



Flexible modes of anadromy in Baltic sea trout: making the most of marginal spawning streams

K. E. LIMBURG*‡, P. LANDERGREN*, L. WESTIN*, M. ELFMAN† AND P. KRISTIANSSON†

*Department of Systems Ecology, Stockholm University, SE-620 35 Färösund, Sweden and †Department of Nuclear Physics, Lund University, SE-221 00 Lund, Sweden

(Received 9 January 2001, Accepted 8 June 2001)

From examination of the ratios of strontium to calcium laid down as a lifetime record in the otoliths of sea trout *Salmo trutta* from Gotland, Baltic Sea, it was found that: (1) the shortest stream was used mostly by precociously emigrant or coastally hatched spawners; (2) longer streams had more fish that underwent normal smoltification; (3) sea-caught fish were predominantly coastally hatched (presumably near stream mouths). Furthermore, some otoliths showed no evidence of a freshwater history at all, raising the possibility of a contingent of the coastal population that does not depend on riverine spawning. The results emphasize the importance of the coastal zone as natal and early life habitat for sea trout in the Baltic, particularly with respect to a potential change to a warmer climate which may exacerbate conditions within small, ephemeral trout streams. © 2001 The Fisheries Society of the British Isles

Key words: *Salmo trutta*; otolith microchemistry; variable emigration; Sr : Ca.

INTRODUCTION

Anadromous brown trout (sea trout) *Salmo trutta* L., like several other salmonid species, are adapted to a wide range of aquatic habitats, with freshwater resident as well as anadromous forms coexisting in the same river system (Elliott, 1994). It is generally thought that sea trout require a period of freshwater residency, ranging from one to several years, before transformation to the smolt stage and subsequent seaward migration for further growth prior to maturity (Elliott, 1994). In southern Scandinavia, the most common pattern for sea trout is 1–3 years in fresh water and 1–3 years at sea before first spawning (Titus & Mosegaard, 1989). However, one of the critical problems for populations that use small streams is low water discharge caused by direct human activities such as deforestation, draining of lakes, canalization of watercourses, dam construction, and indirect actions resulting in climate change (as well as natural, secular cycles of climate). Smoltification at a young age (<1 year) is thought to be a response to low water holding capacity in many streams (Borgström & Heggenes, 1989; Titus & Mosegaard, 1989).

On the Baltic Sea island of Gotland, Sweden (58° N 19° E), sea trout use many streams of various sizes for spawning, but smolt production is low due to dry periods during the summer and early autumn (Landergrén, 1999). Some years

‡Author to whom correspondence should be addressed. Present address: SUNY College of Environmental Science and Forestry, Syracuse, NY 13210, U.S.A. Tel.: +1 315 470 6741; fax: +1 315 470 6934; email: Klimburg@esf.edu

only a few streams contain water and two to three cohorts are lost or strongly reduced. Despite this, the spawning population is surprisingly intact in the following years. In fact, in some surveys conducted in the 1970s and 1980s, spawning sea trout were estimated to outnumber stream-produced smolts by a factor of three (Nyman & Westin, 1978; Gydemo *et al.*, 1982). Many hypotheses have been proposed and tested (Landergren & Vallin, 1998) to account for this; the most intriguing hypothesis to date is precocious migration of young-of-the-year (YOY) to the sea (Järvi *et al.*, 1996; Landergren, 1999). If they can survive to adulthood, early migrating sea trout fry or parr could balance the skewed relationship between smolt production and the spawning population. A prerequisite for this assumption is that the young parr can survive an early shift to a brackish water environment, without undergoing smolt transformation, and return at maturity. Feeding and growing fry have been documented in the coastal zone around Gotland (Järvi *et al.*, 1996), but their eventual fate was unknown. Furthermore, a study by Landergren (2001) showed no significant difference in survival or growth between sea trout parr reared in fresh and brackish water.

One of the most important factors for this early migration seems to be the distance between spawning grounds and the sea (Landergren, 1999). Streams with spawning grounds close to the sea are observed to have the largest number of fry leaving (caught at the stream mouth in fry traps). Two of the studied streams can serve as an example. In Ar Brook, with spawning grounds no more than 50 m from the outlet, 500–1000 sea trout parr migrate yearly to the coastal zone during the first months following emergence. In Hultung Brook, with spawning grounds several kilometres from the sea, not a single parr has been caught in the trap. This phenomenon appears to be related to the fierce competition following emergence, whereby less competitive individuals drift or swim downstream (Elliott, 1994). In shorter streams, losers may actually drift or swim out of the freshwater habitat and enter the sea.

Alternatively, numbers of spawning adults could also be augmented if there were successful spawning and recruitment of sea trout outside of the freshwater habitat entirely, for example in the nearshore coastal zone. Coastal spawning has been observed and documented around Gotland (Nordin, 1957; Landergren & Vallin, 1998), particularly near stream mouths, but it has been assumed that even the low salinities in these areas would be high enough to cause egg and fry mortality. Landergren & Vallin (1998) documented low hatching success (<2%) at salinities of 4‰; nevertheless, a small fraction of eggs did hatch and the fry survived. Thus, if these fish could survive both the physical rigours (increased salinity and mechanical disturbances by wave action) and the ecological interactions (predation and competition) of the coastal zone, these individuals might also eventually recruit to the spawning stocks. The salinity in the Baltic Sea ranges from 10 to 12‰ in the southern part to 2 to 3‰ in the Gulf of Bothnia. Around Gotland the salinity varies between 6 and 8‰.

