compared to only 3 (6.2%) among *Pacifastacus*. However, both species preferentially mated with conspecifics. For females of both species, the proportion interspecific matings never exceeded 50% in any pool, not even at the lowest relative density examined (Fig. 3). The preference for conspecific mating partners was also indicated by the fact that all interspecifically mated females of both species were first mated with a conspecific male.

The proportion interspecific matings of total number of matings among *Astacus* females increased with decreasing relative density of the species (r^2=0.98, P<0.001, Fig. 3). The same relationship seemed to be true for *Pacifastacus* females (Fig. 3), but the low number of interspecific matings makes the conclusion uncertain.

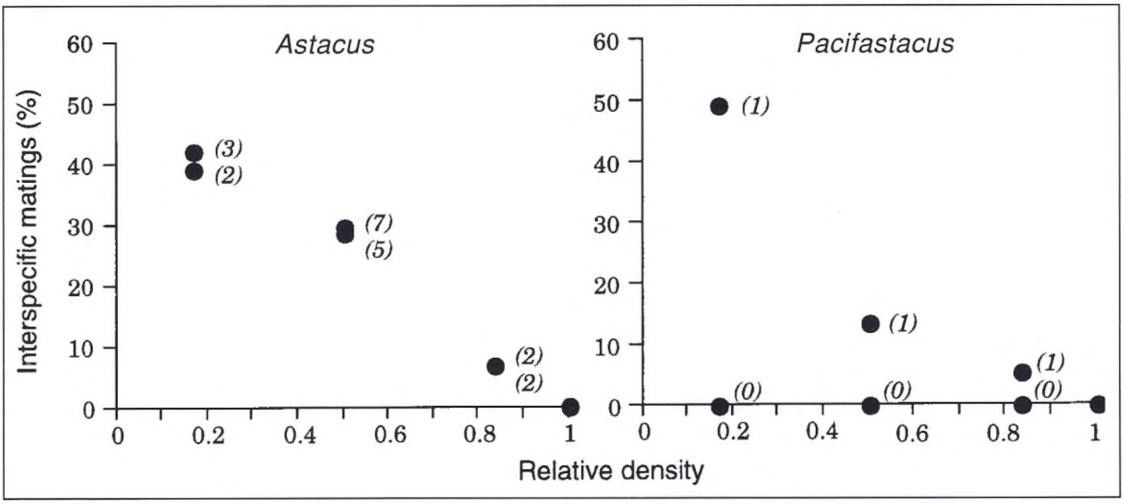

Fig. 3. Proportion interspecific matings of total number of matings for *Astacus* and *Pacifastacus* females in pools with different relative density of the two species. Numbers within brackets denote the number of interspecific matings within each pool.

Table 1. Number of ovigerous females of *Astacus* and *Pacifastacus*, mated with conspecific males, or males of the other species, in December 1990 and May 1991. Four ovigerous, non-mated *Pacifastacus* females were included in the study. N=number of mated or ovigerous females brought indoors on November 1.

			No. of ovigerous	
Species	Mating	N	Dec	May
Astacus	Consp.	20	16	13
Astacus	Intersp.	6	5	0
Pacifastacus	Consp.	20	15	13
Pacifastacus	Intersp.	8	7	0
Pacifastacus	Non-mated	4	2	0

Do *Astacus* and *Pacifastacus* hybridize?

All *Pacifastacus* females and most *Astacus* females that were used in the study of egg survival spawned in the outdoor pools. The transfer of newly spawned females indoors resulted in loss of eggs, and several of the females that were ovigerous on November 1 had no pleopodal eggs in the beginning of December (Table 1). Of the females that were ovigerous in December, all interspecifically mated females of both species, and the non-mated *Pacifastacus* females, had lost their eggs by May. Conversely, of those mated with conspecific males, more than 80% of both species were still ovigerous in May (Table 1). These results indicate that interspecific matings between *Astacus* and *Pacifastacus* will not result in any offspring and, accordingly, it seems unlikely that the two species can hybridize.

Discussion

The results from this study show that *Astacus* and *Pacifastacus* have almost completely synchronous mating periods, and that reproductive interference between the two species occurs. For crayfish species with a restricted, seasonal mating period, similar to that of *Astacus* and *Pacifastacus*, this period is characterized by intense intermale aggression and competition for females (Berrill and Arsenault 1984). Larger males, or males with larger chelae, more frequently initiate and win aggressive encounters and interrupt copulating pairs more successfully than smaller males (Berrill and Arsenault 1982, 1984, Snedden 1990). Additionally, males with larger chelae are better able to secure and more quickly orient females into the copulatory position (Snedden 1990).

Pacifastacus males are strongly dominant over similar-sized *Astacus* males (Söderbäck 1991), and they also have proportionally larger chelae than *Astacus* males. Reproductive interference between the two species should therefore more strongly affect *Astacus* than *Pacifastacus*. In the present study, *Astacus* females showed a higher frequency of interspecific matings than *Pacifastacus* females, and this might imply that *Astacus* is more affected by reproductive interference than *Pacifastacus*. Both species, however, preferentially mated with conspecifics, and all interspecifically mated females were mated with a conspecific male first.

The preference for conspecific mates in both species indicates that some kind of mechanism for reproductive isolation of the two species exists. Pheromones seems to play an important role in the sex recognition in crayfish (Ameyaw-Akumfi and Hazlett 1975), and it has also been shown that chemical cues can contribute to reproductive isolation of crayfish species (Tierney and Dunham 1984). However, interspecific matings have been documented between species that are able to distinguish between con- and heterospecifics chemically, indicating that also tactile and/or visual cues may play an important role in crayfish mate choice (Tierney and Dunham 1984).

The higher frequency of multiple matings, and also of interspecific matings, among *Astacus* females may have been an experimental artefact since crayfish density was artificially high and females were unable to hide after mating. Egg extrusion within a couple of days after mating among *Pacifastacus* females prevented further matings, whereas *Astacus* females, because of their longer period between mating and spawning, may have been artificially forced to multiple matings, and also to interspecific matings.

Since both species preferentially mated with conspecifics, it seems unlikely that interspecific matings should be important for the dynamics of the two species when they are about equally abundant. However, reproductive interference may become increasingly important when the difference in relative abundance increases. In the present study, the frequency of interspecifically mated females increased in the rarer species when the difference in relative density was increased. This pattern was obvious for *Astacus*, but less clear for *Pacifastacus*.

The lowest relative densities of the two species examined in this study were 16.7%. This corresponded to an absolute density of the rarer species of 2.2 crayfish per square meter. In natural populations, where the absolute crayfish density is considerably lower, further increased difference in relative density of the two species may cause problems for the rarer species to find conspecific mates. For example, females of the rarer species risk being mated with a male from the other species while searching for conspecific mates. Furthermore, when *Astacus* is the rarer species, dominating *Pacifastacus* males may outcompete *Astacus* males for females, and may also disrupt copulating *Astacus* pairs. It seems therefore likely that an *Astacus* population at low relative density should be more affected by reproductive interference than a *Pacifastacus* population in the corresponding situation.

The only way to quantify the importance of reproductive interference for the dynamics of co-occurring populations is to collect a large number of mated females from natural co-occurring populations and determine the frequency of interspecific matings. Collection of mated females during the short period before spawning is, however, problematic because females of both species remain hidden after mating (Söderbäck, pers. obs.).

The development of *Astacus* and *Pacifastacus* populations in Lake Skillötsjön, a Swedish lake where the two species have co-occurred since 1973, supports the assumption that reproductive interference should be unimportant when the two species are equally abundant. From initially low densities, the density of both species increased during the first ten years of co-occurrence, with *Astacus* being the more numerous species (Svärdson et al. 1991). Thereafter, the density of *Astacus* started to decline, while *Pacifastacus* continued a rapid increase. In the last years, the density of *Astacus* has declined dramatically, and in 1991 this species constituted only a few percent of the total number of crayfish in the lake (Söderbäck 1993). The initial decline of *Astacus* was probably caused by mechanisms other than reproductive interference, presumably a combination of interspecific competition and fish predation (Söderbäck 1993), but the importance of reproductive interference may have increased with decreasing relative abundance of *Astacus*.

In conclusion, I suggest that reproductive interference, together with the effects of interspecific competition and fish predation, contributes to the observed replacement of *Astacus* by *Pacifastacus*. Reproductive interference is probably unimportant when the two species are about equally abundant, but may become increasingly important and hasten species replacement when the difference in relative abundance increases. When the relative abundance of *Astacus* becomes as low as a few percent, the problems to find conspecific mates may cause virtually all matings in the species to be interspecific, and reproductive interference may ultimately lead to the disapperance of *Astacus* from lakes with co-occurring populations.

Acknowledgement

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Nordic J. Freshw. Res. (1994) 69: 144-148

Minimum Size Regulation as a Tool in Crayfish Management Practice

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Abstract

Noble crayfish management practice varies considerably between countries, with minimum harvest sizes ranging 70-120 mm total length with corresponding weights 10-60 g. Noble crayfish have allometric growth and increase some 40-50% in weight during one season in the 90-100 mm size interval. Female noble crayfish mature at a size of 62-85 mm total length and number of attached eggs are low, i.e. less than 200. Mean size of females in trap catches are lower than mean size at maturity. There is a market for crayfish smaller than 90 mm total length both for consumption and for stocking, and these often constitute more than 75% of catches. We therefore recommend a national minimum harvest size of 90-95 mm total length, and if neccessary as in stunted population local exemptions from the minimum harvest size should be given.

Keywords: crayfish, *Astacus astacus*, management, harvest, minimum size.

Introduction

Noble crayfish (*Astacus astacus*) have been exploited for centuries, and are economically important due to their recognition as a delicacy (Holdich and Lowery 1988, Westman et al. 1990). Present noble crayfish harvest is probably less than 10% of the historic record (Westman et al. 1990), and the reduction is due to habitat loss and pollution, crayfish plague (*Aphanomyces astaci*), stocking and dispersion of alien and native crayfish (e.g *Astacus leptodactylus* which is invading areas with other native crayfish species), eel stocking and overfishing (Holdich and Lowery 1988, Westman et al. 1990). The remaining noble crayfish populations are often heavily exploited. Various restrictive regulations are employed to ensure the maintenance of the brood (Westman et al. 1990). In general, the present management schemes are based on the traditions for crayfish catching and trade practices. Present regulations have been questioned (Lindqvist 1977, Huner et al. 1991, Momot 1991), and the aim of this article is to discuss the need of a minimum harvest size regulation of crayfish fisheries based on current literature.

Present minimum harvest size limits

The noble crayfish are found in at least 20 European countries ranging from Italy and Greece in the south to Fennoscandinavia in the north, and from France in the west to Russia in the east. National management regulations include restrictions on the catching season and size (Westman et al. 1990). National minimum harvest size limits vary from 70-120 mm total length (Fig. 1). There are large variations in the general management framework between various countries, and when local regulations are accounted for the differences become even larger (Westman et al. 1990). The regulations probably reflect the variations in cultural traditions related to the catching and consuming of crayfish. In Finland the 100 mm minimum harvest size limit was established in the 1890s appar-

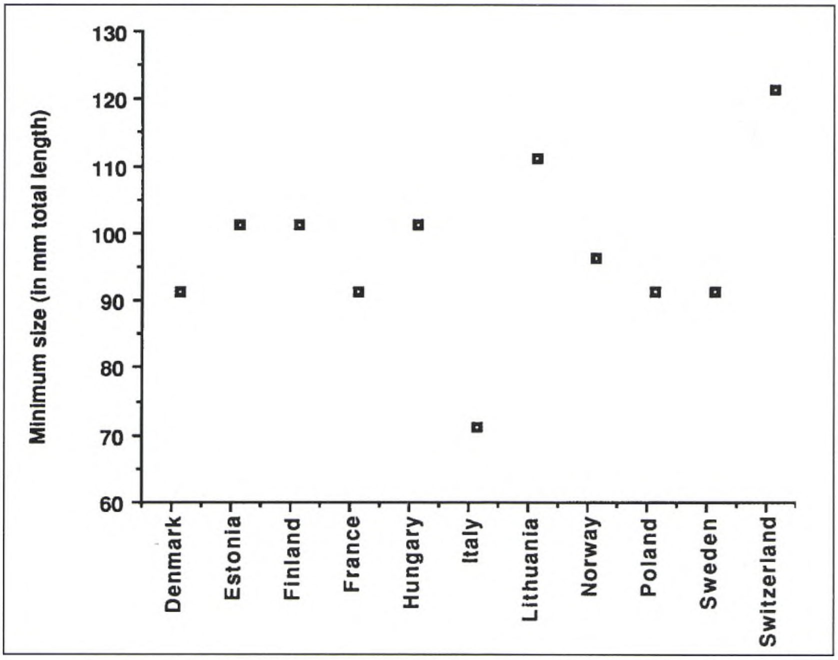

Fig. 1. Minimum size limits for noble crayfish *Astacus astacus* in eleven European countries (Westman et al. 1990, Tuusti et al. 1993, Aloyzas Burba pers. comm.)

ently on the basis of purely commercial considerations (Huner et al. 1991). In 1993, the size limit were removed in the new act for Finland, however, size limits are common in the local regulations (M. Pursiainen, pers. comm.).

Selectivity of baited traps

Noble crayfish is harvested using a wide array of methods and equipment. Recreational catching for home consumption include catching by hand, baited sticks and net balances. Baited traps are however the most widely used catching gear (Westman et al. 1990). Baited traps catch noble crayfish down to 50 mm total length (Abrahamsson 1966, Westman et al. 1978), however, the catchability decreases with size and is low for crayfish smaller than 75 mm total length (Qvenild and Skurdal 1989). The selectivity curve is influenced by the mesh size of the traps (Qvenild and Skurdal 1989). Most of the catch often consist of small crayfish, and the mean size of the catch is in the 80-85 mm total length size interval (Huner et al. 1991, Skurdal et al. 1993). Handling, as small crayfish are caught, sorted and released, may increase mortality (Qvenild and Skurdal 1989). Thus modifications of traps which reduce small sized fraction would benefit production and reduce the need of control.

Markets for small crayfish

It has been suggested that small crayfish are protected as they are not attractive for consumption (Huner et al. 1991, Momot 1991). However, we believe that those fishing for recreation and home consumption, as well as the commercial market will accept small noble crayfish (at least down to some 80-85 mm total length) for consumption. Some of the imported frozen crayfish are in this size interval. Small crayfish will be especially attractive if the price is reduced compared to large crayfish which may fetch US $ 20-50 per kilo. Even with a reduced price small crayfish may considerably increase the fishermens´ outcome at least on the short term. Crayfish of small size groups are also attractive for stocking purposes and may also obtain high prices in competition to those produced from hatcheries.

Size, growth and price

The minimum harvest size limit range from 70-120 mm total length and this correspond to a weight of some 10-60 g. Adult noble crayfish molt once or twice a year and may grow some 5-15 mm per year (Svärdson 1949, Abrahamsson 1966, 1972, Odsjö 1971, Malmqvist 1976, Jørgensen 1985, Skurdal and Qvenild 1986, Pursiainen et al. 1989b, Andersen and Helmgard 1990). The growth is allometric and the weight increase for males may be at least some 40-50% during one season in the 90-100 mm total length size interval (Fig. 2). One kg consist of 43 crayfish 90 mm total length or 29 crayfish 100 mm total length. If natural mortality is low (i.e. less than 30%), and the crayfish grow well, increased minimum size implies increased yield. However, the adverse effect of large males on recruitment have to be considered as well. Since large crayfish fetch higher prices this means that delayed harvest could increase profits even if growth is balanced with mortality. Thus the optimal harvesting size is depending on growth, mortality and price.

