Bull. Fr. Pêche Piscic. (1995) **337/338/339** : 231-239

NOTE DE SYNTHÈSE SUR LA SÉLECTION DE NICHE SPATIALE ET LA COMPÉTITION CHEZ LE JEUNE SAUMON ATLANTIQUE *(SALMO SALAR)* ET LA TRUITE COMMUNE *(SALMO TRUTTA)* EN MILIEU LOTIQUE.

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RÉSUMÉ

La sélection de l'habitat analysée à partir d'un ensemble de données récoltées sur des cours d'eau hétérogènes du point de vue spatio-temporel doit être interprétée en fonction du site et de l'échelle d'étude. La microniche spatiale fondamentale du juvénile de saumon Atlantique et de truite commune est caractérisée en été par une forte préférence pour une faible valeur de la vitesse de courant focale en raison d'une stratégie de gain énergétique basée essentiellement sur une prise alimentaire de la faune dérivante qui permet de maximiser les comportements de prise de position et d'attente du poisson. Cette microniche est également dépendante de la taille : chez le saumon, les plus gros parrs sont tolérants ; par contre chez la truite, une préférence accrue pour les habitats profonds est observée lorsqu'elles grossissent. La niche effective de la truite est relativement plus structurée par des valeurs élevées de la profondeur d'eau et des valeurs faibles de vitesse de courant lorsqu'elle est comparée à celle du saumon caractérisée par de faibles hauteurs d'eau et par des vitesses de courant élevées. Ces différences proviennent d'une plus grande tolérance du saumon pour les fortes vitesses de courant, combinée à un déplacement de la niche de cette espèce par suite d'une compétition avec la truite qui est plus agressive. Cette compétition interactive et interspécifique aboutit à une réduction de la niche spatiale effective chez le Saumon lorsque les paramètres vitesse de courant et profondeur d'eau sont pris en compte simultanément, et pas chez la truite.

SYNTHETIC NOTE ON SPATIAL NICHE SELECTION AND COMPETITION IN YOUNG ATLANTIC SALMON *(SALMO SALAR)* AND BROWN TROUT *(SALMO TRUTTA)* IN LOTIC ENVIRONMENTS.

SUMMARY

Habitat selection data from spatio-temporally heterogeneous streams must be interpreted in the light of site and scale studied. The fundamental spatial microniche in summer in both young Atlantic salmon, *Salmo salar*, and brown trout, *S. trutta*, is characterized by strong preference for low snout water velocities, because of the principal drift-feeding strategy of energy-intake maximizing sit-and-wait. The strategy is described by a simple model. Fundamental niche is size-structured, with larger parr being more dynamically robust in salmon, whereas trout show increasingly strong preferences for pools as they grow. Realized niche in trout is deep-slow relative to salmon's swift(-shallow) niche, which is a result of greater tolerance for higher water velocities in salmon combined with competitive niche displacment in the presence of the more aggressive trout. Interspecific interference competition cause a narrower spatial niche with respect to both water velocity and depth in salmon, but not in trout.

INTRODUCTION

Studies of spatial niche and (micro)habitat selection often focus on the importance of abiotic factors in regulating population numbers. However, biotic factors can also influence animal populations. This is particularly obvious in spatially heterogenous environments such as running waters where spatial segregation by species, body size and social hierarchy can be the result of competitive interactions. Temporal variability of the environment may further influence population regulation; directly or by interacting with biotic factors, to alter resource availability and use.

Habitat selection is generally regarded as a trade-off between potential energy intake and risk (HART, 1993), and variation in these two factors causes individual variation in survival, growth and reproductive success. Spatial heterogeneity implies an unequal availability of energy and potential risk. Therefore, within a species' generation, spatial heterogeneity is an important factor in regulating density-dependent processes in populations.

Stream-living salmonids, in particular territorial or localized dominance hierarchy species (BACHMAN, 1984), may be assumed to have evolved adaptive behavioural tactics to utilize and buffer the spatial diversity in most stream environments. Habitat selection is, therefore, likely to be an important factor in their life history strategies. A major role in the decline of stocks of wild Atlantic salmon (*Salmo salar* L.) has been the loss of suitable freshwater habitat (BAGLINIÈRE *et al.,* 1990). A similar hypothesis may be posed for brown trout (*S. trutta* L.), although extensive stocking confound the issue for this species. The two species have a similar ecology, are sympatric and interact in most streams in Europe. Thus, the quantity and quality of suitable freshwater habitat is of great importance in the ecology and management of these species. This selected review briefly summarizes results from studies on important aspects of fundamental niche, i.e. niche occupied in the absence of competitors and predators, and contrasts these results with realized spatial niche of young Atlantic salmon and brown trout. Here we emphasise the energy constraints set by water velocities resulting in a general model for microposition choice, and the importance of competitive interactions in habitat selection. Influence of environmental variability will be dealt with elsewhere (HEGGENES *et al.*, unpubl.).