In this study, the microchemical properties of otoliths of adult sea trout were used to assay the recruitment success of various life history forms. Specifically, the ratios of strontium to calcium (Sr : Ca) in otoliths were determined as a lifetime tracer of residence in waters of different salinity (Limburg, 1995; Tzeng, 1996; Secor & Rooker, 2000) by collecting adult fish returning to spawn, as well

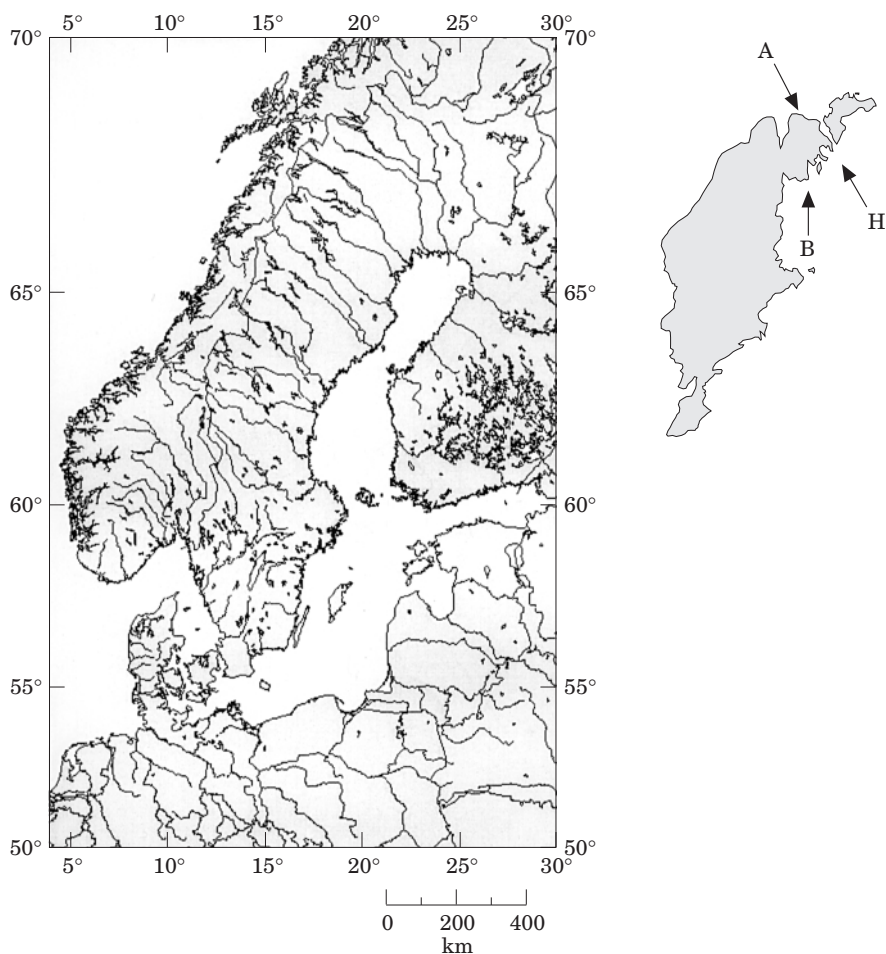


FIG. 1. Map of the Baltic Sea and Gotland. Inset shows location of study streams. A, Ar Brook; B, Bångån Brook; H, Hultung Brook. (Map created with KK+W Digital Cartography, <http://www.aquarius.geomar.de/omc/>).

as fish recruited to the marine stock. The aims were: (1) to observe whether precociously emigrating fry survive and recruit to the coastal and spawning stocks; (2) to observe whether other modes of anadromy occur, not requiring a strict sequence of smoltification; (3) to test whether stream size itself is a factor in the production of smolts *v.* non-smoltifying recruits.

MATERIALS AND METHODS

DESCRIPTION OF THE STUDY AREA

The sea trout used in this study were sampled in three streams on northern Gotland (Fig. 1). Ar Brook is very short (0.25 km), with only a few spawning grounds and close to the sea. A 4 year study (Landergren, 1999), where smolts and spawners were monitored at a weir, revealed that for every smolt produced within Ar Brook, 2.5 spawners returned (Table 1). Hultung Brook is *c.* 3.5 km long with the main spawning areas some kilometres upstream. In this stream there were 1.3 spawners for every smolt

TABLE I. Numbers of smolts and returning spawners observed in the study streams

Origin	1995–1996 Smolt/ spawners	1996–1997 Smolt/ spawners	1997–1998 Smolt/ spawners	1998–1999 Smolt/ spawners	Mean \pm s.d.
Ar	16/42*	20/22*	20/35*	14/78	17.5 \pm 3.0/44 \pm 23.9
Hultung	45/42*	77/62*	98/74*	45/176	66.3 \pm 25.8/88.5 \pm 59.7
Bångån	—/45	—/54	—/61	—/58	54.5 \pm 7.0

*From Landergren (1999).

recorded (Table I). Bångån Brook, 4 km long, is the largest watercourse with the first spawning ground *c.* 2 km from the outlet. No smolt record is available for Bångån, but the spawning population is fairly constant with *c.* 60 \pm 20 (s.d.) sea trout ascending the stream each autumn.

FISH COLLECTION AND PROCESSING

From 1995 to 1999, adult spawners were collected at random in the study streams by means of electrofishing and fish traps; total lengths (L_T) and fresh masses (W) were measured and sex determined. Non-spawning fish in the coastal zone around Gotland were collected with assistance from sport fishermen and household gillnet fishermen, so that not all sea-caught fish had complete records of sex or size. Fish heads were frozen for later removal of otoliths.

In addition, sea trout parr were reared in the laboratory at the Ar field station on northern Gotland, their adipose fins were clipped, and they were released after *c.* 3 months in the coastal zone *c.* 100–300 m from the mouths of the study streams. A number of these were recovered and their otoliths removed for analysis.

In the laboratory, sagittal otoliths were removed from the fish skulls, cleaned, dried and mounted with cyanoacrylate glue on petrographic slides. Otoliths were ground in the sagittal plane to expose the core and polished to a surface smoothness of 0.5 μ m.

OTOLITH ANALYSES

Otoliths were examined under a stereomicroscope and ages (year) determined by reading increments. Increments were counted in all fish by one reader (KEL), and in some cases were verified by a second reader. Often the seasonal patterns in zinc uptake by the otoliths (see below) helped to resolve questionable increments. All otoliths were read at least twice. Lifetime, mean annual growth (cm year^{-1}) was calculated as L_T divided by the age.

Microchemical analyses were conducted on the otoliths, primarily to measure ratios of strontium to calcium (Sr : Ca) as a proxy for salinity. Most of the analyses on wild fish ($n=82$) were made using nuclear microscopy combined with proton induced X-ray emission analysis (μ PIXE analysis) at the Department of Nuclear Physics, University of Lund (Malmqvist, 1996). The high resolution and rapid data collection enabled the entire otoliths to be mapped in 45–65 min (cf. 11–12 h with wavelength-dispersive spectroscopy, WDS) and enabled trace quantities of zinc to be measured as well. Whereas Sr : Ca varied with salinity, Zn : Ca showed seasonal variations as was recently observed in other salmonids (Halden *et al.*, 2000) and which facilitated age determination. Another seven otoliths of wild fish were analysed with a WDS electron microprobe at the Department of Geosciences, University of Uppsala. On these, point transects were made, originating at the otolith core and extending to the outer edge of the otolith.