Sexual maturation and fecundity

Noble crayfish females reach sexual maturity at a size of 62-85 mm total length whereas males mature at a size of 60-70 mm total length corresponding ages of 3-5 years (Svärdson 1949, Cukerzis 1984, Taugbøl et al. 1989, Andersen and Helmgard 1990, Skurdal et al. 1993). Size at maturity is variable between populations and the mean size of mature females varied between 76-95 mm total length in six Norwegian populations (Taugbøl et al. 1989). Furthermore, the proportion of mature females varies both between localities and between years and is often less than 50% (Svärdson 1949, Abrahamsson 1972, Cukerzis 1984, Jørgensen 1985, Huner and Lindqvist 1989, Pursiainen et al.1989a, Taugbøl et al. 1989, Gydemo 1989, Andersen and Helmgard 1990, Skurdal et al. 1993). Crayfish females in Scandinavia often spawn in alternate years (Skurdal and Qvenild 1986, Huner and Lindqvist 1989, Pursiainen et al. 1989a, Huner et al. 1991). Ovarian and pleopod egg numbers are positively correlated to length, and pleopod egg numbers are 53-92% of ovarian egg number

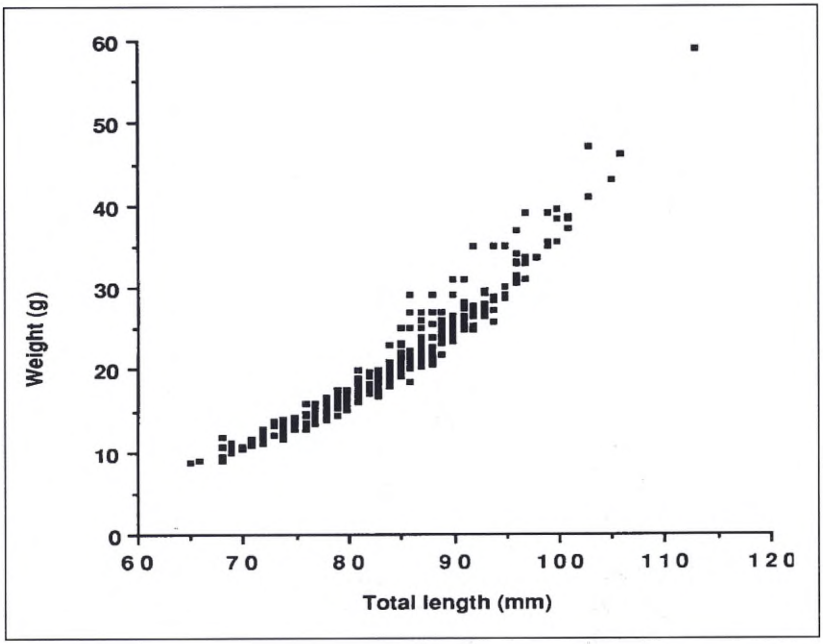

Fig. 2. Length-weight relationship for male noble crayfish from Lake Steinsfjorden, Norway 1981-92 (N=322).

(Svärdson 1949, Abrahamsson 1972, Cukerzis 1984, Jørgensen 1985, Huner and Lindqvist 1986, 1989, Pursiainen et al. 1989a, Taugbøl et al. 1989, Gydemo 1989, Andersen and Helmgard 1990, Skurdal et al. 1993).

Experience with exploitation

In Lake Steinsfjorden, Norway, the regulations have changed several times since 1910 due to complaints regarding size and catch reductions. Exploitation increased during the late 1970s, and yield and population size were reduced by some 50% due to high exploitation and removal of non-legal sized crayfish. Thus, even though the fishery was regulated with a minimum size of 95 mm total length, it may in part be considered as a fishery operating without size limits since enforcement is insufficent. No response in growth, size at maturity, or fecundity due to the increased exploitation could be detected. In 1983, trap mesh size was increased from 17.5 mm to 21 mm to reduce the fraction of non-legal sized crayfish in the trap catches; however no effects on the population was registered. In 1989, the legal season was reduced from five to two weeks and this reduced total trap effort by 45%. The yield and the fraction of large crayfish have since then increased (Qvenild and Skurdal 1989, Skurdal et al. 1993).

The noble crayfish population in Valkealampi pond in Finland apparently responded to increased exploitation by increased growth whereas fecundity remained unchanged (Huner and Lindqvist 1989).

Minimum harvest size

Noble crayfish stock composition is highly variable, and in some lakes few individuals reach the size of 90 mm total length. This has been pointed out as a special problem in Finland (Huner et al. 1991) but also exists in Sweden and Norway and probably in other countries as well (Svärdson 1949, Taugbøl et al. 1989). The minimum harvest size limitation should ensure that females spawn at least once before trapping. Based on the data reviewed a minimum harvest size of 90-95 mm total length will be sufficient to obtain this. The size at the first maturity for noble crayfish ranges from 62-85 mm total length and the mean size of mature females ranges from 76-95 mm total length. In Lake Steinsfjorden the mean size of mature females varies between 83-87 mm total length and the mean size in trap catches between 83-89 mm. Thus if there are no size restrictions, traps represent a potential for recruitment overfishing (Momot 1991). If mature females are protected noble crayfish are able to withstand high exploitation levels (Skurdal et al. 1993).

When arguing for a national minimum harvest size of 90-95 mm total length, we know that in some lakes this will not be the optimal size limit. In Lake Væleren in S.E. Norway (Taugbøl et al. 1989) and also in several Swedish and Finnish lakes (Svärdson 1949, Huner et al. 1991) few crayfish are larger than 80 mm total length and females may reach sexual maturity in the 60-80 mm size interval. Obviously, a minimum harvest size of 90-95 mm total length would be disadventageous in such localities. However, we will argue in favour of giving exemptions in such lakes rather than reducing the minimum harvest size in general. If a growth response to increased exploitation takes place, this will reduce the need for permanent exemptions. Furthermore, in some lakes with large crayfish increasing the minimum harvest size to 100 mm total length is recommended, however, this can be implemented by the local landowners on the basis of local conditions. We must however point out that more data from experimental fisheries with reference localities is needed to further improve the management scheme for noble crayfish and to quantify efforts for noble crayfish fisheries.

There is a common responsibility among nations for the conservation and wise utilization of noble crayfish. When different countries have different regulations this can enhance violations of the regulations. By exporting non-legal sized crayfish from one country to another, fishermen have a considerable potential for increasing profits from catching noble crayfish. This may be very tempting in lakes where undersized crayfish account for some 75-95% of the trap catches. As our borders become more open and trade regulations are changed there is an increased need for a more common legal harvest size.

It is often argued that local landowners should take the responsibility for managing their crayfish populations. As long as their management practices do not threaten the mere existence of the noble crayfish, it is not considered to be a problem even if their fishery regulations are far from optimal. However, it must be considered that it is a national mangement task to assure that noble crayfish resources are harvested in an optimal way. We must also focus on enforcement as rules in themselves not are sufficient for protecting crayfish. Enforcement is also needed to reduce the plague spread risk.

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Size regulations is debated in the crayfish society and we would like to extend our gratitude to our colleagues for the many stimulating discussions. We also thank M. Pursiainen for valuable comments on the manuscript.

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The RNA Concentration as an Index of Current Growth Rate in Juvenile Signal Crayfish, *Pacifastacus leniusculus*

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Abstract

Because crayfish only increase in body size by moulting, weight differences do not represent a good approximation for current growth. By using a biochemical method determining the content of RNA in muscle tissue, we have demonstrated that it is possible to detect a reduction in the rate of protein synthesis already after two days without food and an increase already the first day after the start of refeeding. Values returned to normal after a further four days. The method used yields suitable estimates of the current growth rate for short term studies of crayfish.

Keywords: growth, starvation, RNA-concentration, signal crayfish.

Introduction

Like all crustaceans, crayfish can only increase in size by moulting (Lowery 1988). Although protein synthesis also occurs during the period between moults, the weight of the crayfish does not change much during such periods (Stevenson 1972, Lowery 1988). This is because the water content of the tissues is replaced by proteins during somatic growth (Passano 1960). This poses a problem when attempting to estimate the current growth rate during a period of time that is too short to include a moult. The use of changes in weight as an estimate of growth rate in short term studies is therefore not feasible.

To solve this problem a physiological index of protein synthesis, such as the RNA concentration in relation to DNA, protein or weight of the tissue, may be used (Houlihan et al. 1993). Since approximately 80% of the RNA is contained in the ribosomes, determination of the RNA concentration in a tissue will provide an estimate of ribosome numbers, and by that give an indication of the protein synthesis potential (Houlihan 1991, Jobling 1993). The advantage of this technique is that it reflects the rate of protein synthesis, i. e. the current production of muscle tissue. The technique has been widely used to measure the current growth rate in fish and even allows the detection of daily variations in growth (Bulow 1970, Mugiya and Oka 1990, Houlihan et al. 1993).

Using the RNA concentration, it should be possible to assess the relative growth of individuals during the course of behavioural studies on the effects of competition, and in predation risk and feeding studies. Houlihan et al. (1990) have used the RNA method to study short-term changes in the growth rate of starved shore crabs after being given a meal. However, to our knowledge, this technique has not yet been applied to crayfish.

The aim of this study was to find out whether the methodology for estimating RNA concentration in fish is also applicable to crayfish. For the method to be useful in short-term studies, it needs to be sensitive enough to reflect the effects of differences in daily food supply. This was investigated by subjecting juvenile signal crayfish, *Pacifastacus leniusculus,* to progressive starvation and to progressive refeeding following starvation and studying how this affected the RNA content per gram of tail muscle tissue.

Material and Methods

The studies were made in July 1993 at the Institute of Freshwater Research at Drottningholm. The juvenile crayfish used in this study originated from females caught in the wild. They were hatched in February at the Institute. The juveniles were kept in large tanks in a through-flow system, provided with more than adequate shelter, and abundant food, in the form of fish feed and leaves of the black alder, *Alnus glutinosa*. The water supply to the tanks, both before and during the experiment, was pumped from the Lake Mälaren, filtered through a dynamic sand filter, and aerated.

During the feeding experiments 72 juveniles were moved to a thermostatically controlled room and held in individual compartments, each measuring 75 x 40 x 75mm. The experimental animals had a mean weight of 0.72 g ± 0.28 (SD) and a mean total length of 29.5 mm ± 3.4 (SD). They were visually and chemically isolated from each other since each compartment had its own water inlet and outlet. The flow rate through each compartment was 20 ml • min^{-1}. The light regime was 14L:10D with the lights switched gradually on at 06:00. The average water temperature during the experiments was 16.7 °C ± 0.4 (SD).

When the juveniles received food they were fed daily at 09:00 with a modified commercial fish feed granulate (Ewos). The composition of the feed was 50% protein, 13% lipids, 17% carbohydrates, 11% ash, 1% fibre and a water content of 8%. The ration fed to each juvenile was approximately 1% dry weight day^{-1} of each individual's body weight.

To test the effect of starvation on growth rate, 30 juveniles were randomly assigned to five groups. All were fed during the first three days of the experiment. Each day, starting from the fourth and continuing up to the eighth day, a new group of juveniles were starved, by not being given any food during the remaining days. In this way, the five groups represented a starvation gradient of one to five days. A control group of 12 juvenile crayfish were fed throughout the duration of the starvation experiments. All the juveniles were killed and immediately put in a deep freezer at -70 °C between 13:00 and 14:00 on the last day. To test the effect of refeeding on growth rate, 30 juveniles were again assigned to five groups. All these juveniles were fed for two days and then starved for five days. After the starvation period, the juveniles then received food again, but each day one group of juveniles was killed and immediately put in the deep freezer at 13:00. This provided groups of juveniles representing a refeeding gradient from one to five days after a five day period of starvation. There was no significant difference in the mean weights of the experimental groups before the start of the experiment (ANOVA, $F_{10,61}=0.673$, $P>0.7$). Three juveniles escaped during the experiment, decreasing sample size from six to five individuals for the groups starved three and five days and the group refed one day.

Prior to making the RNA analyses, the juveniles were removed from the freezer and immediately muscle samples were prepared by removing the exoskeleton from the tail muscle. The RNA concentration was estimated using a modification of the Schmidt-Thannhauser method (Munro and Fleck 1966). A sample of 50-150 mg of the frozen tail muscle of the crayfish was weighed, to an accuracy of 1 mg, and homogenized in ice-cold distilled water (1.5 ml) in a 10 ml Potter-Elvehjelm type tissue grinder. The grinder was flushed twice with 1.5 ml ice-cold distilled water. Of the precipitate 2.25 ml was put into each of two glass centrifuge tubes. Half that volume (1.125 ml) of 2.1 M ice-cold PCA was added and the tubes were held in an ice-bath for 15 min and centrifuged at 4 °C for 10 min at 2,500 rpm. The supernatant was discarded. The sediment, including the RNA, was hydrolysed in 3 ml 0.4 M KOH at 37 °C for 60 min. Then 0.120 ml of 10 M ice-cold PCA was added and half the total volume (1.61 ml) of ice-cold 2 M PCA was also added to the duplicate tubes. Prior to the final centrifugation at 4 °C for 10 min at 2,500 rpm, the samples were incubated on ice for 15 min. RNA was then quantified by measuring the UV absorbance of the supernatant at 260 nm on a Shimadzu UV-1201 spectrophotometer. The RNA concentration was expressed as mg • g^{-1} of the initial muscle sample.

Due to a power failure, the temperature in the deep freezer in which all the samples were stored rose temporarily from -70 °C to +5 °C over a two day period. However, since it is reasonable to assume that all the samples were equally subjected to the short-lived rise in temperature, the results can therefore still be interpreted, provided that only the relative values are used. Ten crayfish muscle samples stored in the same freezer had been analysed for RNA concentration prior to the failure. They were reanalysed and we found that on average 41% of the RNA was lost. However, we could not detect any systematic bias as regards either weight or initial RNA concentration, since there was no significant correlations between crayfish size or initial RNA concentration and the amount of RNA lost.

A two-tailed Student *t*-test for unpaired observations was used to assess the statistical significance of the differences between mean RNA concentration of the control group and those of the starved and the refed groups. Significance was accepted at $P<0.05$.

Results and discussion

The mean RNA concentration of the continuously fed juveniles (control group) was 0.86 mg • g^{-1}. This value was used as the base-line (100%) against which the mean values for the other groups were compared (Fig. 1). After one day of starvation there was no detectable difference in the mean RNA concentrations of the control and experimental groups (Fig. 1). However, already after two days starvation, there was a significant decline in the concentration to about 80%, a level that remained fairly steady for all the juveniles that were starved for three to five days. After one days refeeding, the RNA concentration in the juveniles rose to 87% of the base level and already then the difference was not significant compared to the non starved juveniles. However, although the difference in RNA concentration noted on the first day after refeeding started was not significant, mean RNA concentration increased gradually from the first up to the fifth day as shown by the positive correlation found between the number of days of refeeding and the RNA concentration ($r=0.61$, $df=28$, $F=15.9$, $P<0.001$).

