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RELATIONSHIPS BETWEEN TEMPERATURE, POPULATION DENSITY AND GROWTH IN A SEATROUT POPULATION (*S. TRUTTA* L.) OF THE KERGUELEN ISLANDS (TAAF)

by

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ABSTRACT

Brown trout was introduced in the Kerguelen Islands (subantarctica) in 1958. Since then, acclimatized populations colonized adjoining rivers and differentiated themselves into migratory and sedentary forms in lakes or in the sea.

In the Kerguelen rivers, virgin of indigenous fish and characterized by an elementary structure, relationships between environmental factors and trout population parameters are more direct and thus easier to demonstrate.

The sea trout population of the Baie Norvegienne (S.W. Kerguelen) has been sampled for eighteen years. Annual growth increments in the river and in the sea were backcalculated and validated ; population densities were determined by electrofishing inventories in test areas representative of the different biotas ; mean annual temperatures were obtained from the recordings of the meteorological station at Port-aux-Français close to the study area.

Examination of correlations with growth showed a highly significant effect of temperature for the age groups first year in the river and first and second year at sea that were not submitted to a strong spatial competition ; and no effect of temperature among age groups second and third year in the river for which favourable areas and feeding resources were less abundant due to a highly significant increase in population density.

I - INTRODUCTION

"Although readily observed and easily measured, growth is one of the more complex activities of the organism" (Brett, 1979).

The relationship between growth and environmental factors implies to take into account food consumption and therefore any abiotic factor is necessarily involved in interactions between growth and a powerful biotic factor (Brett, 1979). Consequently, it is very difficult to establish a quantitative relationship between growth and environmental factors in natural fish populations, as opposed to experiments in controled conditions.

It appears clearly that the simpler the environment of a population, the better the understanding of the influence of environmental factors on the growth of a cohort. As far as brown trout is concerned, such a simplified type of environment exists in the Kerguelen subantarctic Islands, where acclimatized populations have developped since 34 years ago in small rivers virgin of other fish species and of macroinvertebrates (Davaine and Beall, 1982 a). During a long term study on population dynamics of migratory and sedentary trout, a clear change in the size of certain age groups became evident and led us to seek the causes of this evolution among the factors which varied in a continuous fashion. During the 24-year study period, mean annual temperature increased regularly at the same time as fish densities in a developping population.

II - MATERIAL AND METHODS

2.1 Environmental conditions

The Kerguelen Islands (6 500 km^2) are located slightly to the South of the Antarctic convergence which bounds the Antarctic Ocean. The violent westerly winds impose a cold temperate climate with regular precipitations. The short torrentuous rivers flow over a basaltic layer or glacial alluvia and form sequences of long riffles cut by rapids and pools. Each habitat type is very homogenous and comparable between rivers. Aquatic vegetation is reduced to a few briophytes and filamentous algae in summer. Trees and shrubs are absent.

The two study streams, Rivière du Château and Rivière Norvégienne (Fig. 1) as well as the shallow (1-5 m deep) bay in which they empty, are close to the permanent station of Port-aux-Français (Fig. 1). Fresh and salt water temperature variations are closely related to air temperature. Correlation between mean monthly air temperatures recorded at the meteorological station in Port-aux-Français and mean montly water temperatures in the Rivière Norvégienne is highly significant (r = 0.95). Because of this, we used in this study mean annual air temperatures in Port-aux-Français which insure homogenous values for long time series. Because of the season inversion with respect to the Northern hemisphere, and the need to account for the whole summer growing season between two winter growth stops, the annual mean is calculated from 1 July to 30 June.

2.2 Fish populations

2.2.1 Origin

Brown trout from the Baie Norvégienne rivers come from the introduction of a single stock from the Basque country (France). Twenty-4 year old individuals were released in the Rivière du Château in 1962 (Davaine and Beall, 1982 a). As early as the first generation, trout migrated to the sea and some fish colonized the 2 neighboring streams, Rivière Norvégienne and Rivière des Albatros. Thereafter, sedentary and migratory subpopulations developped in each river of the Baie Norvégienne. A population dynamics study showed that sea trout wintered systematically in fresh water, but did not "home" in the generally accepted sense (Thomas *et al.*, 1981 ; Davaine and Beall, 1982 b). A population genetics study showed no differences between the migrant and sedentary forms (Guyomard *et al.*, 1984). Thus, it is possible to consider the sea trout from the Baie Norvégienne as an homogenous, constantly mixed population. The rivers are juvenile rearing areas and allow the production of the sedentary fraction.

2.2.2 Population inventories

The River Norvegienne, because of its smaller size, was selected for intensive population dynamics investigations. It was divided into sections and subsections, the latter being representative of an homogenous habitat type (pool, riffle ...) as determined by a precise topographic and morphological mapping. Every year from 1973 to 1982, about 50 % of the total surface area of rapids and riffles, where most of the trout in their first two years can be found, and 100 % of the pools, where older fish gather preferentially, were sampled by electrofishing. The population density variations by habitat type determined on the Rivière Norvégienne were considered to be representative of that in the Rivière du Château, because of the physical homogeneity of these two rivers, of the annual mixing of the sea trout population, and of the apparent stability of their distribution in relation to the relative size of these two streams (Thomas *et al.*, 1981).

2.2.3 Study of growth

From 1970 to 1987, 2 477 sea trout were sampled. Age and brood year were determined by scale reading. Age determinations were validated with known-age fish (Beall and Davaine, 1982, 1988). Fish with a smolt age of 1 and 4 or more were few and thus were eliminated, as well as some very old trout when age could not be ascertained precisely. Sample size for this study and the back-calculation of growth was 2 179 trout, with 1 212 2-year smolts and 967 3-year smolts.

The model used for back-calculation (Beall *et al.*, 1991) took into account allometry differences between the freshwater and the marine growth. It gave the best fit to the data while fullfilling the condition of use of linear regression. It was preferred to the Dahl-Lee model, which is more correct from a mathematical point of view as noted by Françis (1990), but gave biased underestimates of length at the first and second winter (30 and 8 %, respectively). A possible bias in back-calculated lengths caused by the Lee phenomenon could be ignored because all cohorts were represented by fish of each age group. Correspondance between the back-calculated size distribution of trout at 1-and 2-year with the lengths observed during winter sampling in the River Norvegienne testified to the fiability of the model.

III - RESULTS

3.1 Evidence for a year effect

Analysis of back calculated length at different ages (Fig. 2 and 3) for 2-and 3-year smolts from the 1963 to 1982 brood years showed that size at age 1 and 2 and at sea migration of 2-year smolts varied little with time, whereas size at age 3 and at sea migration of 3-year smolts decreased notably. On the other hand, size after 1 and mostly 2 summers in the sea seemed to increase significantly. We did not take into account cohorts like 64 and 65, and 82 because samples were too small (n < 10).

