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FACTORS AFFECTING UPSTREAM AND DOWNSTREAM MIGRATION IN ANADROMOUS EUROPEAN SALMONIDS AND CATADROMOUS EEL

by

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ABSTRACT

Outward migration in salmonids and eels from freshwater to sea are influenced by photoperiod, water temperature and flow. Photoperiod is the «zeitgeber», determining the seasonal migration, whereas the two others are finetuning the actual timing of descent. Just before downstream migration occurs, as a result of changed hormonal activities, the salmonid smolts exhibit morphological, physiological and behavioural changes which preadapt them for sea-life. Downstream migration occurs mainly at night, and in salmonids larger individuals descend earlier in the season than small ones. In eel which migrate to sea from August to December, the smaller adults which are males migrate early in the season. Sea survival of Atlantic salmon is influenced by the time of sea entry, it is highest for those entering during a short period in spring and early summer. The main reason for the mortality appears to be predation. During salmonid smolt migration the fish pick up environmental cues which are later used for precise homing as adults. The elvers enter freshwater during summer. In Norway adult salmonids return to estuaries of their home rivers from mid April to late October, Atlantic salmon usually enter the rivers before trout and charr. Within species large individuals return earlier in the season than smaller ones. River ascent is influenced by waterflow and temperature, large individuals are more sensitive to low flow than smaller fish, and may therefore be delayed in the estuary when water discharge is low. Wild and cultured salmonids seem to behave similarly in nature. However, adult behaviour is highly dependent on juvenile experience.

Introduction

The transitions and movement of fish between freshwater and marine environments are often connected to different life history stages, for example through smolt transformation, young salmonids change from parr exploiting freshwater to sea migrating fish. Similarly, yellow eels in freshwater transform to silver eels migrating to their spawning areas in the ocean. The ultimate causes of migrations are probably to increase the product of survival and growth to maximize Darwinian fitness over the entire life cycle (Gross 1987). In cases when a single habitat provide insufficient resources for the entire life cycle, fitness is increased by moving between different habitats supporting variable needs during the ontogeny (Northcote 1978).

Atlantic salmon, brown trout and Arctic charr are anadromous; they spend their first part of life in freshwater, then move to sea for feeding, and then return with high precision to spawn in the river they left as smolts. Anadromous brown trout and Arctic charr usually stay overwinter in freshwater. Eels are catadromous, i.e. they enter freshwater as juveniles, stay there for several years, and return to sea for spawning.

Seaward migration may be obligatory or facultative in anadromous fish species. In many rivers there is facultative migration of salmonids: some individuals of a cohort migrate, others become freshwater resident. Both inner and outer factors contribute to whether or not the fish will migrate. The inner factors are determined by (1) genetics and (2) earlier experience of the fish linked to growth rate and metabolic rate and sexual maturation (see Jonsson & Jonsson 1993). External or outer factors are those like: photoperiod, water temperature, water flow, tidal changes, light intensity, etc.

In this paper we will give a general description of upstream and downstream migration of Atlantic salmon, brown trout, Arctic charr and European eel, discuss mechanisms, in particular those influencing outer factors and discuss possible strategies for the migratory patterns. Several of the data reviewed are based on Norwegian experiments from the River Imsa, and in Atlantic salmon and brown trout most of the knowledge has been gained by using hatchery-reared fish.

Downstream migration

General introduction

Downstream migration of salmonids and eel may have several motivations. In anadromous salmonids fish migrate to sea to gain weight, and are called smolts. Catadromous eel migrate to sea to spawn. Salmon that survive spawning return to sea either in late autumn/early winter, or in spring. Males tend to descend earlier than females. Survivors return for spawning in subsequent years; small salmon are annual spawners whereas large fish spawn annually or biennially (B. Jonsson *et al.* 1990; N. Jonsson *et al.* 1990, 1991).

Smolting in salmonids is under hormonal control and is characterized by a number of physiological and behavioural changes which preadapt the young fish for sea life, while still in fresh water (e.g. Thorpe *et al.* 1985; Hansen *et al.* 1989a, Saunders *et al.* 1994). During transformation from parr to smolt, the fish becomes silvery and the body form becomes more stream-lined, making the fish fit for a pelagic life at sea. During smolting the salmonids lose their positive rheotactic freshwater behaviour to become a schooling fish destined to live close to the sea surface. At the same time several different physiological changes take place, making the fish able to adapt to and osmoregulate in sea water. During smolting the fish also imprint to (learn) cues used for homing. The downstream smolt migration is probably synchronized by changing day-length, whereas water temperature and water flow seem to be key factors

initiating the migration (Thorpe & Morgan 1978; Ruggles 1980; Jonsson & Ruud Hansen 1985; Hesthagen & Garnås 1986; Hvidsten *et al.* 1995).

Light

The photoperiod is the seasonal «zeitgeber» that prepares the fish for migration. However, as the length of days on the same date is equal all years, this is not a factor adapting the fish to migrate during optimal conditions. To do this, other variability like water discharge and temperature are needed.

Smolt migration usually takes place during the darkest period of the night, but towards the end of the smolt migration period migrating smolts are also observed at daytime (Österdahl 1969; Thorpe & Morgan 1978). The fact that smolts move downstream at night may be an adaptation to avoid potential predators (Solomon 1982). However, day-time migration has been observed in northern Russia. For instance Baksthansky *et al.* (1976; 1977) maintain the pike (*Esox lucius*) in rivers in northern Russia had difficulties capturing salmon smolts in sunny weather, when light ripples occurred on the surface of shallow water. At high latitudes in areas with midnight sun, smolts of Atlantic salmon and brown trout have been observed migrating during hours of strong sunlight (see Thorpe & Morgan 1978 for review). In a north Swedish river at 64 degrees north Österdahl (1969) observed a change from nocturnal migration pattern in late May and early June to diurnal pattern in late June. There was no information of the length of the night during the smolt run, but on this latitude in May and June the nights are short and it never gets really dark. Even farther south daytime migration may occur. Solomon (1978) observed in the River Piddle, U.K. that large numbers of Atlantic salmon smolts migrated at bright sunlight, whereas brown trout smolts had definite peak of migration in the early hours of the night. Moreover, Fraser *et al.* (1993) maintain that late descending smolts tend to migrate more during day-time because of the higher water temperature, and thereby increased activity to avoid endothermic predators like birds.