SITE AND SCALE CONSIDERATIONS

Fish are distributed between habitat patches in a nonuniform way. If a stream is sampled at random and certain environmental characteristics of patches are measured, generalized probability functions for habitat selection can be constructed through correlational analyses. Unless one hypothesizes a causal mechanism for spatial niche selection, great amounts of data are necessary to generalize trends. It is a logical problem to extrapolate such data beyond the study stream and range of habitat conditions sampled, until potential «universal» patterns are established (MORANTZ *et al.*, 1987).

Also, questions about predictability (e.g. suitability of habitat) depend on the scale at which they are asked. In heterogeneous natural streams, designated patch size is likely to affect the form of the resulting probability functions. Furthermore, events within any one patch may be highly variable and unpredictable, while events on a larger scale may be relatively stable.

In general, two scales are adopted in stream habitat studies. A «mesohabitat» scale focuses on quantifying physical characteristics of habitat patches (< 50 m^3), and equates to «habitat-type» (e.g. a riffle or run or pool) in small streams - medium sized rivers (1st - 5th order). «Microhabitat» studies focus on stream points, i.e. the snout position of the individual fish, and usually the immediate vicinity providing additional information, i.e. patches up to 1 m^3. On a third and large scale, «macrohabitat» descriptions refer to stream reaches and orders and is a product primarily of habitat observations coupled with data on geomorphology and climate (VANNOTE *et al.*, 1980).

The aspect of temporal scale has attracted less attention than spatial scale. Most studies are done during daytime in summer and at low waterflows. However, temporally variable water flows and temperatures are pervasive environmental factors that affect behaviour and spatial niche selection in salmon and trout and other streamfishes (CUNJAK, 1988 ; HEGGENES *et al.*, 1993 ; FRASER *et al.*,1994).

FUNDAMENTAL SPATIAL NICHE IN YOUNG ATLANTIC SALMON IN SUMMER

Snout water velocity is the most consistent variable that defines the fundamental spatial niche of Atlantic salmon parr (MORANTZ *et al.*, 1987 ; HEGGENES and SALTVEIT, 1990). Parr prefer snout velocities in the range 5 - 25 cms^{-1}, and select these by moving up and down in the water column or laterally within a habitat patch. The fundamental niche is size-structured with the small parr (< 7 cm) having the more restricted niche. Apparently as a result of a specific rheotactic response, the young and small parr avoid the slowest flow areas (HEGGENES and BORGSTRØM, 1991). Probably more as a result of physical stress, all salmon parr avoid the fastest flowing (> 100 cms^{-1}) stream areas. Parr generally avoid deep stillwater areas of > 2 m (GIBSON, 1993 ; but see HUTCHINGS, 1986).

Salmon parr also avoid stream areas with sand and mud where substrates are finer than pebbles (< 16 mm) (KARLSTRØM, 1977), which also appear to be part of an specifically defined spatial niche.

REALIZED SPATIAL NICHE IN YOUNG ATLANTIC SALMON IN SUMMER

Mean (or surface) water velocites, usually in the preferred range 30-50 cms^{-1}, are often rated as the more important mesohabitat variable. These velocities are usually in combination with coarse substratum (16-256 mm), because these two variables are correlated (KARLSTRØM, 1977 ; BAGLINIÈRE and CHAMPIGNEULLE, 1982 ; HEGGENES and SALTVEIT, 1990 ; Fig. 1). The large pectoral fins of salmon parr confer a morphological adaptation allowing greater exploitation of swift waters (JONES, 1975). However, salmon parr demonstrate flexibility with respect to preferred water velocity range, and the realized spatial niche depends on fish size, intra- and interspecific competition, and predation. During, and immediately following emergence, the small parr (or fry) are vulnerable to passive downstream displacement, depending on discharge and fish size and condition. Water depth is of relatively little importance in large rivers which abound with water depths within both suitable and tolerable ranges for salmon parr (KARLSTRØM, 1977 ; MORANTZ *et al.*,1987). Water depth is, however, an important factor in small streams where suitable depths are restricted (KENNEDY and STRANGE, 1986 ; HEGGENES, 1990), and also in estuarine (CUNJAK, 1992) and lacustrine (HUTCHINGS, 1986 ; PEPPER *et al.*, 1992) environments. Small parr (< 7 cm) generally use shallow areas (< 25 cm), but widen their realized depth niche in response to reduced competition and probably also predation (KENNEDY and STRANGE, 1986).