If instead of size at a given age, growth at different ages is correlated with brood year (Table 1), the following observations can be made :

3.1.1 In freshwater

- no year effect for the first growth year, whatever the smolt age ;
- no effect for the second year of 2-year smolts ;
- a significant negative effect for the second year of 3-year smolts, which are always smaller at age 2 than trout which smolt as 2+ ;
- a highly significant negative effect for the third year of 3-year smolts.

The results for 3-year smolts are illustrated in figure 4. A strong decrease of the size at sea migration can be noted.

3.1.2 In the sea

- a highly significant positive effect during the first year for 2-and 3-year smolts, for which growth had notably improved ;
- a highly significant positive effect during the second year for 2-and 3-year smolts.

These results are shown in figure 5.

Thus, the year effect is significant in some trout categories. It acts negatively on the river growth of 3-year smolts, and positively on sea growth of all fish.

3.2 Evolution of environmental parameters

3.2.1 Year-temperature relationship

During the study period, mean annual temperature increased significantly (Fig. 6 and Table 1), with cyclical variations of about 5-year periodicity. This warming phase is illustrated by fast melting glaciers and the disappearance of low lying permanent firns.

3.2.2 Year-population density relationship

From 1973 to 1982, population density in all age groups increased significantly in rivers (Fig. 7 and Table 1). This is particularly true for trout younger than two years in the juvenile rearing zones, but also for older fish in pools.

3.3 Growth-temperature relationship

3.3.1 In the river

The table 1 shows the following results :

- a highly significant positive relationship during the first year for 2 year smolts, but none for 3-year smolts ;
- a non significant relationships in the second year for all fish ;
- a nearly significant ($p = 0.06$) negative effect in the third year for 3-year smolts (Fig. 8).

3.3.2 In the sea

Table 1 and figure 9 show a highly significant relationship between growth during the first and second season in the sea and annual temperature for 2-and 3-year smolts.

3.4 River growth-population density relationship

No significant correlation was found between second year growth of 2-and 3-year smolts and 1+ trout juveniles in rearing zones. Likewise, no relationship was observed in the third year for 3-year smolts.

IV - DISCUSSION AND CONCLUSION

During the sampling period, a growth evolution took place in the sea trout from the Baie Norvegienne. Freshwater growth of juveniles tended to remain stable during the first year, then to decrease starting from the second year. This phenomenon was clearly demonstrated for 3-year smolts only. Inversely, sea growth increased notably from the smolt stage to the following winter and during the second stay in the sea, independantly from smolt age. During this time period, mean temperature increased gradually (about 1°C in 23 years), a phenomenon already noted in New Zealand by Salinger (1982), and juvenile population density was multiplied 8 times in 10 years. This steady population increase is a normal phenomenon in the colonization phase. The first trout released in the Rivière du Château spawned at the earliest during the winter of 1962, and some migratory second generation individuals which colonized the Rivière Norvegienne could not have reproduced before the winter of 1966, more probably 1967. When electrofishing inventories started in the Rivière Norvégienne in 1972, the population was only in its second generation and started to augment with the increase in reproductive potential due to larger numbers of spawner, but also to the age and size of sea trout. It should be noted that the river was totally protected from fishing and that some trout may spawn 6-7 times in succession.

The low temperatures (1-5°C) slow down gastric evacuation and the digestion rate which tends toward 0 when temperature is about 0°C (Brett, 1979). The decrease in digestion rate, in conjuncton with the decrease in appetite, appears as the chief limiting factor of food consumption and thus of growth at low temperatures (Brett, 1979) whatever the prey abundance.

When temperature increases towards an optimum (12.8°C for brown trout fed on maximum rations, Elliott, 1975), the maximum meal size increases as well as the digestion rate, and growth rate augments even more rapidly thanks to a better food conversion efficiency (Brett and Higgs, 1970).

In the natural environment, temperature affects numerous other environmental factors, such as secondary production, and prey capturability by an increase of activity rhythms of prey species and trout. Thus, it is safe to assume that, in a fairly stable and homogenous environment such as the littoral kelp beds where food is abundant and sea trout density low, the mean annual temperature increase has a positive influence on marine growth of these trout, independantly from short term adaptative adjustments in behaviour or other factors. This hypothesis is supported by the significant correlation between temperature and sea growth.

In freshwater, this correlation exists only among first year juveniles distributed over extensive shallow riffle zones, where aquatic meïofauna is abundant and adapted to their small size. Moreover, competition with other age groups is negligible. As far as the second and third freshwater years are concerned, an explicative hypothesis would be that positive effects of temperature are masked by the negative effects of intraspecific competition resulting from the concomitant increase in population density. These two factors evolving simultaneously, it would be normal that neither one correlates with parr growth in the second and third year.

The increase in growth differential between 2-and 3-year smolts during the second year could be explained by the facts that the majority of 2-year smolts are the largest in their age group and that, as competitive pressure augments, growth differences between dominant and dominated fish also increase (Brett, 1979). Competition for food increases in second year fish not because they share to some extent the production zones with first year trout, but because they seek larger preys available in the exogenous drift of terrestrial invertebrates (Wojtenka and Van Steenberghe, 1982), aquatic invertebrate macrofauna being absent from the streams.

During the third year, the majority of parr changes habitat and gathers in deeper but also smaller zones where food competition with older sedentary trout becomes fierce. This would explain the strong growth decrease of 3-year smolts in the third year.

Although the precise study of the influence of environmental factors on animal populations can be efficiently conducted in experimental conditions only, it is necessary to regularly confront this knowledge to the real life situation. With this in mind, long term ecological studies, integrating maximum variations in environmental parameters, and taking place in structurally simple ecosystems such as the Kerguelen Islands, could be of real value to understand the complexities of interactions in a natural system.

