



The impact of marine fish predation on Atlantic salmon smolts (*Salmo salar*) in the Tana estuary, North Norway, in the presence of an alternative prey, lesser sandeel (*Ammodytes marinus*)

M.-A. Svenning^{a,*}, R. Borgstrøm^b, T.O. Dehli^b, G. Moen^b,
R.T. Barrett^c, T. Pedersen^d, W. Vader^c

^a Norwegian Institute for Nature Research, Department of Arctic Ecology,
Polar Environmental Center, NO-9296 Tromsø, Norway

^b Norwegian University of Life Sciences, Department of Ecology and Natural Resource Management,
PO Box 5003, NO-1432 Ås, Norway

^c Zoology Department, Tromsø University Museum, NO-9037 Tromsø, Norway

^d Norwegian College of Fishery Science, University of Tromsø, NO-9037 Tromsø, Norway

Received 27 February 2005; received in revised form 6 May 2005; accepted 9 June 2005

Abstract

The Tana river, in northern Norway has the largest wild Atlantic salmon stock in the world. Each summer more than 1 million smolts, representing nearly 20% of the total number of Atlantic salmon smolts produced annually in Norwegian rivers, descend through the large estuary of this river. Several marine fishes feed in the estuary during the summer months, and because the descending smolts are suitable prey, predation by these species was expected to be significant for the survival of the smolts.

In 2000 (mid-June to early August), nearly 500 cod (*Gadus morhua* L.), saithe (*Pollachius virens* L.), whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*) and sea trout (*Salmo trutta*) were caught by hand jigging and troll fishing in the estuary and inner part of the Tana fjord before, during and after the smolt run. Based on analyses of the fish stomach contents, lesser sandeel (*Ammodytes marinus*) was found to be the dominant prey, while no remains of Atlantic salmon, including otoliths, were found. We conclude that neither marine fishes nor anadromous trout are significant predators on salmon smolts in the estuary and inner fjord, probably due to a large abundance of lesser sandeel. Sandeel may thus be a key factor for the status of the Tana river as one of the world best Atlantic salmon rivers, by reducing the high smolt and post-smolt mortality as observed in several other estuaries and fjords.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Predation; *Salmo salar*; Salmon smolts; Sandeels; Marine fish; Tana estuary/fjord

* Corresponding author. Tel.: +47 77750412; fax: +47 77750401.

E-mail address: martin.svenning@nina.no (M.-A. Svenning).

1. Introduction

Predation by fish is the major cause of predation mortality of fishes in many marine boreal ecosystems (Bax, 1998). Studies of growth and survival suggest that growth-mediated predation is the dominant source of recruitment variability within populations (Friedland et al., 2000). The main mortality on Atlantic salmon smolts is believed to occur from entry into the estuary through to and during the first months of the post-smolt stage (Hansen and Quinn, 1998). Survival from smolts to mature fish varies considerably between populations, from less than 5% (Hansen and Quinn, 1998) to 30–40% (Crozier and Kennedy, 1993).

Whereas few fish have been identified as important predators on salmon smolts, marine species such as cod (*Gadus morhua* L.) and saithe (*Pollachius virens* L.)

did prey heavily on Carlin-tagged smolts in the estuaries of two rivers (Surna and Orkla) in mid-Norway. The predators appeared to aggregate in the estuaries and fed on salmon smolts that left the river mouth, resulting in a mortality of up to 24.8% in these small, restricted areas (Hvidsten and Møkkelgjerd, 1987; Hvidsten and Lund, 1988). Cod and saithe, and piscivorous birds such as gannets (*Morus bassanus*), mergansers (*Mergus* spp.) and cormorants (*Phalacrocorax carbo*) have also been observed to consume post-smolts during their migration from the rivers to the oceans (Hvidsten and Lund, 1988; Feltham, 1990, 1995; Dieperink et al., 2002; Montevecchi et al., 2002).

