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F. Schiemer, M. Zalewski & J. E. Thorpe (eds). The Importance of Aquatic-Terrestrial Ecotones for Freshwater Fish

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Land/Inland water ecotones: intermediate habitats critical for conservation and management

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Introduction

In the 20th century the utilisation of natural resources, the emission of pollutants and the degradation of landscape has increased beyond a critical level. Only during the last two decades has the predictive ability of environmental sciences gained strength and become the basis for modern conservation and environmental management procedures. This is especially true for aquatic ecology, where a series of new concepts and theories arose (e.g. the biomanipulation concept Shapiro *et. al.* (1975); role of land/water ecotones — Naiman *et al.* (1988); river continuum concept — Vannote *et al.* (1980); flood pulse concept — Junk *et al.* (1989)).

In the 21st century, freshwater will be one of the most precious and most threatened resources, and the restoration and management of inland waters will have high priority; this will require the application of environmentally responsive engineering and technology.

Control of environmental quality will require several levels of resolution:

1. at the catchment area level, e.g. maintenance of landscape patchiness, pollution control,
2. at the ecotone level (e.g. control of non-source pollution and siltation, maintenance and restoration of biodiversity),
3. at the level of the aquatic ecosystems (e.g. biomanipulation of lakes and reservoirs, Shapiro & Wright, 1984; self-purification processes of rivers, Zalewski *et al.*, 1992).

The last two aspects especially are strongly dependent on the structure and function of aquatic ecotones.

Ecotones are interfaces, whose properties, scale and significance depend upon the particular ecological problem under discussion. As transition zones, their extent depends on the properties which are in transition. Consequently, the concept is multifaceted, dynamic, and difficult to constrain structurally within Holland's definition (1988). Naiman *et al.* (1988) noted that ecotones represent regions of high variance along environmental gradients. This important statistical property is a key factor in the applicability of the concept. It emphasises the localised relative diversity of structure and functions, and thereby implies that they have particular importance for the conservation of the biological resources associated with them. The primary goal of biological conservation is the maintenace of genetic continuity of the component species within systems; this ensures the maximum responsiveness of those species to environmental change. Maintenance of such genetic variety is facilitated by maintening environmental variety. Just as the nature of individual variation gives meaning to average measures in population biology, it is the nature of the variation of their component properties which gives significance to ecotones.

Hypotheses about the importance and influence of ecotonal habitats on freshwater fish biology were articulated during a meeting in Krakow, Poland, in 1990 (Zalewski *et al.*, 1991). The ecotone concept has been treated with considerable latitude in this volume. The term is used in a rather broad sense in order to focus on various significant aspects of terrestrial/aquatic interfaces on fish and fish populations.

Besides its relevance for practical applications, the ecotone approach has been profitable in creating opportunities to test general ecological hypotheses, e.g. on the relationships between habitat stability and life-history strategies; on the correlation of environmental complexity with genetic diversity; on the relevance of complementary landscape structures for population dynamics of species.

Ecotones — their forms and functions for fish

In freshwaters, from the fish's point of view, ecotones take several forms: as littoral zones in ponds, lakes and reservoirs, or as bank structures and flood plains in rivers. In addition to the lateral land/water margins, vertical transitions, between the bed sediments and stepwise longitudinal transitions, e.g. between riffles, cascades and pools, are significant.

Ecotones are important for fish as spawning grounds and as habitats — particularly during the early life stages. The structural qualities of the shoreline determine the degree of cover available to avoid predators and wash out effects during floods, as well as to provide conditions for overwintering.

Marginal zones usually provide the highest food availability, both by autochthonous production (e.g. Wetzel, 1990) and allochthonous material from the adjacent terrestrial zones. Beyond these direct functions as habitat and resource, the ecotones mediate the conditions for fish development by functioning as a filter for light, nutrients, sediments etc.