Analyses using WDS involved visually locating the core of the otolith with transmitted light, then laying out a transect of 30–50 points spaced 20–40 μ m apart traversing the otolith from the core to the outer posterior edge (a so-called ‘life-history transect’). The parameters for operation were: accelerating voltage, 20 kV; current, 20 nA; electron beam

diameter, 15 μm . Strontium was counted for 40 s on the peak and 40 s on the background (only on one side, to avoid the strong interference from a second order Ca K- α peak). Calcium was counted until a precision of at least 0.1% was reached (usually <20 s), and background was counted for 10 s on each side of the peak. Strontianite (SrCO_3) and calcite (CaCO_3) were used as calibration standards. The detection limits were $0.03 \pm 0.004\%$ mass for both elements.

μPIXE analyses were made at the Lund Nuclear Microprobe facility, using a standard 2.55 MeV proton beam. X-rays were detected with a Kevex Si(Li) detector of 50 mm^2 active area and a measured energy resolution of *c.* 155 eV at the 5.9 keV Mn K α peak. A thick absorber (mylar + aluminium) was used during the analysis to suppress the Ca X-ray peaks; this permitted increasing the current to enhance the signals of Sr and other trace elements. The total charge was *c.* 1 mCoulomb. The normal procedure for a scan was to raster as much of the otolith as possible in a grid of 128×128 pixels. Following data collection, the data sets were normalized to counts per charge.

To verify that elevated Sr : Ca indeed reflected the more saline conditions of the Baltic Sea, otoliths were analysed from laboratory-reared fish, raised either entirely in fresh water, or fresh water and then transferred to Gotland sea water (mean salinity 6.74‰). Additionally, otoliths were analysed from four sea trout caught along the Swedish west coast (salinity range 20–25‰).

RESULTS

VALIDATIONS AND COMPARISONS WITH OPTICAL FEATURES

Otoliths from fish reared either entirely in fresh water, or transferred to Gotland coastal sea water, showed clear and consistent differences in the otolith Sr : Ca ratio (Fig. 2). Otoliths of fish exposed to 6.74‰ (averaged over time) showed an increase over six-fold above the ratios of freshwater-exposed fish; however, fish caught on the Swedish west coast (where salinities vary from 20–25‰) showed an additional increase of only 1.6-fold Sr : Ca (Table II).

In general, Sr : Ca ratios do not correspond with optical zonations within otoliths, unless a migration event corresponds to a seasonal event, e.g. a movement in the spring or autumn (Fig. 3). Conversely, zinc accumulation demonstrated a seasonal pattern, with Zn : Ca density patterns reflecting the seasonal zonations observed visually (Fig. 3).

VARIATION IN FRESHWATER-SEAWATER RESIDENCY MODES

A wide variety of habitat use was documented in the otoliths of fish caught in Ar, Hultung, and Bångån streams, as well as in the coastal zone of Gotland (Fig. 4). In addition to fish that left as smolts at ages ranging from 1 to 4 years old [Fig. 4(a)–(d)], other lifestyles included maturation in fresh water [Fig. 4(e)], and discrete movements among areas of different salinity including movement between fresh water and very low salinity [e.g. near the mouth of a stream entering the sea; Fig. 4(g), (h)] and precocious emigration [Fig. 4(j)]. More surprising were the numbers of otoliths with elevated Sr : Ca throughout the entire otolith matrix, indicating no experience with fresh water at all [Fig. 4(k), (l)]. In other words, these fish entered the sea, or were born there, without undergoing smolt transformation.

Whether the fish had a marine or freshwater resident mother is also readily visible (Figs 2–4), because marine-origin mothers deposit Sr in the egg. As the embryo develops, the Sr is incorporated into the embryonic otolith and is visible as a core of elevated Sr : Ca in these maps. Thus, cross-generation information