A test whether the nocturnal behaviour was a direct response to low light intensity or an innate rhythm, supported the direct response hypothesis, and it was observed that hatchery smolts released in the evening descended faster than smolts released in the morning, and artificial illumination of parts of the river at dark, reduced the speed of descent (Fig. 1) (Hansen & Jonsson 1985). However, large numbers of hatchery smolts released in the morning schooled downstream during daytime. In such cases a number of wild smolts joined the schools opposite to the usual situation with night descent.

Silver eels migrate downstream during night (Deelder 1954), and the migratory activity depends on the light intensity (Haraldstad *et al.* 1985; Vøllestad *et al.* 1986). In Dutch inland and Baltic waters the maximum activity of silver eels occurred around the last quarter of the lunar cycle (Frost 1950; Lowe 1952; Jens 1952/53), while in the upper Rhine maximum activity occurred before the moon's last quarter (Jens 1952/53). Boëtius (1967) and Edel (1976) showed that silver eels held in tanks in complete darkness with constant temperature and water flow, had an innate rhythm correlated with the lunar phase. Vøllestad *et al.* (1986) studied the effect of light on the migratory activity of European silver eels in the River Imsa, Norway. They found that illumination of the water surface at a weir in the river (0.007 to 0.15 lux) significantly reduced the eel descent. Furthermore, during nights with moon light they found that most silver eels descended during the first dark period after sunset when light intensity was less than 0.06 lux, and stopped when the moon appeared over the horizon and shone on the river. Thus, the lunar cycle seems to have no effect on the eel migration other than the effect mediated by variation in illumination of the river.

Temperature

Water temperature is one proximate factor initiating downstream migrations in fish. It fine tunes the preparation to migration by influencing the rate of physiological processes and influences the rate of migration up and downstream through its effect on metabolic rate and activity. In a number of studies it has been shown that increasing water temperature in the spring is important for the initiation of the smolt run (e.g. White 1939; Mills 1964; Österdahl 1969; Bagliniere 1976; Solomon 1978; Jonsson & Ruud-Hansen 1985; Jonsson *et al.* 1989). Several authors have reported that downstream migration of smolts of Atlantic salmon and brown trout occurs at about 10°C or slightly above (White 1939; Mills 1964; Österdahl 1969; Solomon 1978). Jonsson & Ruud-Hansen (1985) examined if water temperature, waterflow, cloudiness and lunar cycle influenced the timing of Atlantic salmon smolt migration in the River Imsa; but only temperature was shown to influence the migration. The development in water temperature between 9 April and 16 May explained 91, 95 and 89 % of the yearly variance in date of 25, 50 and 75 % yearly cumulative smolt descent, respectively. There was not observed any threshold temperature above which the run started, and the smolts started to descend at temperatures between 5.8-11.2°C. The smolt run started early in years when the water temperature was high or when the increase in temperature was rapid. The conclusion was that in the River Imsa the timing of smolt descent was controlled by a combination of actual temperature and temperature increase in the water during spring rather than triggered by a specific water temperature or a specific number of degree-days.

In brown trout several observation have shown that also in this species the time of descent was correlated with rising water temperature in the spring (Solomon 1978; 1982).

The water temperature may also be important for the start of the spawning migration of silver eels downstream rivers and the speed of descent. Vøllestad *et al.* (1986) observed that the run of silver eels started yearlier in years with low than with high water temperature during July and August, and most eels descended at temperatures between 9 and 12 °C (Fig. 2). The recapture-rate in a fish trap in the River Imsa of tagged eel displaced upstream was highest at 9°C and decreased at both higher and lower temperatures. No threshold temperature at which the run started was observed. Water temperature could not, however, explain why the eels migrated faster late in the season (Vøllestad *et al.* 1994). This seemed to be caused by increased motivation, influenced by the date (photoperiod).

Waterflow

High waterflow in rivers provides downstream movement in a large number of fish species, and the downstream migration of salmonid smolts has been reported by several authors to be initiated by increased water flow (e.g. Berry 1932, 1933; Allen 1944; Österdahl 1969; Hesthagen & Garnås 1986). In the River Orkla, Norway Hesthagen & Garnås (1986) observed that migration of Atlantic salmon smolts was initiated by the first spring peak in water discharge when the water temperature was 2-3 °C. Significantly more smolts migrated when the flow was increasing, followed by a decline in the water temperature than when the conditions were opposite.

The water flow in rivers appears to influence the direction of migration and the speed of descent. The water current is the vector that transport smolts downstream (Thorpe 1982). It has been hypotethized that smolt migration is a result of a passive displacement (Tytler *et al.* 1979, Thorpe *et al.* 1981), although this hypothesis has gained little general support (Thorpe & Morgan 1978, Solomon 1978, Kennedy *et al.* 1984 Bourgeois & O'Connell 1988).