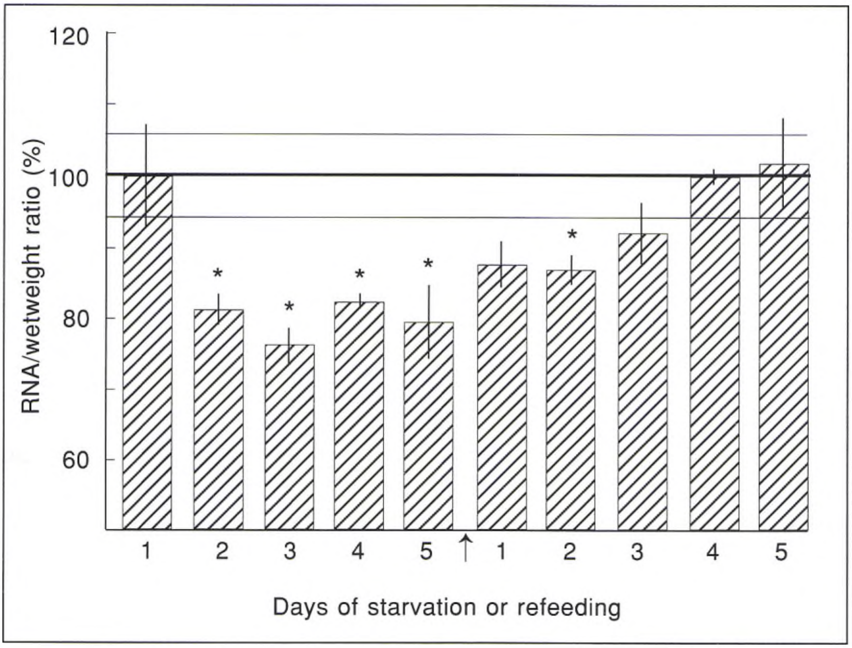

Figure 1. Percentage effects of starvation and refeeding, in relation to time, on the RNA/wetweight ratios in tail muscle of juvenile signal crayfish. The horizontal lines indicate the mean values ± SE for the continuously fed control group. Vertical bars indicate the mean values ± SE of 5 or 6 crayfish. * indicate significant differences compared to the control group. The arrow indicates when refeeding starts.

The general pattern shows that, already after two days of starvation, juvenile signal crayfish showed a response to the lack of food by a reduction in their capacity to produce proteins. The level did not decrease any further, however, and remained stable after up to five days starvation. The initial recovery of the protein synthesis was quite prompt, when refeeding started and after four days refeeding the level had recovered to that of the continuously-fed group. This pattern is what one would expect if the RNA concentration provides a true indication of current growth. In a comparable experiment on juvenile rainbow trout, *Oncorynchus mykiss,* Mugiya and Oka (1990) found almost identical patterns in the decline and increase of RNA concentration (RNA/DNA ratio) in response to food availability. As in the present study, it took two days of starvation before the values declined significantly and they also noted an immediate, but gradual, response to refeeding. Houlihan et al. (1990) found that after seven days of starvation, the level of RNA concentration (RNA/protein ratio) of shore crabs, *Carcinus maenas,* had already increased nine hours after a meal to a level comparable to that of non-starved individuals.

It would seem from our results that the RNA concentration can be used to detect small differences due to feeding regimes and, hence, the method is suitable for use in assessing relative growth rates over very short periods of time. Furthermore, the method will be useful for assessing the growth patterns of wild populations of crayfish for which the previous history of the individuals is not known.

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Comparative Growth from Length Composition and Mark-recapture Experiments for Noble Crayfish (*Astacus astacus*) and Signal Crayfish (*Pacifastacus leniusculus*) in Finland

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Abstract

A large number of crayfish studies have been carried out in 17 natural waters and in culture by the Finnish Game and Fisheries Research Institute (FGFRI). In many of the lakes, studies of noble crayfish (*Astacus astacus*) and signal crayfish (*Pacifastacus leniusculus*) have been monitored for several years and data acquired over a long period. It has been shown in south and central Finland that signal crayfish grow faster than noble crayfish under similar conditions because of more frequent moulting and greater length increment per moult. In southern Finland a considerably higher proportion of mature signal crayfish moult two or three times a year, whereas mature noble crayfish generally moult only once or twice. In allopatric populations signal crayfish grow faster than noble crayfish during their first summer and by the end of their second growing season they are as large as four-summer-old noble crayfish. However there were large variations in growth for both species. In sympatric populations 0+ noble crayfish were 21 mm in total length (TL), whereas signal crayfish had already attained 30 mm in TL. 1+ noble crayfish measured 42 mm, compared to an average of 62 mm for signal crayfish. After their third summer (2+) noble crayfish averaged 64 mm in length, by which time the signal crayfish had reached 100 mm. In both species it has been observed that the males grow faster than the females, and length increment has been seen to slow down with increasing size. In central Finland the growth rate was as fast as in southern Finland.

Keywords: *Astacus astacus, Pacifastacus leniusculus,* growth rate, length, moult.

Introduction

At present there are two freshwater crayfish species in Finland; the native noble crayfish (*Astacus astacus*) and the introduced signal crayfish (*Pacifastacus leniusculus*). The noble crayfish, due to intensive stockings, was once spread to all major watercourses up to the polar circle. Due to the crayfish plague, which spread into Finland from Russia in 1893, the stocks of the noble crayfish have suffered great losses (e.g. Westman 1991). Nowadays catchable noble crayfish populations have in fact vanished from thousands of waters in spite of intensive stocking activity.

The signal crayfish was introduced into Finland in 1967 (Westman 1973, 1991). In the period 1967-92 approximately 300,000 signal crayfish were stocked in 138 water bodies, mainly located within the natural range of noble crayfish. More than 190,000 of stocked signal crayfish were one summer old juveniles (Järvenpää and Kirjavainen 1992). Only a few signal crayfish stockings occurred north of this latitude of which Lake Kermajärvi (66°N) represents the world's northernmost stocking locality (Westman 1991). For the conservation of native noble crayfish Finnish fishery authorities have made a strategy for spreading signal crayfish only to former crayfish waters devastated by the plague in southern Finland. Stockings with the plague resistant signal crayfish are expanding because this species is shown to reproduce as fast, grow as rapidly and taste as good as the noble crayfish (Westman 1991, Westman et al. 1992a).

The purpose of this study is to compare the yearly growth rate, the length increment per moult and the moulting frequency of *A. astacus* and *P. leniusculus* in southern and central Finland. Crayfish anglers, water body owners and the authorities responsible for making crayfish stocking decisions are keenly interested in the productivity of both species in association with management of the stocks. Some results have been presented elsewhere (Pursiainen et al. 1988, Westman et al. 1992 b, Westman et al. 1993).

Material and methods

The FGFRI has been monitoring noble and signal crayfish populations in selected waters for more than 20 years. Most of these studies have been directed towards allopatric populations. However, one study was carried out on sympatric populations of noble and signal crayfish in Lake Slickolampi (Westman et al. 1992c, Westman et al. 1993).

For catching adult crayfish in 1976-77 Swedish-type two-mouthed baited cylinder traps were used (Abrahamsson 1971), and from 1978 onwards narrow-mouthed baited cylinder traps of the so-called Evo-trap type were used (Westman et al. 1979a). Traps with mesh size 8 mm were baited with roach and distributed at 5 m intervals in the littoral zone. Juveniles were collected by electric fishing (Westman et al. 1979b) and by dredge sieving (Odelström 1983). Thousands of crayfish have been individually marked using electric cauterization (Abrahamsson 1965, Westman and Pursiainen 1979) or waterproof pen. With repeated fishing in the same or following summers the length increase and moulting frequency of the marked specimens has been registered. Ages have been determined from length frequency distributions and data collected from mark-recapture studies.

The length of the carapace (CL) was measured using Vernier callipers from the tip of the rostrum to the posterior edge of the carapace (Fitzpatrick 1977). For calculating the regression between CL and total lenght (TL), the TL was measured on a measuring board while the crayfish was lying on its back. The CL has been converted to the TL by using different regression models for both species and sexes. In Lake Slickolampi, Lake Karisjärvi and Lake Vuorijärvi it was possible to use lake specific regression models. In other waterbodies we used the regression model of Lake Slickolampi for noble crayfish and the regression model of Lake Karisjärvi for signal crayfish.

To compare growth of signal and noble crayfish we have used data from 6 and 13 waters, respectively (Table 1). Furthermore, we have also used data from cultured juveniles from FGFRI's Evo State Fisheries and Aquaculture Research Station.

Results

Growth-rate

The body lengths (TL) of the various age groups of signal and noble crayfish in different water bodies in southern and central Finland are presented in Table 2 and Fig. 1. The mean size of noble crayfish increased from 19 mm for one-summer-old individuals to 79 mm for four summer old individuals and to 90 mm for five-summer-old individuals. The fastest growth at age 3+ was noted in the mesotrofic Lake Katumajärvi and at age 4+ in the mesotrofic Lake Avusjärvi, where the mean density of noble crayfish aged two summers or more was <1 crayfish/m^2. The slowest growth was found in the oligotrofic River Raudanjoki, where the mean density of crayfish aged two summers or more, averaged 4.1 crayfish/m^2 (Westman et al. 1986).

Table 1. Experimental waters. Eight of the waters*) have been described elsewhere (e.g. Westman et al. 1986, Pursiainen et al. 1988, Westman et al. 1992 b,c, Nylund et al. 1993).
Trophiclevel: Tot P <10 μg/l = oligotrophic; Tot P 10-30 μg/l = mesotrophic; Tot P >30 μg/l = eutrophic.
Species: *P.l.= Pacifastacus leniusculus*, *A.a.= Astacus astacus*.

Water	Coordinates	Area (ha)	Trophiclevel	First introduction	Species
Lake Karisjärvi*	61°58´N 25°32´E	10.8	Oligotr.	1968-1969: 618 mature (100 mm) *P.l.*	*P.l.*
Lake Slickolampi*	60°01´N 23°34´E	4.2	Oligotr.	1971: 900 2-stage (10 mm) *P.l.*	*P.l.* & *A.a.*
Lake Vuorijärvi*	61°39´N 24°49´E	13	Oligotr.	Date unknown *A.a.*	*A.a.*
Lake Ormajärvi*	61°06´N 24°58´E	645	Eutr.	1989:2860 0+ (30 mm) *P.l.*	*P.l.* & *A.a.*
Lake Kukkia*	61°20´N 24°40´E	3,640	Oligotr.	1989:1200 0+ (30 mm) *P.l.*	*P.l.* & *A.a.*
Lake Vekuna*	61°19´N 24°36´E	73	Oligotr.	1989: 743 mature (90mm) *P.l.*	*P.l.*
Lake Pälkänevesi*	61°23´N 24°29´E	4,620	Oligotr.	1974: 250 2-stage (10 mm) *P.l.*	*P.l.*
River Raudanjoki*	60°40´N 24°10´E	2 km	Mesotr.	Native	*A.a.*
Lake Särkemä	61°08´N 24°40´E	15	Mesotr.	1990: 650 0+ (26 mm) *A.a.*	*A.a.*
Lake Kankaistenjärvi	61°01´N 24°39´E	274	Oligotr.	1987:1300 0+ (20 mm) *A.a.*	*A.a.*
Lake Katumajärvi	61°00´N 24°32´E	381	Mesotr.	1989: 600 0+ (30 mm) *A.a.*	*A.a.*
Lake Iso-Kilpastin	61°23´N 25°10´E	25	Mesotr.	1989:1000 0+ (17 mm) *A.a.*	*A.a.*
Lake Haarajärvi	61°14´N 25°11´E	14.8	Mesotr.	1988: 450 0+ (28 mm) *A.a.*	*A.a.*
Lake Nerosjärvi	61°17´N 24°52´E	14.8	Mesotr.	1988: 450 0+ (28 mm) *A.a.*	*A.a.*
Lake Valkiajärvi	61°17´N 25°12´E	8	Oligotr.	1987:1930 0+ (15 mm) *A.a.*	*A.a.*
Lake Haaraj.-Valkjärvi	61°14´N 25°11´E	3.6	Mesotr.	1977-79:1268 mature *A.a.*	*A.a.*
Lake Avusjärvi	61°16´N 24°48´E	200	Mesotr.	1988:1500 1+ (25 mm) *A.a.*	*A.a.*
River Palsankoski	61°21´N 24°59´E	2 km	Oligotr.	1989:1000 0+ (18 mm) *A.a.*	*A.a.*

Corresponding values for signal crayfish were 29 mm for 0+ individuals and 105 mm for 3+ individuals. Signal crayfish males were larger than females in the age groups 1+, 2+ and 3+. The fastest growth was observed in Lake Ormajärvi which is eutrofic and the slowest growth in the oligotrofic Lake Pälkänevesi. Densities are in both lakes about one crayfish/m^2. Some *P. leniusculus* males had reached 100 mm at the end of their second growing season and 130 mm at the end of their third growing season.

In Lake Slickolampi, with sympatric populations, 0+ *A. astacus* averaged 21 mm in TL, and had increased 10 mm (91%) in total length after

Table 2. The average total length (mm) of different age groups for signal crayfish and noble crayfish in different waterbodies in southern and central Finland and in culture at FGFRI's Evo State Fisheries and Aquaculture Research Station. Juveniles (0+ signal and noble crayfish. and 1+ noble crayfish) have been collected by electric fishing and dredge sieving. Older specimens have been caught by traps except River Raudanjoki (collected by electric fishing) and Evo culture (collected by hand).

SIGNAL CRAYFISH (*Pacifastacus leniusculus*):

Water	0+				1+				2+				3+			
	x	s.d	range	*N*	x	SD	range	*N*	x	SD	range	*N*	x	SD	range	*N*
Lake Karisjärvi ♂	30.3	1.76	26-33	4	84		70-100	110	106		82-124	425				
♀	"	"	"	4	84		64-96	145	96		80-116	430				
Lake Slickolampi ♂	30.2	2.85	26-34	65	75.6	5.74	74-79	94								
♀	"	"	"	65	72.6	7.33	69-75	81								
Lake Ormajärvi ♂					85.2	6.35	73-100	29	105.7	8.39	91-126	40	115.8	9.18	104-143	28
♀					82.9	5.59	75-90	8	97.9	7.88	77-113	36	109.4	8.36	92-121	17
Lake Kukkia a) ♂					81.6	5.18	70-90	14					111.0	5.09	104-120	6
♀					81.6	6.84	72-94	12					105.0	7.13	96-126	14
Lake Kukkia b) ♂					81.4	6.30	73-93	12								
♀					79.5	5.84	70-90	13								
Lake Vekuna ♂					79.4	9.04	52-95	39								
♀					77.9	5.30	70-89	37								
Lake Pälkänevesi ♂					68.1	9.38	59-82	6	98.9	12.1	81-136	31				
♀					66.2	8.30	55-73	5	93.9	6.72	77-102	23				
Evo/Culture/selected * ♂	35.4	4.53	25-60	607	73.3	7.30	47-93	428	85.9	8.53	65-111	336	95.7	8.46	65-118	141
♀	"	"	"	607	74.3	7.40	41-92	440	85.3	6.01	72-119	302	90.3	10.4	58-113	112
Evo/Culture/norm. **	25.4		15-35	1500												
Evo/Culture/predated #	30.3		20-60	300												
TOTAL ♂	28.6		26-34		78.6		47-100		99.1		65-136		107.5		65-143	
♀					77.4		41-96		93.3		72-119		101.6		58-126	

* Selected for improvement of breed, not in total-average at age 0+, ** Produced on the basis of natural cycle of the species,
# Predated artificially incubated, not in total-average

NOBLE CRAYFISH (*Astacus astacus*):

Water	0+				1+				2+				3+				4+			
	x	SD	range	*N*	x	SD	range	*N*	x	SD	range	*N*	x	SD	range	*N*	x	SD	range	*N*
L. Slickolampi	21.4	1.55	19-30	173	41.8	4.35	37-48	328	63.6	3.59		13								
River ♂ Raudanjoki ♀	15.5 15.5		14-17 14-17	45 44	35 33		25-45 25-41	152 140	54 49		46-62 42-56	141 101	70 62.5		63-77 57-68	203 95	82 73		78-86 69-77	90 95
L. Särkemä									71.6	1.15	74-76	3	78.9	15.6	72-94	2				
L. Kankainen									75.4	8.08	70-84	3	82.8	11.3	72-104	9				
L. Katumajärvi													89.1	9.98	80-100	4	97.4	10.5	88-120	18
L. Kilpastin													83.1	10.4	74-108	9				
L. Haarajärvi													84.0	5.77	86-96	4	90.2	7.13	80-102	10
L.Nerosjärvi																	98		76-110	14
L.Valkiajärvi																	92			1
L.Haarajärven-Valkjärvi													78.2	5.89	72-102	29				
L. Avusjärvi																	100		80-120	10
R.Palsankoski									72.8			1								
Evo/Cult./ ♂ selected * ♀	27.2 27.2	2.44 2.44	22-32 22-32	112 112	50.1 49.6	5.65 5.46	38-72 38-63	783 774	64.9 62.7	7.22 7.19	55-85 48-79	768 760	68.1 64.8	7.74 6.34		172 154	77.4 70.2	8.46 5.78		128 114
Evo/Cult./ norm **	19		14-25	750																
Evo/Cult./ predated #	26		20-35	250																
TOTAL	18.6		14-30		41.9		25-72		66.5		42-85		78.6		57-108		89.8		69-120	