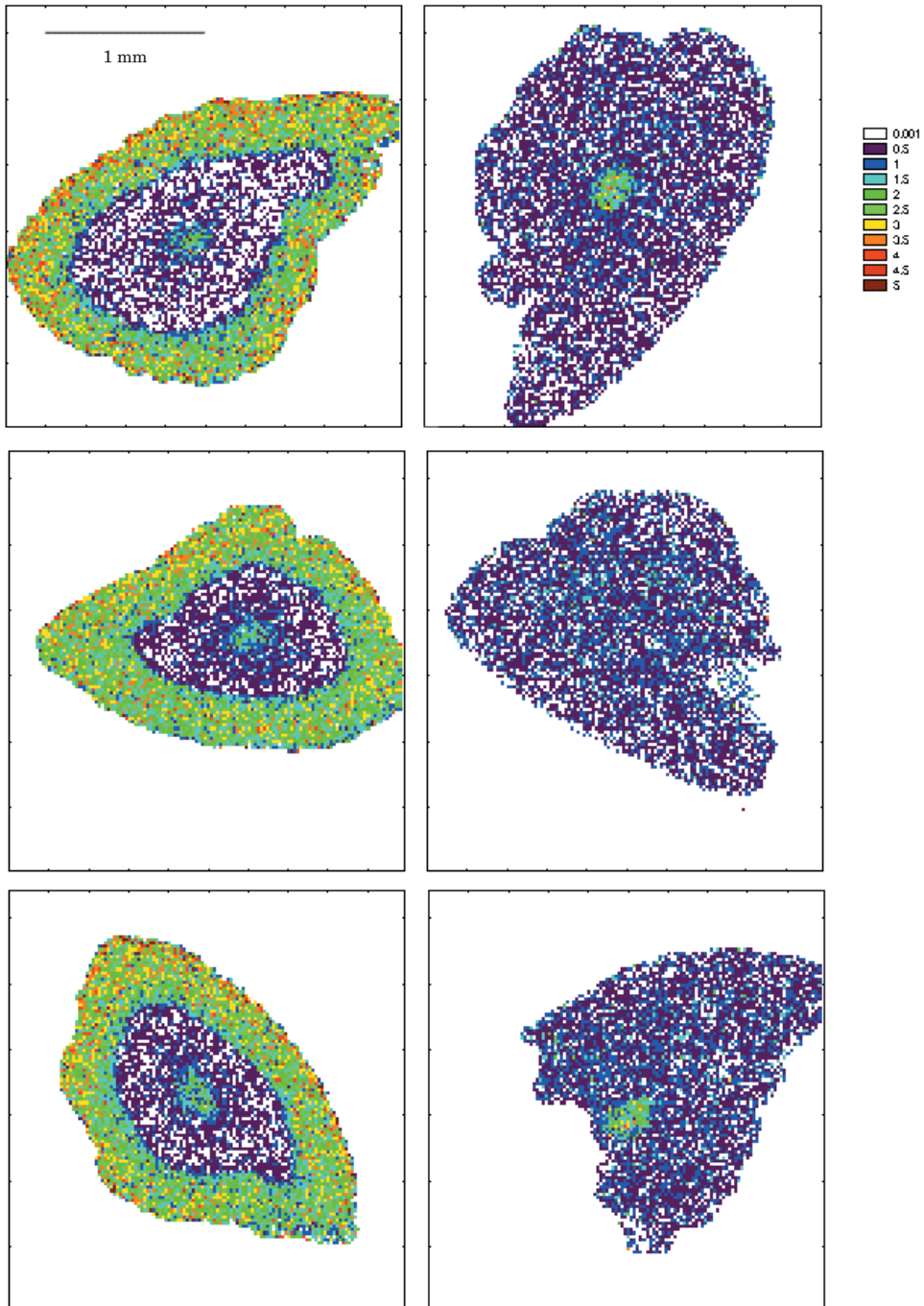


FIG. 2. Validations of Sr uptake by otoliths of juvenile sea trout ($n=6$) reared at different salinities. Values are Sr : Ca ratios taken directly from the microPIXE X-ray maps. Otoliths on the left are from fish reared initially in fresh water, then transferred to ambient coastal water (average salinity 6.74‰). Otoliths on the right are from fish reared entirely in fresh water. Note that the middle freshwater fish lacks Sr in its core, indicating its maternal parent was a freshwater resident. The otolith at the bottom right is broken (posterior missing).

TABLE II. Mean values of Sr : Ca from outer portions of otoliths of six laboratory reared brown trout and four Swedish sea trout

Salinity (‰)	Mean Sr : Ca	S.D.	<i>n</i>
Laboratory reared, entirely fresh water			
0	0.368	0.157	60
0	0.298	0.130	63
0	0.340	0.154	60
Laboratory reared, transferred to ambient sea water			
6.74	2.183	0.233	55
6.74	2.048	0.265	57
6.74	2.060	0.233	46
Wild, caught on Swedish west coast			
20–25*	3.38	0.56	106
20–25*	3.78	0.72	123
20–25*	3.29	0.74	151
20–25*	2.85	0.70	133

Pixel values on the otolith outer sections (i.e. laboratory or marine phase) were averaged to produce the means reported above (*n* refers to number of pixels used for each fish).

*Estimated salinity.

is available, and it is clear that freshwater residents can have marine-origin mothers and *vice versa* (Fig. 4). This phenomenon of Sr deposition in eggs appears to be a family characteristic of salmonids (Kalish, 1990; Halden *et al.*, 1995; Volk *et al.*, 2000). In the present samples, 91% (79 individuals) had marine-origin mothers.

The observation (Table I) of fewer smolts per spawners in a short stream (Ar Brook) relative to a longer one (Hultung) was strikingly borne out in the retrospective analysis of otoliths. The relative frequency of fish that had smolt-transformed *v.* those that apparently missed the smolt stage decreased as a function of stream length (Fig. 5; ANOVA of life histories as a function of site of capture $F_{3,76}=4.86$, $P<0.005$). Fish lacking a smolt stage also exceeded smolts amongst the fish collected in the sea. Fish that had been fin-clipped at age 3 months and released directly into the sea were recovered in Bångån and Ar Brooks, and from the sea, but not from Hultung Brook (Fig. 5). Of these, three remained at sea after release, three moved into fresh water and remained there for 1–2 years before migrating out, and the others moved first into weakly brackish water (e.g. near a river mouth) before moving offshore into higher salinity. Otoliths of the fin-clipped fish that remained at sea had substantially higher Sr : Ca ratios (range 3.5–4.5) throughout their seawater phases compared to the fish reared in Gotland coastal sea water (Table II). These higher ratios were also observed in some wild fish. Such elevated ratios may indicate movement to areas of higher salinity, or some other physiological or environmental change (e.g. dietary differences).

Fish were also classified by habitat use histories (Fig. 6). These were divided as: fish that spent 1–4 years in fresh water (normal) before emigration to sea (FW to SW); fish that used the nearshore coastal zone (with low salinity) as their