V - BIBLIOGRAPHY

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Table 1 - Linear correlations between cohort growth and years, temperature and population density

TYPE OF RELATIONSHIP			CORRELATION	PROBABILITY	SIGNIF.
1 - <u>YEAR EFFECT ON GROWTH</u>					
RIVER	1st year	Smolt 2 and 3	. 0.24	0.322	NS
	2nd year	Smolt 2	. 0.37	0.127	NS
		Smolt 3	- 0.55	0.019	S
	3rd year	Smolt 3	- 0.89	< 0.001	HS
SEA	1st year	Smolt 2	+ 0.71	0.001	HS
		Smolt 3	+ 0.83	< 0.001	HS
	2nd year	Smolt 2	+ 0.73	0.001	HS
		Smolt 3	+ 0.85	< 0.001	HS
2 - <u>YEAR EFFECT ON TEMPERATURE</u>			+ 0.75	0.001	HS
3 - <u>YEAR EFFECT ON POPULATION DENSITY</u>					
RIVER	2nd year	(1+ Fish)	+ 0.84	< 0.01	HS
	3rd year	(2+ Fish)	+ 0.63	0.05	(S)
	4th year	(3+ Fish)	+ 0.83	< 0.01	HS
4 - <u>TEMPERATURE EFFECT ON GROWTH</u>					
RIVER	1st year	Smolt 2	+ 0.67	0.002	HS
		Smolt 3	. 0.34	0.165	HS
	2nd year	Smolt 2	. 0.25	0.311	NS
		Smolt 3	. 0.15	0.562	NS
	3rd year	Smolt 3	. 0.37	0.122	NS
SEA	1st year	Smolt 2	+ 0.83	< 0.001	HS
		Smolt 3	+ 0.58	0.009	HS
	2nd year	Smolt 2	+ 0.73	0.001	HS
		Smolt 3	+ 0.66	0.002	HS
5 - <u>POPULATION DENSITY EFFECT ON GROWTH</u>					
RIVER	2nd year	Smolt 2	. 0.47	0.197	NS
		Smolt 3	. 0.08	0.839	NS
	3rd year	Smolt 3	. 0.05	0.896	NS

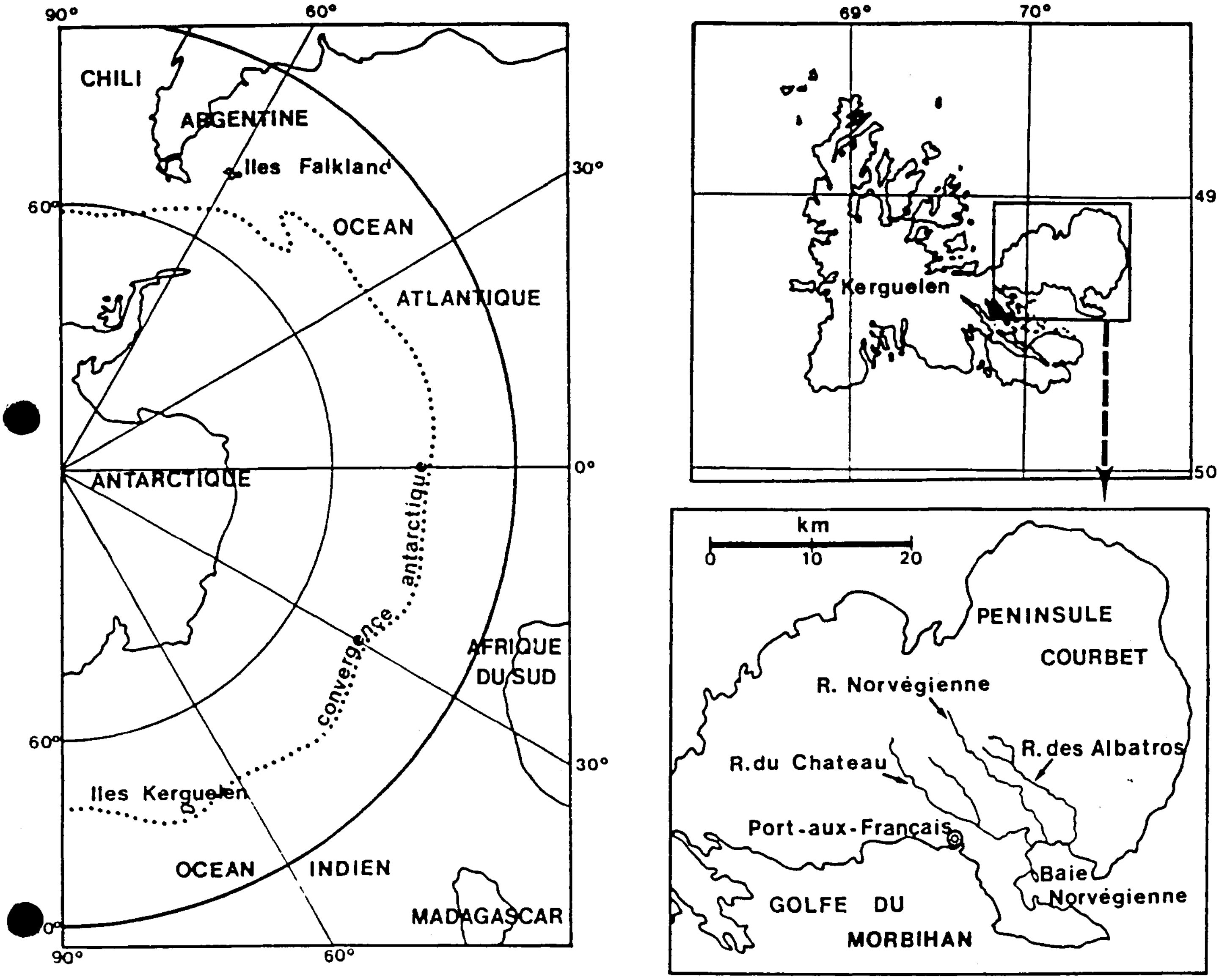

Figure 1 - Geographical situation of the Baie Norvégienne in the Kerguelen Islands (TAAF)

