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DETERMINANTS OF GEOGRAPHICAL VARIATION IN THE AGE OF SEAWARD-MIGRATING SALMON, *SALMO SALAR*

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SUMMARY

(1) Using data from 182 rivers throughout the geographical range of the Atlant salmon, *Salmo salar*, we tested the hypothesis that the time taken to reach the migrato smolt stage of the life-cycle was dependent on feeding and growth opportunities, and the in turn were dependent on temperature and daylength (since salmon feed only in daylight

(2) The mean age of smolts in a river was positively and strongly correlated with latitud when considering west and east Atlantic populations separately. There were significa differences, however, between the Canadian and European rivers, such that when the da were combined, latitude explained only 6·1% of the variation in age of smolts.

(3) However, over 82% of the variation in smolt ages in the same data set was explain by an index of growth opportunity, which took account of annual changes in bo temperature and daylength. Thus the mean age of smolts, while varying fivefold over t 40° latitudinal range of the species, could be predicted relatively accurately from annu temperature and photoperiod records.

INTRODUCTION

The eggs of Atlantic salmon (*Salmo salar* L.) are laid in the beds of freshwater streams, a the young fish (parr) remain in these streams until they reach the migratory smolt phas The smolts then migrate downstream to the sea in the late spring. Within a river syste there is variability in the age at which the parr metamorphose into smolts, with common two or three age-classes undertaking the smolt migration each year. However, t variation in the age of smolts within rivers is less than that between rivers. It has long be recognized that a crude relationship exists between the latitude of a river and the mean a of its smolts: the further north the river, the older the age at smolting (e.g. Dahl 1910; All 1941; Jones 1959; Symons 1979; Power 1981). Similar correlations have been found in s trout *Salmo trutta* L. (Fahy 1978; L'Abee-Lund *et al.* 1989). It has been assumed that the relationships are due to temperature (Jones 1959). Symons (1979) found a negati correlation between the length of the growing season (taken as the number of days per ye when the water temperature exceeded 7 °C) and mean smolt age for a small sample of sev rivers across the geographical range of the salmon, while Power (1981) demonstrated similar relationship for a larger number of Canadian rivers. This critical temperature w chosen because young salmon reduced or ceased feeding at 7 °C (Allen 1940; Saunders Henderson 1969). However, Higgins & Talbot (1985) have shown that at any giv temperature, food intake and turnover rates are higher when daylengths are increasi than when they are decreasing. A similar negative correlation between growing season a smolt age has recently been found in Norwegian sea trout (L'Abee-Lund *et al.* 1989).

Recent experiments in controlled laboratory conditions have revealed mu
environmental influences on developmental rates in juvenile salmon (Thorp
now know that the physiological decision of whether or not to migrate in a gi
made some 9 months beforehand: after this time fish that will smolt have hig
than those that will defer migration for a further year (Metcalfe, Huntingfo
1986, 1988), leading to the development of a bimodal size distribution (Th

Dominant fish have a higher probability of being amongst the early migrat
do subordinates of similar initial size (Metcalfe *et al.* 1989). However, n
experiments have shown that the overall proportion of fish in a populatio
early is dependent on growth conditions up to the summer decision point: t
conditions, the greater the percentage of early-migrating fish (Thorpe *et al.* 19
parr do not feed in darkness (Higgins & Talbot 1985), and therefore growt
dependent on temperature: daylength can also limit maximum growth rat
experimental shift in the annual photoperiodic cycle, such that high water t
coincide with short (rather than long) days, results in a lowered growth rate a
proportion of early-migrating fish (Thorpe *et al.* 1989). In a series of such n
experiments, these authors showed that an index of growth opportunity in
summer (which took account of both temperature and daylength) was a hig
predictor of the proportion of fish that smolted after only 1 year unde
conditions.