The Tana river in northern Norway is the most productive Atlantic salmon river in western Europe, and >150t of salmon are caught in the river each year (Svenning et al., 2005). For some weeks each summer,

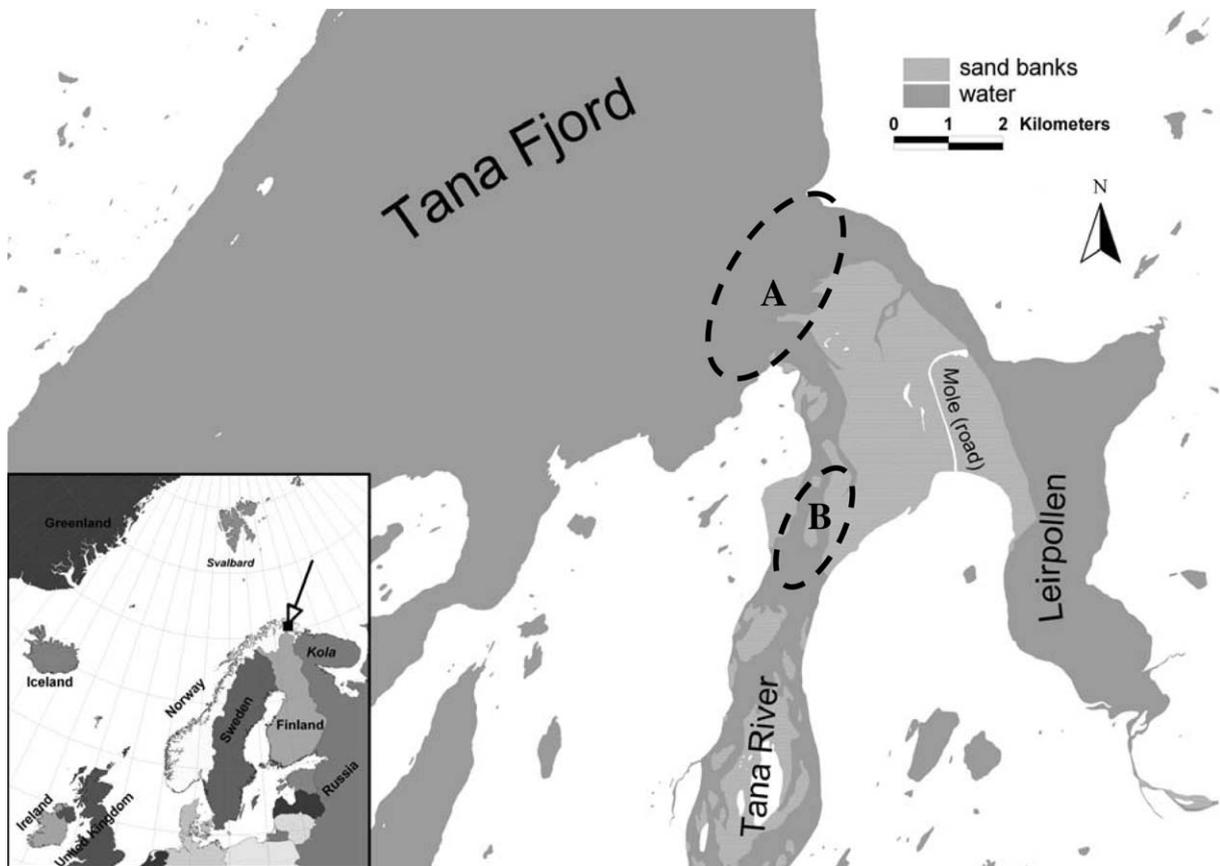


Fig. 1. Map of the Tana river estuary and fjord showing the area where the fish sampling – by hand jigging (A) and troll fishing (B) – was conducted 20 June–11 August 2000.

Table 1
Number of fish caught for stomach analysis in the Tana estuary/fjord from 20 June (week 25) to 11 August (week 32) 2000

		No. of fish caught in the weeks			No. of stomachs with contents (total)
		25–28	29–32	Total	
Cod	<i>G. morhua</i>	107	103	210	138
Haddock	<i>M. aeglefinus</i>	29	92	121	89
Saithe	<i>P. virens</i>	8	60	68	26
Whiting	<i>M. merlangus</i>	7	33	40	20
Cusk	<i>B. brosme</i>	1	0	1	0
Flounder	<i>P. flesus</i>	0	1	1	0
Sea trout	<i>S. trutta</i>	0	56	56	44
Total		152	345	497	317

probably more than a million salmon smolts descend through the estuary, representing about 20% of the total number of smolts produced annually in Norwegian rivers (Svenning et al., 2005). A study of the effect of a potentially serious predator, the goosander (*Mergus merganser*) showed that their predation on salmon smolts in the Tana estuary was very low in

1981 and 2000 (Svenning et al., 2005). Their diet was instead dominated by lesser sandeel (*Ammodytes marinus*) which was very abundant in the estuary during the whole summer, including during the seaward migration of salmon smolts through the estuary.