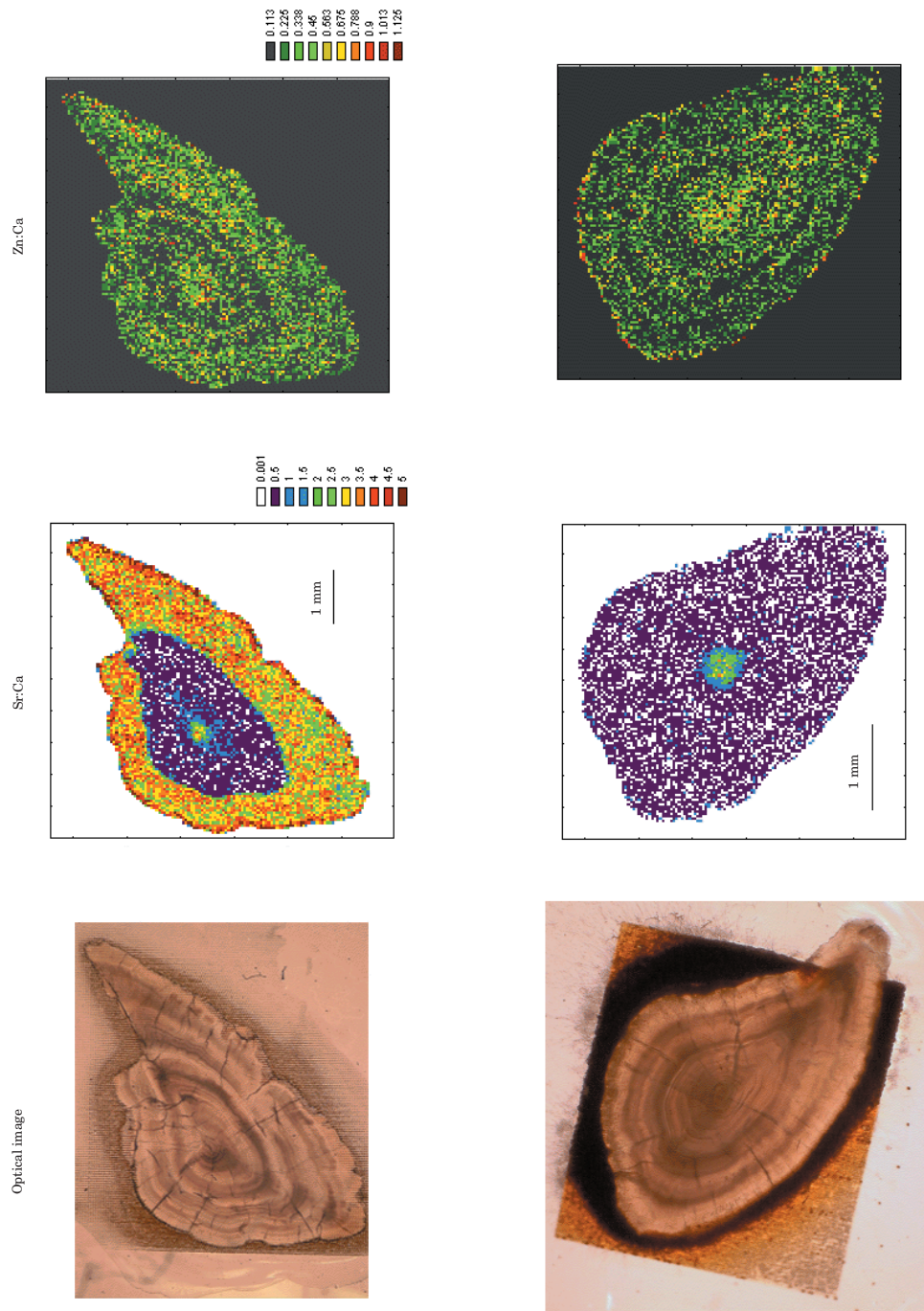


Fig. 3. Comparisons of optical v. microchemical features of otoliths from two adult brown trout. From left to right, the images are optical micrographs, Sr : Ca maps, and Zn : Ca maps of the same otolith. Top row shows otolith from a 4+ year old male caught outside Ar Brook that left fresh water after 2 years; bottom row is from a 3 year old resident male collected in Bångån Brook. Note similarities between Zn : Ca fluctuations and optical zonations.