We now extend this approach to field data, to examine the extent to which
and daylength can be used to predict the age of smolt migration of Atlantic salm
over the entire geographical range of the species (given by MacCrimmon &

METHODS

Data on the mean age of migrating smolts in a river were obtained from t
literature for rivers throughout the range of the Atlantic salmon, from 43
from 72°W to 52°E; details of the data set are given in Appendix 1. The rivers
into three broad geographical regions: the eastern Atlantic coast of Cana
Europe (from Spain to Norway, and including Iceland) and eastern Europe (
rivers draining into the Baltic and the White Sea). We determined the lati
river, or in the case of long rivers, the latitude of the upper reaches sinc
presumed to contain the salmon populations.

The maximum growth rate of salmon is assumed to be limited by a combi
temperature and the daylight hours available for feeding. An index of an
opportunity (*G*) for each river was calculated as:

$$G=\Sigma T_i \cdot D_i$$

where T_i is the mean air temperature in excess of 5·5 °C in month i, and D_i is
daylight in month i. Mean monthly air temperatures were obtained from Cha
Canadian rivers) and Steinhauser (1970; European rivers). It would have been
use water temperatures, but these data were not available for the majori
Therefore, air temperatures have been used as the best (and most s
approximation; these tend to be highly correlated with average water tem
salmonid streams (e.g. Elliott 1984). Although the actual temperature at whi
salmonids ceases varies slightly according to acclimation temperature (Ellio
may show some variation between salmon stocks, as a compromise we ha

value of 5·5 °C as the lower temperature limit to growth, as used by Power (1981). The ho of daylight each month were calculated as the duration of daylight (including civil twilig at that latitude on the 15th of each month multiplied by the number of days in that mont

Data were obtained for fifty-two Canadian, 101 western European and twenty-ni eastern European rivers in total.

RESULTS

The mean age at which salmon smolts migrated to sea was strongly correlated w latitude within each of the three geographical areas (Canada, western and east Europe), with salmon in rivers further north taking longer to reach the smolt st (Fig. 1a–c). However, when the three groups were combined into a single data set, resulting correlation was poor and explained only 6·1% of the variation in mean smolt