While goosanders are thus probably ruled out as important predators of salmon smolt in the Tana river,

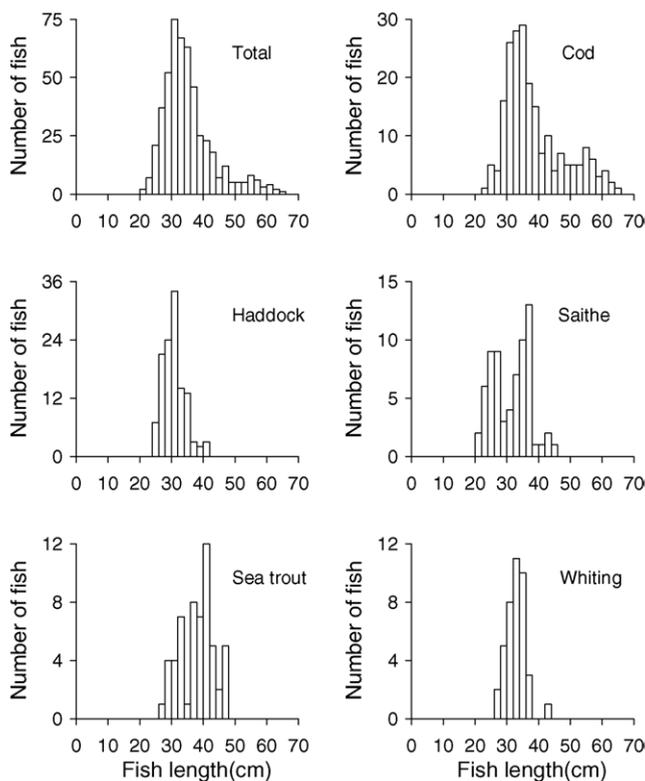


Fig. 2. Length frequency distribution of fish caught in the Tana estuary/fjord between 20 June and 11 August 2000.

there remain several species of potential fish predators which are present in the estuary. These include cod, saithe, haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and sea trout (*Salmo trutta*) (Hvidsten and Møkkelgjerd, 1987; Grønvik and Klemetsen, 1987; Jiang and Jørgensen, 1996; Temming et al., 2004). For these predators, Atlantic salmon smolts of 25–30 g would presumably be ideal prey.

This study addresses the predation on salmon smolts by these species in the Tana estuary, taking into consideration their size and the role sandeels play as an alternative prey.

2. Materials and methods

The Tana river in Finnmark, North Norway, is partly a border river between Finland and Norway (Fig. 1). It is a large river with mean average discharge at $163 \text{ m}^3 \text{ s}^{-1}$ and with a maximum as high as $2740 \text{ m}^3 \text{ s}^{-1}$ in late May (Niemi et al., 2001). According to earlier tagging experiments, the main smolt run in the river is between 15 June and 25 July (Svenning et al., 2005).

In the lower part of the river especially, sand is the main bottom substrate, and large sand banks dominate the inner 2–3 km of the fjord and the estuary. The estuary is shallow (0–3 m), but is bisected by a deeper (2–3 m) channel formed by the river (Fig. 1). The large sand banks are excellent habitats for sandeels (*Ammodytes* spp.). In 2000, the main descent of the smolts through the estuary was estimated to be in the first 2 weeks of July (Svenning et al., 2005).

To determine levels of fish predation in the estuary on Atlantic salmon smolts descending the river, predatory fish were sampled by hand jigging or trolling from a small (5 m) open boat in the estuary and the inner part of the fjord from 20 June to 11 August 2000 (Fig. 1). Each fishing effort was quantified according to number of fishermen and time spent fishing. Samples were collected over 32 days, covering the whole day and night periods, and all the tidal phases.

All captured fish were weighed ($\pm 0.5 \text{ g}$), and their (standard) length measured ($\pm 0.5 \text{ mm}$). The stomachs were opened in the laboratory under a stereo microscope, and food items were identified to the lowest possible taxon. The degree of fullness and % volume of the different food items were estimated for each

sample. When possible, the lengths of all prey fish were measured. Free otoliths were identified to species using Härkönen (1986) and a reference otolith collection. The frequencies of occurrence of prey species or prey groups were estimated in order to describe the diet width of the predator species. The % volumes of prey species and prey groups were estimated to quantify each category's contribution to the diet. Empty stomachs were excluded from this estimation.