* Selected for improvement of breed, not in total-average at age 0+, ** Produced on the basis of natural cycle of the species,
# Predated artificially incubated, not in total-average

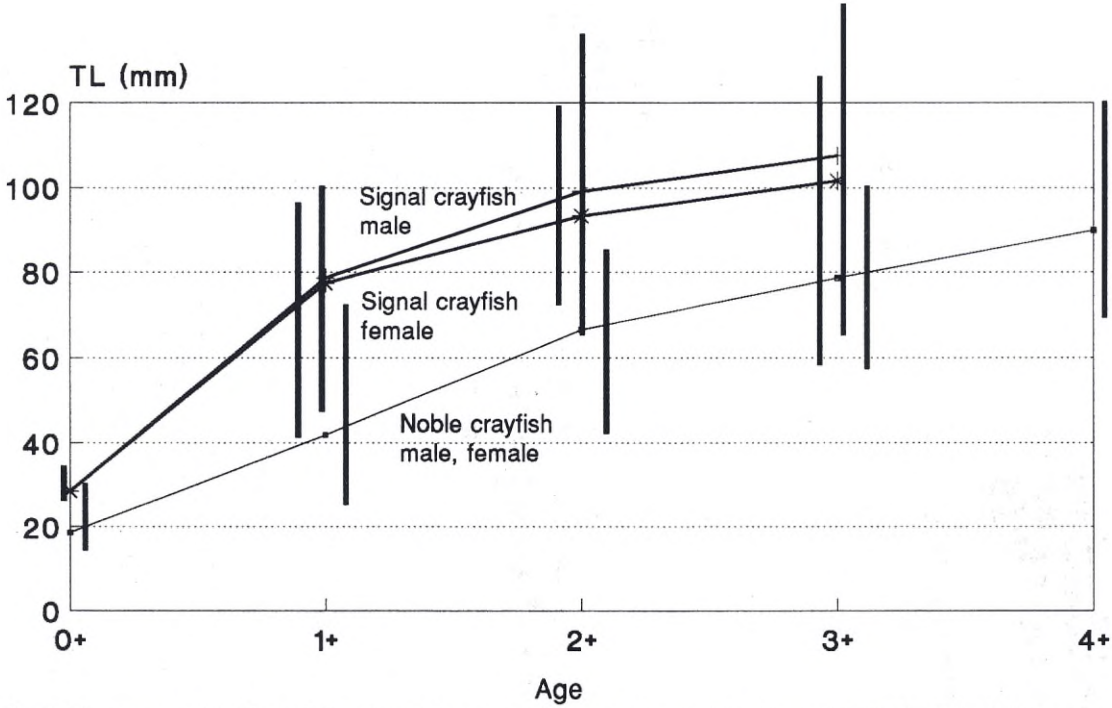

Fig. 1. The average total length (mm) and the range of the smallest and the longest individual for different age groups of *Astacus astacus* and *Pacifastacus leniusculus* in 13 noble crayfish lakes and 6 signal crayfish lakes in southern and central Finland.

leaving the mother. Corresponding values for *P. leniusculus* were 30 mm and 20 mm (200%), respectively. 1+ *A. astacus* were on average 42 mm in TL, and had increased 21 mm TL (100%) during their second summer. Corresponding values for *P. leniusculus* were 60 mm and 30 mm (100%), respectively. 2+ *A. astacus* were on average 64 mm in TL, and had grown 25 mm (60%) since the age of 1+, by which time the signal crayfish had reached 100 mm (for further details, see Westman et al. 1993).

The moulting frequency and length increment

In Lake Karisjärvi signal crayfish males moulting twice a year were mainly 80-100 mm (TL) long. Females >80 mm and males >100 mm moulted only once a year. Male signal crayfish >70 mm grew on average 12.4 mm per moult (SD 1.01, N=45) and females grew on average 8.5 mm (SD 0.96, N=35) (t-test, $P < 0.001$). The average length increment per moult decreased with increasing size (Fig. 2).

In Lake Slickolampi in 1987-91, 64% of the signal crayfish males and 37% of the females moulted more than once a year. Similarly, 17% of male noble crayfish and only 6% of female noble crayfish moulted more than once a year. The largest proportion of the signal crayfish moulted three or four times per year. In 1987-91, signal crayfish males grew on average 9.4 mm and females 9.0 mm in total length per moult (t-test, $P>0.05$ NS). Within the same period noble crayfish males grew on average 8.9 mm and females 5.8 mm in total length (t-test, $P<0.001$).

In Lake Vuorijärvi 65% of male noble crayfish >70 mm moulted once a year and the rest of the males twice. 81% of the females moulted once and only 19% twice a year. The mean in-

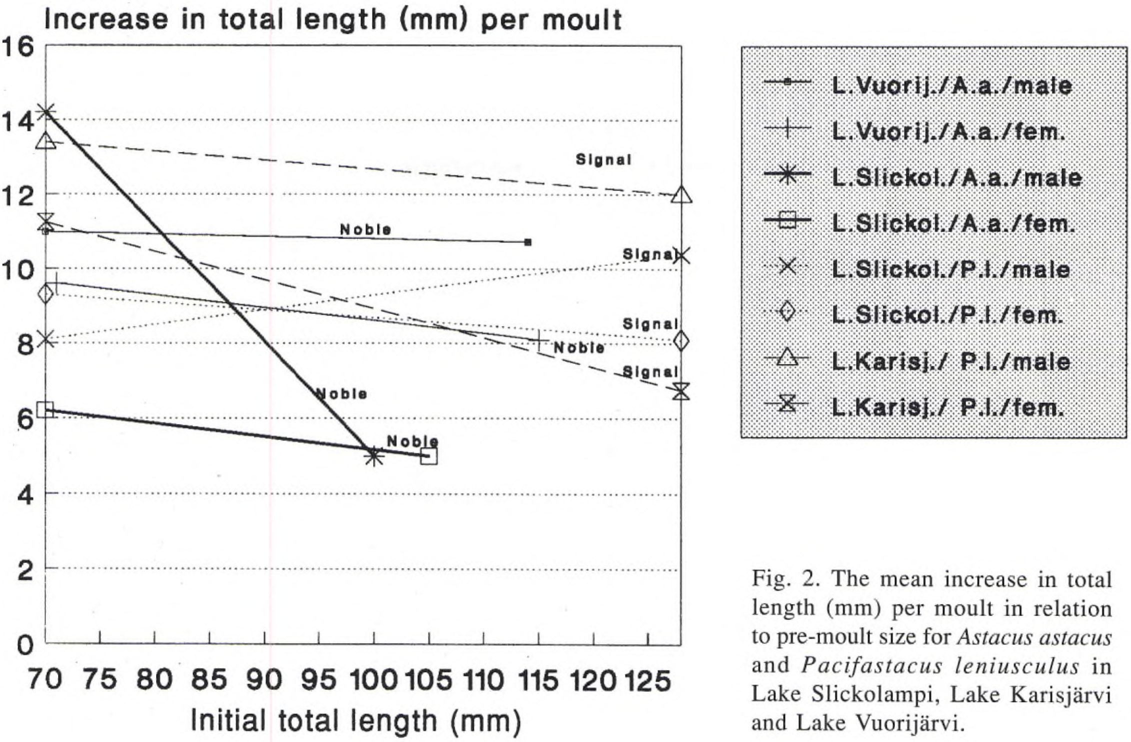

Fig. 2. The mean increase in total length (mm) per moult in relation to pre-moult size for *Astacus astacus* and *Pacifastacus leniusculus* in Lake Slickolampi, Lake Karisjärvi and Lake Vuorijärvi.

crease in total length per moult was 10.4 mm for noble crayfish males and 8.7 mm for females (*t*-test, $P<0.001$). The increase in length during moult did not appear to be dependent on initial length in this case (Pursiainen et al. 1988).

Discussion

The growth of stocked signal crayfish has been exceptionally fast in southern and central Finland compared to noble crayfish after stocking. However, there were large variations and overlap in growth for both species. As stated by Lowery (1988), signal crayfish stands out as being the fastest growing of the northern temperate zone crayfish species for which data is available. Individuals have reached 100 mm in TL within three years in both the British Isles and Sweden (Hogger 1986, Abrahamsson 1971). In Lake Slickolampi the growth rate of *P. leniusculus* was almost twice as high as that of *A. astacus*.

The annual growth depends on moulting frequency and growth per moult. Many environmental factors influence the moulting frequency of crayfish, of which temperature, food supply and population density are the most important (Svärdson 1949, Armitage et al. 1973, Gydemo 1989, Lowery 1988, Pratten 1980).

The length increase per moult depends on the size of crayfish; large individuals do not grow as much as the smaller ones (Abrahamsson 1971). This was also noted in Lake Karisjärvi. The highest increases in length per moult were registered for 70 mm (TL) male signal crayfish and the lowest for large female noble crayfish.

The higher growth rate in signal crayfish compared to noble crayfish is mainly due to a higher moulting frequency but also a greater increase in length per moult (Westman et al. 1993). In Finland offspring of signal crayfish hatch about one week earlier than noble crayfish and the rapid growth rate in signal crayfish seems to start already after hatching (Westman et al. 1993).

Although second-stage signal crayfish are a little bit shorter than noble crayfish, they are about 50% longer than noble crayfish at the end of their first growing season(Westman et al. 1993). The difference in weight is even larger. The growth rate seems to be faster in lakes with sparse crayfish populations. In more dense populations the growth rate is not so good (Abrahamsson 1965, Abrahamsson 1972).

The comparison between different signal and noble crayfish populations is valid only if the environmental conditions are equal. The best situation is if both species live together in the same lake (sympatric populations as in Lake Slickolampi). Also the sampling methods should be identical. The trapping method makes it possible to evaluate only *A. astacus* longer than 65 mm (Pursiainen et al. 1988), although in sparse populations trapping selects fast growing animals and there are differences in trappability between species (Westman et al. 1992c).

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Survival of Juvenile Signal Crayfish (*Pacifastacus leniusculus*) in Relation to Light Intensity and Density

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Abstract

During 1991-92 juvenile signal crayfish were studied at the Simontorp hatchery in Sweden. In two different experiments, I tested the hypothesis that higher illumination would enhance juvenile survival rate, possibly a result of lowered juvenile activity. To be able to evaluate the significance of density dependent factors, a third experiment was carried out, where juveniles were reared individually. There was a positive correlation between juvenile survival and light intensity. At a light intensity of 600 lux, the mean juvenile survival was 75%, being significantly better than the survival rate of 49%, at a light intensity of 325 lux. When juveniles were reared individually, the mean survival was 83% which was significantly better than for individuals reared at a density of 100 per m^2. The experiments indicate that it is possible to achieve an acceptable survival in laboratory experiments with crayfish juveniles, during the first three to four month after hatching. To accomplish this it is important to use fresh food, to have shelters in excess, to have a complex habitat, and a light intensity of at least 600 lux. To minimize death caused by cannibalism, a density of less than 100 juveniles per m^2 seems to be advisable for the signal crayfish.

Keywords: Crayfish, *Pacifastacus leniusculus*, light intensity, density, food.

Introduction

In previous laboratory studies the survival rates of newly hatched crayfish juveniles have been lower than expected. D'Abramo et al. (1985) had a maximum survival rate of 42% after 100 days when the density was 200 juveniles/m^2. Mason (1979) studied juveniles of the signal crayfish for 80 days with a maximum survival of 47% at a density of 130 juveniles/m^2. In outdoor experiments the survival and growth has been reported to be better in comparison with laboratory studies (Pursianinen et al. 1983, Ackefors et al. 1989). According to Celada et al. (1989) and Taugböl (1989) the factors affecting survival and growth of juveniles are water temperature, water quality, food, photo period, density, handling, competition, cannibalism, pathological processes and the heterogeneity of the environment. It seems urgent to evaluate the significance of these factors because of the need for a high survival rate and normal growth when using crayfish juveniles for experiments and for stocking natural waters. How is it then possible to increase juvenile survival in laboratory experiments? Firstly, death caused by nutrient deficiencies can be avoided by adapting food levels as much as possible to the organisms nutrient requirements. Secondly, intraspecific competition and cannibalism can be reduced by increasing the structural complexity of the habitat and by lowering the juvenile density (Mason 1979). Thirdly, increased juvenile growth and survival could be achieved, by reducing crayfish activity and stress. Several studies have revealed that temperature, light intensity, the length of the dark period, population density and food shortage, influence crayfish activity. (Abrahamsson 1983, Ipsen et al. 1984, Hamrin 1987, Westin and Gydemo 1988). In this study I evaluated the effects of different light intensities on survival of juvenile crayfish. I expected that light intensity affected juvenile activity and, hence, juvenile survival. The aim was also to evaluate if it was possible to rear juvenile signal crayfish during laboratory experiments, at a density of 100 juveniles/m^2, and still have an acceptable survival rate after three to four months.

Material and methods

This investigation was made during 1991-92 at the Simontorp hatchery in the south of Sweden. Egg bearing females were trapped in October every year in the Rögle ponds outside the city of Lund. The hatching was manipulated to start in February the following year. The investigations were conducted in four recirculating water systems supplemented with well water. 10% of the water was changed weekly. The water quality was stable with a pH value of 7.7 and a calcium content of 70 mg • l^{-1}. The maximum values of ammonia and nitrite were 0.15 mg • l^{-1}, and the water was always saturated with oxygen during the experiment. The light regime was 15L:9D and industrial fluorescent light was used. The juvenilecrayfish in the different experiments were fed every second day in excess, with a liquidised suspension of egg, fresh chopped earthworms, and green peas. Live *Artemia salina* where also given to the juveniles. The artemia were fed freshwater algae (*Chlorella* sp.) prior to being given to the crayfish. Excessive food was removed but no other cleaning was performed.

Experiment 1

During 1991, 67 tanks were supplied with 150 second stage juveniles per tank (162/m^2) with an initial average weight of 29 mg. There were four separate systems, and each system had a biofilter and supplied 21 tanks. The tanks had a bottom area of 0.92 m^2 (220 cm by 42 cm). The tanks were filled to a depth of 15 cm, and contained 6 building bricks, each containing 28 holes (each hole had a diameter of 1 cm), and a potato sack (made of plastic), filled with small plastic pipes. During the experiment, each tank was supplied with fresh macrophytes (*Elodea canadensis*, *Nitella opaca* and *Chara* sp.), collected from the Rögle ponds. 75% of the total bottom area of the tanks were covered with either bricks, plastic pipes or macrophytes. The temperature varied between 15 and 20 °C with an average temperature of 18 °C. The light intensity that each tank recieved, varied in a gradient between 20 and 360 lux. Surviving juveniles were counted after 107-124 days. Total length and cheliped losses were measured in the juveniles from one system (21 tanks).