However, tests carried out in the River Imsa have at least partly given support to the passive displacement hypothesis. There, lake reared salmon smolts migrated at irregular times (Hansen 1987), both wild and hatchery-reared, were considerably delayed or lost when transplanted to lakes upstream the natural smolt producing area (Hansen *et al.* 1984), and smolts displaced farther upstream in the main river migrated more quickly downstream at high waterflow than low (Youngson *et al.* 1989). The water current seems to give the fish a directional cue. The smolts appear to actively move out into the main current of the river to avoid being caught in backwater and sloughs (Hansen & Jonsson 1985). Thus, the descent is not passive. Observations made on Atlantic salmon (Bourgeois and O'Connell 1988) and on smolts of lacustrine salmonids as sockeye salmon (*Oncorhynchus nerka*) (Groot 1965) and Arctic charr (*Salvelinus alpinus*) (B. Jonsson pers. obs.) where smolts in lakes have been observed to migrate faster than the downstream current velocity, suggest that local adaptations in this trait may also occur in salmonids naturally reproducing above lakes.

It has been observed that catches of European silver eels increased with a rise in the water level (Frost 1950; Lowe 1952; Jens 1952/53; Deelder 1954). Moreover Tesch (1977) maintained that increased water discharge encouraged the eels to migrate, and Vøllestad *et al.* (1986) observed that the run of silver eels in the River Imsa started earlier in autums with high water discharge than in autums with low flow.

Estuaries and fjords

Knowledge of salmonids in the marine phase is scarce. In Norway, Atlantic salmon leave estuaries and fjords relatively quickly, and move into oceanic waters and stay there for 1-4 years, whereas brown trout and Arctic charr feed and grow close to the river, and they stay in the sea a couple of months each summer (e.g. Jensen 1968; Jensen & Berg 1977; Finstad & Heggberget 1993). In estuaries schools of post-smolts are probably displaced with the surface current, and the movement is influenced by the tide and the direction of the water flow (Carlin 1969; Holm *et al.* 1982; Thorpe 1988; Pethon & Hansen 1990; Jonsson *et al.* 1993).

Jonsson *et al.* (1993) recently summarized the migration pattern of hatchery reared postsmolts of Atlantic salmon tagged and released in the River Imsa. When leaving the river the fish seemed to move along the Norwegian coast northwards and gradually enter oceanic waters as recaptures decreased northwards. Similarly Carlin (1969) observed that hatchery reared salmon smolts released in the River Lagan on the Swedish west coast moved northwards along the Danish coast. Some moved into the Atlantic after they had passed Denmark; others continued in the NNW direction along the Norwegian coast to the feeding areas into the Norwegian Sea. As post-smolts, Atlantic salmon feed on surface insects, crustaceans and small fish like sand-eel and herring (e.g. Morgan *et al.* 1986; Levings *et al.* 1994).

There is surprisingly very little information about postsmolts of brown trout and Arctic charr. The smolts move to sea in the spring and stay in estuaries and fjords during the summer. Results from tagging brown trout smolts revealed that the great majority of the fish was recaptured less than 100 km away from their home rivers (e.g. Jensen 1968; Jonsson 1985; Berg & Berg 1987; Berg & Jonsson 1989; Sundal 1991; Lund & Hansen 1992). The same pattern has also been observed in Arctic charr (Nordeng 1977; Jensen & Berg 1977). The main food items in marine waters have been reported to be different crustaceans, fish and polychaets (Pemberton 1976; Fahy 1983; Grønvik & Klemetsen 1987).

In Norway the first sexually mature Atlantic salmon enter estuarine areas in late April, beginning of May, whereas for example in Scotland salmon may enter estuaries and rivers

throughout the year. However, in both areas the large individuals usually enter before the smaller ones (e.g. N. Jonsson *et al.* 1990; Shearer 1992). There is also suggested that run timing of Atlantic salmon differs genetically between salmon populations (Fig. 3), probably as a result of local adaptation (Hansen & Jonsson 1991). The return migration of salmon is an active process, and the migratory speed decreases when the fish approach fjords and estuaries, suggesting that the homing navigation is more complicated than in open waters, or that salmon await suitable conditions for upstream migration (Hansen *et al.* 1993). The feeding activity of salmon ceases when the salmon approach their home rivers (Hislop & Shelton 1993). In Norway brown trout feed mainly in fjords, and the length of their migration is positively correlated with the distance from the river mouth to the Norwegian base line (Sundal 1991). The length of the migration is not significantly correlated with fish size, fish age or river size.

Upstream migration

In Norway salmonids enter rivers in summer and autumn, the oldest individuals ascend before younger ones. In small rivers water flow limits the ascent of in particular larger salmon. In such cases salmon may enter rivers late in the season and small fish may come before the larger ones (N. Jonsson *et al.* 1990). In general, small rivers harbour only small salmon, whereas large rivers support both small and large fish (N. Jonsson *et al.* 1991).

Water flow and water temperature are important environmental variables that influence upstream migration of fish to freshwater (Jonsson 1991). Their effect, however, may differ among rivers. For instance, water flow appears to be an important factor stimulating upstream migration in rivers with highly fluctuating water levels during the migratory period, while water temperature appears to be more important in rivers with stable water discharge.

Water flow

In various fish species water flow influences both the timing of river ascent and the intensity of migration (e.g. Jellyman & Ryan 1983, Potter 1970, Asplund & Södergren 1975, Libosvársky 1976, van den Berghe & Gross 1989, N. Jonsson *et al.* 1990). In the River Imsa, the number of ascending adult Atlantic salmon increased with increasing water discharge (N. Jonsson *et al.* 1990). Furthermore, in Deer Creek Junior, Washington, the ascent of female coho salmon increased with raising stream level (van den Berghe & Gross 1989). Similarly, Saunders (1960) observed in Eilerslie Brook, Prince Edward Island, that adult Atlantic salmon entered the river during autumn freshets, and remained at the head of the estuary during periods of low flow. Potter (1988) tracked Atlantic salmon in the estuary of the River Fowey, south-west England. He observed that most fish entered freshwater during periods of increased freshwater discharge. Low river flow delayed the migration of salmon into the river, and many fish stayed for several weeks or even months in the estuary before entering freshwater. One reason may be that they move quite large distances away from the river mouth and do not detect all floods.