3. Results

3.1. Fish capture

A total of 497 fishes, from seven species, were caught between 20 June and 11 August in the Tana estuary/fjord (Table 1). Their lengths varied from 20 to 65 cm, with a dominance of individuals between 25 and 45 cm (Fig. 2). Cod (42.3% by number) and haddock (24.3%) dominated, but saithe (13.7%), sea trout (11.3%) and whiting (8.0%) was also frequently captured. Only one flounder *Platichthys flesus* and one cusk *Brosme brosme* were caught.

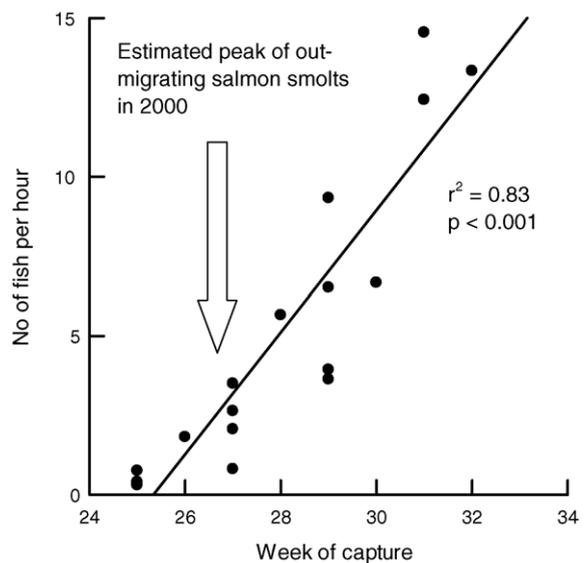


Fig. 3. Number of fish caught per person per hour in the Tana estuary/fjord between 20 June (week 25) and 11 August (week 32) in 2000. The estimated peak of out-migration of Atlantic salmon smolts in 2000 is marked with an arrow.

Catch per unit effort (CPUE) increased from less than 1 fish per hour in June/July to 15 fish per hour in late July/August (Fig. 3). The increase in CPUE was significantly positively correlated to date of capture for cod ($r^2=0.56$, $p=0.001$), haddock ($r^2=0.47$, $p=0.003$) and sea trout ($r^2=0.33$, $p=0.025$), but not for saithe ($r^2=0.18$, $p=0.22$) and whiting ($r^2=0.13$, $p=0.29$).

3.2. Diet

From the 497 fish, 452 stomachs (91%) were analyzed, and of those 317 (70%) contained food remains (Table 1). The frequency of empty stomachs varied from 13% in haddock to 50% in whiting. Fish prey was found in approximately 95% of the stomachs that contained food remains; for cod (88.4%), whiting (95.0%), saithe (76.9%) and

sea trout (100%), while only 12.4% of the haddock stomachs contained fish remains. By volume, fish constituted only 9.8% of the haddock stomach contents, in contrast to 76% (in saithe) to 100% (in sea trout) for the other four fish species (Fig. 4A).

Six prey fish species were found in the fish stomachs, and among these lesser sandeel dominated (Fig. 4B). No remains of Atlantic salmon were found in any of the analyzed fish stomachs. In the cod stomachs, sandeel made up 80.1% by mass, herring 3.6%, capelin 2.7%, flounder 7.5%, saithe 1% and haddock 5.1%. In saithe only sandeels (94.0% by mass) and cod (6.0%) were found, while haddock and whiting had been eating sandeels (84.4% and 92.6%, respectively), and herring (15.6%) and capelin (7.4%), respectively. In the sea trout stomachs, sandeels were the only prey species found.