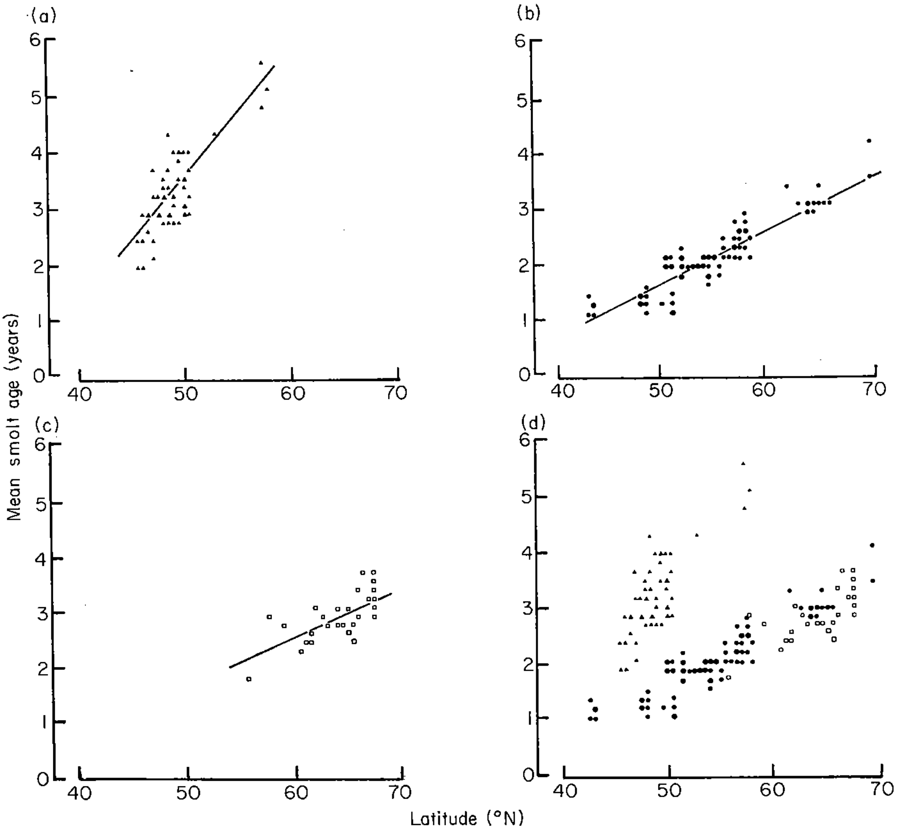

FIG. 1. The relationship between the latitude of a river and the mean age of migrating smolts in different geographical areas. Larger symbols signify superimposed data points. (a) Canada ($Y=bX-a$ where b ($\pm$S.E.)$=0{\cdot}225\pm0{\cdot}023$, $a=7{\cdot}749\pm1{\cdot}135$; $n=52$, $r^2=0{\cdot}659$, $P<0{\cdot}001$). (b) Western Europe ($b=0{\cdot}097\pm0{\cdot}004$, $a=3{\cdot}195\pm0{\cdot}229$; $n=101$, $r^2=0{\cdot}846$, $P<0{\cdot}001$. (c) Eastern Europe ($b=0{\cdot}084\pm0{\cdot}020$, $a=2{\cdot}620\pm1{\cdot}325$; $n=29$, $r^2=0{\cdot}388$, $P<0{\cdot}001$). (d) All rivers combined ($n=182$, $r^2=0{\cdot}061$).

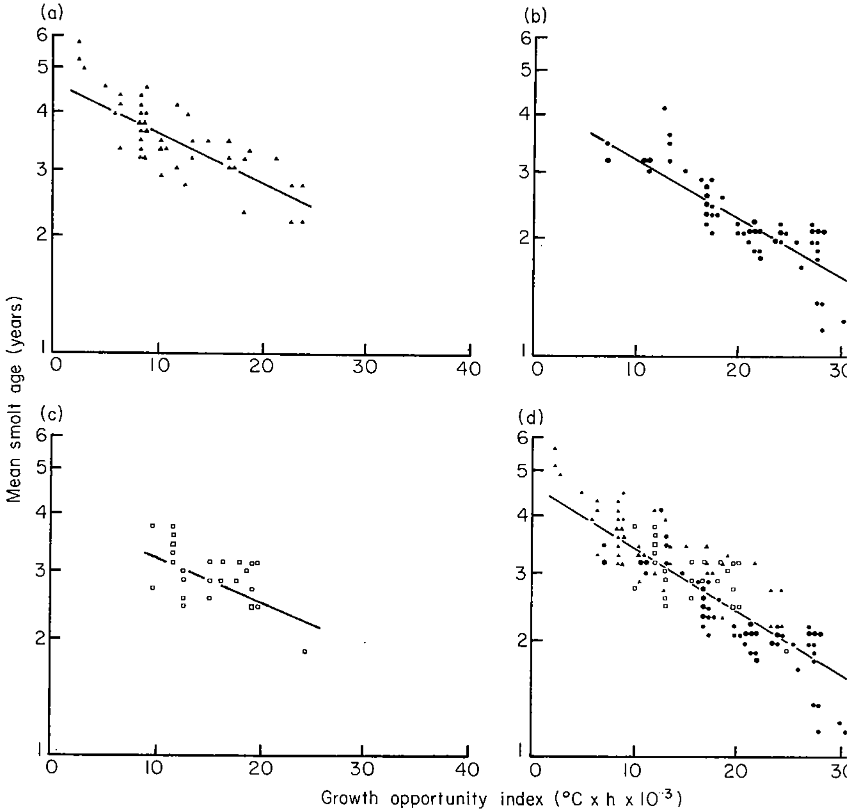

FIG. 2. The relationship between the index of growth opportunity and the natural logarit
mean age of migrating smolts in rivers in different geographical areas. Larger symbols
superimposed data points. (a) Canada ($Y=bX+a$ where a ($\pm$S.E.)$=1{\cdot}548\pm$
$b=-0{\cdot}0291\pm0{\cdot}0034$; $n=52$, $r^2=0{\cdot}591$, $P<0{\cdot}001$). (b) Western Europe ($a=1{\cdot}503\pm$
$b=-0{\cdot}0365\pm0{\cdot}0018$; $n=101$, $r^2=0{\cdot}810$, $P<0{\cdot}001$). (c) Eastern Europe ($a=1{\cdot}424\pm$
$b=-0{\cdot}0252\pm0{\cdot}0059$; $n=29$, $r^2=0{\cdot}403$, $P<0{\cdot}001$). (d) All rivers combined ($a=1{\cdot}612\pm$
$b=-0{\cdot}0397\pm0{\cdot}0014$; $n=182$, $r^2=0{\cdot}823$, $P<0{\cdot}001$).