High water discharge during the upstream migration appears to be more essential for large than small salmon, this may be most pronounced in small rivers. In small rivers, the water flow appears to be more limiting to the ascent of large multi-sea-winter salmon than the grilse. For instance, in the River Imsa (annual mean water discharge: $5 \text{ m}^3 \text{ s}^{-1}$) the number of ascending multi-sea-winter but not one-sea-winter Atlantic salmon, was correlated with increasing water discharge (Fig. 4) (N. Jonsson *et al.* 1990). The grilse seem to enter freshwater soon after they arrive from the sea whereas the larger multi-sea-winter fish delay until water flow in the autumn becomes favourable. The large adults probably need more

water to become completely submerged, and sufficient motivated to ascend the river. Similar results were found for coho salmon in the Deer Creek Junior, where large females entered the creek at peak discharge and progressively smaller ones entered as waters receded. There, however, no similar trend was found among males (van den Berghe & Gross 1989). In larger rivers, like the River Dee, Scotland, large and old salmon are not delayed relative to the grilse. The older salmon both return in early spring and ascend the river before the later returning grilse (Hawkins 1987).

Upstream migration during very high and rapidly flowing water appear disadvantageous for the fish, because of increased energetic costs relative to low flow situations. However, this increased cost may often be balanced by the increased protection offered by the increased flow.

Large rivers, with high water discharges, may aid the fish in finding the mouth of the river they are going to enter (Malmqvist 1980; Jellyman & Ryan 1983). This is supported by the fact that the number of fish straying to other rivers seem to decrease with increasing river size (Hansen 1980; Berg & Jonsson 1989), and that salmon released directly in the sea as smolts, enter the largest among the nearby rivers when they return as adults (Hansen *et al.* 1989b).

The connection between water flow and river ascent seems also reflected in the adult size of Atlantic salmon in rivers. In rivers with mean water discharge between 1 and 40 m³s⁻¹, there was positive correlation between adult size and water discharge (Fig. 5). In larger rivers, there was no similar trend (N. Jonsson *et al.* 1991).

Water temperature

In rivers with small fluctuations in water levels during the migratory period, water temperature appears to be more important factor stimulating upstream fish migration. For instance, importance of increasing water temperature for the ascent of elvers has been noted by several authors (e.g. Gandolfi *et al.* 1984; Hvidsten 1985; Vøllestad & Jonsson 1988; Martin 1995). In the River Imsa, the annual number of ascending elvers of European eels (*Anguilla anguilla* L) varied strongly, and was positively correlated with temperature in the river (Fig. 6) (Vøllestad & Jonsson 1988). In the Arno River, Italy, on the other hand, differences in temperature between sea and river water seem to play an important role in the ascent of elvers (Gandolfi *et al.* 1984). Marked migratory movements occurred when river and sea water showed differences in temperature not exceeding $\pm 3-4^{\circ}\text{C}$. Movements decreased when temperature difference in either direction was greater.

Water temperature in rivers appears also to stimulate the spawning migration of many species. Davies & Sloane (1987) studied the upstream migration of spawning brown trout and rainbow trout in Liawenee Canal, Great Lake, Tasmania, 1949-1985. They found that brown trout migrated upstream from early April to mid May and rainbow trout from late August to early November. Brown trout migrated predominantly over the temperature range 6-10°C, while rainbow trout migrated mainly over 5-11°C. Furthermore, rainbow trout migration occurred at high flow conditions and was positively correlated with canal flow increases, whereas brown trout migrated during low canal flow. Some authors have found that the upstream migration starts above a threshold water temperature or at preferred temperatures. According to the literature, these temperatures vary within and among species (Sørensen 1951; Matsui 1952; Smith 1955; McKenzie 1964; Rembiszewski 1970; Kuznetsov 1976; Leggett 1976; Malmqvist 1980; Gandolfi *et al.* 1984; Helfman *et al.* 1984; Hvidsten 1985; Sørensen & Bianchini 1986; Hutchinson & Mills 1987; Naismith & Knights 1988). Fish are poikilothermic animals and their activity are dependent on the temperature in the water. At

low temperatures they are less active than at higher temperatures. On the other hand, the activity at higher temperatures require higher energetic costs. Thus the upstream migration is expected to occur at temperatures above a minimum, but not at too high temperatures. For instance, at low temperatures upstream migrating fish may have problems with passing obstacles. Jensen *et al.* (1989) found that Atlantic salmon were unable to pass waterfalls in the River Vefsna if the water temperature was below 8°C. An example illustrating how high water temperature may decrease the intensity of upstream migration was published by Elson (1969). When studying the intensity of Atlantic salmon migration in the Northwest Miramichi River he found that the ascent increased with increasing water temperature up to 24-25°C (the lethal upper temperature limit is about 30°C) and then decreased. Hawkins (1989) noticed that when water temperature in River Dee, Scotland, exceeded 20°C adult Atlantic salmon remained in the sea.

Migration versus recidency

Many fish populations have both resident and migratory individuals. For anadromous salmonids there may be good growth opportunities in salt water, but on the other hand the natural mortality may be higher in the marine environment. The decision about migration versus residence probably depends partly on individual growth rate or a character correlated with growth rate like rate of metabolism, partly on heridity (see Jonsson & Jonsson 1993; Thorpe 1994). Females often dominate among migrants and males among residents. The reason is probably that females maximize their fitness by growing larger, because their reproductive success generally increases with body size.