The realized spatial niche is size structured. Larger parr (> 7 cm) have a considerably wider niche in summer than small parr, and tolerate a wide range of habitat conditions, including deeper habitats (> 20 cm), and a wide range of water velocities (10-70 cms^{-1}) with coarser substrates (64-512 cm).

FUNDAMENTAL SPATIAL NICHE IN BROWN TROUT IN SUMMER

The most consistent characteristic of spatial niche selection in brown trout is, as for young Atlantic salmon, the very narrow niche window for snout water velocity (RINCON and LOBON-CERVIA, 1993, HEGGENES *unpubl.*). A second consistent characteristic is that spatial niche selection in brown trout is size-structured. However, this latter characteristic appears to be the result of intraspecific competition, and thus part of the realized spatial niche.

REALIZED SPATIAL NICHE IN BROWN TROUT IN SUMMER

Small trout parr (< 7-8 cm) are abundant in shallow, swift stream areas (< 20-30 cm depth, 10-50 cms^{-1} water velocities) with cobble substrates. Larger trout have increasingly strong preferences for deep-slow stream areas, especially pools, which provide more cover. Unlike young Atlantic salmon, large brown trout have a narrower spatial niche than small parr. This is, however, a size effect. Whereas salmon parr in the lotic environment normally have a maximum size of 18-22 cm, resident brown trout may grow to a considerably greater size (30-60 cm), resulting in a progressively stronger spatial niche competition and more restrictive spatial requirement (HEGGENES *unpubl.*).