For management purposes a detailed and quantitative understanding of the various fish/ecotone interactions is required. Significant attributes of ecotone quality and their descriptors have been discussed in this volume, especially in the papers of Kolasa & Zalewski, Schlosser, and Bretschko.

One such attribute is ecotone morphology, i.e. shape, extent and composition. Shape refers the to sinuosity, contortion and complexity of wetlands as well as lake and river margins; this is for example expressed by indices of shoreline and littoral development, or by the areal extent of littoral zones and flood plains. Composition considers the vegetational structure (e.g. guild composition, height, density and canopy closure).

Besides the quality of local ecotone structure, the network (form and connectivity) of habitat patches and ecotones within a landscape context is significant:

Most fish species will not only exploit different parts of their habitat differentially to cover various requirements, e.g. feeding, shelter, spawning, but also require a sequence of habitat types over the course of their ontogenetic development. Compound effects of landscape structure must therefore be taken into consideration. Schlosser (t.v.) distinguished the following factors as particularly decisive for population dynamics and community composition of fish:

(a) habitat complementation, which refers to the spatial proximity of non-substitutable habitat types and their connectivity (Dunning *et al.*, 1992),
(b) habitat supplementation (i.e. facultative habitat use by a species),
(c) source and sink areas (zones differently endowed as spawning and nursery zones; sources are zones of high recruitment from which less well endowed sink areas are stocked),
(d) neighbourhood effects, i.e. the permeability between differently endowed patches.

Further descriptors of ecotones consider their functions as sources or sinks of material and as filters or barriers between the patches they connect. This not only holds true for energy, light, inorganic and organic nutrients, siltation (see Rabeni & Smale, t.v.) or toxic substances, but also with regard to ecotones functioning as a habitat for interacting biota: prey, predators or carriers of fish parasites and diseases.

Critical attributes of ecotones and their variance depend on spatial and temporal scales. In order to quantify their role, these attributes must be measured in a manner appropriate to the specific biological problem at hand; they must then be related to the appropriate performance measures such as species' occurrence, developmental rates and production, population structure and biomass, genetic diversity, community structure, life history strategies a.s.o..

Just as the physical qualities of ecotones change temporally, so do the physiological and behavioural responses of fishes towards them:

Fish vary dramatically in size and requirements during ontogeny. Associated with this variation is a complex array of life-cycles and habitat-use patterns (see Schlosser, t.v.).

Drastic ontogenetic niche shifts occur during the early life history and during the reproductive period; these shifts are often bound to the lateral fringes of water bodies. A good match between the narrow requirements during the critical period and the structural and functional properties of the ecotones is decisive for population dynamics (Schiemer *et al.*, 1991; Schiemer & Zalewski, 1992).

The hierarchical structure of spatial and temporal scalings addressed above is particularly obvious in the case of flood plains. They basically represent ecotones between rivers and terra firma. Their boundaries contain a hierarchy of transition zones such as the river margins, the interlink between river and backwaters, the interception of backwaters with wetland areas.

During early life history the structural properties of the shoreline, in the dimension of a few metres, and their short-term changes (e.g. in hours) due to continuous water level fluctuations determines habitat quality. Resolution of the river-backwater continuity is significant on a larger scale (km), while habitat complementation (see above) on the order of 10–100 km may be relevant for certain anadromous species (see Schiemer & Zalewski, 1992, Agostinho & Zalewski, t.v.).

The resolution of the appropriate temporal and spatial scalings at which ecotonal properties are relevant for specific requirements of characteristic species is not only decisive for successful research, it is also a major research objective in itself.

Ecotone effects on fish in rivers

The energy of flowing water and the obstructions caused by geomorphology, boulders and large organic debris derived from riparian areas are significant in creating lateral and longitudinal heterogeneity; this in turn influences fish diversity, biomass and production in rivers.