Some fish in a salmon population mature sexually as parr in the river. These fish are chiefly males (Jones 1959), although a few completely freshwater populations occur in northern Europe (Berg 1985) and a large number in Newfoundland and Labrador (Sutterlin & Maclean 1984). Under rearing conditions, parr maturity is also common, and advanced developmental rates seem to increase the frequency of early maturing fish (Thorpe 1989). In mature parr, the probability of later smolting is reduced, but maturation does not rule out a later smolting completely (Saunders *et al.* 1982; Hansen *et al.* 1989c; Berglund *et al.* 1991).

Experiments carried out in the R. Imsa revealed a 30% reduction in the proportion of migrants from mature parr, compared with corresponding immatures (Hansen *et al.* 1989c). However, it is possible to increase the proportion of the mature males that will migrate by keeping them in heated water during winter (Berglund *et al.* 1991). A similar effect may be achieved by stripping the mature parr in the autumn (Hansen *et al.* 1989c; Greenstreet 1992).

Survival

Many factors determine the survival and return of salmon, although many of them are poorly known (e.g. Saunders 1983). The parr-smolt transformation (smolting) and the post-smolt stage (the period just after the smolts have left the rivers) is of particular interest in salmon ranching, because this period is critical for survival in the sea (Browne *et al.* 1983).

The timing of smolt migration seems to be crucial for an optimal survival and return of the salmon (Larsson 1977; Cross & Piggins 1982; Hansen 1987), hence this timing may be a result of adaptation to the prevailing environmental conditions in the local area. When hatchery-reared salmon smolts are retained in freshwater, they will desmolt, and males will tend to mature the coming autumn (Lundqvist & Fridberg 1982). However, when retained in seawater, these fish will survive poorly when released in late summer and autumn, despite

their larger size at release (Hansen & Jonsson 1986; 1989). This is not the case in Baltic salmon (*Salmo salar*) (Eriksson 1988) where experiments with delayed release have demonstrated that these fish survive better than those released in the spring. Similarly in Atlantic brown trout delayed release had positive effect on survival (Jonsson *et al.* 1994). The reason why delayed release is positive in some, but not all cases is difficult to explain, but may be linked to physical conditions and predator species in the systems (see Larsson 1984; Eriksson 1988).

It is well known that the physiological state of smolts and post-smolts changes with time, and in particular when smolts are retained in freshwater. However, the mechanisms behind the observations that there is an optimal time for smolt migration («migration window») are less well understood, but predators, diseases, parasite abundance and food conditions may be factors causing the mortality.

Atlantic salmon are subjected to heavy mortality as smolts and post-smolts in estuaries and fjords due to predation by different animals. Important predators are different species of birds like gulls, cormorants, herons and mergansers (Huntsman 1941; White 1957; Reitan *et al.* 1987; Kennedy & Greer 1988), and fishes like Atlantic cod, saithe, pollack and sea trout (Hvidsten & Møkkelgjerd 1987). Some of these predators are dependent on vision to search for their prey. It has therefore been speculated whether predation pressure on released salmon smolts is smaller when they are released in the dark than during daylight. Experimental releases of salmon smolts at Ims gave no significant difference in return rate of smolts released in the morning and smolts released in the evening (Hansen & Jonsson 1986).

In the estuaries of the River Surna and River Orkla, mid-Norway heavy predation of fish, mainly cod, has been observed on both released hatchery-reared and wild smolts (Hvidsten & Møkkelgjerd 1987). A significantly improved survival of hatchery-reared smolts was obtained when smolts were transported by a well-boat and subsequently released in the ocean outside the River Surna (Gunnerød *et al.* 1988), but straying of the returning adults increased considerably.

In Norwegian rivers draining areas with high snow fall, the current velocity increases considerably during snow melt, and the water turbidity of the water increases. Both in the River Gaula and River Surna hatchery-reared smolts improved their survival significantly when they were released at high water discharge within the normal period of migration (Fig. 7) (Hvidsten & Hansen 1988), as was also observed in rivers in Maine, USA (Hosmer *et al.* 1979). Reasons for this may be that because smolts move close to the water surface (Holm *et al.* 1982) and descend more quickly at high current velocity (Youngson *et al.* 1989), they may be less vulnerable to predation from marine fish species in the estuary at high than at low water flow. The high turbidity may also make the smolts less visible for the predators.

smolt migration, estuaries,

Experiments carried out in the River Imsa show that the average survival-rate of hatchery-reared smolts is only half of that in wild fish (B. Jonsson *et al.* 1991). This difference may be due to both different selection pressures in hatcheries and nature, and to differences in smolt quality (e.g. physical condition) and release methods. Survival may be 30 times higher in hatcheries than in nature, so inferior fish may survive in hatcheries. Moreover, the physical fitness of hatchery fish at release may be lower than that of wild conspecifics because of lower physical activity in the hatchery tanks than in the wild. A third difference is that hatchery fish have little experience in catching natural food and avoid predators. However, they have been shown to learn extremely quickly (Stradmeyer & Thorpe 1987).