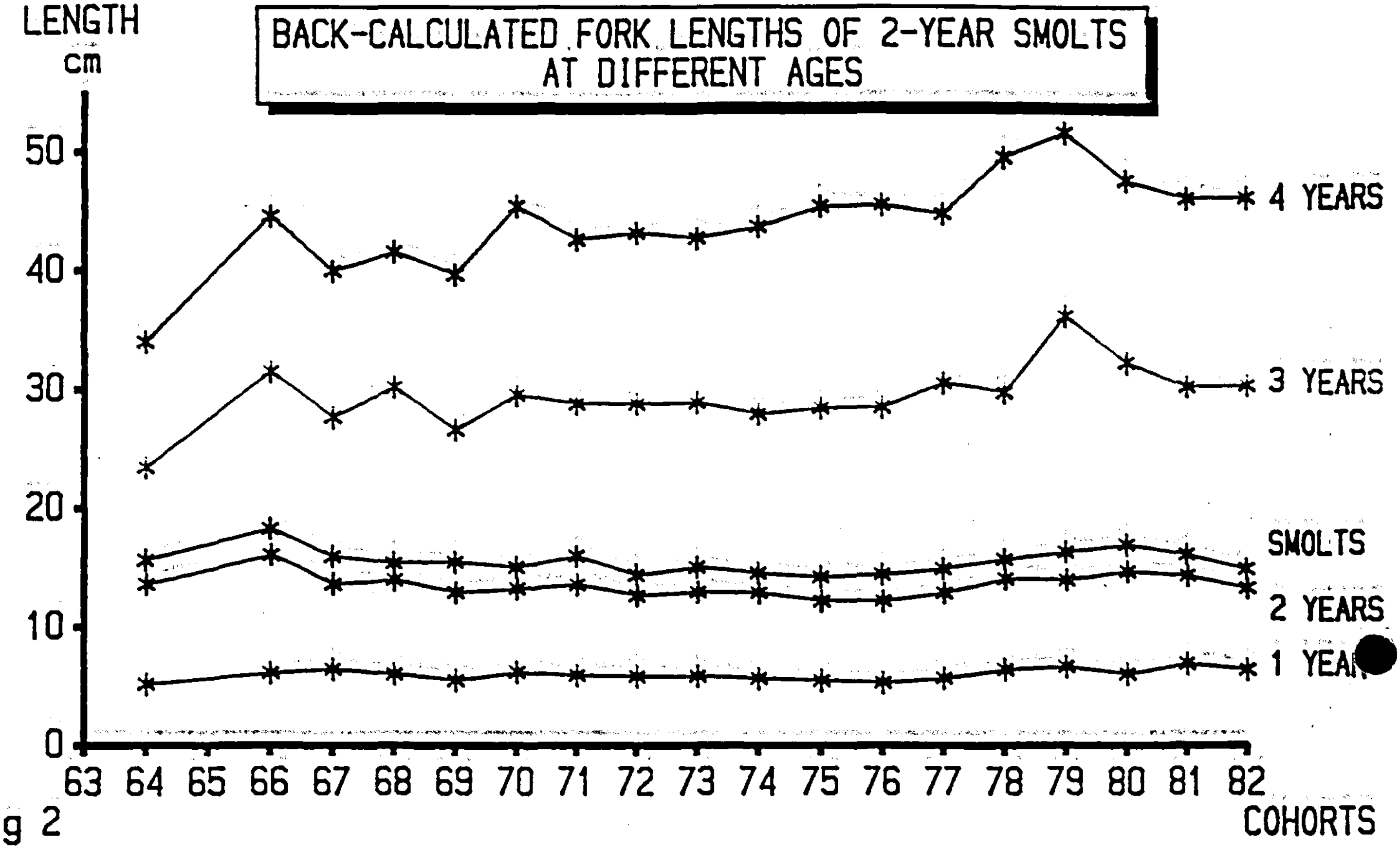
LENGTH cm
BACK-CALCULATED FORK LENGTHS OF 2-YEAR SMOLTS AT DIFFERENT AGES
50
40
30
20
10
0
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
COHORTS
4 YEARS
3 YEARS
SMOLTS
2 YEARS
1 YEAR

Fig 2

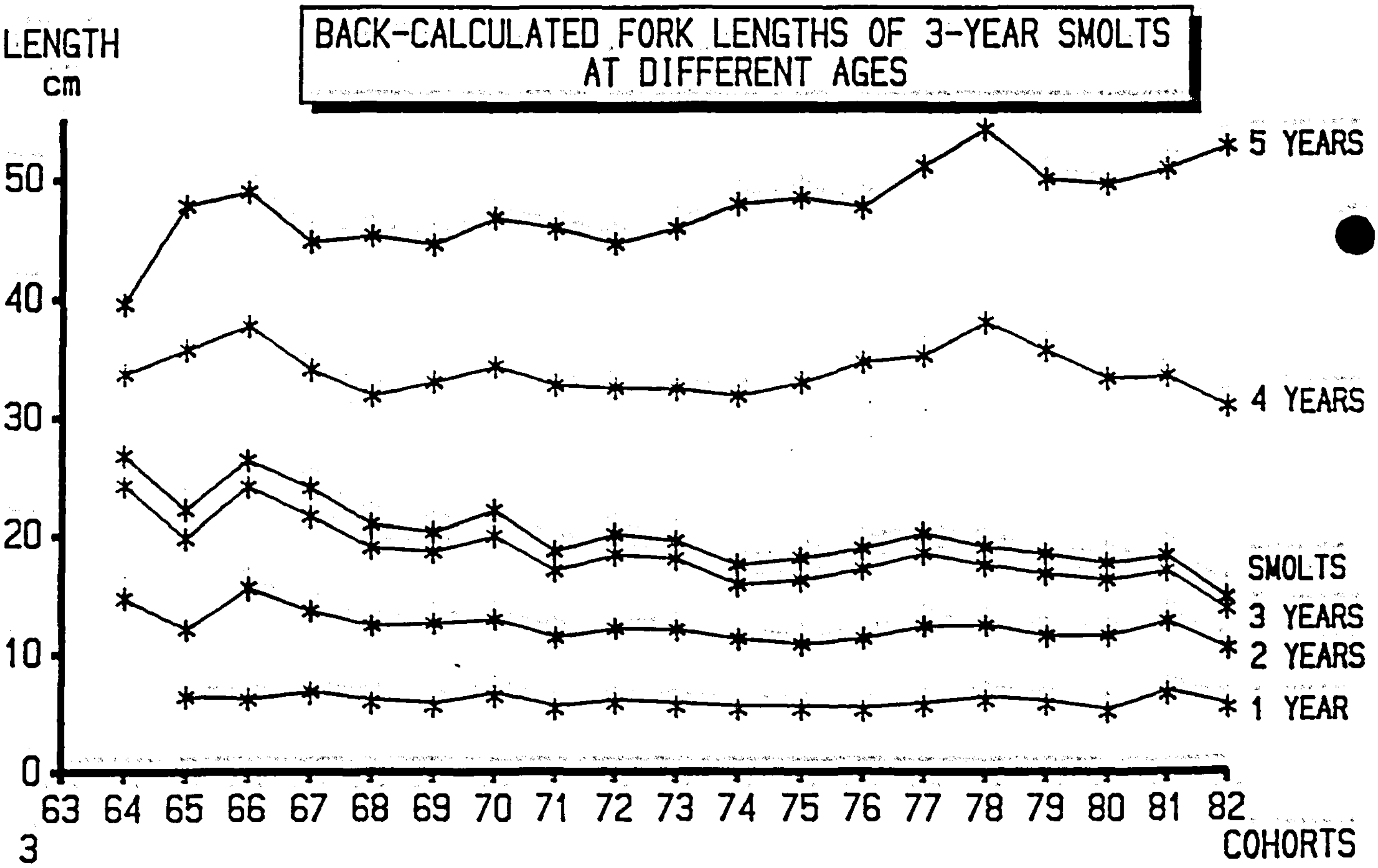
LENGTH cm
BACK-CALCULATED FORK LENGTHS OF 3-YEAR SMOLTS AT DIFFERENT AGES
50
40
30
20
10
0
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
COHORTS
5 YEARS
4 YEARS
SMOLTS
3 YEARS
2 YEARS
1 YEAR

