Understanding the distribution and abundance of species is one of the cornerstones of ecological science. Therefore, insight is required in the resource requirements of species, their life history, intra- and interspecific interactions and their response to environmental conditions (Townsend et al., 2000). Similarly, understanding the distribution of species as affected by pollution requires a specific analysis of the parameters determining the persistence of species in disturbed environments. Here it will be attempted to evaluate whether traditional ecological concepts on the distribution of species can be used to analyze the impacts of toxicants. The insight generated in this thesis on specialized river insects coping with large variations in water quality will be reviewed.

In many studies, physical characteristics shaping differences in riverine habitats, are often recognized as major factors governing the distribution
of species (for example Allen, 1995; Ward, 1992; Leland and Fend, 1998; Rempel et al., 2000). Riverine ecosystems consist of a diverse array of habitats along the longitudinal axis of a river, varying profoundly in many physical factors (Allen, 1995; Ward, 1992). In undisturbed lotic ecosystems aquatic insects (and other aquatic species) are (more or less) predictably structured according to longitudinal gradients in, for example, current velocity, substrate composition or oxygen regime (for example Hynes, 1970; Statzner et al., 1988; Charvet et al., 2000). Also resource requirements of riverine organisms predict the shifts in the relative abundance of feeding guilds over the longitudinal profile of a river, as described by the river continuum concept (Vannote et al., 1980). The ability of a species to maintain a viable population in its specific river habitat, however, depends on its response to the prevalent environmental conditions (Townsend et al., 2000). The ways in which tolerances and requirements of species interact and match the conditions and resources provided by certain habitats are addressed in the niche concept: numerous environmental conditions together build a multidimensional hypervolume within which a certain species can maintain a viable population (Hutchinson, 1959). On the large longitudinal scale of rivers ranging from groundwater-fed streams to low-land rivers, temperature is, for example, considered to be a factor of major importance in determining the distribution of species by influencing various life-cycle aspects (Ward, 1992). Insects can maintain viable populations only within certain temperature limits, as demonstrated for caddisflies by Lowe and Hauer (1999). On the other hand, an increase in the temperature, caused by human influences such as cooling water discharges, has been shown to enable the invasion of (exotic) species from other climate zones (Rajagopal et al., 1999). Thus, the habitat characteristics and (complex interactions between) the numerous environmental conditions add up to a set of locally defined selective forces which act as 'filters' selecting certain (indigenous) species from a much larger pool of potential inhabitants.

Can the presence of contaminants also be thought of as being dimensions in the multidimensional niche? Consequently, can the impact of toxicants be analyzed analogously to the analysis of natural conditions? Since species specific responses of aquatic insects to different degrees of pollution are apparent (chapter 2), toxicants could act analogous to other dimensions, like for example temperature, in defining conditions that discriminate the distribution of species. The absence of species in the
severely polluted large European rivers in the 1960/70s and the mortality of aquatic organisms after the Sandoz accident in 1986 (chapter 1), clearly illustrate that the temporal persistence of species could indeed be affected by the presence of toxicants in the field. Therefore we argue that a disturbance by environmental contaminants, due to anthropogenic activities, can cause niche dimensions to vary outside of the normal range or introduce previously non existing dimensions. Subsequent shifts in the abundance of species could be expected, therewith impairing the structure or functions of the riverine ecosystem. However, whereas changes in for example current velocity, temperature, and light result in a (more or less) predictable annual cycle of seasonal succession of species (Patrick, 1975; Allan, 1995), the run-off of environmental contaminants superimposes a large proportion of unpredictability on this regularity: minute changes in concentrations of chemicals, due to for example accidental spills, could result in large changes in niches and therefore in the dominance of opportunistic versus specialized species. Indeed in the present thesis it was demonstrated that the maximum peak concentrations of organophosphorous insecticides in the field are in the same order as the observed effect levels for sensitive juvenile river insects determined in the laboratory (chapter 2). Riverine insects, that require stable environmental conditions because of their relative long life-cycle, are likely not able to maintain populations in rivers which are frequently disturbed by such accidental peak concentrations of contaminants. Simultaneously, this example shows that spatial and temporal aspects of pollution in relation to the life-cycle characteristics of the organisms, determine the extend to which contaminants impair the persistence of species. For example, not only the concentration and kind of chemical spilled are determining the effects on biota, but also the frequency and seasonal timing at which the organisms are exposed to it. Considering this relationship between chemical stressors and life-cycle characteristics of the exposed riverine species, also chemicals present during longer periods at concentrations below acute lethal effect levels could prevent species to persist in certain habitats. For copper, maximum field concentrations do not reach acute effect levels (chapter 2), but the average load in for example the river Meuse is in the same order as the observed behavioral effect levels for *H. angustipennis* (chapter 2). These behavioral responses are likely to reduce the fitness of organisms (Blaxter and Ten Hallers-Tjabbes, 1992) and therewith indicative for potential life-cycle effects. Conditions that are steadily sub-optimal such as a continuous exposure to low concentrations of copper, as well as peak
Concluding remarks

exposures such as pesticide spills, may therefore limit the distribution of species. Especially the species with a sensitivity above average and/or species with relative long life-cycles are prone to local extinction.

It can be expected that chemicals interact with each other as well as with other environmental conditions. Mixture toxicity is an example of such an interaction: in the present thesis, experiments revealed that the tested model toxicants contribute to mixture toxicity below their individual effect levels (chapter 4.1). Adverse effects in the field are, therefore, not determined by the effects of (incidental discharges of) individual compounds only. In the field, mixture toxicity has indeed been demonstrated to be responsible for adverse effects on riverine invertebrates (Stuijzfand, 1999). Similarly, interactions between environmental contaminants and other limiting conditions can be expected. Considering the large differences in response types to these different dimensions, such interactions can be expected to appear in a variety of ways: in chapter 4.2 it was demonstrated that the combined effect of copper and low oxygen is much higher than can be expected based on the effects of both factors separately. Since in the field the lowest oxygen concentrations often coincide with the highest toxicant concentrations, it was concluded that 'multiple stress' actually occur in large rivers carrying complex pollution and that under such conditions adverse effects of chemicals on riverine biota can be unexpectedly high. Simultaneously it was shown, however, that such interactions between multiple stressors are compound specific: no synergistic effects of a combination of lowered oxygen and diazinon were found (chapter 4.2). Similar contrasting observations have been reported for the effects of temperature, salinity and food availability on the toxicity of chemicals (Heugens et al., in press). On the other hand, there are also variables in complexly polluted rivers, such as elevated concentrations of nutrients or organic waste, that may mask or (over-) compensate the response of certain organisms to toxicants (De Ruiter and Hendriks, 1996; Dubé and Culp, 1996; Stuijzfand, 1999).

Based on the results of the experiments presented in this thesis, we argue that in rivers suffering from a complex pollution, chemicals and other environmental factors act together in re-structuring the niches of benthic invertebrates. This is consistent with the manifold observations on changing biodiversity in polluted rivers (for example Doledec et al., 1999; Delong and Brusven, 1998). When general ecological principles are
used to put our limited understanding of the impact of pollution on specialized river insects in perspective, it becomes clear that spatio-temporal aspects of environmental contaminants in relation to life-cycle characteristics of the organisms are critical in regulating the persistence of species.

REFERENCES