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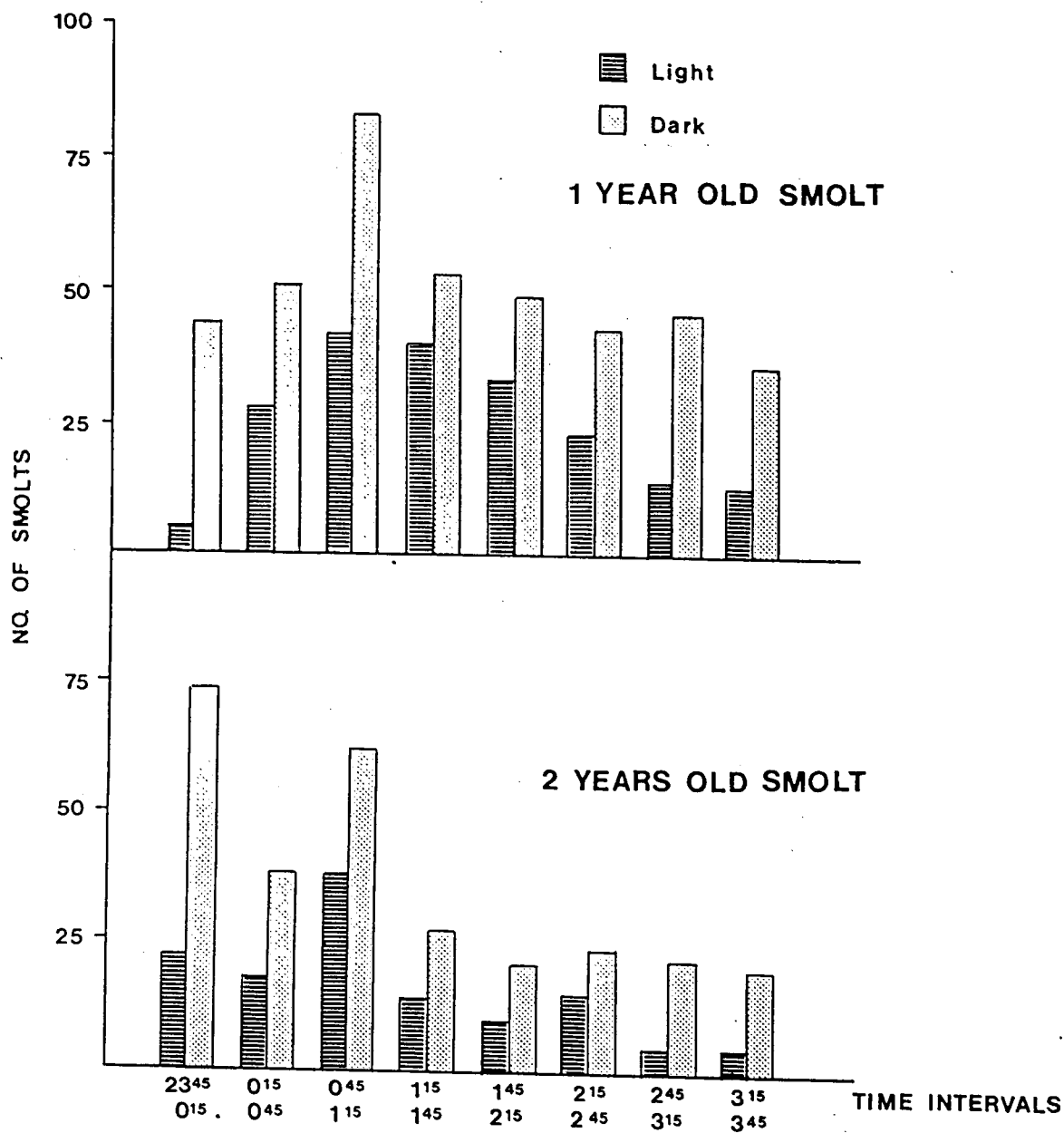
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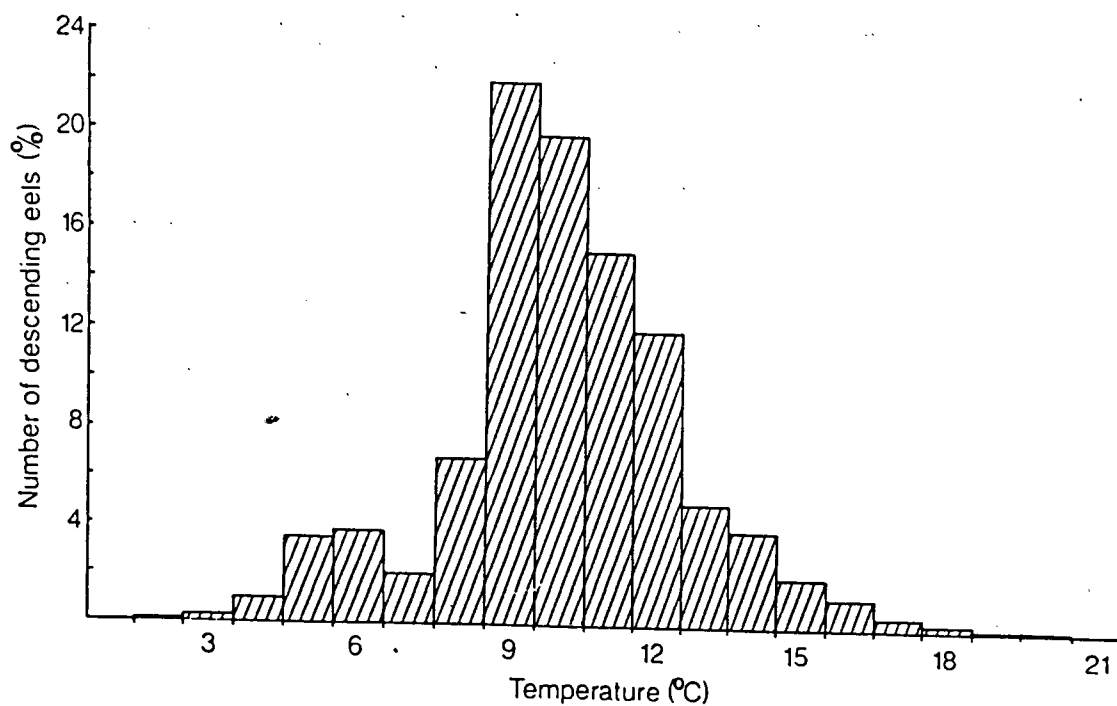
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Figure 1. From Hansen & Jonsson (1985)