Experiment 2

Six hatchery containers with a bottom area of 0.16 m^2 (40 cm by 40 cm) were placed in two tanks (three per tank). The containers were filled to a depth of 15 cm. One building brick, plastic pipes, and macrophytes totally covered the bottom of the container. Containers were stocked with 15 juveniles resulting in a density of 100/m^2. Three containers recieved an illumination of 600 lux and the remainder 325 lux. The temperature varied between 16 and 21 °C, with an average temperature of 18.5°C. After 112 days the number of surviving juveniles were counted.

Experiment 3

To be able to evaluate the significance of density dependent factors, 20 juveniles were put in each of four hatchery containers (40 cm by 40 cm) for 109 days, receiving an illumination of 225 lux. The containers were filled to a depth of 15 cm. Each container was divided in 20 separate compartments and every compartment contained one juvenile. Juveniles were counted after 42, 60 and 109 days. Although the juveniles were separated at the beginning of the experiment, some juveniles managed to escape and enter other compartments. This was most evident in one of the containers, and this container was excluded from the analysis. Experiment 2 and 3 were carried out in the same system during 1992.

Results

Experiment 1

A positive correlation was found between juvenile crayfish survival and light intensity (*r*=0.57, *F*=31.0, *P*<0.001, *df*=66, y=0.067x + 33.8, Fig 1). The mean survival rate was 47% (range 20-69%). In the same experiment, juveniles from one system (21 tanks) were measured. Of the 1362 surviving juveniles, 259 (19%) had lost at least one cheliped during the experiment. The juveniles suffering from cheliped loss, had a mean length of 18.7 mm (SD=1.5, *N*=21). The intact ones had a mean length of 20.1 mm (SD=1.6, *N*=21). The difference was significant (paired, two tailed *t*-test; *t*=6.3, *P*<0.001, *df*=20).

Experiment 2

The mean survival rate for the juveniles in hatchery containers, receiving 600 lux was 75%. This survival rate was significantly higher compared to crayfish exposed to 325 lux, where juveniles had a mean survival rate of 49% (Mann-Whitney U test; *P*<0.05, *N*=6). Epiphytic algae covered the walls of the hatchery containers receiving 600 lux but was insignificant in the other tanks as well as in the tanks in experiment 1 and in experiment 3.

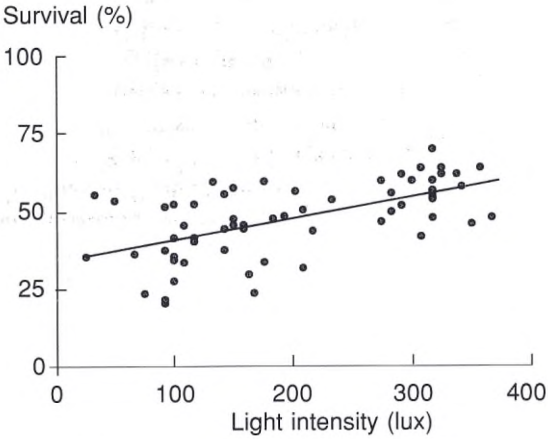

Fig. 1. The percent of surviving signal crayfish juveniles in 67 tanks after 107-124 days, correlated with light intensity (Experiment 1).

Experiment 3

The mean survival rate of juveniles living separately was 98% after 42 and 60 days, and 83% after 109 days. The maximum survival after 109 days was 95% and the minimum 70%. All surviving juveniles were normally pigmented and the mean length was 21.7 mm (SD=4.4, *N*=50). 7% of the juveniles had lost at least one cheliped during the experiment. Three juveniles were unable to shed their exoskeleton and died during moulting. The survival was significantly better for juveniles reared separately, compared to those reared together at a density of 100/m^2, and illuminated by 325 lux in experiment 2 (Mann-Whitney U test; *P*<0.05, *N*=6).

Discussion

The effects of light intensity on survival

The experiments reveal that an increased light intensity has a positive effect on juvenile survival. The higher survival rate could be explained in several ways. Previous studies have shown that crayfish locomotor activity is affected by changes in illumination (Blake and Hart 1993, Hamrin 1987, Söderbäck 1992), and in light intensity (Westin and Gydemo 1988, Ipsen et al. 1984). When Ipsen et al. (1984) studied juvenile noble crayfish during laboratory conditions, they concluded that juvenile activity not only was correlated with hours of darkness, but also with decreasing light intensity. The increased survival rate at higher light intensities in this study, could be a result of reduced cannibalism, and reduced number of conflicts, as a consequence of a low juvenile activity. An alternative explanation for the high survival rate at higher light intensities is that the increased amount of available food e.g., epiphytic algae, could directly enhance juvenile survival but also indirectly by reducing the food searching activity of juveniles. Further studies are needed to asses the factors influencing juvenile survival in relation to light intensity.

Juvenile density and survival

The individually reared juveniles had a higher survival rate than juveniles reared at a density of 100/m². This is in agreement with the results presented by Celada et al. (1989). They had a higher juvenile survival in isolated animals than in groups of three. The results from this and several other studies (Ackefors et al. 1989, Celada et al. 1989, Westman 1973, Mason 1979) indicate, that density dependant factors causes increased mortality. D'Abramo et al. (1985) state that the maximum density possible for juvenile signal crayfish in culture during the first 30 days is 150/m², and Gydemo and Westin (1989) showed that a density of 100/m² was possible for 3.5 cm large noble crayfish juveniles when shelters were in excess. When Jonsson (1992) studied juvenile crayfish the survival rate was higher for the noble crayfish but the growth was better for the signal crayfish, when reared at equal densities. Since the signal crayfish is more aggressive than the noble crayfish (Cukerzis 1986, Söderbäck 1991), it is probably wise to rear the former at lower densities than the noble crayfish. The results in this study indicate that it is appropriate to have a density of less than 100 juveniles/m² during three to four months after hatching. To improve the growth rate the results in this investigation indicate that it is important to prevent cheliped losses. Animals which had lost a cheliped were significantly smaller than the intact ones, which is in agreement with the results presented by Hirvonen (1992) and Bowler and Brown (1977). When crayfish loose a cheliped, a new one is regenerated during moulting (Aiken and Waddy, 1992), at the expense of overall body growth.

Suitability of the diet

In nature, juvenile crayfish feed on a variety of invertebrates, epiphytic algae and zooplankton (Goddard 1988). Juveniles are also well adapted to filter feeding (Thomas 1979, 1986). Therefore, I expected that a diet based on natural and fresh food should be suitable. When juveniles were fed individually the survival was comparatively good. When Celada et al. (1989) fed individually reared juveniles with several fresh and artificially compounded diets, the survival was much lower. The maximum survival was 44% after 80 days when fresh aquatic plants were added to a crab protein reference diet for crustacean. In this study the mean survival, when the juveniles were fed individually, was 98% after 60 days and 83% after 109 days. This suggests that a diet based on natural and fresh food is advisable for experiments with newly hatched crayfish. Further the juveniles were normally pigmented and few of them had died because of the moult death syndrome (MDS), which has been quite common in feeding experiments with crustaceans (Baum et al. 1991).

In conclusion, the results indicate that with fresh food, shelters in excess, a complex habitat and with a light intensity of at least 600 lux, is it possible to achieve a good survival of newly hatched signal crayfish even when reared together. To minimise death caused by cannibalism, a juvenile density of less than 100/m², during three to four months, is advisable.

Acknowledgement

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NOTES AND COMMENTS

On Catching of Noble Crayfish (*Astacus astacus*) in Estonia

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Yearly accounts of catching permits have served as a basis when estimating the conditions of the Estonian crayfish populations. The uniform order of catching crayfish and the permit system makes it possible to unify the results and to assess the distribution of crayfish populations, their ability of reproduction and the distribution of "burn spot disease". As catching devices crayfish dipnets have been used. Fixing the beginning and the end of catching, the number of sized crayfish (10 cm and longer) caught per net-hour or the yield calculated. This method give us some rough estimate of the crayfish abundance in Estonia and the possibility to get a general information from the crayfish resources during catching season annually. In the best crayfish water bodies, the yield has reached up to 50 crayfish per net-hour. Unfortunately, such figures are exceptions. The mean yield on the mainland is 1-2 and on the Island of Saaremaa 3-4 sized crayfish per net-hour. The numbers represent the water bodies for which catching licenses are given.

Protection of crayfish resources has been the prime motive for making a system of crayfish catching licenses. The number of permits issued has been considerably smaller than the crayfish resources would permit. It is due to a considerably large scale of poaching. The number of permits has been corrected annually according to the catching results previous years. The number and list of water bodies where hobby catching is allowed has been changed continuously. At present, more than 130 watercourses and 135 lakes have been registered as crayfish habitats (Fig. 1). Some 10 lakes and 10 rivers on the mainland and 8 water bodies on the Island of Saaremaa are regarded as good crayfish water bodies. The remaining crayfish populations are satisfactory or poor from the reproduction point of view. The crayfish catches during the last 14 years are shown in Fig. 2. The number of caught crayfish achived its peak in 1983, reaching 30 thousand sized crayfish. During the following two years the situation changed drastically due to the death of crayfish populations in 15 mainland water bodies. Crayfish deaths occurred in Rivers Kaave, Reiu, Laanemetsa, Nurtu, Päärdu, Nóva, Vihterpaly, Kloostri, Angerja, Enge and Vidva, Lakes Uljaste and Saare and other water bodies. Unfortunately, we are not able to find all cases of eradications. The crayfish in River Kaave and the Laanemetsa brook died due to pollution and the crayfish of the Angerja brook due to dredging. It is possible that crayfish plague occurred in some water bodies as well. Up to now, re-occurrence of a crayfish population has been noted in Lake Saare. Other populations are very sparse and we need to make series of transplantations to increase these populations.

A third of the total catch originate from the numerous water bodies on Island of Saaremaa. According to the results of catch accounts of 1984-85, the number of sized crayfish decreased and thus crayfish catch on Saaremaa was prohibited beginning from 1985. The hobby fishing was restored two years later but the number of licenses issued was considerably smaller than crayfish resources would permit.

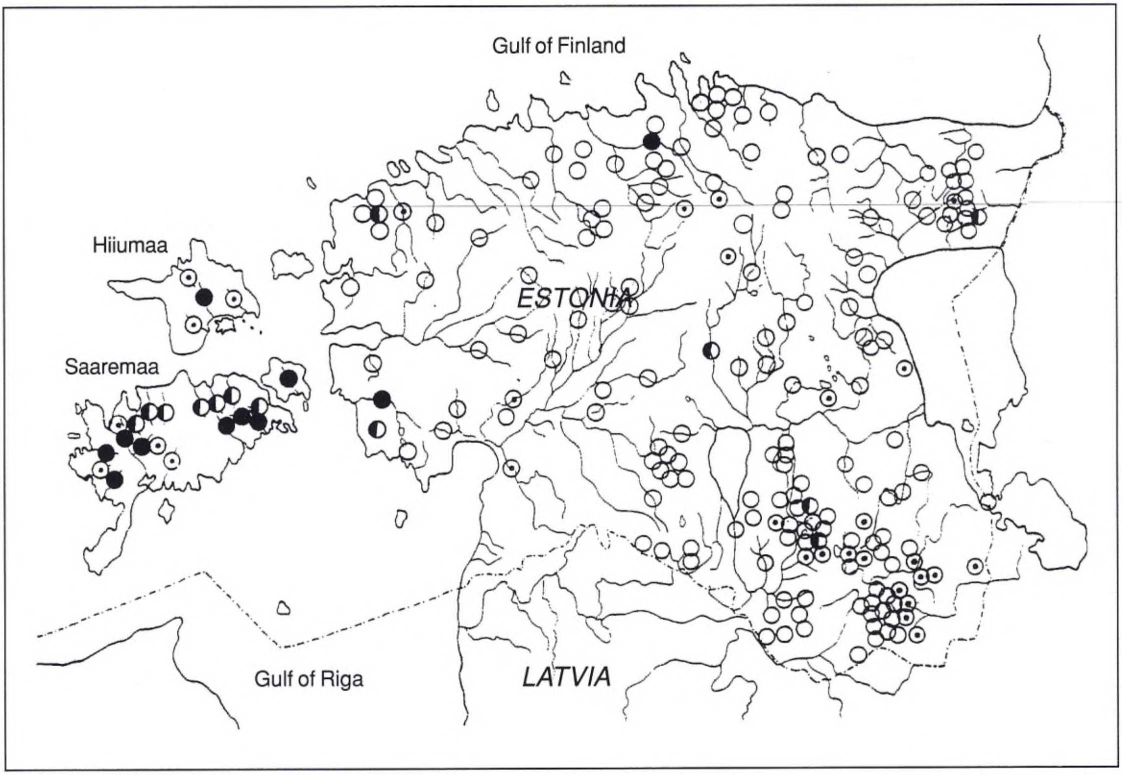

Fig. 1. Distribution and number of sized nobel crayfish (10 cm and longer) caught with one dipnet per hour during one night: ○ <1, ⊙ 1-2, ◐ 2-3, ● >3.

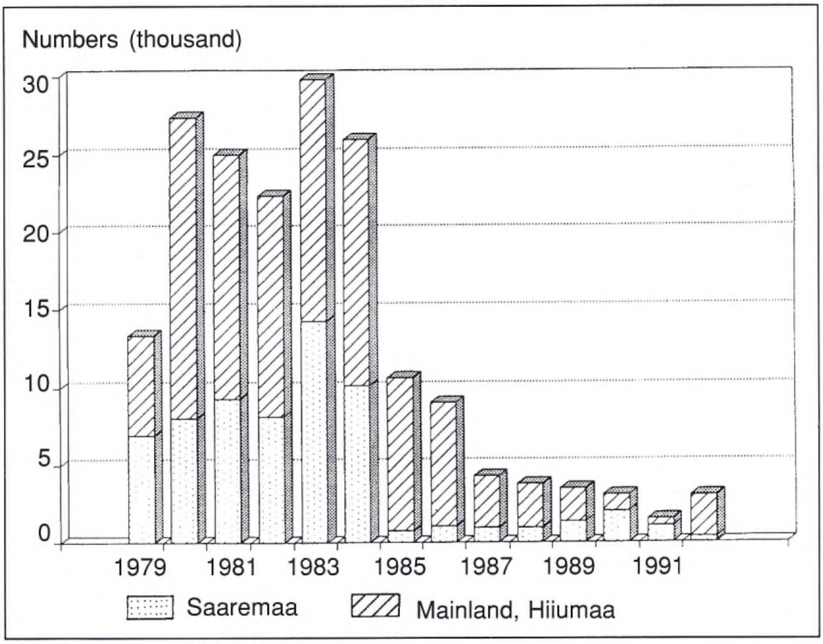

Fig. 2. The number of sized noble crayfish caught in 1979-92.

On catching licenses there has been regular information about the distribution of "burn spot disease". In the north and north-east of Estonia there are some heavily infected crayfish populations, where more than 50% of specimens have spots (Fig. 3). The spreading of "burn spot disease" possibly is related to poaching and the use of undesinfected catching equipment.

The islands of Estonia have remained uninfected by plague. Therefore the crayfish of Saaremaa, Muhu and Hiiumaa Islands are of great value as stocking material for natural water bodies as well as for crayfish breeding. Since 1970 about 150 thousand specimens have been transplanted from the strong populations, mainly from the Island of Saaremaa into former crayfish waters of the the mainland. Stocking of crayfish is controlled by the Ministry of the Environment and its local bureaus. Traditionally, restoration of crayfish stocks is carried out in September every year. Unfortunately, the size of the restored crayfish populations have remained small.

There have been some attempts to hatch noble crayfish. In 1989 the total outcome was 8,000 juveniles. The hatching of crayfish can be considered as a beginning of crayfish farming in Estonia.

The most discussed question in recent years is the introduction of signal crayfish (*Pacifastacus leniusculus*). However, since the national authorities claim that the introduction of signal crayfish in Estonia is not desirable Estonia is one of the last countries in Europe where no alien crayfish species have been introduced.