Fig 3

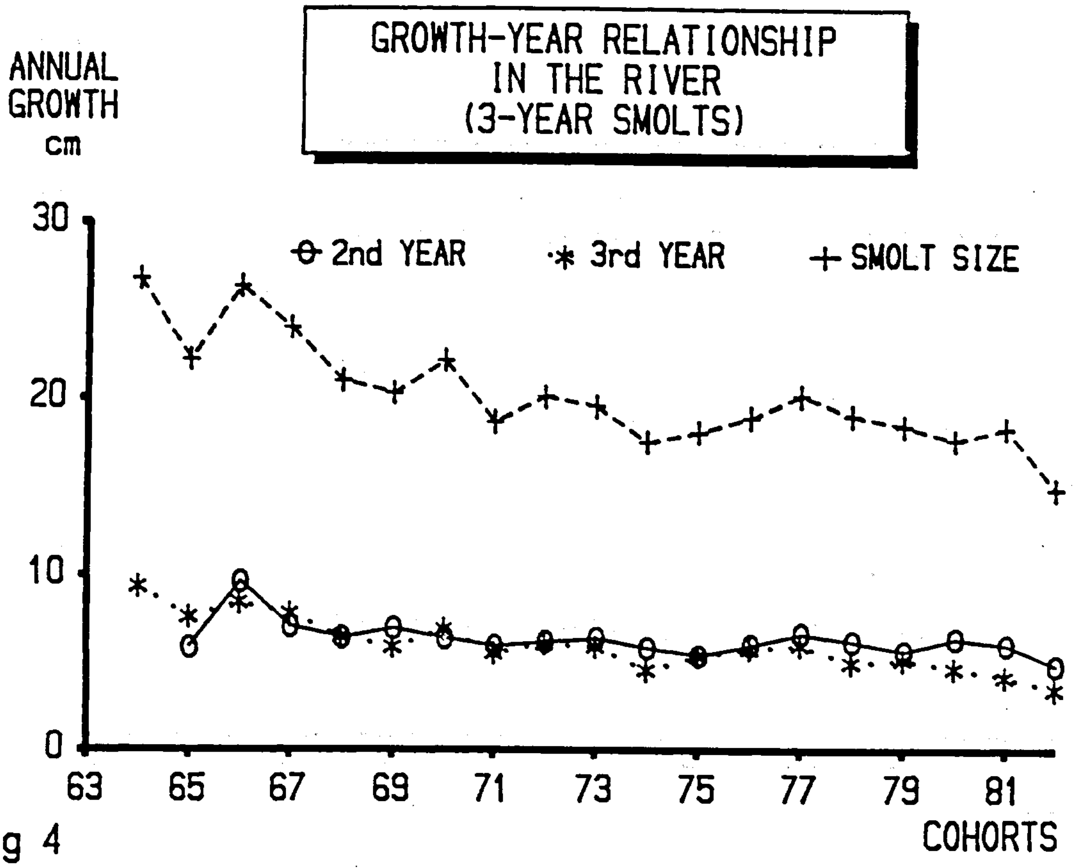
GROWTH-YEAR RELATIONSHIP
IN THE RIVER
(3-YEAR SMOLTS)
ANNUAL GROWTH cm
30
20
10
0
2nd YEAR
3rd YEAR
SMOLT SIZE
63
65
67
69
71
73
75
77
79
81
COHORTS

Fig 4

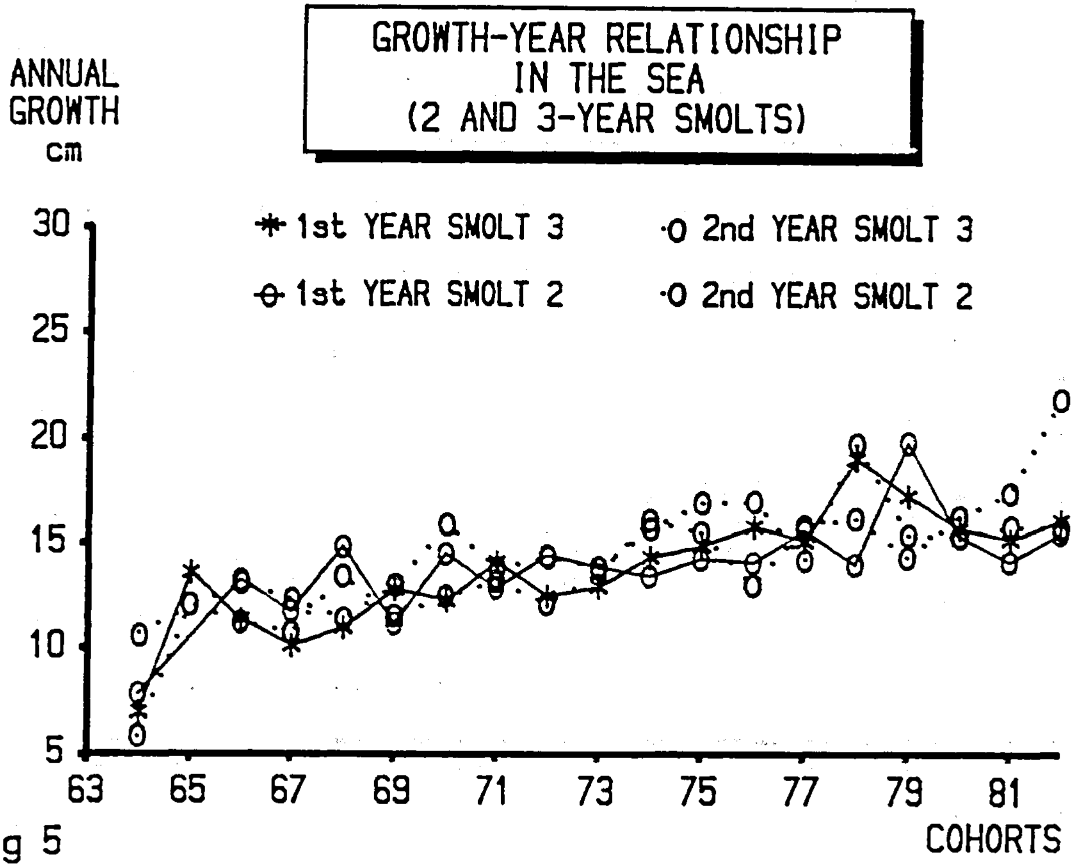
GROWTH-YEAR RELATIONSHIP
IN THE SEA
(2 AND 3-YEAR SMOLTS)
ANNUAL GROWTH cm
30
25
20
15
10
5
1st YEAR SMOLT 3
2nd YEAR SMOLT 3
1st YEAR SMOLT 2
2nd YEAR SMOLT 2
63
65
67
69
71
73
75
77
79
81
COHORTS