The heterogeneity and structural qualities of the shoreline and the river bed are responsible for the diversity of the fish fauna and the habitat value for different ontogenetic stages. Structure provides not only refuges for fish, but also microhabitats for food organisms, velocity patterns and organic drift. This is of direct significance for energy expenditures in station maintenance, for foraging and for escape from predators. Behaviourally, the visual isolation conferred by increased structural complexity of a stream bed allows it to be occupied by higher numbers of otherwise territorially aggressive individuals (Kalleberg, 1958); this contributes to higher population and production levels. Small-scale habitat characteristics are apparently more important for small than for larger fish: this holds true during ontogenetic development (see, e.g. Schiemer & Zalewski, 1992) but is also evident in the habitat use by small riverine fish, where small-scale heterogeneity and short-term changes in flow are significant (Zweimüller, t.v.).

The positive relationship between channel morphology and heterogeneity as well as fish diversity, both inter- and intraspecifically, is well documented; it has been tested by revitalisation programmes of degraded river systems (e.g. Jungwirth *et al.*, t.v.).

The significant effect of riparian vegetation for creating habitat diversity and determining instream processes has been demonstrated by Penczak, t.v. Concomitant losses in fish diversity and production are observed when streamside vegetation is removed, but can be restored if the vegetation zone is allowed to regenerate.

Power & Power's contribution (t.v.) pinpoints the gradient of low to high ecotone significance in various climates. In the high arctic, seasonal ice cover controls the transfer of material from land to water; it also excludes fish for long periods from marginal habitats and forces them into pools. Thus, marginal features are significant at different times.

The significance of source and sink areas and neighbourhood effects in rivers have been clearly demonstrated by various authors. Schlosser, for example, was able to demonstrate that beaver ponds function as a population source for interconnecting streams in North America. Schiemer *et al.* (1991) have shown that in the large regulated rivers of Europe only limited areas of the inshore zones provide nurseries for rheophilic species; these areas function as source areas. The population decline of former mass fishes in large European river systems, as for example *Chondrostoma nasus L.*, is a result of insufficient source areas.

Ecotone effects in lakes and reservoirs

As in rivers, the littoral zone of stagnant water bodies is functionally very important (see Wetzel, 1992), and ecotone effects are multiple and complex. They influence fish populations decisively via spawning success, as habitats, as shelter against predation or wave action and as feeding zones. Fish assemblages, population density and structure, i.e. the strength of year classes, are not only dependent on the extent and structure of the marginal zones, but also on the magnitude, timing and predictability of water level fluctuations.

The dependence upon ecotones as habitats is particularly high during early life history and decreases often with age. Inshore zones are often protective, fry-supportive habitats with a high and diverse food availability, allowing rapid growth in order to survive the critical phase in development (Matena, Simonian *et al.*, t.v.). Littoral development generally correlates with fish yield.

The strongly differing form and extent of ecotones in reservoirs – from geometrically regular artificial embankments, steep former river banks, to extensively flooded shallow areas – in combination with different patterns of water level fluctuations, provide good 'experimental' conditions to study ecotone effects on fish populations (Duncan & Kubecka, t.v.). The extent of vegetated margins or seasonally flooded vegetation is decisive for the success of phytophils and phytolithophils, which usually represent the main spawning type. In European reservoirs with poor ecotone development, perciforms (esp. *Perca, Stizostedion, Gymnocephalus*) prevail. They are less dependent on marginal structures and have a pelagic larval phase. A correlation could be established between the extent of marginal zones and the relationship of cyprinids to percids (see Fig. in Duncan & Kubecka, t.v.); this reflects spawning success primarily.

In the artificial and geometrically regular drinking water reservoirs of London, the littoral zone is very weakly developed and the reservoirs are characterized by low fish abundance. Water level fluctuations disturb the spawning success, especially of species spawning at the fringes.

Water levels in reservoirs usually exhibit short-term and seasonal fluctuations. Oscillations in year classes may be a consequence. High water levels in spring and early summer guarantee success, while low water levels depress recruitment. Short-term fluctuations of approximately 50 cm per day can eliminate whole year classes of a species.