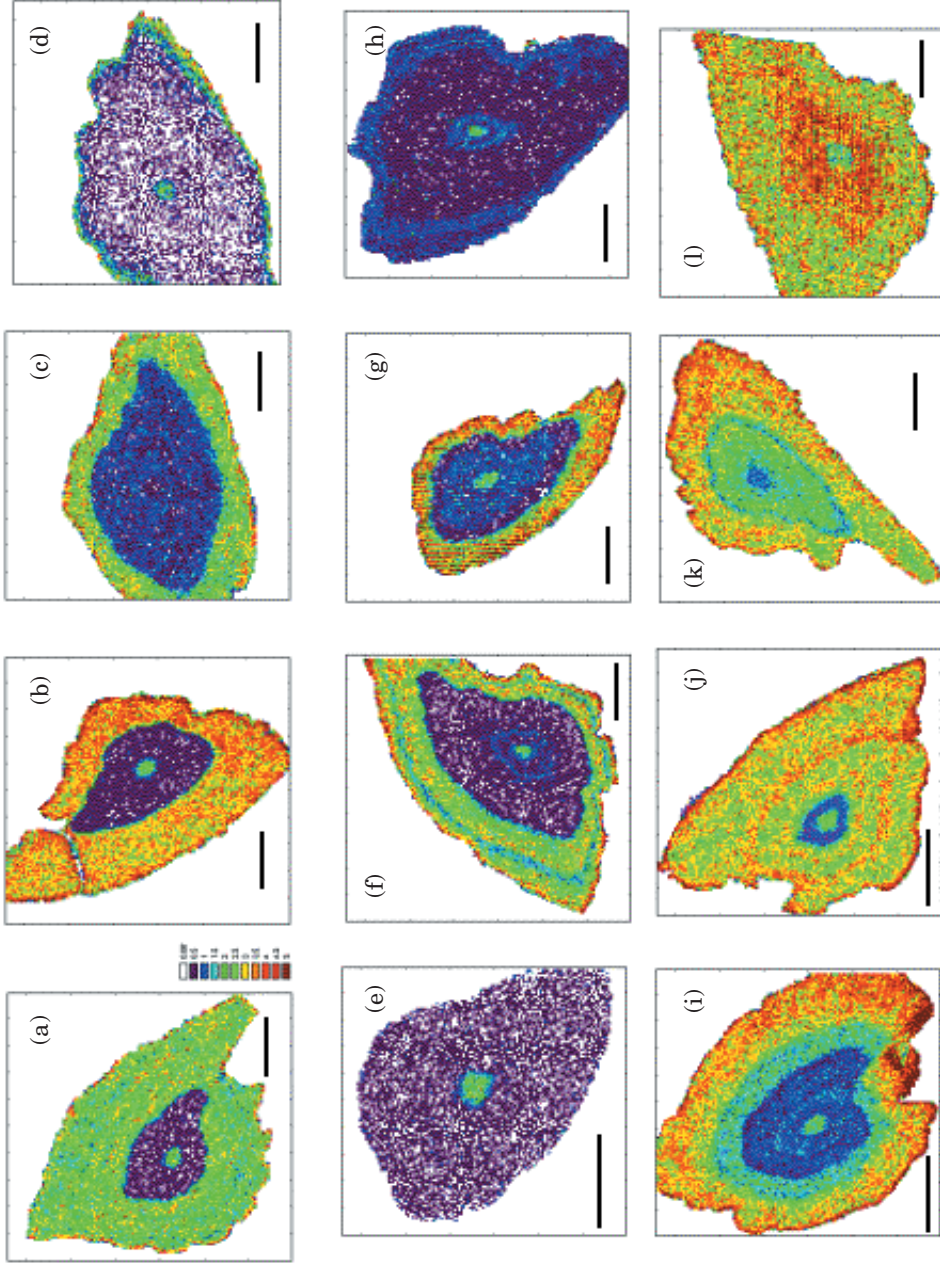


FIG. 4. Variations in life history habitat use in Gotland sea trout, as evidenced by differences in Sr:Ca ratios in otoliths. Otoliths from fish that underwent a normal smolt transformation, at ages (a) 1, (b) 2, (c) 3, and (d) 4 years, respectively; (e) a freshwater resident (and sexually precocious) male; (f) a fish that moved between fresh and slightly brackish waters before migration to sea; (g) a fish that used the coastal zone (weak salinity), then moved into fresh water for a period before migration to sea; (h) a fish that moved solely between weakly brackish and fresh water. Otoliths with different and abrupt changes in habitat including (i) a fish that moved into waters of increasing salinity in successive years; (j) a precocious emigrant; and two fish lacking any freshwater experience (k), (l). Note that one of these (k) has low Sr:Ca in its core, indicating a freshwater mother. Horizontal bars represent 1 mm.

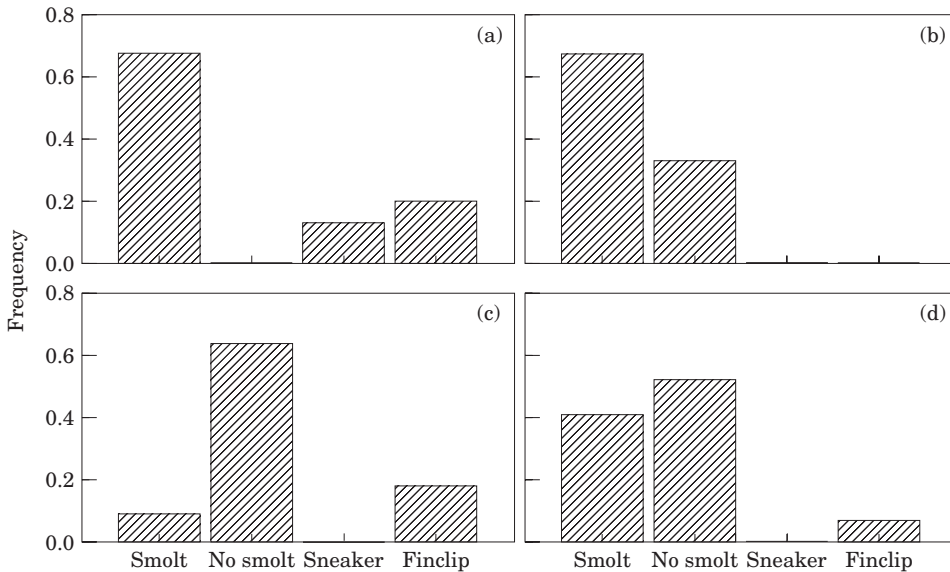


FIG. 5. Life histories of fish collected in three spawning streams: (a) Bångån Brook (4 km), (b) Hultung Brook (3-5 km), (c) Ar Brook (0-25 km), and of fish collected at (d) sea. Smolt, had migrated from fresh water to sea water after at least 1 year's freshwater residency and assumed to have undergone a smolt transformation; No Smolt, fish had either migrated shortly after emergence or had used a low salinity coastal zone, or higher salinity zone, without extended residency in fresh water; Sneaker, sexually precocious males; Finclip, laboratory-reared individuals that had been released at age 3 months into the sea.

juvenile rearing habitat, and either remained there or moved into waters of higher salinity (Coastal); freshwater residents (FW only); precocious emigrants (Precocious); and fish that appeared to spend their entire lives in higher salinity (Marine). Within streams, highest frequencies (27%) of precocious emigrants were found in Ar Brook and lowest (0%) in Bångån Brook; highest frequencies of normal anadromous forms were found in the latter (93%). Sixty per cent of the fish collected in Ar had been reared in the coastal zone, as was a substantial fraction (41%) of fish collected at sea. Marine residents were only collected at sea, constituting 7% of the fish collected there. Normal anadromous fish made up another 41% of sea-caught fish, while precocious emigrants constituted 4.5% of the sea-caught sample.

Lifetime mean annual growth (cm year^{-1}) by habitat use category was similar for all groups except for freshwater residents (Fig. 7), which was around half that of the other groups. Age at capture by habitat use category did not show significant differences ($P=0.18$). There were significant differences between growth by site of capture (ANOVA excluding fin-clipped fish, $F_{3,69}=5.92$, $P=0.0013$), but this was related at least in part to the differences in mean \pm s.e. age of fish captured at each site, with oldest fish captured in Hultung ($4.8 \text{ years} \pm 0.37$) and younger fish collected at sea (3.7 ± 0.16).

DISCUSSION

Flexibility in brown trout life histories is well documented (Jonsson, 1985; Elliott, 1994; Thorpe, 1994), but the present study is the first to demonstrate that

