

8 Ecological Concepts Important for the Interpretation of Effects of Chemicals on Aquatic Systems

ROBERT C. PETERSEN Jr. and LENA B.-M. PETERSEN

Summary

Some ecological concepts usually not considered in ecotoxicology are presented and their importance in assessing the effects of hazardous substances on aquatic systems at the population, community and ecosystem level are discussed.

At the population level the distribution of mortality is briefly reviewed. It is pointed out that contrary to the mortality curve for commonly used laboratory organisms such as *Daphnia*, many aquatic populations experience most of their mortality at the beginning of the life cycle. Results of a chronic study using the stream invertebrate, *Hydropsyche siltalai*, demonstrates how this high natural mortality can mask the effect of two toxic chemicals, arsenite and 4,5,6-trichloroguaiacol. The masking of the effect of the chemicals is an example of population compensatory mortality and it is suggested that this may complicate the interpretation of chemical effects data.

At the community level the problems associated with interpreting effects data are linked to the lack of objective criteria. It is suggested that the study of a small group of ecologically related organisms, a guild, can provide more information on the effect of toxic substances than the study of the whole community. This approach is illustrated with a study of a guild of stream dwelling invertebrates in a metal polluted river. A key to this analysis is the recognition of the difference in species sensitivity and it is suggested that the specialist-generalist concept can be used to predict which species will be most affected by toxic substances. An ecological specialist with a narrow set of niche dimensions will be relatively more sensitive to toxic stress (stenotoxic) than a more generalist (eurytoxic) species. It is then suggested that the prediction of which species will be most sensitive should be coupled to its ecological role in the community with special attention paid to keystone species. Not all species are of equal importance to system structure and function as is illustrated with examples from the ecological literature and field studies of a metal-polluted river.

The ecological concepts discussed are expanded into a set of recommendations or decision rules for the interpretation of the effect of toxic substances on aquatic systems. They are; (1) the population mortality distribution should be known since natural mortality may mask the effect of a toxic chemical through compensatory mechanisms, (2) guilds of ecologically related species will provide more information on toxic effects than whole communities, (3) species with broad ecological niches (generalists) will be more tolerant to toxic stress

(eurytoxic) than species with narrow specialized niches which will be less tolerant to toxic stress (stenotoxic), (4) knowledge of the keystone species and the effects on it are important for understanding ecological effects, and (5) structural properties of communities are less conservative and will be affected first and to a greater extent by a toxic agent than functional properties.

8.1 Introduction

The purpose of this chapter is to present several ecological concepts not usually considered in the assessment and interpretation of chemical effects data on aquatic organisms. This approach is based on ecotoxicology which if viewed as a subdiscipline of ecology (Moriarity 1983) can be paraphrased from Truhaut (1977) and Krebs (1972 in Begon et al. 1986) and defined as the study of the effects of pollutants on the interactions that determine the abundance and distribution of organisms. The interactions are both between organisms and between the organism and its environment. It is the effect of pollutants on these interactions that is our concern here.

The chapter is arranged in a hierarchical structure of ecological concepts that are important for interpreting effects at the population, community and ecosystem level. First we will review the types of mortality that aquatic populations can experience over a life cycle. Mortality is an obvious concern and can be considered a cornerstone of the disciplines toxicology and ecotoxicology. However, the mechanisms of mortality and its distribution during a life cycle in natural populations has not been thoroughly considered by ecotoxicologists. This may be due to the carry over from laboratory toxicity tests where natural mortality such as that occurring in the control, is considered a flaw in the experimental design and is, therefore, kept at a minimum. In natural populations of most aquatic organisms, except for some exceptions commonly used in laboratory culture, high mortality is a common occurrence during a short period at the beginning of the life cycle.

We will then review the common techniques of interpreting the effects of chemicals on communities. These techniques are primarily counts of species and we suggest that these analyses by themselves do not provide enough information. As an alternative we recommend the study of discrete but integral units of communities and illustrate this approach with examples using guilds, specialist-generalists, and keystone species.

We then recognize the ecosystem as an organizational unit above that of the community. In the chapter we use the term ecosystem primarily to take advantage of work done on stress in ecosystems and the problem of cumulative environmental effects. In both of these the effects of chemicals which are usually thought of as working at the individual level are magnified up the hierarchy of system organization and may be best conceptualized at this higher level.

This discussion is selective and presents concepts not previously covered from an ecotoxicological point of view. For a more general discussion of ecotoxicology the reader is referred to Moriarity (1983), Sheehan et al. (1984), and Butler (1978).