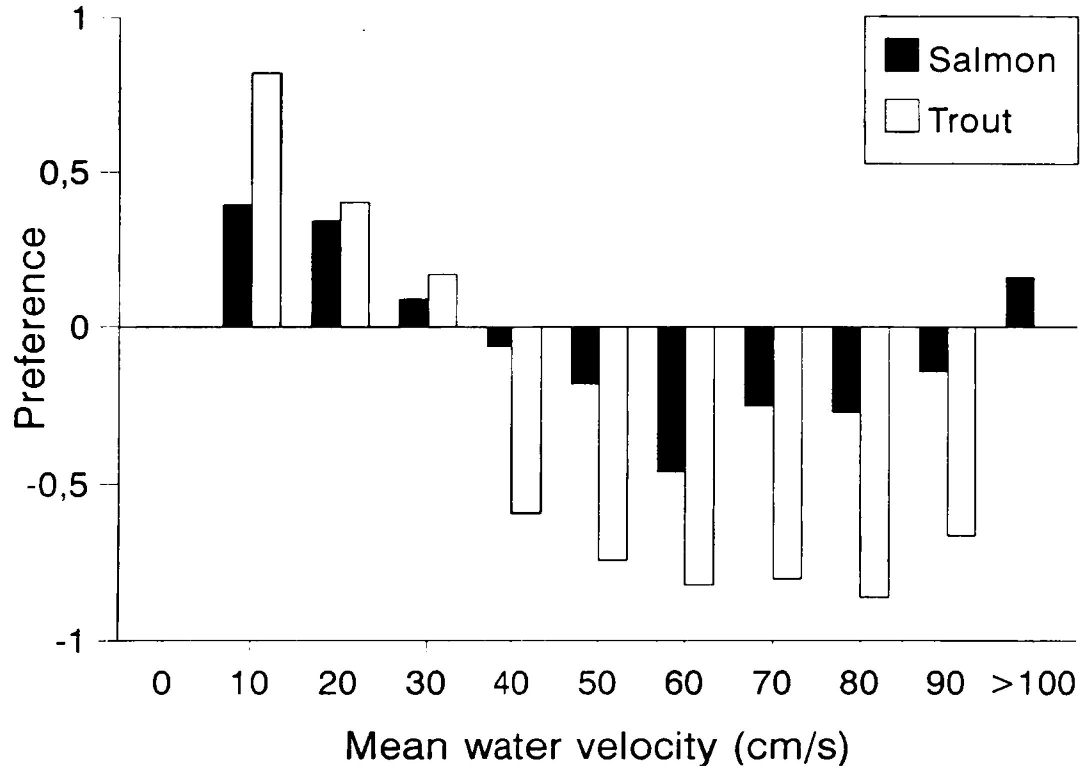

Figure 1 : Vitesses moyennes préférées par les jeunes saumons Atlantique et les jeunes truites dans un ruisseau. Les saumons sont plus tolérants que les truites, comme le montre la plus faible amplitude. Les truites évitent les zones où l'écoulement est rapide et préfèrent les mésohabitats plus lents.

Figure 1 : Mean water velocity preferences by young Atlantic salmon and trout in a stream. Salmon are more tolerant than trout, as indicated by the lower amplitude. Trout avoid fast flowing areas and prefer slower mesohabitats.

Several attempts have been made to assess the relative importance of habitat variables in habitat selection by brown trout, but there has been little consensus in distinguishing between realized and fundamental niche. Most studies rate water depth as the most important habitat variable defining spatial niche selection in brown trout, especially for larger fish and in smaller streams (KENNEDY and STRANGE, 1986 ; HEGGENES *unpubl.*). Other studies conclude that variables interact strongly such that no one can be singled out as more important than others (HEGGENES and SALTVEIT, 1990), or that a size-structuring effect may explain the situation for young parr, but not for the larger fish (BAGLINIÈRE and CHAMPIGNEULLE, 1982). Such confusion is likely the combined result of Liebigs 'law' of the minimum and Shelfords 'law' of tolerance, i.e. different variables are likely to limit populations in different streams, either through approaching the critical minimum or limits of tolerance. The emerging consensus is that depth and cover most affect the distribution of brown trout.

THE GENERAL MODEL FOR MICROPOSITION CHOICE IN SUMMER

That salmon and trout consistently and «universally» exhibit a narrow niche window for snout water velocities, has formed the basis for reasonably predictive models of microposition choice in salmonids under certain favourable and stable physical conditions (FAUSCH, 1984 ; HUGHES and DILL, 1990). The causal mechanism is elegantly explained by optimal foraging theory, i.e. microposition choice was determined by maximum net energy intake, with the focus on potential energy gain rather than risk. In streams spatial competition also substitute for direct competition for food and reduced risk (CHAPMAN, 1966), since drift-feeding is the main foraging strategy. Therefore the net energy gain potential of a holding station, i.e. both cost and gain, is determined through spatial requirements ; the single parameter of micro water velocities (HILL and GROSSMAN, 1993). Preferable positions are in low velocity micro-niches (reduced energy expenditure) close to a swift current (increased energy potential), and the fish will seek to maximize the difference between the cost and energy gain curves (Fig. 2). The principal foraging strategy in summer has been characterized as a cost-minimizing sit-and-wait strategy (BACHMAN, 1984). However, since the cost curve is rather flat while the energy potential (drift availability) curve peaks due to dramatically decreased capture success at higher velocities (HILL and GROSSMAN, 1993), the principal foraging strategy in salmonids in summer is better described as an energy intake-maximizing sit-and-wait strategy (Fig. 2).