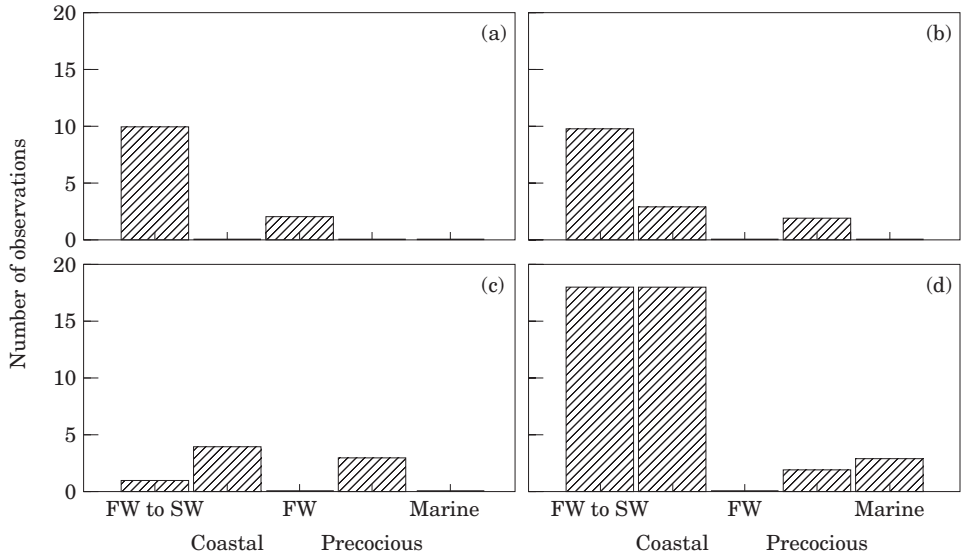


FIG. 6. Habitat use histories of sea trout, by point of capture: (a) Bângân Brook, (b) Hultung Brook, (c) Ar Brook, (d) sea caught. FW to SW, fish that moved from fresh water to sea water after freshwater residency of at least 1 year; Coastal, fish that had used the coastal zone as their early life habitat; FW only, freshwater residents; Precocious, fish that had emigrated within a few months of hatching (as determined by the location of elevated Sr : Ca in relation to the formation of the annulus); Marine, fish that had elevated Sr : Ca ratios throughout the entire otolith.

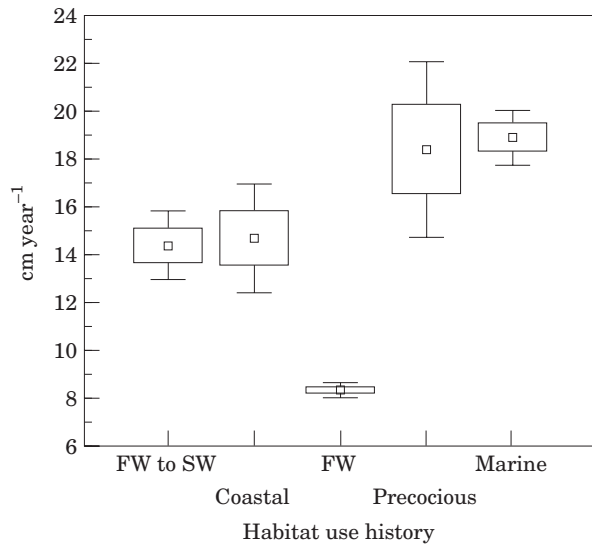


FIG. 7. Box-plots of ANOVA results of lifetime mean annual growth (cm year^{-1}) of fish classified by predominant habitat use. \perp , ± 1.96 S.E.; \square , ± 1.00 S.E.; \square , mean. Classification as in Fig. 6.

S. trutta can survive to reproductive maturity in a saline environment without passing through a freshwater phase. In standard seawater challenge tests, typically run at or near full-strength sea water, brown trout showed a size

relationship to seawater tolerance (Ugedal *et al.*, 1998), but challenges at brackish salinities more typical of the Baltic Sea have not been conducted.

Although 500–1000 fry and young parr have been regularly observed migrating (or drifting) out of Ar Brook within 3 months of emergence, the frequency of precocious emigrants actually recruited to the coastal and spawning stocks is low (8.5%). On the other hand, fish that reared either in the nearshore coastal or, apparently, offshore environments constitute another 33% of the wild fish assayed. Taken together, 41.5% of wild recruited fish in the present study appear not to have undergone a smolt stage. Järvi *et al.* (1996) assumed that the fry they observed in the nearshore zone around Gotland had emigrated from natal streams, but according to the present results, many of these fry may instead have been hatched in the nearshore zone, presumably near stream mouths where salinities were <4‰. Lifetime growth did not differ from fish that had undergone a normal smolt transition (Fig. 6).

Among the streams reported on here, adult spawners, lacking a smolt stage, outnumbered smolted adults by seven to one in the shortest stream (Ar Brook), whereas smolted adults outnumbered non-smolts by a factor of 2 in Hultung Brook (3.5 km) and were the only form of anadromous fish found in the largest watercourse (Bångån, 4 km long). Thus, the likelihood of a given stream's production of *S. trutta* being supported by 'exogenous' spawners appears to increase with decreasing stream size. Larger streams not only should have more suitable spawning and nursery habitat than small streams, but should also suffer fewer 'dry-out' episodes.

The mechanism that promotes the movement of 'exogenous spawners' into streams is unknown. However, salmonids generally home to natal streams by olfactory cues (Hasler, 1971). If much of the coastal spawning that takes place is actually in the vicinity of a stream mouth, then the stream effluent may still impart a characteristic odour, albeit dilute, to the juveniles when they imprint. Springs from the same stream might also emerge within the coastal gravel beds, as an extended hyporheic zone. Whether or not imprinting is possible on dilute stream water could be tested experimentally, but at this time, the issue of stream fidelity is unresolved for the Gotland populations.

Sea-caught individuals lacking a smolt stage also outnumbered the smolted recruits at sea (23 *v.* 20 individuals; Fig. 5). Of these sea-caught fish, three individuals were identified by their Sr : Ca ratios as having solely experienced marine water. This raises the possibility of the existence of a separate contingent of sea trout lacking any dependence on stream spawning. The genetic basis for salinity tolerance in *S. trutta* is unknown, but it appears as if there is at least some capacity within the coastal population around the island of Gotland to tolerate the ambient brackish salinities, similar to some Pacific salmon (Thorpe, 1994). This phenomenon is not isolated to Gotland; in a separate, pilot study of sea trout spawning in the River Em on the southeastern Swedish coast, five of seven adult sea trout also displayed no evidence of freshwater experience, based on otolith Sr : Ca ratios (K. E. Limburg, unpubl. data). Does this contingent represent a distinct genotype? Alternatively, the maternally-donated otolith Sr may obscure evidence of early residency of the egg in fresh water.

The fact that successful spawners can recruit to streams from coastal habitats, particularly to smaller streams, has implications for population resilience in the

face of a potentially warmer climate in the future. Concern has been raised about the potential effects of climate change on salmonids (Jensen, 1992; Hinch *et al.*, 1995; Minns *et al.*, 1995) including both changes in freshwater spawning habitats and marine conditions. For example, Jensen (1992) predicted that in Norway both temperature and precipitation is expected to increase, resulting in substantially higher winter but lower summer runoff. If the same holds true in the vicinity of Gotland, then flash floods and dry-outs in small streams would increase and year-classes produced there would be expected to fail more frequently. Similarly, medium-sized streams might be expected increasingly to dry out in a warmer climate. However, because coastal zones near stream mouths appear to serve as extended spawning and nursery habitat, stream populations appear to be buffered by recruitment of fish originating from the coastal zone.