Top down effects of fish

Top down effects by fish can a) either influence ecotones themselves or b) affect other compartments of the aquatic ecosystem. Via recruitment these effects can be dependent on ecotones:

Fish feeding and mechanical action are known to influence the vegetational structure of the littoral zones. Such influences can initiate feedback mechanisms amplifying or dampening system processes. Species feeding on macrophytes or benthos in the littoral zones can enhance or depress ecotonal structure, depending on population density of fish. One can speculate that intermediate densities result in the highest degree of structure.

An interesting example was presented by Kolasa & Weber (t.v.), who found that foraging activity of carp creates local passages and opens water patches among emergent plants. The heterogeneity so created may in turn enhance survival and growth of carp fry and juveniles (Fig. 1/1).

On the other hand, complex top down effects on the dynamics of lake and reservoir systems and in turn on water quality may occur. The spawning success and population dynamics of species having different trophic ecologies, — zooplanktivorous, herbivorous or piscivorous — can have far-reaching effects via feeding activity, mechanical action, and sediment reworking. Feedback loops can be initiated for example via internal loading, food chain control or phytoplankton/macrophyte antagonism. By size-specific feeding on zooplankton, roach or perch for example exert the well known top-down effects on phytoplankton and trophic conditions. This can change the delicate balance between macrophytic and phytoplankton growth (Fig. 1/2). Spawning success of benthivorous species such as bream can enhance the internal loading by high population levels of adults (Fig. 1/3).

Finally, the spawning success of piscivorous fish such as pike or pike-perch will have controlling effects on other species (Fig. 1/4).

Relevance of the ecotone concept in practice

The increasing intensity of land use is reflected in degradation of land/water ecotones and ecological functions. In certain fields the ecotone approach is apparently particularly important, e.g. in river engineering, in the biomanipulation of reservoirs and lakes, and in nature conservation with regard to maintaining biodiversity. The book presents examples of ways in which the ecotone approach can be applied:

Many river systems have been simplified by man for limited usages such as drainage channels, ship transport channels, or for power generation. A consequence of this loss of physical diversity has been widespread losses of biological diversity. However, as our understanding of the dependence of biota on the ecotonal habitats of rivers has increased, rational restoration programmes have been devised and tested;