(Fig. 1d). A comparison of the regression lines corresponding to the three ge
areas revealed highly significant differences in regression slopes (Covarianc
$F_{2,176}=27{\cdot}13$, $P<0{\cdot}0001$); salmon from Canadian rivers undertook the smolt n
a much older age than European fish at the same latitude.

When the same data on mean smolt ages were plotted against the index
growth opportunity G, significant correlations were again obtained w
geographical region (Fig. 2a–c). Furthermore, combining the data into
resulted this time in a highly significant correlation that explained 82·3% of tl
in mean smolt age (Fig. 2d). There is no apparent difference between
geographical areas in the form of the relationship, although a covariance a
revealed a marginally significant difference in regression line slopes (F
$P=0{\cdot}044$).

DISCUSSION

The older age of smolts at a given latitude in North America compared with Europe clearly influenced by temperature; the North Atlantic Drift produces a much warm climate on the eastern coast of the Atlantic than on the west. However, daylength has additional effect, since European rivers will be further north than the correspondi Canadian rivers that experience the same temperature regime; they will therefore ha much longer daylengths during the warmest part of the year, so allowing the fish to fe more. This difference may be appreciable: the Ste Marguerite river in Canada and t Simojoki in Finland both experience monthly mean temperatures of 15·5 °C in July, b the daylength during this warmest month at the Simojoki is 38% longer (24 h compared 17·4 h).

Combining both temperature and daylength variations into a single index of grow opportunity produces a highly significant predictor of average age of smolt migrati throughout the geographical range of the salmon. The strength of the correlation perhaps surprising, given the relatively crude temperature measurements and the fact th it was not possible to take into account variations in stream productivity. Moreover, t index of growth opportunity is somewhat simplistic in assuming that growth ra correlate positively with temperature, since the relationship is actually more of parabola, growth declining as the upper lethal limit is approached (Elliott 1982). It likely that some of the more southerly populations experience summer temperatu above the optimum for maximal growth; however, it is difficult to correct for this beca (i) the temperature that maximizes growth in salmonids varies both with food availabil and acclimation temperature, and (ii) the temperature–growth relationships have not been determined precisely for this species (Elliott 1982). We have therefore been forced ignore this factor; no doubt some of the remaining variation in smolt ages would explained if the index of growth opportunity took into account both river productiv and optimal temperatures for growth.

Statistically significant differences in smolt ages between the three geographical ar remain even when using the index of growth opportunity. The same temperature a daylength regime that produces a mean smolt age of 3·00 in western Europe wo produce mean smolt ages of 3·14 in eastern Europe and 3·41 in Canada. While differences are small, they may be a result of not taking into account the fact mentioned above; they may also arise from genetic variability between the population different areas.

It is unclear whether salmon stocks from cold environments are genetically bet adapted to growing at low temperatures. Jensen & Johnsen (1986) suggested that this the case, although their evidence was a negative correlation between the length of growing season in a river (taken as number of days per year above 7 °C) and the me number of such 'growth days' required to produce a smolt. This measure of gro opportunity does not control for variations in temperature above 7 °C, nor for differen in daylength. The analyses presented here suggest no adaptation, since it is the logarit of smolt age that is linearly related to the index of growth opportunity (Fig. 2); thus, relationship with temperature is not simply additive and fish in cold rivers tak disproportionately long time to reach the smolt stage. Previous studies have dem strated heritable differences between salmonid stocks in characters such as parr b morphology, developmental timing and behaviour that appear to be adaptations to lo environments (e.g. Riddell & Leggett 1981; Riddell, Leggett & Saunders 1981; Strut

& Stewart 1986; Taylor 1988; Thorpe 1989). Juvenile growth rates of diffe under controlled conditions also show some variation (e.g. Naevdal *et al.* 1979 *al.* 1987); whether such variation is adaptive remains to be seen.