8.2 Assessment of Toxic Effects at the Population Level

8.2.1 Mortality Distribution in Aquatic Populations

An opinion shared by many ecotoxicologists is that immature or neonatal stages are more susceptible to chemical agents than are adult organisms. This may be due to differences in detoxification mechanisms between young and adult organisms, or rates of excretion of toxic chemicals (Rand and Petrocelli 1985). For example, it was found that for fish the maximum acceptable toxicant concentration (MATC) could be estimated by using shorter tests with early developmental stages instead of a complete life cycle test (McKim 1985). McKim (1977) reviewed 56 life cycle tests and found that the estimated "no-effect" concentrations were virtually identical, in 80% of the cases, for the short embryo-larval-juvenile phase and the lengthy life cycle test. In the rest of the cases the differences were factors of 2 or less. A serious difficulty arises, however, when this generality, that early life stages are sensitive to toxic substances, is applied to aquatic populations, since many species of organisms experience naturally high rates of mortality in the immature stages (Deevey 1947; Slobodkin 1961; Hutchinson 1978).

There are 4 basic patterns of survivorship that have been recognized to occur in populations. Fig. 1 represents the 4 types of survivorship (mortality) of 1000 individuals over a 52-week univoltine life cycle. The 4 types are idealized models since there are few examples of populations conforming exactly to any one model. Type I is indicative of a population where the major number of deaths occur at the end of the life cycle, the adult senescence model. This may be an appropriate model for the demography of human populations and certain parthenogenetic invertebrates such as rotifers and cladocerans (Hutchinson 1978). Even in many human populations this model may not exactly describe the survivorship of individuals since in many countries high infant mortality will give the curve a sharp drop at the beginning. Type II is mathematically equivalent to a constant number of deaths through time. Adult bird populations have a nearly constant mortality and approach type II (Ricklefs 1973). Type III is the mortality curve of a population which experiences a constant proportion of deaths and results in an exponentially decreasing population size. This is the common pattern for fish (Ricker 1946; Allen 1949) and aquatic

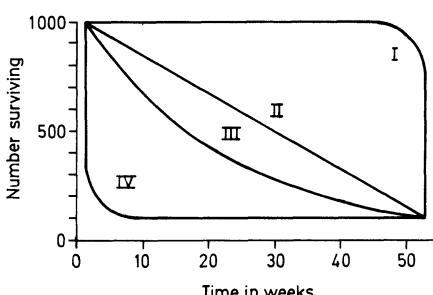


Fig. 8.1. Hypothetical survival of 1000 individuals of species with 1-year (52 week) life cycles where 10% (100) survive (for explanation see text)

insect populations (Neese and Dugdale 1959; Waters 1969; Waters and Crawford 1973; Gillespie and Benke 1979; Benke 1984) especially when mortality during the first few days of the life cycle is excluded (Petersen and Petersen 1988). Type IV is a decreasing power function where the population experiences most of its mortality in the very early life stages. Many aquatic populations including fish and most invertebrates experience mortality somewhere between a type III and IV (Deevey 1947; Slobodkin 1961; Waters 1969) especially when a large (> 100) number of eggs are produced per female.

A clear distinction is made between the two extreme types of survivorship, type I and IV. In type IV a large number of young are produced unprotected into an environment, maternal resources are used to produce the maximum number of individuals and parental care is absent. In type I only a few young are produced at a time, maternal resources are shared by these few and parental care is commonly given. Both the rotifers and cladocerans are parthenogenetic and produce relatively large and few offspring at any one time (Pennak 1953; Hutchinson 1978). The larger size seems to give the young an advantage against mortality due to predation (Zar 1980) but advantages of beginning life nearly full-grown must also play a part. In *Daphnia* the eggs are allowed to hatch in the brood pouch, a form of parental care, before the young are released (Pennak 1953) which would give it an additional advantage when entering the population.

Low juvenile mortality is one of the reasons why both rotifers and cladocerans have become animals of choice in laboratory studies. Day old *Daphnia* when used in the toxicological testing should have a mortality in the control not in excess of 5% (Gieger et al. 1980). In the calculation of the toxicity of a compound it is important that the effect of the toxicant can be separated from other causes of mortality. This is done by correcting for mortality occurring in the control by using Abbott's correction where the corrected proportion, $P_{cor} = (P_{obs} - C) / (1 - C)$ with P_{obs} the observed proportion and C the mortality occurring in the control (Finney 1947). Abbott's correction subtracts the mortality in the control from the experimental value and assumes that mortality due to the toxicant and mortality due to the background conditions are additive. In laboratory toxicity testing minimizing background mortality reduces the importance of this assumption.