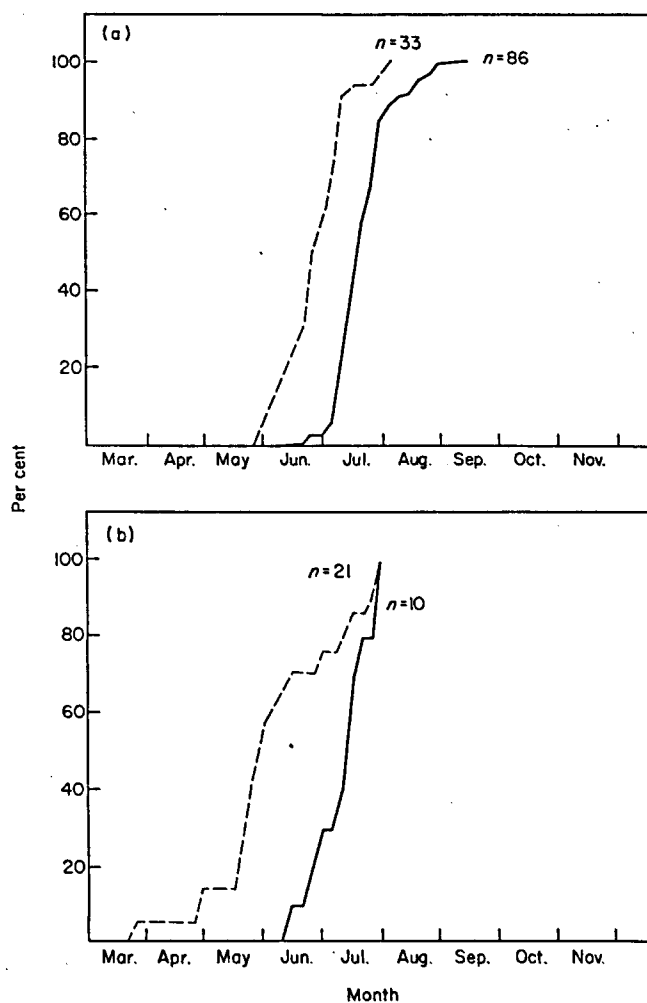
Number of salmon smolts recaptured in the fish trap during 30-min intervals (15 min with light on and 15 min with light off).

Figure 2. From Vøllestad *et al.* (1986)



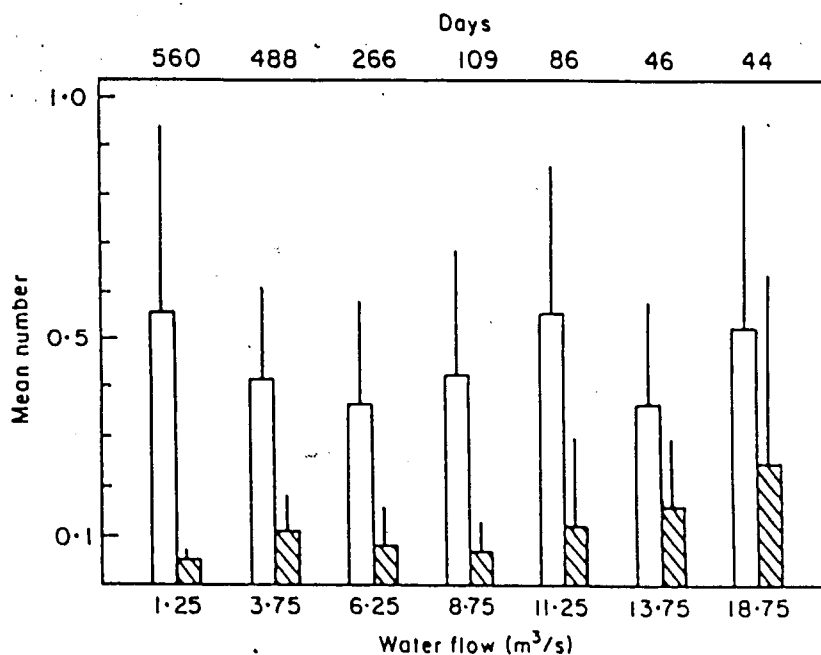
Percent silver eel descent ($N = 36\,494$) at temperatures between 2 and 20°C in the River Imsa during 1975–84.

Figure 3. From Hansen & Jonsson (1991)



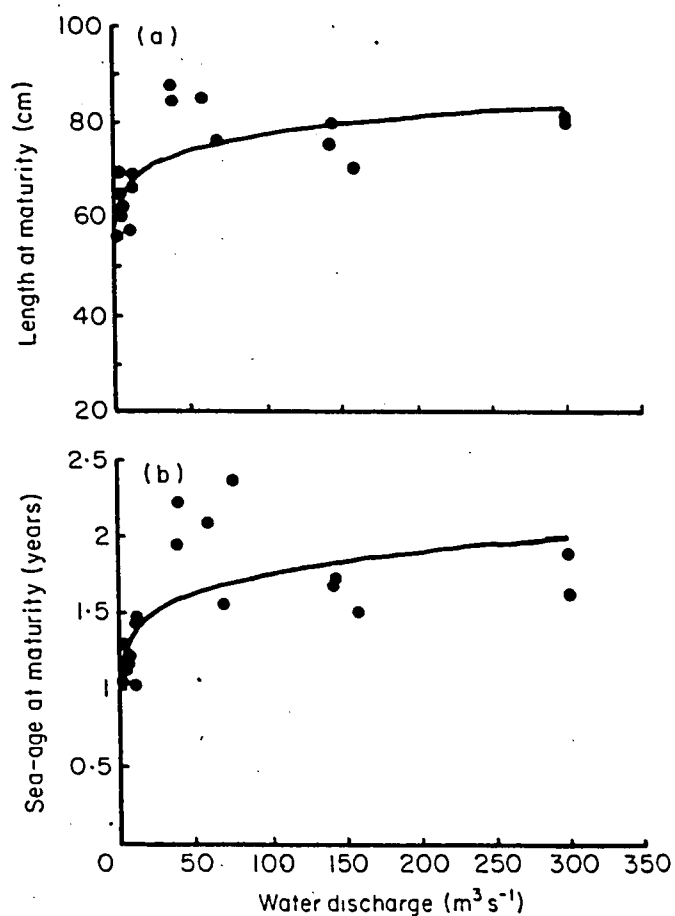
Cumulative recaptures of (a) one-sea-winter and (b) two-sea-winter salmon in Norwegian coastal fisheries of smolts released in the River Imsa 1981. ----, R. Figga stock; ----, R. Imsa stock.