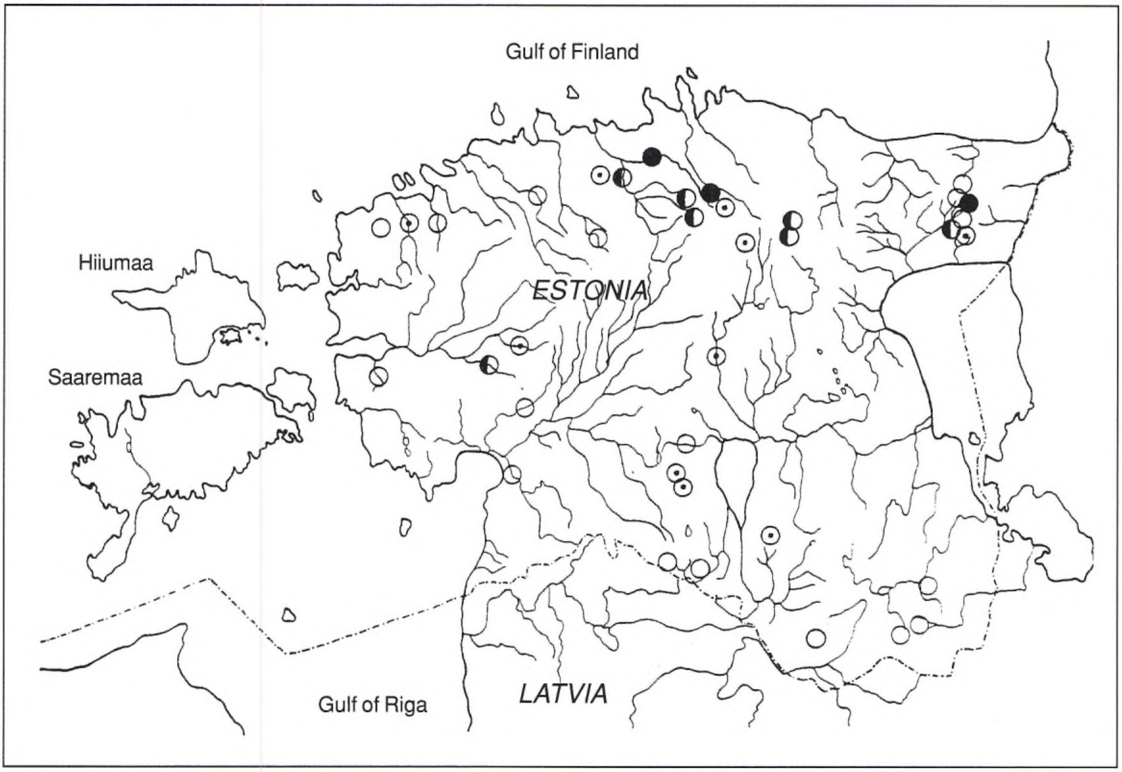

Fig. 3. Distribution of "burn spot disease" in Estonia and percentage of infected mature specimens in populations: ○ 1-15, ⊙ 15-30, ◐ 30-45, ● 45-60.

Facts about Crayfish in Lithuania

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Lithuania numbers more than 722 rivers and rivulets, 2,500 lakes, each covering an area of more than 0.1 km^2, and some 1,500 smaller lakes that occupy 1.5% of the total area of the Lithuanian territory.

Historical notes

In 1578 the Livonian Chronical wrote that there was plenty of crayfish in Lithuania. They were important objects of export. From 1890 to 1914 Lithuania was the most important centre in Europe for purchase and export of crayfish. Seven to eight million crayfish were exported from here annually.

In the period 1925 to 1930 crayfish were sent to Germany and France for breeding purposes. In 1949 and 1950 2,900 and 31,200 kg, respectively, were trapped in Lithuania. Exportation was temporarily revived between 1952 and 1967 (Sestokas 1973).

The abundance of crayfish stimulated to different research activities. In 1883 M. Girdwoyn investigated 10 lakes abundant in crayfish and suggested transplantations of crayfish to lakes with sparse populations (Sestokas and Cukerzis 1983). In 1899 the first booklet on crayfish was published in Lithuanian. However, it was not until 1956 that more systematic investigations were started by J. Cukerzis. In the period 1963 to 1969 his group investigated and obtained data from 404 waterbodies with crayfish. In 1972 the laboratory of Carcinology was formed and it was active until 1984.

Crayfish species and distribution

In Lithuania the research on crayfish resources was first started in about 1970. The investigations showed that crayfish inhabited 444 lakes or 17% of all lakes studied (Sestokas 1973). At present, three (maybe four) crayfish species inhabit Lithuanian waters (Fig. 1).

Astacus astacus - native in Lithuania. It is the most widely distributed species, the occurrence of which coincides with the part of Lithuanian territory abounding in lakes. According to earlier data *A. astacus* inhabited 91.5% of the lakes rich in crayfish. It is assumed that the patchy distribution of *A. astacus* in the area is related to anthropogenic effects (Cukerzis 1973).

Astacus leptodactylus is widely spread in the north-western parts of Lithuania, probably due to introductions from Latvia and Byelorussia at the end of the last century. It was supposed that *A. leptodactylus* was resistant to crayfish plague and therefore it was introduced to replace *A. astacus*. In 1970 *A. leptodactylus* was present in 8.5% of the lakes with crayfish populations and in 4.4% of the lakes they co-existed with *A. astacus* (Sestokas 1973).

Pacifastacus leniusculus from Sweden was introduced into some isolated lakes in 1972. There are no data available on the distribution of this species at present.

Cambarus affinis. It is supposed that this crayfish species has reached the waters of south Lithuania from Poland and the Kaliningrad region (Russia).

Situation of commercial crayfish catches

In recent years the amount of commercially harvested crayfish originate from one single fish farm. Besides, during several years two old fishermen trapped *A. leptodactylus* together with fish in Lake Apvardai (Table 1).

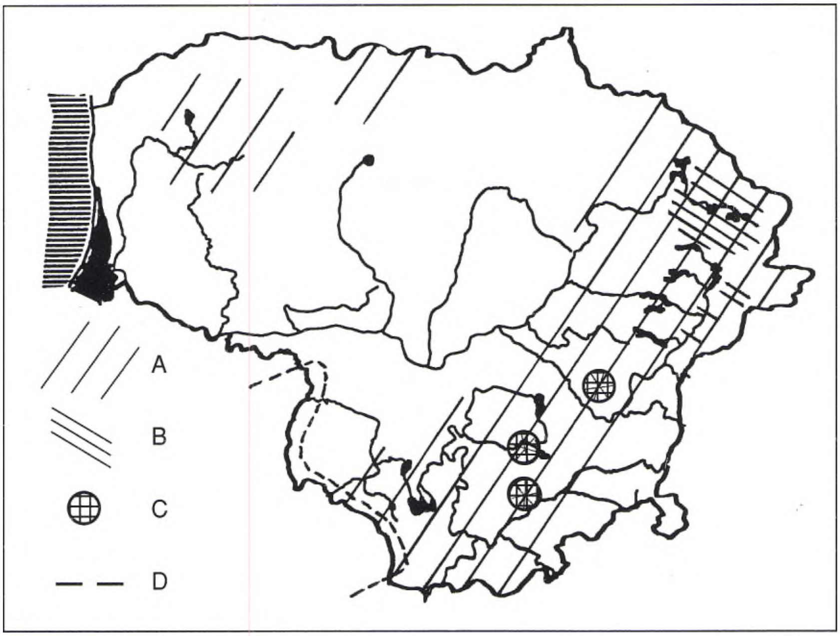

Fig. 1. Distribution of crayfish species in Lithuanian waters.
A = areas mainly inhabited by *Astacus astacus*,
B = areas where *Astacus leptodactylus* may be found,
C = localities where *Pacifastacus leniusculus* introductions have been made,
D = areas where *Cambarus affinis* can be found.

Table 1. The official total catches of *A. leptodactylus* in Lake Apvardai.

1990	1991	1992
430 kg	200 kg	no fishing

Unofficial catches are higher by many times. Several instances are known when more than two thousand specimens have been caught in a lake during one night.

The present situation in scientific research

Since 1984 when the laboratory of Carcinology headed by Prof. J. Cukerzis was abrogated, no structural division was left at the Institute of Ecology or anywhere else where all the scientific workers could be engaged in crayfish research problems. The scientists who remained at the Institute proceeded with their previous work. However, at present crayfish is being used as test objects for certain branches of science: physiology, behaviour, biochemistry, microbiology and toxicology. Currently, all research efforts at the Institute are focused more on fundamental investigations and not on applied ones. Today, the studies on crayfish at the Institute of Ecology are being carried out by three scientists: A. Burba - behaviour and the effects of anthropogenic factors, G. Mackeviciene - metabolism, L. Michenieni - microflora.

Crayfish protection and restoration

The measures for crayfish protection in Lithuania are considered to be good, even it they are formal. The Department of Environmental Protection limited the catching of crayfish in 1985-92 to 94 lakes (total area 6,292.8 ha), 6 ponds (503 ha) and 35 rivers (total length 1,387 km). Unfortunately, the crayfish resources have not been investigated in these lakes and all available information is based on reports of local inspectors.

These limitations should help to increase crayfish resources and, as well, serve the transplantation programme carried out by this department. In 1991 2,752 adult individuals of *A. astacus* were transplanted from one lake into two lakes and one rivulet with sparse populations. In 1992 8,208 adult individuals of *A. astacus* were transplanted from five lakes and seven rivers into nine rivers, three lakes and three stream ponds.

In Lithuania capture of legal-sized crayfish (from 11 cm) is allowed during the period July 15 until November 1.

The future

Until now, almost no efforts have been made on crayfish aquaculture in Lithuania. Only in 1963-64 some efforts were made to rear crayfish in fish ponds. Besides, crayfish breeding and rearing have been performed under experimental conditions with the purpose of using them for scientific experiments.

We now hope that crayfish cultivation will attract farmers and business men in Lithuania. In the near future two main problems have to be solved:

1. The investigations of crayfish resources and their management.
2. Aquaculture studies.

Currently the privatization process is taking place in Lithuania. Individual persons and organizations rent lakes. Amateurish fishery clubs are being established instead of the uniform society of fishery. We believe that an establishment of either an amateurish or a commercial fishery demands scientific investigations in order to save our resources from ruthless exploitation.

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On the Restoration of Noble Crayfish in Sweden

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Introduction

Crayfish are of importance from several aspects. Ecologically they can act on several trophic levels and being the largest invertebrate in fresh waters they can have a considerable impact on the ecosystem. Economically they are one of the most valuable freshwater species. Socially they have, at least in the Nordic countries, a great importance. Thus, it is of interest to preserve existing populations and increase the production by restoration and enhancement.

The reasons for the need of restoration are on one hand diseases, viz. the crayfish plague that since its first appearance in Europe has devastated approximately 90% of the native crayfish stocks. On the other hand, man has depleted and devastated crayfish populations by direct and indirect ecosystem changes. Thus, the question of restoration arises.

Strategies for restoration

One easy way is to replace the native species with an introduced "homologue". The true, long-term, effects of such introductions cannot be predicted, only guessed. The history of transplantations and introductions are not encouraging. As a matter of fact the author has not been able to find one single introduction in fresh waters with a native fauna that can be claimed to be fully successful from a biological point of view. However, from a shortsighted economical point of view there gives numerous examples. Nyman (1991) stated that "the dominant ethics of the so called developed world has for centuries been: if a species does not have a direct commercial value to us, it can be ignored or even exterminated".

Dealing with crayfish restoration in Sweden, Finland and Denmark means dealing with two species, the introduced American signal crayfish, *Pacifastacus leniusculus* (Dana), and the native noble crayfish, *Astacus astacus* (L.). Restoration with signal crayfish means restoration of crayfish fishery for economical purposes. Restoration of noble crayfish populations means restoration of crayfish for conservation purposes, but also for economical puposes, since for cultural as well as market economical reasons, a "native" product generally has a higher value, especially if in short supply.

Thus, when the decision is taken to restore crayfish populations, it must be decided whether it is the crayfish fishery or the native crayfish species that is to be restored. If it is the crayfish fishery, the easy choice is to introduce signal crayfish with the probable risks of making the crayfish plague permanent in the water system and eradicating remaining noble crayfish populations. Most likely the signal crayfish will develop a fishable population. However, Swedish experiences show that the price drops with time and increased supply, owing to the numerous introductions and present day economical argument cannot be expected to last. Also, possible adverse effects of the signal crayfish are still not too well known. From the few instances where signal crayfish and noble crayfish live together, apparently without crayfish plague present, the signal crayfish is the most successful and the noble crayfish populations are decreasing (Fjälling and Fürst 1985, Svärdson et al. 1991, Söderbäck 1993). The problem of competition between crayfish species was known and considered a risk connected to the introduction of signal crayfish (Svärdson 1965). It is also assumed that introduced *P. leniusculus* contributed to the extinction of *Pacifastacus nigrescens*, an endemic species in California (Holdich 1988).

The more difficult way is to restore the native crayfish. In Sweden at least, the statement "once crayfish plague - always crayfish plague" has ruled for many years, implying that it does not make sense trying to restore noble crayfish except for in certain areas. It is more vulnerable to the crayfish plague and therefore the risk of new attacks is present. However, in many of the cases of alleged new plague outbreaks, crayfish plague has not been confirmed. The causes of disappearance of crayfish may in many cases be sought after elsewhere. Finding the reasons may be more difficult but is essential for a successful restoration.

Possible reasons to declining crayfish stocks are (adapted from Nyman 1991):

- Habitat degradation: e.g. drainage, deforestration, water level regulation, dredging, filling, harbours, dams, vegetation removal, sedimentation.
- Water quality degradation: pollution: e.g. acidification from acid rain, heavy metal discharge, nutrient loadings from agriculture, forestry and municipal sources leading to eutrophication and oxygen depletion.
- Introduction of exotic species or populations: e.g. extermination through competition, predation, diseases.
- Fishing: fishing is selective. Overfishing may cause ecosystem changes through inter- and intraspecific alterations of the fauna.
- Diseases other than crayfish plague: e.g. *Saprolegnia* sp. has been proved to the cause of mass mortality (Fiskeriverket 1993, Vey 1977, Söderhäll pers. comm.). Parasites and diseases are more likely to occur and have severe effects when habitat and water quality deteriorates.

These possible reasons alone or, probably more common, interactive, can all have severe influence on the ecosystem resulting in altered paths of interaction and a more hostile ecosystem for the noble crayfish. The net effect is not only a decrease or extermination of the crayfish but also more adverse conditions for the noble crayfish to deal with when trying to recover. The noble crayfish, being a more K-selected species, is less aggressive and fecund relative to the signal crayfish. This is one factor that could explain why signal crayfish has been successful in waters where reintroductions of noble crayfish has not been successful and the reappearance of crayfish has not been confirmed. One path of interaction is illustrated with the mass-removal of predacious fish using Rotenone in some small lakes on Åland (Storberg 1978). The crayfish population grew very rapidly after the treatment.

Restoration methods

There are no universal methods for restoration. What is successful in one case may not work in another. With present day knowledge on ecosystem interactions and sustainable management of natural crayfish populations, a lot of work in these fields is needed. A general scheme can, however, be applied:

- Identify the state and causes to the state. In the preceeding section a number of possible reasons were listed. They can be responsible for the state alone or interconnected and may have effects in other parts of the water system than where they are situated. When determining the status of the crayfish population, it is necessary to perform thorough investigations and not only rely on trap catches and a general decrease in numbers. The general rule of "fishable stock size" as has been applied in Sweden, defined as one crayfish CPUE, is worthless for a number of well known reasons.
- Determine which measures that are necessary to take and which are possible. It may be sufficient to create new suitable habitats, or a changed water regulation scheme may be applied. New wetland areas to retain water and decrease run-off nutrient loadings may be created. Has the fish fauna changed and could it be changed back to the previous state?
- Decide methods. The methods chosen must take into account the whole ecosystem, not only the waterbody. In most cases manage-

ment schemes must be imposed and in many cases also legislative measures. One absolute requirement is to minimize the risks for crayfish plague attacks by not allowing introductions of signal crayfish anywhere in the water system. When deciding methods, cooperation is necessary between various interested parties. These are the fishing-right owners, the farmers who are using fertilizers, the environmental protection authorities and conservation groups, industry, communities etc.