INTERSPECIFIC COMPETITIVE INTERACTIONS

Habitat segregation may result from competitive interactions (interactive segregation; interference or exploitative competition), or from selective differences (selective segregation). Reduced amplitude or displacement of spatial niche optima and/or breadth in sympatry compared with allopatry indicate, by definition, competitive interactions. In salmonids such interactive segregation usually results from aggressive interactions together with subtle specific differences in spatial niche breadth (HEARN, 1987). Sympatric brown trout and young Atlantic salmon overlap considerably in their habitat use (HEGGENES and SALTVEIT, 1990, Fig. 1), suggesting potential interspecific competition provided that resource demand exceeds availability. Young Atlantic salmon tend, however, to be distributed more in the swift shallow habitats, often with finer substrates, than trout (Fig. 1) (KARLSTRØM, 1977 ; BAGLINIÈRE and ARRIBE-MOUTOUNET, 1985) and further from the river banks, whereas brown trout parr are more abundant in the shallow and slow-flowing streambank areas. In smaller streams, salmon parr tend to be restricted to intermediate depths (15-40 cm), while trout parr and older trout also occupy the deepest, pool-like areas. This depth distribution is a result of interactive spatial competition with brown trout. In the absence of brown trout, salmon use a wider depth range (LINDROTH, 1955 ; HEGGENES, 1990), but prefer the deeper stream areas (KENNEDY and STRANGE, 1986). They also increase in density in pools. Where other pool-dwelling species are abundant (cyprinids, percids), density of salmon parr in pools and slow water is reduced (BAGLINIÈRE and ARRIBE-MOUTOUNET, 1985). Thus, young Atlantic salmon are fundamentally tolerant with respect to water depths. However, the realized spatial niche is often restricted to a narrower range because of interference competition with brown trout, i.e. interactive segregation. In the absence of brown trout, young Atlantic salmon expand their spatial niche to also include relatively slow-deep estuarine and lacustrine habitats (HUTCHINGS, 1986 ; CUNJAK, 1992 ; PEPPER *et al.*, 1992). This is presumably a response to reduced interspecific competition (GIBSON and COTE, 1982), and an example of different habitat selection caused by ecological release in allopatry (HEARN, 1987).

Habitat segregation in trout and salmon is often the combined effect of depth and velocity. Allopatric salmon may also colonize more slow-flowing stream areas (KARLSTRØM, 1977 ; KENNEDY and STRANGE, 1986 ; HEGGENES, 1990). The importance of higher water velocities in the distribution of sympatric Atlantic salmon, is therefore presumably the combined expression of morphological selection potential, i.e. salmon's greater tolerance towards higher water velocities because of the larger pectoral fins, and interference competition, i.e. dominance by the more aggressive trout (KALLEBERG, 1958) occupying the more slow-flowing areas.

Habitat selection in brown trout is less affected by interspecific competition, as brown trout is usually dominant over other salmonids (KALLEBERG, 1958 ; GATZ *et al.*, 1987). It has been reported that brown trout in allopatry colonize more fast-flowing areas than when in sympatry with salmon (KARLSTRØM, 1977). The occasional presence of young trout in deep water, appears to be related to the presence of young salmon in the fast and shallow areas (BAGLINIÈRE and ARRIBE-MOUTOUNET, 1985) or the absence of larger trout (below).