Fig 5

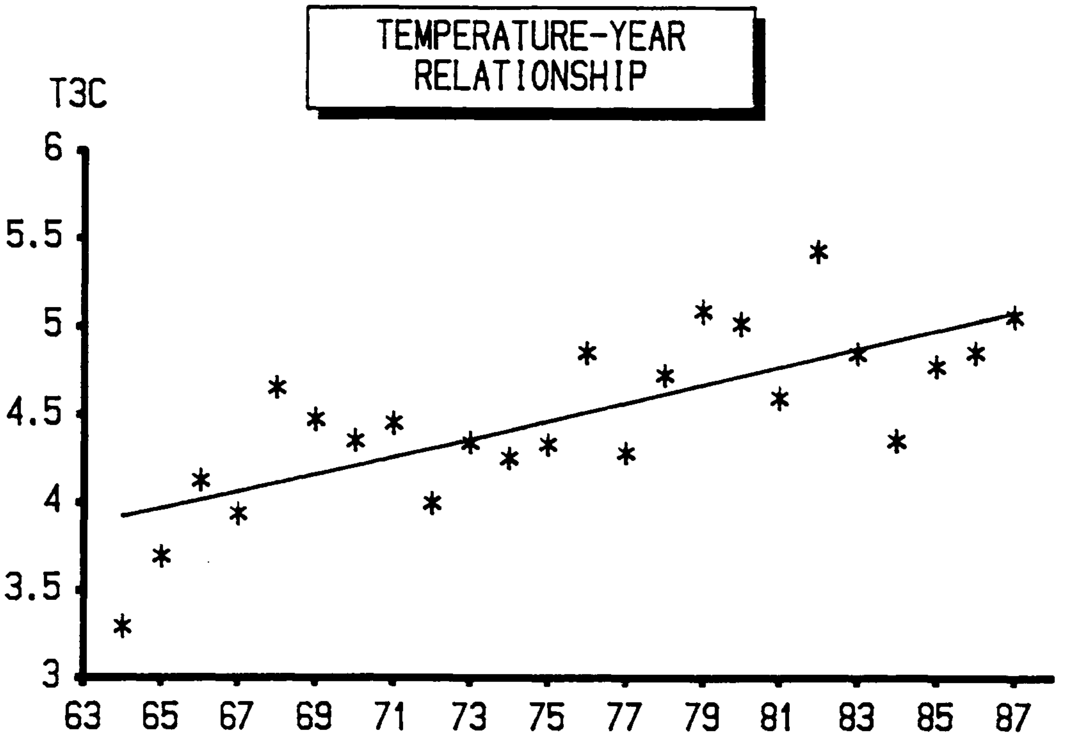
TEMPERATURE-YEAR RELATIONSHIP
T3C
6
5.5
5
4.5
4
3.5
3
63
65
67
69
71
73
75
77
79
81
83
85
87
YEARS

Fig 6

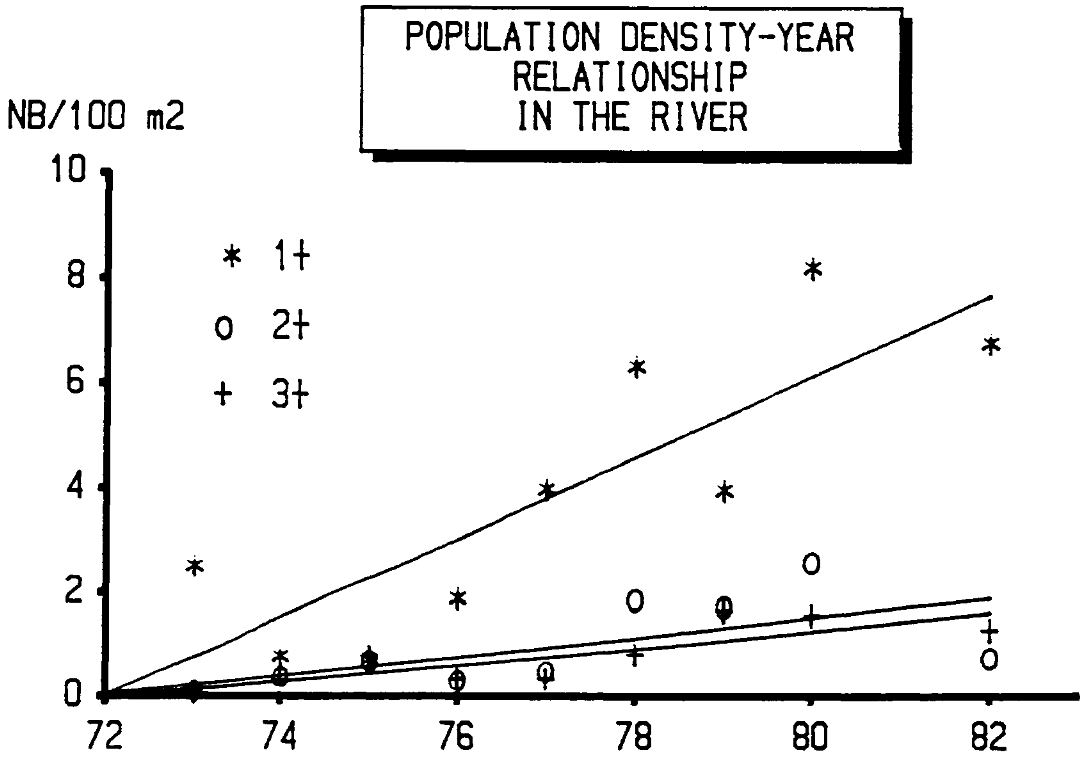
POPULATION DENSITY-YEAR RELATIONSHIP IN THE RIVER
NB/100 m2
10
8
6
4
2
0
* 1+
o 2+
+ 3+
72
74
76
78
80
82
YEARS