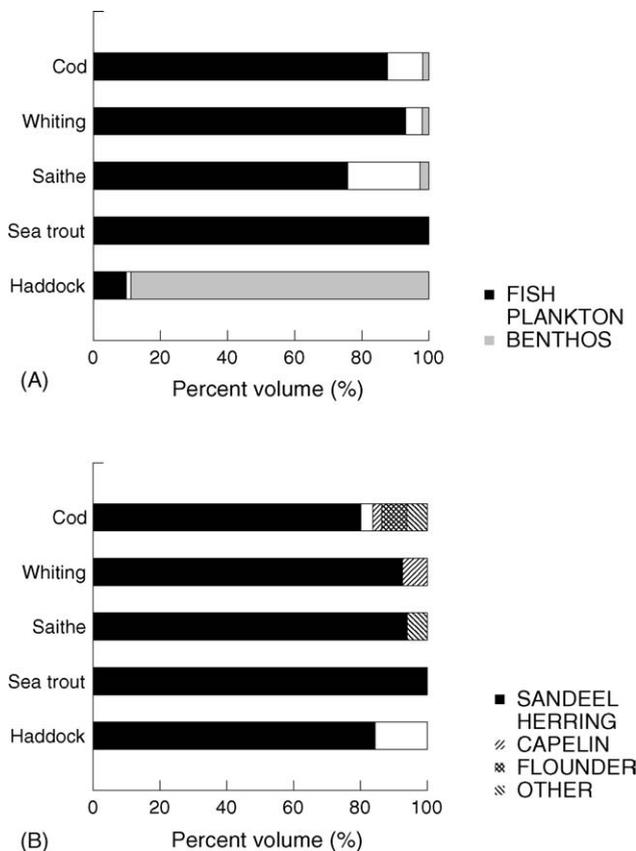


Fig. 4. The stomach contents of fish sampled in the Tana estuary/fjord between 20 June and 11 August 2000, in groups (A) and in fish species (B).

Of the prey fish that could be measured precisely ($n = 369$), the lesser sandeel ranged from 3.5 to 18.2 cm (mean 13.2 cm, $n = 330$), flounders from 2.5 to 16.2 cm (mean 9.8 cm, $n = 13$), herring from 6.7 to 18.1 cm (mean 13.2 cm, $n = 14$), haddock from 12.0 to 21.7 cm (mean 16.9 cm, $n = 4$), saithe from 13.6 to 13.9 cm (mean 13.8 cm, $n = 2$) and capelin from 8 to 13.5 cm (10.4 cm, $n = 6$).

Although lesser sandeel strongly dominated as prey, their size varied strongly between the predatory fishes. The mean size of sandeels consumed was around 13 cm (i.e. 1 year old) in cod, sea trout and whiting, and 7.6 cm (young-of-the-year) in saithe (Fig. 5). The size of the prey fish (sandeels) increased with the size of the cod

($p = 0.002$) and sea trout ($p = 0.001$), while no such correlation was found for haddock, saithe and whiting ($p > 0.05$ for all species) (Fig. 6). Individual cod, sea trout and whiting with body lengths below 40 cm, had, however, consumed sandeels up to 17–18 cm.

4. Discussion

Previously registered salmon smolt runs in the Tana river were between 15 June and 25 July (Svenning et al., 2005; Davidsen et al., 2005). Catches of smolts in trawls made between the estuary and the mouth of the Tana fjord by the Norwegian Marine Research Institute on 5–22 July 2000 indicated a peak run through the estuary during the first week of July (Svenning et al., 2005). Thus, our sampling of predatory fish in the estuary, between 20 June and 11 August 2000, most probably covered the main smolt run.

Fish predators have a prominent ontogenetic change in diet from a predominance of invertebrates in small individuals to a predominance of fish in larger fish. The proportion of fish in the cod diet often increases in fish longer than 40 cm, and cod may swallow fish prey that are up to 55% of their own length (Pedersen and Pope, 2003). The preferred prey mass is estimated to be about 2–4% of the cod predator mass (Nilssen et al., 1994). During the period 1974–1981, the mean length of more than 11 000 salmon smolts from the Tana river varied between 16.2 and 16.8 cm, and their mean weight between 31 and 35 g (Svenning unpublished). Thus the Tana salmon smolt would be expected to be a preferred prey of a cod weighing 1–2 kg or being 40–55 cm in length, and even cod as short as 35 cm may prey on smolts (Hvidsten and Møkkelgjerd, 1987).

Although more than 450 stomachs of cod, saithe, whiting, haddock and sea trout were examined during the main smolt run in the Tana river, no salmon smolts or otoliths from salmon smolts were found among any of the stomach contents. Based on earlier studies in the rivers Orkla and Surna in central Norway, where saithe and cod were important predators on salmon smolts (Hvidsten and Møkkelgjerd, 1987; Hvidsten and Lund, 1988), this result was unexpected. All predator fish species in the Tana estuary, except saithe, had consumed prey fish within the size range of the Tana smolts, and, based on the numbers of fish caught and the frequency of prey fish per predator, cod and sea