Figure 4, From N. Jonsson *et al.* (1990)



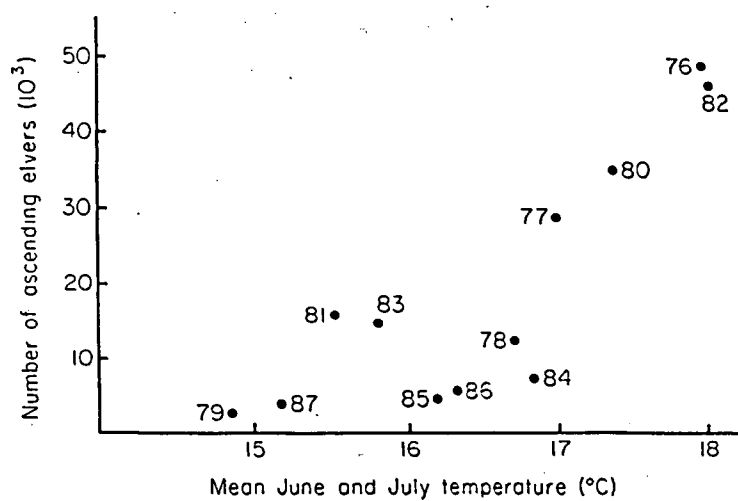
Annual mean number of Atlantic salmon that spent one (\square ; $N=668$) or more (hatched ; $N=133$) winters at sea ascending into the fish trap at the outlet of the River Imsa per day at water discharges of 0–2.49 (1.25) m^3/s , 2.5–4.99 (3.75) m^3/s , etc. during June–October 1976–1988. Vertical lines give 95% confidence limits of the annual means.

Figure 5. From N. Jonsson *et al.* (1991)



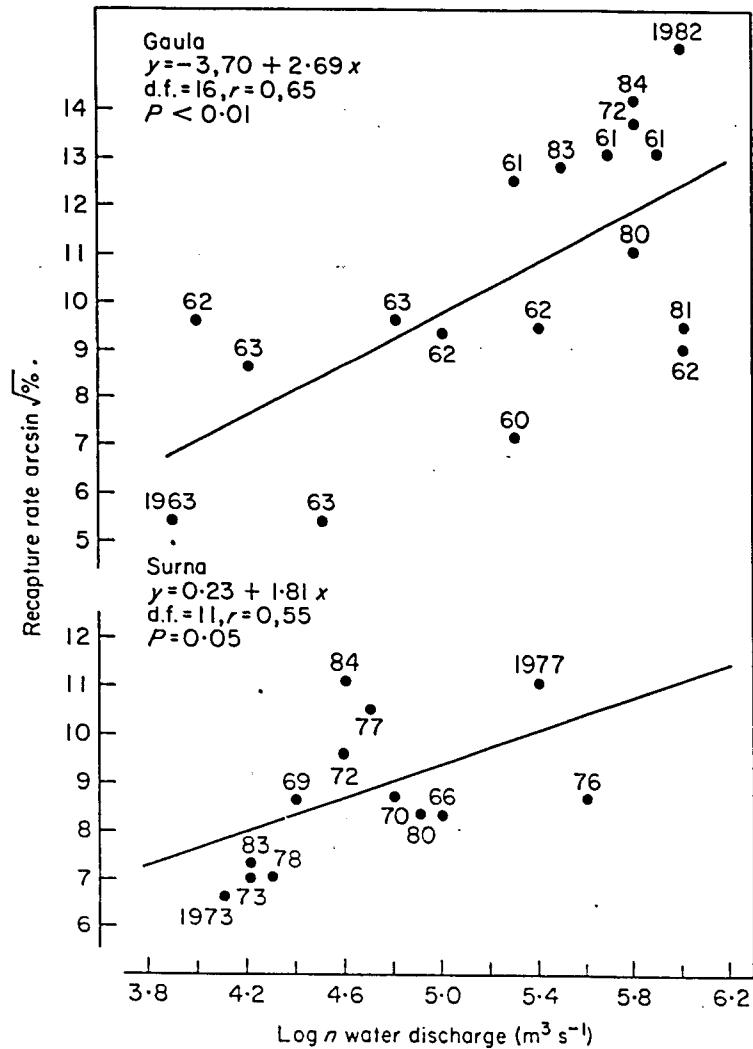
Relationship between (a) length at sexual maturity (L cm) and (b) mean sea-age at sexual maturity (A years) of Atlantic salmon and yearly mean water discharge ($W \text{m}^3 \text{s}^{-1}$) (regression lines: (a) $L = 58.15 W^{0.06}$, $r^2 = 0.53$ and (b) $A = 1.05 W^{0.11}$, $r^2 = 0.41$).

Figure 6. From Vøllestad & Jonsson (1988)



Relationship between mean June and July water temperature in the River Imsa between 1975 and 1987, and the total number of ascending elvers and young yellow eels in the various years.

Figure 7. From Hvidsten & Hansen (1988)



Regression of total adult recapture rate on log n water discharge at release of Atlantic salmon smolts stocked in the Rivers Surna and Gaula. Data from 1960–1984.