Fig 7

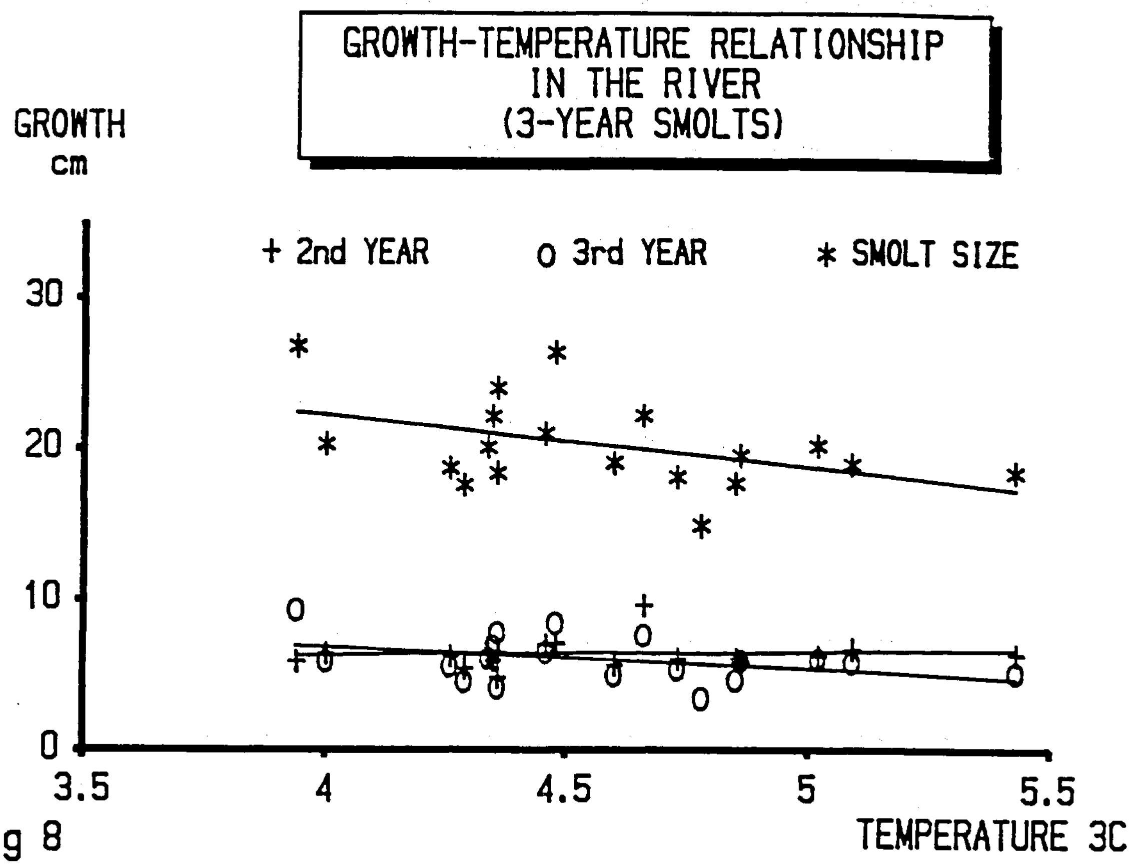
GROWTH-TEMPERATURE RELATIONSHIP
IN THE RIVER
(3-YEAR SMOLTS)
GROWTH
cm
+ 2nd YEAR
o 3rd YEAR
* SMOLT SIZE
30
20
10
0
3.5
4
4.5
5
5.5
TEMPERATURE 3C

Fig 8

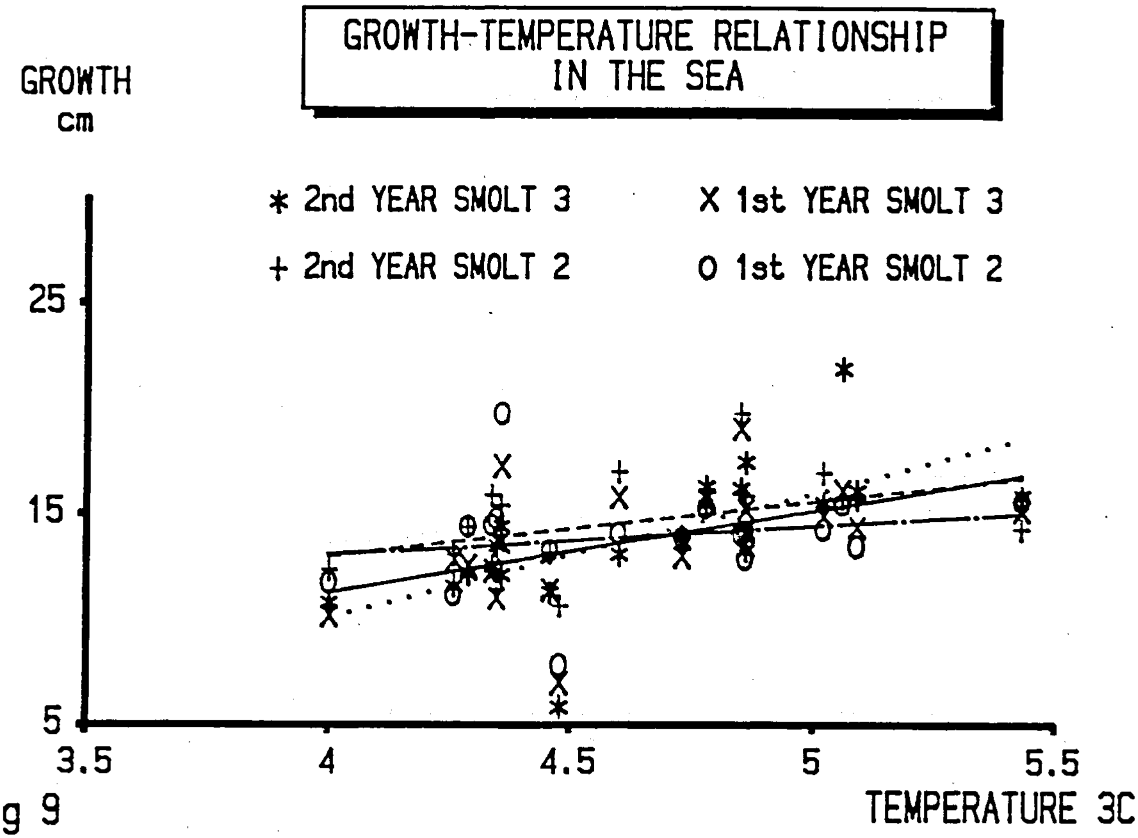
GROWTH-TEMPERATURE RELATIONSHIP
IN THE SEA
GROWTH
cm
* 2nd YEAR SMOLT 3
X 1st YEAR SMOLT 3
+ 2nd YEAR SMOLT 2
O 1st YEAR SMOLT 2
25
15
5
3.5
4
4.5
5
5.5
TEMPERATURE 3C