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APPENDIX

Details of rivers used in the analysis, arranged within each country in order of latitude.

Canada

Pol (Bagliniere & Champigneulle 1986)
Big Salmon (Bagliniere & Champigneulle 1986)
Morell (Bagliniere & Champigneulle 1986)
Miramichi (Bagliniere & Champigneulle 1986)
Cains (Chadwick, Randall & Leger 1986)
Branch (Chadwick, Randall & Leger 1986)
Renews (Chadwick, Randall & Leger 1986)
Salmonier (Chadwick, Randall & Leger 1986)
Little Codroy (Power 1981)
Grandy's (Chadwick, Randall & Leger 1986)
Terrenceville (Chadwick, Randall & Leger 1986)
Kedgwick (Chadwick, Randall & Leger 1986)
Patapedia (Bagliniere & Champigneulle 1986)
Robinson's (Chadwick, Randall & Leger 1986)
Ste Marguerite N. E. (Bielak & Power 1986)
Ste Marguerite (Bielak & Power 1986)
Grand Cascapedia (Power 1981)
Terra Nova (Dempson, Myers & Reddin 1986)
Gander (Power 1981)
Harry's (Chadwick, Randall & Leger 1986)
S.W. Brook (Power 1981)
Gambo (Chadwick, Randall & Leger 1986)
Wings Brook (Hutchings 1986)
Laval (Bielak & Power 1986)
Humber (Power 1981)
Indian Bay (Chadwick, Randall & Leger 1986)
Exploits (Dempson, Myers & Reddin 1986)
Mistassini (Bielak & Power 1986)
Campbellton (Chadwick, Randall & Leger 1986)
Godbout (Bielak & Power 1986)
Jupiter (Power 1981)
Sops Arm (Chadwick, Randall & Leger 1986)
Pigou (Randall & Power 1979)
Natashquan (Bielak & Power 1986)
Nabisipi (Bielak & Power 1986)
Olomane (Bielak & Power 1986)
Corneille (Power 1981)
Mingan (Bielak & Power 1986)
St Jean (Bielak & Power 1986)
Etamamiou (Bielak & Power 1986)
Romaine (Bielak & Power 1986)
Matamek (Bagliniere & Champigneulle 1986)
River of Ponds (Chadwick, Randall & Leger 1986)
Moisie (Power 1981)
Bouleau (Randall & Power 1979)
Gros Mecatina (Bielak & Power 1986)
W. Arm Brook (Evans, Rice & Chadwick 1984)
St Genevieve (Chadwick, Randall & Leger 1986)
Sandhill (Power 1981)
George (Symons 1979)
Koksoak (Power 1981)
Leaf (Lee & Power 1976)

Western Europe

Spain

Sella (Martin Ventura 1987)
Esva (Martin Ventura 1987)

France

Gave D'Oloron (Bousquet & Marty 19
Nive (Bousquet & Marty 1987)
Adour (Symons 1979)
Scorff (Bagliniere & Champigneulle 198
Blavet (Fontenelle *et al.* 1980)
Elle (Bagliniere *et al.* 1987)
Steir, Odet & Jet (Fontenelle *et al.* 1980
Aulne (Bagliniere *et al.* 1987)
Elorn (Bagliniere *et al.* 1987)
Leguer (Bagliniere *et al.* 1987)
See and Selune (Bagliniere *et al.* 1987)
Bresle (Fournel, Euzenat & Fagard 198
Meuse (Philippart 1987)