Thus, in order to successfully restore crayfish populations, national strategies must be developed. The World Conservation Strategy launched jointly by UNEP, IUCN and UNEP in 1980 may serve as a basis. The strategy aims to preserve genetic diversity, maintain essential ecological processes and to ensure the sustainable use of species and ecosystems. This can be accomplished by Aquatic Diversity Management Areas, ADMA (Nyman 1991).

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Results from the group discussions

Interspecific and intraspecific interactions

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The members of the group were Anabela Jensen, Denmark; David Lodge, U.S.A.; Tiit Paaver, Estonia; Trond Taugbøl, Norway; Paula Henttonen, Jouni Tulonen, Kai Westman and Markku Pursiainen, Finland; Björn Söderbäck, Anders Jonsson, Mikael Svensson (secr), Lennart Edsman, Pia Keyser, Javier Dieguez-Uribeondo, Sweden.

Objectives

The group discussion focused on factors regulating population with special emphasis on interspecific and intraspecific interactions of crayfish in the Nordic countries. Three major items relevant to the Nordic crayfish species were identified: a) the reasons for the appearance of non-recovering *Astacus astacus* populations, b) temperature as a factor limiting geographical distribution of *Astacus astacus* and *Pacifastacus leniusculus*, and c) effects of crayfish parasites and diseases.

Background

Non-recovering *Astacus astacus* populations

Severely reduced populations of *Astacus astacus*, failing to recover from plague infections, acidification and liming and other catastrophic events have been observed in all Nordic countries. There may be several reasons for this phenomenon, including interspecific and intraspecific regulation, and/or abiotic regulation. The cause of the initial reduction may or may not be the reason why the crayfish population does not recover. Lack of historical data on the cause of events and population size before the reductions was considered to be a general problem.

Although the reason for a drastic reduction of crayfish populations is often unknown, crayfish plague, (*Aphanomyces astaci*), is often also thought to be the main factor in cases where documented evidence of the plague is not available. Signs similar to those of crayfish plague (e.g. mass mortality, brown spots on carapace and limbs, broken chelipeds) may have been observed, but the plague fungus has not been adequately identified in the laboratory. Samples collected from the populations are often too old for identification of *A. astaci*. Several other reasons for mass crayfish mortality are possible, but rarely documented. The life cycle of crayfish plague is well known, as are the defense reactions of the host. Yet it seems that the plague behaves differently in natural conditions as compared with the laboratory. The hypothesis that some noble crayfish could be resistant to the plague has not been verified in the laboratory, and field evidence is lacking. Data on the length of time an infected noble crayfish can survive during the cold period of the year is also lacking. One explanation for the non-recovering *A. astacus* populations propounded was that the plague spreads back into the lake when the crayfish population becomes dense enough to be catchable.

Because it has not always been possible to identify *A. astaci* when mass mortality of crayfish has occurred, the question of other lethal diseases has been raised. The influence of

Psorospermium haeckeli on the population level is not clear since *P. haeckeli* has been the subject of general interest for a short time only. Cases of mass mortality of crayfish, sparse populations or a slow growth rate of crayfish often coincide with *Psorospermium* in certain lakes, without implying that *Psorospermium* is the main reason for these phenomena.

In addition to the direct effect on survival and growth, parasites and diseases might have an indirect effect by changing the behaviour of crayfish so that they become more vulnerable to predation. Until now, only *Thelohania* and *Aphanomyces* are known to cause this effect. However, other diseases and parasites may act in the same way.

One possible explanation for the failure of *A. astacus* populations to recover is altered interspecific and intraspecific interactions following a drastic reduction in population size. In general, there have been few studies on the interspecific interactions between crayfish and other organisms in lakes and rivers. In a variable environment (after a plague episode or after an environmental disaster) the relationships between different species may change. This change is difficult to predict on the basis of current knowledge. Predation possibly influences the recovery of crayfish populations and predation from fish might have been underestimated on some occasions. The crayfish itself is a factor changing the abiotic and biotic environment and its own physical habitat. The loss of crayfish from the lake will influence the habitat, e.g. vegetation increases and shelters become filled with sediment.

Abiotic factors in crayfish lakes and rivers change slowly or more rapidly, usually as a consequence of human activities. Both eutrophication and acidification result in abiotic and biotic changes in the ecosystem. Pollution and toxins are suspected to be one explanation for the slow recovery of the crayfish population. However, contrary to the common belief that crayfish are sensitive to polluted waters, productive crayfish populations are sometimes found even when exposed to industrial waste water.

Temperature as a factor limiting geographical distribution of crayfish and the implications for restocking

The distribution of *A. astacus* populations seems to be limited by temperature in the north of Norway, Sweden and Finland. However, the optimum temperature range for *A. astacus* and *P. leniusculus* is not documented, and it is reasonable that the optima for the two species would differ. If there are differences between the two species (or between different phenotypes of each species), this will certainly be important when deciding which species should be restocked and will affect the outcome of exploitation. The following hypothetical model for choice of species where either species it is possible to choose was suggested (Fig 1):

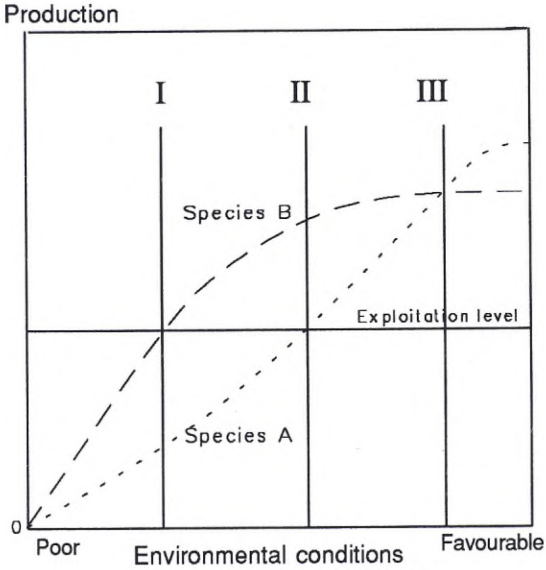

Fig. 1. Choice of crayfish species (or phenotype) for stocking in relation to environmental conditions.

If species (or phenotype) A has a higher optimum carrying capacity than species (phenotype) B when environmental conditions are good (III), it should be chosen for stocking lakes/rivers. However, when environmental conditions are more harsh (I), species (or phenotype) B, which has a higher carrying capacity (or optimum population size) in sub-optimal conditions should be chosen when it is above exploitation level. When environmental conditions are close to optimum for both species, other factors than carrying capacity should be used when deciding the issue.

Crayfish parasites and diseases

Crayfish plague (*Aphanomyces astaci*) was recognized as the most important parasite of the native crayfish species in the Nordic countries. However, *Psorospermium haeckeli*, the fungus *Saprolegnia parasitica*, white-tail disease (*Thelohania contejeani*), burn-spot disease, (*Ramularia astaci*) and other parasites should all be considered.

Crayfish plague is without doubt the most dangerous known crayfish disease, and it has caused widespread economic losses in Europe. Apparently there are diagnostical problems when identifying the plague since the analyses involve isolating *A. astaci*, sporulation, and infection of healthy animals. Firstly, this is difficult, and a well-equipped laboratory is needed. Secondly, fresh samples of crayfish (still alive) are needed, and thirdly, it is time consuming, which makes the analyses expensive. As regards microscopical determination of the plague, the hyphae is sometimes not found, especially when the crayfish is degraded and covered with other fungi. If other indications are used to determine crayfish plague, e.g. mass mortality, brown spots on the cuticula and broken legs, other diseases and environmental changes may cause similar symptoms. In many cases this will lead to a false diagnosis.

The time lapse before restocking after the outbreak of crayfish plague was discussed. Cage experiments 1-2 years after the outbreak can be used to confirm that crayfish plague is no longer present in the water before restocking. In a few cases restocking has been done the same year.

When the plague has struck a population there are no general rules as to which species should be used for restocking - *Astacus* or *Pacifastacus*. The latitude, situation and nature of the water body, as well as the vicinity of other crayfish populations should be considered before a decision is taken.

There may be several reasons why repeated attacks of crayfish plague, "chronic plague", occur. Either all crayfish were not killed in the previous attacks, or the plague spreads again from another infected population. However, another possible reason might be that the plague does not behave as it is believed to do in natural waters. It could also be a question of the population density and/or, resistance of crayfish (*A. astacus*). The question of whether infected crayfish could carry *A. astaci* for a long time when water temperature is low was again raised.

The potential parasite *Psorospermium haeckeli* was regarded to be widespread and common in *Astacus*-populations in the Nordic countries. However, it is more rarely found in *Pacifastacus* populations. Its taxonomic position is unknown. Groups of fungi, algae, and even parasitic dinoflagellates have visible features similar to those of *P. haeckeli*. Signs of the defence reactions of the host against *Psorospermium* are dependent on crayfish species. It is not possible to answer the question of whether *Psorospermium* is a real parasite of crayfish or a commensal before we know more about its life history.

Under certain conditions the fish pathogen, *S. parasitica*, can cause mortality in crayfish, and its virulence on crayfish species is being studied. White-tail disease, (*T. contejeani*), has not been a major problem in Nordic countries. Because of the increasing frequency of *Thelohania* in artificially acidified lakes in Canada, the status of this disease deserves to be followed. Burn-spot disease, (*Ramularia astaci*), and Branchiobdellids are more common in Estonia than in the Nordic Countries. They are not regarded as a serious health problem, but they can reduce the price of crayfish or create difficulties in selling crayfish.

We know too little about bacteria and viruses in crayfish. Vibrio have been reported to cause problems in softshell production in U.S.A. and the connection between bacteria (e.g. *Aeromonas hydrophila*) and mortality of *A. astacus* held in a recirculating water system in Kuopio is currently being studied. Infectious pancreatic necrosis virus (IPNV) is known to be transferred by crayfish.

Recommendations

Non-recovering *Astacus astacus* populations

More must be known about the history of crayfish populations. Data on the distribution of crayfish in the Nordic and Baltic countries is sparse and scattered. There is therefore a need to compile data on crayfish populations within all the Nordic countries. There is also a need to compile data on proven instances of crayfish plague as well as data on other obvious reasons for the disastrous reductions in crayfish populations.

The effect of predation and competition upon the recovery of reduced crayfish populations needs to be studied more thoroughly. Little attention has been paid to this question, although this has been one of the most fundamental problems in crayfish management. Studies should focus on the effects of predation and competition on recovering crayfish populations, especially in situations where there have been physical changes in crayfish habitat.

Data should be collected on the basis of questionnaires and from known sources about lakes/rivers with non-recovering populations. Possible areas to be covered should be predatory species (mammals, birds and fish) and their changes, limnological and environmental factors, changes within the drainage area, crayfish exploitation levels and population characteristics such as population age and size. The first steps should be to specify the questions to be included, by correspondence. Questionnaires should then be distributed within countries and the data compiled.

Temperature and restocking of crayfish

Laboratory experiments must be conducted to study the effect of temperature on crayfish distribution. The experiments should focus on the duration of the cold period and on the critical minimum temperature for different periods of the life cycle. Experimental results should also be compared with data from the species "original" distribution area. The results should thereafter be verified in field experiments.

Crayfish parasites and diseases

Although the host-parasite relationship between the crayfish plague and the crayfish is well known, too little attention has been paid to the situation in natural environments. The behaviour of crayfish plague in lakes and rivers must be studied more in greater depth. More information on the ecology and interaction between the plague and crayfish (at population level) is needed. Thus, the help of an epidemiologist is recommended. The effect of crayfish parasites and diseases (other than crayfish plague) as a possible constraint on the recovery of crayfish populations must be studied. The influence of parasites and diseases on the behaviour of crayfish (exposing them to increased predation) also needs to be studied.

To put an end to conjecture speculation, the life cycle, spreading and infection mechanisms of *Psorospermium* should be ascertained. The influence of this organism on individual crayfish and crayfish populations should be studied. The choice of method (microscopical examination of tissue samples or digestion of the crayfish, a relative or a quantitative scale) for finding *Psorospermium* in crayfish needs to be assessed.

Crayfish Management in the Nordic and Baltic countries

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The members of the group were, Magnus Appelberg, Arne Fjälling (secr), Magnus Fürst, Rolf Gydemo and Tommy Odelström from Sweden; Eilif Byrnak, Peter Gertz-Hansen and Henrik Jörgensen from Denmark; Japo Jussila, Teuvo Järvenpää and Jorma Kirjavainen from Finland; Aloyzas Burba from Lithuania; Tiit Paaver and Janus Tuusti from Estonia and Jostein Skurdal from Norway.

Objectives

The main aims include a better protection and conservation scheme for native crayfish in the Nordic and Baltic countries, and developing management tools for achieving a high and sustainable yield of crayfish of attractive size from natural water bodies.

Background information

Crayfish species and distribution

There is only one native species in the Nordic and Baltic countries, the noble crayfish (*Astacus astacus*). It has been discussed whether noble crayfish have been introduced to Sweden and Norway. Distribution is strongly influenced by stocking, and at present self-perpetuating stocks are found as far north as 67°N in Finland, 61°N in Sweden and 63°N in Norway. The narrow-clawed crayfish (*Astacus leptodactylus*) has spread into Lithuania, Latvia and Finland and is also found in Denmark. Signal crayfish (*Pacifastacus leniusculus)* have been stocked in Sweden, Finland, Lithuania and Denmark. Spiny-cheek crayfish (*Orconectes limosus*) have probably spread to localities in Denmark and Lithuania.

Threats

Habitat loss, pollution, acidification and crayfish plague (*Aphanomyces astaci* Schikora) have reduced noble crayfish populations throughout their area of distribution. Noble crayfish production is also adversely affected by the stocking and dispersion of alien and native crayfish (e.g. the alien signal crayfish *Pacifastacus leniusculus*, and spinycheek crayfish *Orconectes limosus*, and the native narrow-clawed crayfish *Astacus leptodactylus*). Eel stocking and overfishing have also depleted stocks. In many localities crayfish abundance have been greatly reduced without any known sign of disease or other disastrous factors. In such cases, there has been speculation as to whether *Psorospermium haeckeli* has contributed to the loss.

Status of crayfish stocks

The noble crayfish has been eradicated from most of the previous productive lakes and rivers. The present catch is probably less than 10% of historic records in spite of the many new crayfish localities which have been stocked. Compared to their pre-plague distribution, noble crayfish are presently mainly confined to low productive localities, i.e. patchy distributions at high latitudes and/or altitudes.

The pre-plague catches of noble crayfish in the Nordic and Baltic countries exceeded 2,000 tonnes, whereas present catches are less than 200 tonnes (Table 1). The present total annual European catch of all crayfish species is estimated at approximately 7,000-8,000 tonnes. Of this quantity noble crayfish comprise only some 220 tonnes or some 2-3% of the total European catch. Noble crayfish fetch a high price and thus probably represent some 10-20% in value of the total crayfish catch.

Table 1. Past and present catch of noble crayfish (*Astacus astacus*). Factors other than the plague have also contributed greatly to the decline in catches (all figur catches in tonnes).