While there is agreement that most aquatic organisms have a survivorship curve not like rotifers and cladocerans it is difficult to form generalities about the mortality models presented in Fig. 8.1. Petersen (1974) was able to follow the emergence, egg deposition and first instar mortality of a population of *Nigronia serricornis*, a semivoltine megalopteran predator, common in streams in the eastern United States. These stream insects lay their eggs on overhanging vegetation which makes them easy to find and count. Along a 93-m stretch of stream, there were 10,746 eggs laid. Of these, 69% hatched giving an initial population density of 115 larvae/m² of riffle habitat (Fig. 8.2). In the following 125 day sampling period the *Nigronia* population underwent a typical type III mortality curve or negative exponential with a constant proportion of the larvae being lost per day. However, *Nigronia* is a reclusive predator with a three year

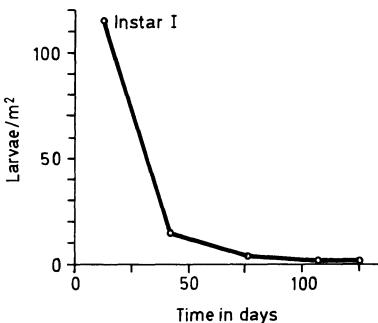


Fig. 8.2. Survivorship curve of a natural population of *Nigronia serricornis* (Megaloptera: Corydalidae) with an instantaneous mortality rate of -0.015 per day (data redrawn after Petersen 1974)

life cycle and after the first 125 days the population density reached a level of 4 larvae/m² which was maintained throughout the remainder of the life cycle. Most, if not all, mortality was restricted to a brief period at the start of the life cycle. Therefore, if the initial population density is known and measured for 3 years, a type IV mortality curve is the appropriate model. But if either the initial estimate is missing or the entire period not considered, a type III will be the better model.

For univoltine aquatic insects most mortality occurs in the early life stages, with low but measurable mortality occurring throughout the entire life cycle. Petersen (1989) has examined in detail the survival of three coexisting species of hydropsychid caddisflies from instar I through pupal stage in a small woodland stream in southern Sweden, over a one year life cycle. Larval survival for the one year life cycle was adequately represented for all three species by a type III negative exponential survivorship curve, $N_f = N_i e^{-bx}$ where N_f is the final population density and N_i is the initial population density with r^2 values of 0.92 for *Hydropsyche siltalai*, 0.90 for *H. saxonica* and 0.88 for *H. angustipennis* (Fig. 8.3). While there was a constant proportion dying throughout the larval period, the absolute number of deaths was highest in the first few weeks of the life cycle.

High mortality in early life stages is usually attributed to density dependent biotic factors such as predation or competition for food or space. Mortality rate, in general, is considered to be density dependent if the assumptions of the Verhulst-Pearl logistic equation of population growth are applicable (Pianka 1983). While it is true that both density dependent and density independent factors contribute to population mortality, density dependent factors tend to dominate, especially during the high mortality, early in the life cycle.

In the study of three coexisting species of hydropsychid caddisflies, Petersen (1989) reports data that when recalculated shows mortality rate correlated ($r=0.97$) with initial population density. A similar observation can be made with data reported by Cuffney and Minshall (1981) for another hydropsychid caddisfly, *Arctopsyche grandis*. A high mortality rate was observed in a year with a high initial population density, a low mortality rate in a year when the initial population was low.

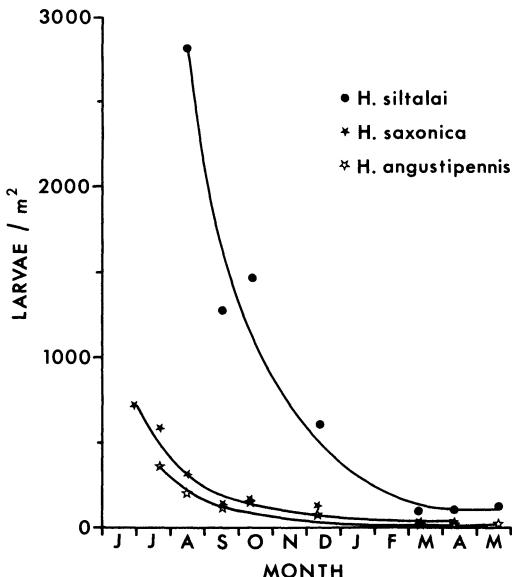


Fig. 8.3. Survivorship curves for natural populations of three species of net spinning caddis-flies, *Hydropsyche saxonica*, *H. angustipennis* and *H. siltalai*. The first point on the left of each curve represents the first appearance of instar I larvae (data redrawn after Petersen 1989)