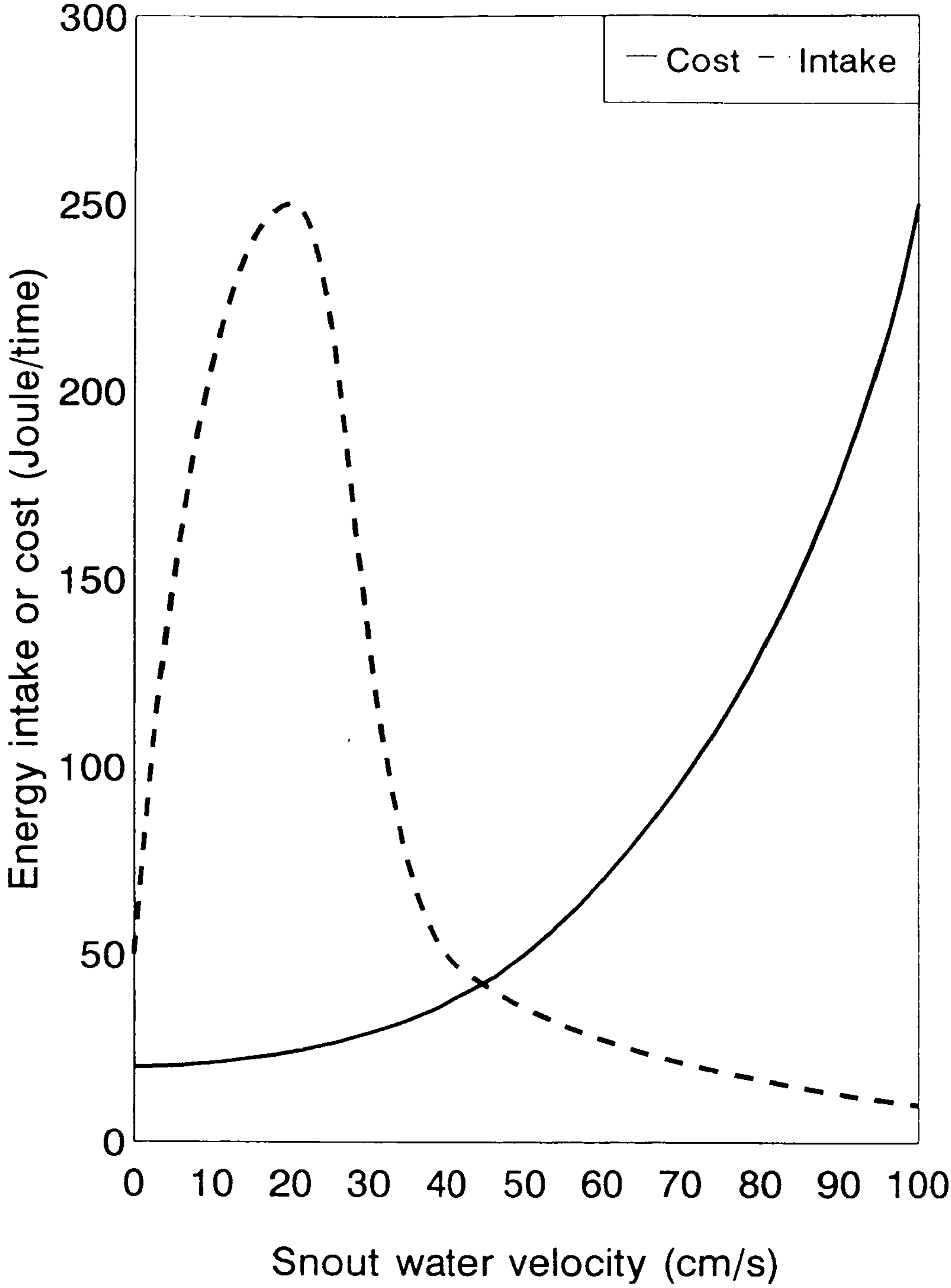

Figure 2 : **Modèle de choix de microposition par des salmonidés se nourrissant sur la dérive, basé sur le gain énergétique net. Les truites et les saumons sélectionnent des microhabitats dans la colonne d'eau qui maximisent la différence entre les courbes de dépense et d'entrée d'énergie (nourriture), c'est-à-dire le gain énergétique net.**

Figure 2 : **Model for microposition choice by drift feeding stream salmonids based on net energy intake. Salmon and trout select water-column microhabitats that maximize the difference between the cost and energy (food) intake curves, i.e. net energy gain.**

INTRASPECIFIC COMPETITIVE INTERACTIONS

Intraspecific size or year-class competition may influence survival and growth (see GIBSON, 1993), and habitat selection in salmon parr (SYMONS and HELAND, 1978). Effects may vary, depending on population densities (HEGGENES and BORGSTRØM, 1991). Social interactions are evident. Dominant parr may be aggressive (SYMONS and HELAND, 1978) and the presence of large salmon or trout can depress feeding in salmon parr (STRADMAYER and THORPE, 1987 ; HUNTINGFORD *et al.*, 1993). Such interactions may influence microposition choice by subordinate parr (KEENLEYSIDE and YAMAMOTO, 1962 ; GIBSON, 1988). Size-structured habitat selection, particularly for depth in brown trout (BOHLIN, 1977 ; HEGGENES *unpubl.*), is presumably an effect of intense intraspecific competition for space. Larger and dominant individuals colonize deep-slow habitats, while smaller and thus subordinate individuals are restricted to shallower more fast-flowing areas. Dominance is almost exclusively determined by size in both species (BACHMAN 1984, HUNTINGFORD *et al.*, 1990), and there are indications that smaller trout occupy the deep-slow areas in the absence of larger trout (BAGLINIÈRE and CHAMPIGNEULLE, 1982).

Aggressiveness in both species is related to temperature, and is reduced at lower temperatures (FRASER *et al.*, 1993 ; HEGGENES *et al.*, 1993), and in salmon also with slow water flows (GIBSON, 1988). Aggressiveness is also related to density and food supply (KALLEBERG, 1958).

In conclusion, the fundamental micro-niche in both species is characterized by a narrow preference for low snout water velocities. It is, therefore, reasonably predictive. Selected mesohabitats are deep-slow in trout relative to salmon which are more tolerant towards high water velocities. Interference competition with trout results in spatial niche contraction in salmon.

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