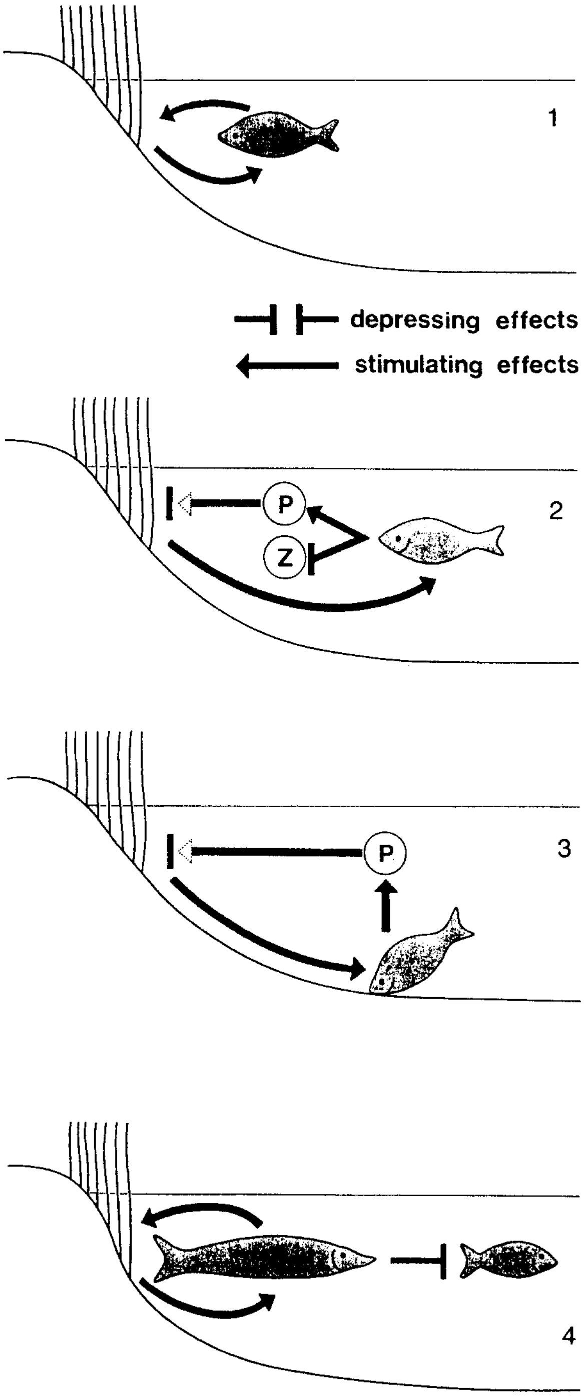

Fig. 1. Possible process loops via fish, initiated by ecotone development. P = phytoplankton; Z = zooplankton. 1. Herbivorous or benthivorous feeding in the littoral zone (e.g. rudd or carp), stimulating ecotone structure. 2. Effects of zooplanktivores (e.g. roach or perch), enhancing phytoplankton. 3. Effects of benthivores (e.g. bream), enhancing internal nutrient loading. 4. Piscivores (e.g. pike), controlling populations of other fish species.

one result is the reinstatement of some of the relevant physical variation to particular stream and river systems, with dramatic increases in biological variety, fish diversity, biomass, and production (Jungwirth *et al.*, Muhar *et al.*, t.v.).

Biomanipulation, i.e. the control of food chain relationships to influence the trophic state of water bodies has become a major management tool for water quality control. In Europe, for example, good recruitment of cyprinids and percids — dependent on spawning success and larval survival in the littoral zone — tends to reduce the ability of large zooplankton such as *Daphnia* to prevent phytoplankton blooms. Control of water level fluctuations provides opportunities for manipulating stocks by drying eggs or disturbing spawning disturbance. The manipulation of land/water ecotones may become a major tool in controlling of water quality by regulating the predators of zooplankton (Zalewski *et al.*, t.v.).

Adaptive characteristics of fish

The adaptive qualities of species with regard to the characteristics of land/water ecotones (e.g. form, heterogeneity, stochasticity of processes) have rarely been addressed to date. Such adaptive characteristics may span from metabolic or behavioural mechanisms to complex life history strategies. Winemillers (1992) life history model, for example, distinguishes three strategies (opportunistic, periodic, equilibrium) on three demographic characteristics of a species: age at maturity, fecundity and juvenile survivorship, could be successfully related to a cline of aquatic habitat size and stability in a large wetland system. The range was from large, permanent channels where equilibrium species dominated to relatively small and temporary channels where opportunistic species prevailed (Wanzenböck & Kerteszy, t.v.).

Population genetics with regard to ecotonal form and function is a key research field (see Coelho & Zalewski, t.v.). 'Environmental heterogeneity' is thought to be a major factor in maintaining and structuring genetic diversity (Nevo, 1988), and fitness in natural populations is a positive function of heterozygosity (Frankel & Soule, 1981). In most types of freshwater ecosystems, fish diversity depends greatly on boundary environments; they are the most diversified, maintain population genetic diversity, and are thus sites for active microevolution (Salo *et al.*, 1986; Naiman *et al.*, 1988).

In conclusion: This issue is presenting the state of investigations on often neglected aspects of linkages between fish and the riparian zones. The dependence of fish on structural and functional attributes of the land/water ecotones proves to be complex but has far-reaching effects. Insight into these relationships opens new perspectives for maintaining biodiversity, applying fish as environmental indicators and — via top-down — in the regulation of aquatic system functions.

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