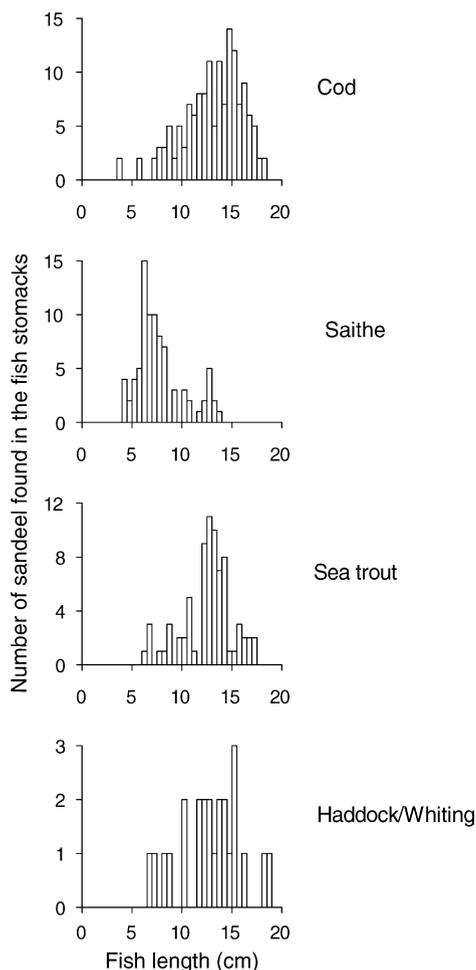


Fig. 5. Length of sandeels found in stomachs of fish sampled in the Tana estuary/fjord between 20 June and 11 August 2000.

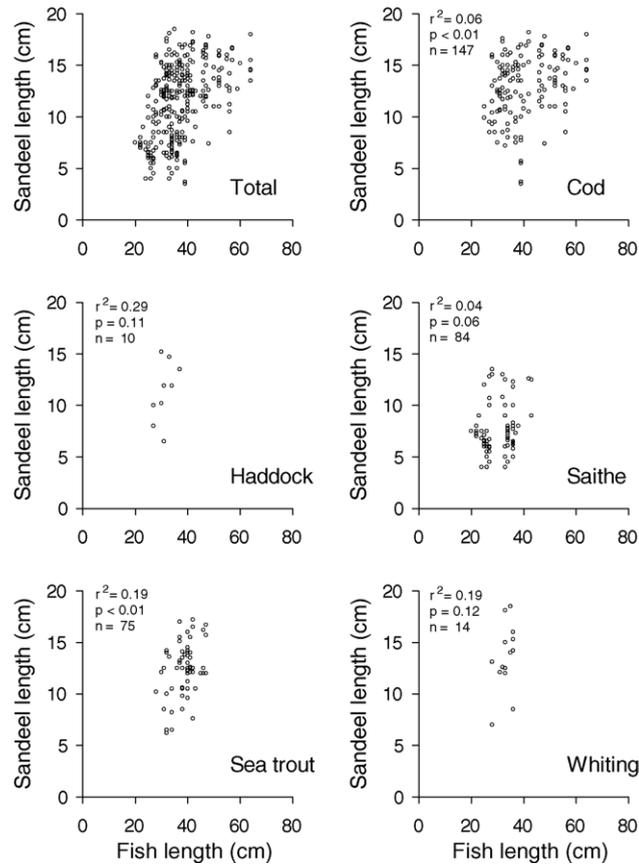


Fig. 6. Relationship between size of fish sampled in the Tana estuary/fjord between 20 June and 11 August 2000, and length of sandeels found in the fish stomachs.

trout were potentially the greatest predator risk for the descending salmon smolts. No sea trout was however caught before 15 July, and the species was thus probably unimportant as an estuarine salmon smolt predator, at least in this year.

Based on the near total dominance in the diet of most of the fish predators, the abundance of lesser sandeel in the Tana estuary is probably large compared to most other Norwegian coastal areas. This large concentration of sandeels in the Tana estuary, their high nutritional value ($22\text{--}29\text{ kJ g}^{-1}$ dry weight, Hislop et al., 1991), their size and their slender body form makes sandeels very attractive and vulnerable as prey. The dominance of sandeels in the diet of the thousands of male goosanders in the Tana estuary, with a corresponding absence of salmon smolt in their diet (Svenning et al., 2005), further emphasizes the importance of this

local sandeel stock in the Tana ecosystem. A similar but slightly lower dominance of locally abundant sandeels in the diet of fish predators during the summer was observed at a coastal bank in south-western Norway (Høines et al., 1995). Whereas lesser sandeel is probably the most abundant fish species in the North Sea (Daan et al., 1990), and an important prey species for many fish, seabirds and marine mammals (Furness, 2002), the species is evidently only locally important in the Norwegian and Barents Seas where capelin and herring are the dominant planktivores and prey species (Sakshaug et al., 1994; Barrett, 2002; Skjoldal, 2004). Smolt survival may be substantially increased by avoiding predation in estuaries and fjords, as documented by the experiments in the Surna river by Gunnerød et al. (1988) and Heggberget et al. (1991). In experiments with groups of two-winter-old smolts released into the