Country	Crayfish plague	Catch	
		Before the plague	Present (year)
Denmark	1907	?	?
Estonia	1890s	>20	0.1 (1990)
Finland	1893	>650	110 (1990)
Latvia	?	?	?
Lithuania	1890s	400	4 (»1970)
Norway	1971,1987	> 40	10 (1990)
Sweden	1907	>1,000	50 (1987)
Total		2,110	174

Management regulations applying to crayfish fishing

Crayfish have been exploited in the Nordic and Baltic countries for several centuries. Crayfish fishing is regulated in various ways. The regulations are aimed at achieving a high and sustainable yield of crayfish of attractive size. National management regulations include restrictions on season and size (Table 2). Season restrictions vary between countries; in Denmark there are specific seasons for the sexes to protect females and their young. Minimum size limits vary from 90-110 mm total length. Estonia and Norway have national rules on mesh size or effort restrictions. In addition to national rules, Norway and Sweden also have local rules adopted by local authorities or land owner associations which impose further restrictions on fishing. There are large differences in the general management framework between the countries (Table 2), and when local regulations are taken into account differences become even larger. The regulations probably reflect the differences in cultural traditions related to the catching and consumption of crayfish. In Finland the 100 mm minimum size limit was established in the 1890s apparently on the basis of purely commercial considerations. Despite their long use, relatively little is known about the effects of various management regulations on wild noble crayfish populations.

To meet local demands European markets have been importing several thousand tonnes of crayfish per year mainly from Louisiana, USA. There is also crayfish trade between various European countries, although statistics are poor Noble crayfish are harvested using a wide array of methods and equipment. Baited traps are the most widely used fishing gear, although recreational catching for domestic consumption also include catching by hand, baited sticks and net balances.

Table 2. Regulations of *Astacus astacus* fisheries in the Nordic and Baltic countries (M=males, F=females).

Country	Season	Minimum size (mm TL)	Mesh size (mm)	Effort restriction	Local rules
Denmark	M:1/4-30/9 F: 1/8-30/9	90			
Estonia	25/7-25/9	100		+	
Finland	21/7-31/10	100**			
Latvia	?	?			
Lithuania	15/7-15/10	110			
Norway	6/8-14/10	95	21		+
Sweden	2nd Wednesday in Aug-31/10*	90			+

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* abolished from 1994 and on, ** abolished from 1993.

Conservation

The noble crayfish (*Astacus atacus*) is the only native crayfish species in the Nordic and Baltic countries. To protect the noble crayfish it is necessary to impose a ban on stocking of alien crayfish which are plague vectors. It is also necessary to ban the import of live crayfish for consumption and ornamental use. Measures to protect crayfish habitat and liming of acidified lakes are needed as well. Some stocking of native crayfish in plague-stricken areas has been successful, indicating a potential for reestablishing native crayfish in such areas.

Crayfish production and market

There is a large demand for crayfish in the Nordic countries; some 2,000 - 3,000 tonnes are imported each year. To increase domestic production native and alien crayfish are stocked and produced in aquaculture facilities. Noble crayfish have been stocked in new localities this century and have increased their northernly distribution considerably in Finland, Sweden and Norway. The alien signal crayfish *Pacifastacus leniusculus* has been stocked in Sweden, Finland, Lithuania and Denmark to restore crayfish production in areas devoid of noble crayfish owing to crayfish plague. Stunting (i.e. slow growth due to high densities or other causes) is a problem in many lakes and this reduces crayfish catch potential significantly in many areas.

Crayfish in the ecosystem

Freshwater crayfish are true omnivores, feeding primarily on aquatic and semi-aquatic vegetation, benthic invertebrates and detritus. Aquatic animals affect their environment and resources through consumption and release. Consumption is harvesting, whereas release may be seen as fertilization, representing recycling for primary production. Crayfish may also be an important catalyst in the turnover of organic matter. Crayfish have high assimilation rates of animal and plant nitrogen (protein). While pelagic components of the aquatic food web are important as both consumers and remineralizers, crayfish serve a primary role as catalysts in the degradation and mineralization of organic matter, with a negligible release of phosphorus. Crayfish may also exert a significant grazing pressure on macrophytes. In the context of eutrophication, crayfish seem to play a positive overall role in the ecosystem.

Methodology for sampling crayfish

Crayfish are collected using various kinds of equipment, including various sorts of traps and baits. There are large variations in selectivity and catchability from one method to another and the results from different studies are therefore not comparable. Variations in catch and catch compositions of baited traps are influenced by biotic (population structure, molting, mating) and abiotic parameters (season, temperature, light, weather, habitat heterogeneity, mesh size, bait and so forth). Abundance estimates thus have serious shortcomings even when mark-recapture methods are used.

Recommendations

Conservation and restoration of crayfish populations

Data on distribution of both native and introduced crayfish species should be undertaken in all countries. Such compilations are presently being done in Estonia, Sweden and Norway. Data on the spread of crayfish plague should also be compiled. The data should be collated in a joint report on the status of crayfish in the Nordic and Baltic countries.

It is very important to intensify action to prevent the spread of crayfish plague. In the EU it is possible to restrict live transfer of crayfish by declaring plague-free zones, introducing a national program to fight plague spread or introducing national restrictions on live crayfish handling and stocking. In addition, epidemiological studies of crayfish plague are needed to understand how crayfish plague is spread and to be able to taken more effective action to reduce the risk of plague spreading.

Efforts to restore lost noble crayfish populations should be increased.

Management of natural populations

Data from experimental fishing is needed to evaluate the effects of various restrictive measures on crayfish catches of both native and alien species. Current data on noble and signal crayfish should be compiled and analysed in order to provide a basis for establishment of an experimental model. The data required for the analysis includes size composition, length increment per molt, molt intervals, size and age at maturity, frequency of mature females, fecundity, recruitment, mortality and yield. A preliminary request has indicated that such data (all or some of them) is available on some 50 noble crayfish and some 12 signal crayfish populations. This data on the population biology of noble and signal crayfish should be published separately, which should also clarify the differences between the species. A population dynamic model should be developed on the basis of the data collected to identify gaps in knowledge. Experimental fishing should then be initiated in selected experimental lakes. The experimental lakes must be thoroughly monitored. A group consisting of Jouni Tulonen (Finland), Magnus Appelberg (Sweden), Peter Gertz-Hansen (Denmark), Aloyzas Burba (Lithuania), Jaanus Tuusti (Estonia) and Jostein Skurdal (chairman, Norway) was appointed to address this issue.

Crayfish in the ecosystem

Crayfish influence organic turnover and co-existing fauna and flora through feeding and competition. Introduction of crayfish and plague outbreaks provide field experimental situations. More research is needed to understand the adverse effect of crayfish on their environment.

Standardizing of methods

Data on present methods should be compiled and attempts should be made to compare the various sampling techniques with regard to catch composition and quantities in order to calibrate the methods. Variance estimates for current methods should also be calculated. New sampling techniques should be developed and tested, particularely non-active methods such as tangling nets, shelters and so on. A group consisting of Markku Pursiainen and Japo Jussila (Finland), Magnus Appelberg (chairman, Sweden), Henrik Jørgensen (Denmark), Aloyzas Burba (Lithuania), Jaanus Tuusti (Estonia) and Jostein Skurdal (Norway) was appointed to address this issue.

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Joint Recommendations of the Nordic Crayfish Workshop April 19-21, 1993, Älvkarleby Research Station

The participants of the meeting agreed upon the following recommendations for the most important work concerning freshwater crayfish in the Nordic and the Baltic countries:

Management of Natural Populations

- Compile current data from crayfish studies in the Nordic countries.
- Form population dynamic models on this basis
- Select experimental lakes.
- Set up an experimental model.

Conservation and restoration

- Compile data on the status of native stocks in the Nordic and the Baltic countries.
- Compile data from several countries on plague spread.
- Document Danish legislative restrictions on the handling of live crayfish within the EU.

Standardizing of sampling methods

- Compile data on present methods.
- Standardize and calibrate present methods.
- Calculate variance for present methods.
- Find and test new methods.

Crayfish plague, *Aphanomyces astaci*

It is necessary to:
- Analyze time series data on plague.
- Conduct epidemiological studies in natural systems.

Psorospermium spp.

It is necessary to:
- Improve our knowledge of the life history of this potential parasite.

Crayfish and the environment

It is important to:
- Compile data on the distribution of the Nordic crayfish species and status of stocks.
- Improve our knowledge of the impact of the Nordic crayfish species on their environment.

Acknowledgements

We are most grateful to Nordisk Forskerutdanningsakademi (NorFa), the Swedish National Board of Fisheries and the International Association of Astacology (IAA) for financially supporting the workshop.

List of Papers presented at the Symposium

Aloyzas Burba	Facts about crayfish in Lithuania
Javier Dieguez-Uribeondo	The fish pathogen *Saprolegnia parasitica* and its virulence on crayfish species
Lennart Edsman	Factors affecting competitive abilities in *Pacifastacus leniusculus*
Magnus Fürst	Report to the Swedish Board of Fisheries about possibilities to restore natural populations of *Astacus astacus*
Rolf Gydemo	Aspects of restoration of noble crayfish
Japo Jussila	Crayfish management in Mikkeli Province in central Finland 1989-92
Henrik Jørgensen	Population size, growth and reproduction of *Astacus astacus* in a Danish lake
Jorma Kirjavainen	The growth rate and increase in length per moult of the noble crayfish and signal crayfish in southern and central Finland
David M. Lodge	Factors affecting crayfish populations and crayfish behaviour
Jostein Skurdal	Do we need regulations for catching crayfish?
Mikael Svensson	The effects of three fish species on survival and shelter selection of juvenile noble crayfish *Astacus astacus* in a pond experiment
Björn Söderbäck	Population regulation in two co-occurring crayfish species *Astacus astacus* and *Pacifastacus leniusculus*
Trond Taugbøl	Crayfish plaque and restoration in Norwegian waters
Jaanus Tuusti	The state of crayfish stock and the results of its research in Estonia
Kai Westman	Development of noble and signal crayfish populations in a small Finland forest lake

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All manuscripts submitted are considered for publication on the understanding that they have not been published, submitted, or accepted for publication elsewhere.

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Decisions of the editors are final.

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Fifty reprints are supplied free of charge. An additional number may be ordered at cost. Price list and order forms for reprints are sent with proofs.

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Language

Manuscripts should be in English. Linguistic usage should be correct. Write in a clear style. Avoid extensive reviews in the Introduction and Discussion. Cite only essential sources of a theory or opinion.

Title

The title should be brief and contain words useful for indexing and information retrieval.

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The abstract should succinctly mirror the content and emphasis of the paper in about 175 words. Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article.

Keywords

Five keywords should be given for indexing and information retrieval.

Text

The first page should contain only the title and author's name and address. Begin the text on page two. The manuscript should be type-written, double-spaced with wide margins and on one side only of good quality paper. Word processor generated manuscripts should be in upper and lower case letters of typewriter quality font. Manuscripts printed by 7 x 9 or 9 x 9 dot matrix printers will not be accepted for publication or review. Underlinings in the text should be avoided. After re-submission please enclose a diskette containing the final version of the manuscript in any DOS-wordprocessing program (e.g. wp 5.1, ws, ms-world).

Illustrations

Submit each diagram, graph, map or photograph in one original and three copies. All illustrations should bear author's name. Tables and legends of illustrations should be written on separate sheets. Do not incorporate the legend in the figure itself. Tables and illustrations should be comprehensible without reference to the text.

Colour plates may be included at the author's expense.

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Units

Use SI units as far as possible.

Nomenclature

Binomial Latin names should be underlined and used in accordance with International Rules of Nomenclature.

References

In the list of references the following usage should be conformed to:

Journal

Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. - Rep. Inst. Freshw. Res., Drottningholm 55: 144-171.

Book

Krebs, J.R. and N.B. Davies. 1991. Behavioural ecology. An evolutionary approach. Third edition. - Blackwell Scientific Publications, Oxford. 482 p.

Chapter

Krebs, J.R. and R.H. McCleery. 1984. Optimization in behavioural ecology. p. 91-121. - In: Krebs, J.R. and N.B. Davies (eds.) Behavioural ecology. An evolutionary approach. Second edition. Blackwell Scientific Publications, Oxford.

In the text references are given:

Svärdson (1976) or, at the end of a sentence (Svärdson 1976).

Titles of journals should be abbreviated according to the World List of Scientific Periodicals. If in doubt, give the title in full.

Do not refer to unpublished material.

Acknowledgments

Keep them short.

Symbols and Abbreviations

The following symbols and abbreviations, as well as others approved for the Systeme International d'Unités (SI), are used in this journal without definition. Any others must be defined in the text at first mention, as well as in the captions or footnotes of tables and in fiugres or figure captions. A variable divided with another variable should be noted as the following example L per min is L min^{-1}.

Time

A colon should be used as the separator between hour and minute and between minute and second. The symbols "h", "min", and "s" are not used, since they are the symbols for hour, minute, and second in the sense of duration or the length of time. Thus "12 h 30 min" expresses a measured time of twelve hours and thirty minutes duration whereas 12:30 refers to the time of

Prefixes

giga (10^{9})	G
mega (10^{6})	M
kilo (10^{3})	k
milli (10^{-3})	m
micro (10^{-6})	µ
nano (10^{-9})	n
pico (10^{-12})	p

Time and Temperature

day	d
degrees Celsius	°C
hour (spell out for diel time)	h
kelvin	K
minute	min
second	s

Spell out year, month, and week.

In Table and Fig.:

year	yr
month	mo
week	wk

Weights and Measures

centimeter	cm
gram	g
kilogram	kg
kilometer	km
liter (exception to SI)	L
meter	m

Spell out hectare and tonne.

Mathematics and Statistics

all standard mathematical signs, symbols, and abbreviations base of natural logarithm	e
common test statistics (F, t, etc.)	
correlation or regression coefficient (multiple)	R
correlation or regression coefficient (simple)	r
degree (angular)	°
degrees of freedom	df
expected value	E
intercept	α
logarithm (specify base)	log
minute (angular)	'
not significant	NS
percent	%
probability	P
probability of type I error (false rejection of null hypothesis)	$P\alpha$

probability of type II error (false acceptance of null hypothesis)	$P\beta$
radian	rad
sample size	N
second (angular)	"
standard deviation	SD
standard error	SE
variance	V or var

Physics and Chemistry

all atomic symbols	
alternating current	AC
ampere	A
becquerel	Bq
candela	cd
chemical acronyms listed in Webster's dictionaries (DDT, EDTA, etc.)	
coulomb	C
dextro	D
direct current	DC
electron volt	eV
equivalent	eq
farad	F
gray	Gy
hertz	Hz
hydrogen ion activity (negative log of)	pH
joule	J
levo	L
lumen	lm
lux	lx
molar	M
mole	mol
newton	N
normal	N
ohm	Ω
ortho	*o*
para	*p*
pascal	Pa
per mille (per thousand)	‰
siemens	S
tesla	T
trishydroxymethyl-aminomethane	tris
volt	V
watt	W
weber	Wb

General (some are restricted)

compass directions (maps and coordinates): east	E
north	N
south	S
west	W
et alii	et al.
et cetera	etc.
filial generation	F
for example	e.g.,
international unit	IU
months (tables, figures): first three letters (Feb, Jun, etc.)	
ploidy	n
sex (tables, figures, hybrid crosses): female	♀
male	♂
that is	i.e.,

Word List

The spelling of the following words is frequently inconsisten in submitted manuscripts. We prefer that authors adhere to the Journal's house style for these commonly used terms:

age-class (n.)
age-group (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
chi-square (n., adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
freshwater (n., adj.)
fresh water (n.)
groundwater (n., adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)
saltwater (adj.)
sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
short term (n.)
size-class (n.)
snowmelt (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
t-test (n., adj.)
warm water (n.)
warmwater (adj.)
year-class (n.)
young-of-the-year (n., adj.)

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