Fig 9

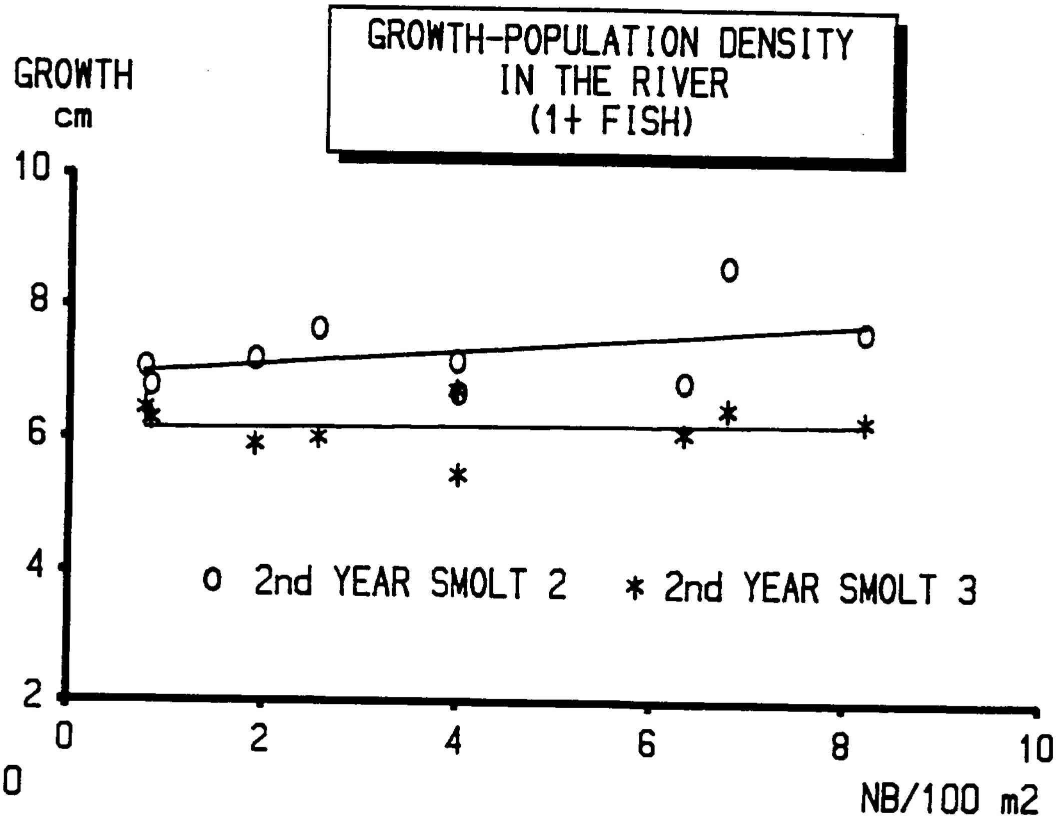
GROWTH-POPULATION DENSITY
IN THE RIVER
(1+ FISH)
GROWTH
cm
10
8
6
4
2
0
2
4
6
8
10
NB/100 m2
o 2nd YEAR SMOLT 2
* 2nd YEAR SMOLT 3

Fig 10

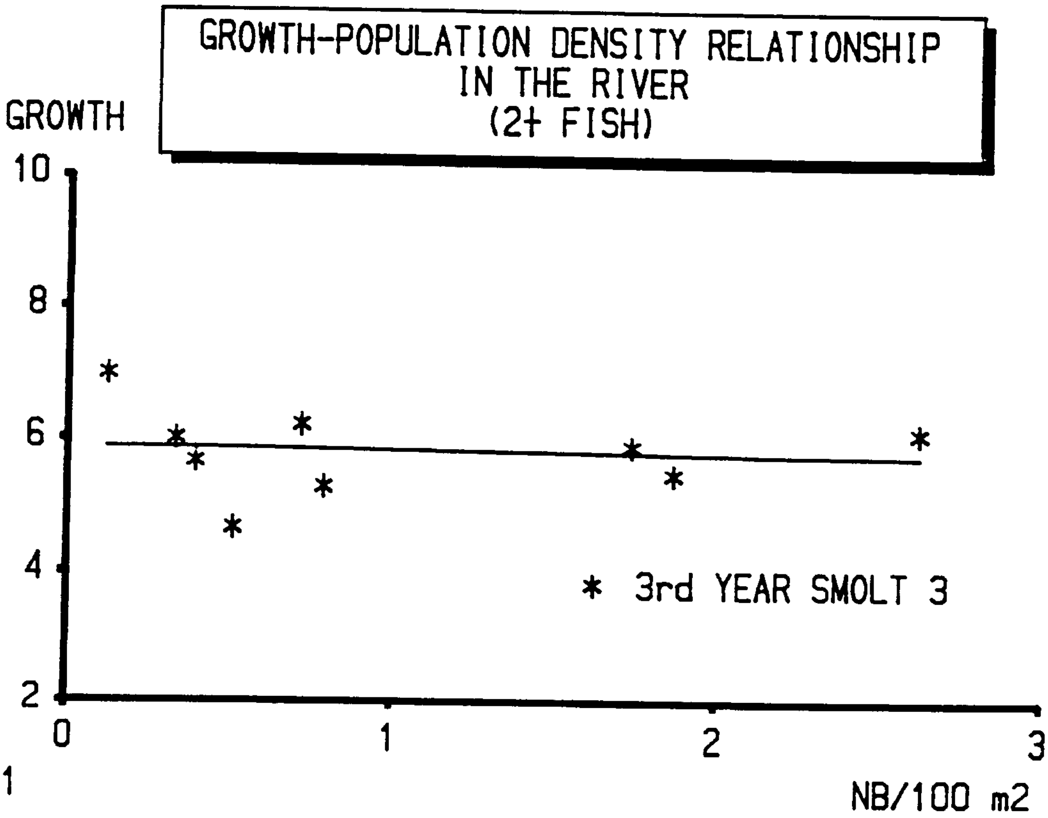
GROWTH-POPULATION DENSITY RELATIONSHIP
IN THE RIVER
(2+ FISH)
GROWTH
10
8
6
4
2
0
1
2
3
NB/100 m2
* 3rd YEAR SMOLT 3

Fig 11