river, the fjord outside or the open sea, the recapture rate as mature salmon increased from 1.2% after release in the river to 4.2% after release in the open sea (Gunnerød et al., 1988; Heggberget et al., 1991). In the Surna estuary and fjord, cod and saithe were important predators (Hvidsten and Møkkelgjerd, 1987), and these experiments indicated that their predation on salmon smolts was a substantial mortality factor.

As observed in other localities, piscivorous fish may congregate to feed on smolts during their migration (Meacham and Clark, 1979; Hvidsten and Møkkelgjerd, 1987; Hvidsten and Lund, 1988), however, the CPUE of potential smolt predators in the Tana estuary and inner fjord increased considerably in the period after the main smolt run. Likewise, a similar increase was observed in the goosander aggregation from June to August–September, culminating with up to 25 000–30 000 birds in the estuary 1–2 months after the smolt run (Svenning et al., 2005), indicating that Atlantic salmon smolts are not the main basis for the aggregation of either goosanders or marine piscivorous fish species in the estuary. While the large and as yet unexploited population of lesser sandeel in the Tana estuary thus attracts large numbers of fish and avian predators, they may also act as an important factor contributing to the status of the Tana river as one of the most important salmon rivers of the world.

The apparent low predation pressure on the salmon smolts in the estuary may, however, be very fragile, as any reduction of the sandeel population may force these large numbers of bird and fish predators to feed on alternative prey species, including salmon smolts. Alternatively, they may simply leave the inner fjord area to seek food elsewhere along the coast. A repeat of our study in years when the sandeel population is low throughout the summer would possibly indicate which of these hypotheses is correct.

References

- Barrett, R.T., 2002. Atlantic puffin *Fratercula arctica* and common guillemot *Uria aalge* chick diet and growth as indicators of fish stocks in the Barents Sea. *Mar. Ecol. Prog. Ser.* 230, 275–287.
- Bax, N., 1998. The significance and prediction of predation in marine fisheries. *ICES J. Mar. Sci.* 55, 997–1030.
- Crozier, W.W., Kennedy, G.J.A., 1993. Marine survival of wild and hatchery-reared Atlantic salmon (*Salmo salar*) from the River Bush, Northern Ireland. In: Mills, D.H. (Ed.), *Salmon in the Sea and New Enhancement Strategies*. Fishing News Books, Oxford, pp. 139–162.
- Daan, N., Bromley, P.J., Hislop, J.R.G., Nielsen, N.A., 1990. Ecology of North Sea fish. *Netherl. J. Sea Res.* 26, 343–386.
- Davidson, J., Svenning, M.-A., Orell, P., Yoccoz, N., Dempson, J.B., Niemelä, E., Klemetsen, A., Lamberg, A., Erkinaro, J., 2005. Spatial and temporal migration of wild Atlantic salmon smolts determined from a video camera array in the sub-Arctic River Tana. *Fish. Res.* 74, 210–222.
- Dieperink, C., Bak, B.D., Pedersen, L.-F., Pedersen, M.I., Pedersen, S., 2002. Predation on Atlantic salmon and sea trout during their first days as postsmolts. *J. Fish. Biol.* 61, 848–852.
- Feltham, M.J., 1990. The diet of red-breasted mergansers (*Mergus serrator*) during the smolt run in N.E. Scotland: the importance of salmon (*Salmo salar*) smolts and parr. *J. Zool.* 222, 285–292.
- Feltham, M.J., 1995. Predation of Atlantic salmon, *Salmo salar* L., smolts and parr by red-breasted mergansers, *Mergus serrator* L., on two Scottish rivers. *Fish. Manage. Ecol.* 2, 289–298.
- Friedland, K.D., Hansen, L.P., Dunkley, D.A., MacLean, J.C., 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES J. Mar. Sci.* 57, 419–429.
- Furness, R.W., 2002. Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. *ICES J. Mar. Sci.* 59 (2), 261–269.
- Grønvik, S., Klemetsen, A., 1987. Marine food and diet overlap of co-occurring Arctic charr *Salvelinus alpinus* (L.), brown trout *Salmo trutta* (L.) and Atlantic salmon *Salmo salar* L. off Senja. *N. Norway Polar Biol.* 7, 173–177.
- Gunnerød, T.B., Hvidsten, N.A., Heggberget, T.G., 1988. Open sea releases of Atlantic salmon smolts, *Salmo salar*, in central Norway, 1973–1983. *Can. J. Fish. Aquat. Sci.* 45, 1340–1345.
- Hansen, L.P., Quinn, T.P., 1998. The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Can. J. Fish. Aquat. Sci.* 55, 104–118.
- Härkönen, T., 1986. Guide to the Otoliths of the Bony Fishes of the Northeast Atlantic. Danbiu ApS, Hellerup, Denmark.
- Heggberget, T.G., Hvidsten, N.A., Gunnerød, T.B., Møkkelgjerd, P.I., 1991. Distribution of adult recaptures from hatchery-reared Atlantic salmon (*Salmo salar*) smolts released in and offshore of the River Surna Western Norway. *Aquaculture* 98 (1–3), 89–96.
- Hislop, J.R.G., Harris, M.P., Smith, J.G.M., 1991. Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *J. Zool.* 224, 501–517.
- Høines, Å.S., Bergstad, O.A., Albert, O.T., 1995. The food web of a coastal spawning ground of the herring (*Clupea harengus* L.). In: Skjoldal, H.R., Hopkins, C., Erikstad, K.E., Leinaas, H.P. (Eds.), *Ecology of Fjords and Coastal Waters*. Elsevier B.V., Amsterdam, pp. 385–401.
- Hvidsten, N.A., Lund, R.A., 1988. Predation on hatchery-reared and wild smolts of Atlantic salmon, *Salmo salar* L., in the estuary of river Orkla, Norway. *J. Fish. Biol.* 33, 121–126.
- Hvidsten, N.A., Møkkelgjerd, P.I., 1987. Predation on salmon smolts (*Salmo salar* L.) in the estuary of the river Surna, Norway. *J. Fish. Biol.* 30, 273–280.