Management of sea trout populations of the island of Gotland has focused on within-stream habitat and on catch quotas (R. Gydemo, pers. comm.). A major conclusion of this study is that nearshore coastal zones are also important as spawning and nursery habitats, particularly those areas associated with the outflows of small streams. Such areas should be protected to enhance spawning and recruitment success of sea trout.

We thank S. Ehrenberg for preparation of the otoliths and H. Harryson for assistance in the WDS analyses. Special thanks are extended to all who participated in the sampling of sea trout otoliths. Financial support was provided by the Swedish Agricultural and Forestry Research Council, the Sustainable Coastal Zone Management programme of the Swedish Foundation for Strategic Environment Research (MISTRA) and the Carl Trygger Foundation.

References

- Borgström, R. & Heggenes, J. (1989). Smoltification of sea trout (*Salmo trutta*) at short length as an adaption to extremely low summer stream flow. *Polskie Archiwum Hydrobiologii* **35**, 375–384.
- Elliott, J. M. (1994). *Quantitative Ecology and the Brown Trout*. London: Oxford University Press.
- Gydemo, R., Nyman, L. & Westin, L. (1982). Gotländska sjöar och vattendrag—en fiskeribiologisk inventering. *Information from the Institute of Freshwater Research* **9** (in Swedish, English summary).
- Halden, N. M., Babaluk, J. A., Campbell, J. L. & Teesdale, W. J. (1995). Scanning proton microprobe analysis of strontium in an Arctic char, *Salvelinus alpinus*, otolith: implications for the interpretation of anadromy. *Environmental Biology of Fishes* **43**, 333–339.
- Halden, N. M., Mejia, S. R., Babaluk, J. A., Reist, J. D., Kristofferson, A. H., Campbell, J. L. & Teesdale, W. J. (2000). Oscillatory zinc distribution in Arctic char (*Salvelinus alpinus*) otoliths: The result of biology or environment? *Fisheries Research* **46**, 289–298.
- Hasler, A. D. (1971). Orientation and fish migration. *Fish Physiology* **6**, 420–510.
- Hinch, S. G., Healey, M. C., Diewart, R. E., Thomson, K. A., Hourston, R., Henderson, M. A. & Juanes, F. (1995). Potential effects of climate change on marine growth and survival of Fraser River sockeye salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 2651–2659.
- Järvi, T., Holmgren, K., Rubin, J.-F., Petersson, E., Lundberg, S. & Glimsäter, C. (1996). Newly emerged *Salmo trutta* fry that migrate to the sea – an alternative choice of feeding habitat? *Nordic Journal of Freshwater Research* **72**, 52–62.

- Jensen, A. J. (1992). Possible effects of climatic changes on the ecology of Norwegian Atlantic salmon (*Salmo salar* L.). *NINA (Norsk Institutt for Naturforskning) Forskningsrapport* **36**, 3–21.
- Jonsson, B. (1985). Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Transactions of the American Fisheries Society* **114**, 182–194.
- Kalish, J. M. (1990). Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. *Fisheries Bulletin, U.S.* **88**, 657–666.
- Landergren, P. (1999). Recruitment of sea trout, *Salmo trutta* (L.) in small coastal streams on Gotland, Sweden. Licentiate in Philosophy Thesis, University of Stockholm.
- Landergren, P. (2001). Survival and growth of sea trout parr in fresh and brackish water. *Journal of Fish Biology* **58**, 591–593. doi:10.1006/jfbi.2000.1460.
- Landergren, P. & Vallin, L. (1998). Spawning of sea trout, *Salmo trutta* L., in brackish waters—lost effort or successful strategy? *Fisheries Research* **35**, 229–236.
- Limburg, K. E. (1995). Otolith strontium traces migratory histories of juvenile American shad, *Alosa sapidissima*. *Marine Ecology Progress Series* **119**, 25–35.
- Malmqvist, K. G. (1996). Particle-induced X-ray emission—a quantitative technique suitable for microanalysis. *Mikrochimica Acta (Suppl.)* **13**, 117–133.
- Minns, C. K., Randall, R. G., Chadwick, E. M. P., Moore, J. E. & Green, R. (1995). Potential impact of climate changes on the habitat and population dynamics of juvenile Atlantic salmon (*Salmo salar*) in eastern Canada. *Canadian Special Publication of Fisheries and Aquatic Sciences* **121**, 699–708.
- Nordin, S. (1957). Öringlek i saltvatten vid Gotland. (Sea trout spawning in salt water at Gotland). *Svensk Fiskeri Tidskrift* **3**, 42–43 (in Swedish).
- Nyman, L. & Westin, L. (1978). *Havsöringen på Gotland-en inventering. Information från Sötvattenslaboratoriet*. Drottningholm, Sweden: Institute of Freshwater Research (in Swedish with English abstract).
- Secor, D. H. & Rooker, J. R. (2000). Is otolith strontium a useful scalar of life cycles in estuarine fishes? *Fisheries Research* **46**, 359–371.
- Thorpe, J. E. (1994). Salmonid fishes and the estuarine environment. *Estuaries* **17**, 76–93.
- Titus, R. G. & Mosegaard, H. (1989). Smolting at age 1 and its adaptive significance for migratory trout, *Salmo trutta* L., in a small Baltic-coast stream. *Journal of Fish Biology* **35**(Suppl. A), 351–353.
- Tzeng, W. N. (1996). Effects of salinity and ontogenetic movements on strontium:calcium ratios in the otoliths of the Japanese eel, *Anguilla japonica*. *Journal of Experimental Marine Biology and Ecology* **199**, 111–122.
- Ugedal, O., Finstad, B., Damsgard, B. & Mortensen, A. (1998). Seawater tolerance and downstream migration in hatchery-reared and wild brown trout. *Aquaculture* **168**, 395–405.
- Volk, E. C., Blakley, A., Schroder, S. L. & Kuehner, S. M. (2000). Otolith chemistry reflects migratory characteristics of Pacific salmonids: Using otolith core chemistry to distinguish maternal associations with sea and freshwaters. *Fisheries Research* **46**, 251–266.