Great Britain

Lynher (Anon. 1971–72)
Fowey (Anon. 1971–72)
Tamar (Anon. 1971–72)
Tavy (Anon. 1971–72)
Camel (Anon. 1971–72)
Hampshire Avon (Berry 1935)
Torridge (Jonas 1921–25)
Axe (Anon. 1970–74)
Taw (Jonas 1921–25)
Test (Anon. 1967–71)
Itchen (Anon. 1967–71)
Usk (Anon. 1966–74)
Wye (Hutton 1913–41)
Cheshire Dee (Jones 1953)
Hodder (Stewart 1960, 1961)
Wyre (Stewart 1960, 1961)
Ribble (Stewart 1960, 1961)
Cumb. Derwent (Jones 1953)
Solway Dee (MacFarlane 1931)
Tyne (Storrow 1930)
Solway Nith (MacFarlane 1938)
Tweed (MacFarlane 1933)
Forth (Menzies 1923)
Tummel (Thorpe 1977)
Almond (Thorpe 1977)
Tay (MacFarlane 1934a)
North Esk (Thorpe 1977)
Loch Shiel (Nall 1928b)
Girnock Burn (Thorpe 1977)
Aberdeen Dee (Menzies 1923)
Aberdeen Don (Menzies 1923)

Findhorn (Menzies 1923)
Spey (Menzies 1923)
Balgy (Nall 1928b)
Conon (Menzies 1928)
Ewe (Nall 1932)
Ullapool (Nall 1928a)
N. Harris (MacFarlane 1934b)
Morsgail (Nall 1932)
Grimersta (Menzies 1927)
Laxdale (Nall 1932)
Uig (Nall 1932)
Hope (Nall 1927)
Thurso (Allen 1944)

Ireland

Waterville (Went & Barker 1943)
Inny (Went 1948)
Bandon (Went 1947)
Lee (Went 1947)
Laune (Went 1947)
Blackwater (Went 1947)
Feale (Went 1947)
Liffey (Frost & Went 1940)
Corrib (Went 1947)
Shannon (Went 1939)
Burrishoole (Piggins 1959)
Owenduff (Went 1941b)
Moy (Went 1947)
Owenmore (Cummins 1963)
Ballisodare (Went 1941a)
Sligo (Went 1947)
Drumcliffe (O'Driscoll 1950)
Erne (Went 1942)
Boyne (Went 1947)
Finn (Went 1972)
Foyle (Went 1972)
Roe (Went 1972)
Bush (Vickers 1977–1979)

Sweden

Hogvadsen (Symons 1979)

Norway

Christiansand (Dahl 1910)
Strynselva (Jensen & Johnsen 1986)

Trondelagen (Dahl 1910)
Alta (Heggberget *et al.* 1986)
Burgoynes (Dahl 1910)

Iceland

Sog (Gudjonsson 1978)
Olfusa-Hvita (Gudjonsson 1978)
Ellidaar (Gudjonsson 1978)
Laxa, Kjos (Gudjonsson 1978)
Grimsa (Gudjonsson 1978)
Thvera (Gudjonsson 1978)
Nordura (Gudjonsson 1978)
Midfjardara (Gudjonsson 1978)
Vididalsa (Gudjonsson 1978)
Laxa, Adaldalur (Gudjonsson 1978)

Eastern Europe

Sweden

Ricklean (Osterdahl 1964)
Kalix Alv (Karlstrom 1977)

Finland

Simojoki (Toivonen & Jutila 1982)

Soviet Union

Daugava (Lischev & Rimsh 1961)
Luga (Kuchina 1939)
Neva (Svetovidova 1935a)
Vodla (Smirnov 1971)
Shuya (Smirnov 1971)
Pyalma (Smirnov 1971)
Severnaya Dvina (Lebedev & Chzhen Chzhen-Dy 1963)
Vyg (Gorskiyi 1935)
Pinega (Smirnov 1935)
Kem (Kazakov 1982)
Mezen (Danilchenko 1935)
Chapoma (Melnikova 1970)
Soyana (Kuchina 1935)
Varzuga (Melnikova 1959)
Strelna (Melnikova 1970)
Umba (Melnikova 1970)
Kolvitsa (Azbelev & Lagunov 1960)
Ponoyi (Svetovidova 1935b)
Iokanga (Azbelev 1967)
Tuloma (Azbelev 1967)
Voronya (Kuchina 1935)
Teriberka (Berg 1935)
Titovka (Azbelev 1967)
Kola (Melnikova 1959)
Pechenga (Azbelev 1967)
Zapdnaya Litsa (Azbelev 1967)