- Jiang, W., Jørgensen, T., 1996. The diet of haddock (*Melanogrammus aeglefinus* L.) in the Barents Sea during the period 1984–1991. ICES J. Mar. Sci. 53, 11–21.
- Meacham, C.P., Clark, J.H., 1979. Management to increase anadromous salmon production. In: Clepper, H. (Ed.), Predator–Prey Systems in Fisheries Management. Sport Fishing Institute, Washington, DC, pp. 377–386.
- Montevocchi, W.A., Cairns, D.K., Myers, R.A., 2002. Predation on marine-phase Atlantic salmon (*Salmo salar*) by gannets (*Morus bassanus*) in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 59, 602–612.
- Niemelä, E., Julkunen, M., Erkinaro, J., Mäkinen, T.S., 2001. Seasonal variation in density of juvenile Atlantic salmon in fluvial shoreline habitats of a large subarctic river. J. Fish. Biol. 59, 555–568.
- Nilssen, E.M., Pedersen, T., Hopkins, C.C.E., Thyholdt, K., Pope, J.G., 1994. Recruitment variability and growth of northeast arctic cod: influence of physical environment, demography, and predator–prey energetics. ICES Mar. Sci. Symp. 198, 449–470.
- Pedersen, T., Pope, J.G., 2003. How may feeding data be integrated into a model for a Norwegian fjord population of cod (*Gadus morhua* L.). Scientia Marina 67 (Suppl. 1), 155–169.
- Sakshaug, E., Bjørge, A., Gulliksen, B., Loeng, H., Mehlum, F., 1994. Structure, biomass distribution, and energetics of the pelagic ecosystem in the Barents sea—a synopsis. Polar Biol. 14, 405–411.
- Skjoldal, H.R. (Ed.), 2004. The Norwegian Sea Ecosystem. Tapir Academic Press, Trondheim, p. 559.
- Svenning, M.-A., Fagermo, S.E., Barrett, R.T., Borgstrøm, R., Vader, W., Pedersen, T., Sandring, S., 2005. Goosander predation and its potential impact on Atlantic salmon smolts in the River Tana estuary, northern Norway. J. Fish Biol. 66, 924–937.
- Temming, A., Gotz, S., Mergardt, N., Ehrich, S., 2004. Predation of whiting and haddock on sandeel: aggregative response, competition and diel periodicity. J. Fish. Biol. 64, 1351–1372.