Density-dependent mechanisms have been used to describe the high juvenile mortality in fish populations (Ricker 1954; Mortensen 1977). Ricker (1954) recognizes two forms of external mortality factors in the exploitation of fish stocks, compensatory and random. Compensatory mortality is density-dependent and occurs early in the life cycle. Random mortality is density-independent and occurs throughout the life cycle. Mortensen (1977) has also observed an early life-stage, density-dependent mortality in brown trout (*Salmo trutta*) and a density-independent mortality which occurs throughout the remainder of the life cycle. In both these studies with fish, the density-dependent mortality occurred just after hatching from the egg and accounted for most of the mortality of the cohort.

Cummins and Wilzbach (1987) suggest that the majority (> 80%) of the natural mortality observed in field populations of stream invertebrates is not the result of predation, competition for food and space, or physical-chemical environmental stress but is rather caused by pathogens which are more effective on early life stages than later in the life cycle. This is supported by a large body of evidence (Anderson and May 1982; May 1983; 1985) suggesting that pathogens are important regulators of animal populations and operate through essentially density-dependent mechanisms (Begon et al. 1986).

8.2.2 Compensatory Mortality in the Interpretation of Effects

Moriarty (1983) has suggested that it is difficult to predict the effect of a toxic substance on a natural population even though a large number of individuals in that population may have been eliminated. In most cases the causes of mor-

tality in natural populations are difficult to separate and to distinguish between additive and compensatory mortality. Additive mortality is that mortality of most concern to ecotoxicologists since it is the mortality added to the population by a specific cause. As mentioned, in laboratory studies experiments are designed to determine the additive mortality due to an added toxicant. This can only be done when other causes of mortality are held to a minimum and can be subtracted using Abbott's correction. However, in natural populations there are many causes of mortality, not all of which add additional deaths to a population. A particular factor such as a parasite, starvation or toxicant may eliminate an individual that would have died from some other cause.

Some of the best examples of how compensatory mortality works comes from wildlife management. In the management of waterfowl populations, where hunting limits have to be set to maintain a certain population level, the primary concern is whether the exploitative mortality e. g. that caused by duck hunters, will add to the existing level of natural mortality or whether this mortality will be compensated for by a reduction in other forms of mortality. Rather surprisingly, it has been found that the annual hunting mortalities of male adult Mallard ducks (*Anas platyrhynchos*) over a 20 year period are largely compensated for by a decrease in other forms of annual mortality (Burnham and Anderson 1984). Similar compensatory mortality mechanisms have been reported for wood pigeons (*Columba palumbus*) (Murton et al. 1974) and in the predation of the winter moth (*Operophtera brumata*) by the pine siskin (*Carduelis pinus*) (Roland et al. 1986). At the community level Connell et al. (1984) has invoked compensatory mechanisms in recruitment, growth, and mortality to explain maintenance of rain forest tree diversity. Obviously, wildlife managers as well as environmental managers would like to keep the level of mortality in populations constant, a level at which population compensatory mechanisms would absorb the mortality caused by mans activities.

In order to examine the effect of compensatory mechanisms on an aquatic invertebrate, the survivorship of the caddisfly *H. siltalai* was followed from the egg stage through instar V for 257 days under 5 concentrations of two toxic chemicals arranged in double 1.4 multiple increases ($1.4 \times 1.4 = 1.96$) namely 18, 35, 69, 135, 264 $\mu\text{g/L}$ 4,5,6-trichloroguaiacol (4,5,6-TCG) and 270, 520, 1020, 2000, 3920 $\mu\text{g/L}$ sodium metaarsenite as As in static, 8 L stream aquaria according to the procedures in Petersen and Petersen (1984). The purpose of the experiment was to compare the effect of a highly water soluble, chemical toxicant, arsenite, to a moderately hydrophobic ($\log P_{ow} = 3.7$) toxicant, 4,5,6-TCG, in an extended, chronic study.

The background mortality of the laboratory population (Fig. 8.4) was similar but more dramatic than that observed for the field population of the same species (Fig. 8.3). In the control microcosm there was $8 \pm 2\%$ (mean $\pm 95\%$ CL) mortality among 3 egg masses with a total of 808 eggs. This mortality consisted of 3% which died in the egg stage and 5% which died as first instars which were unable to leave the egg. No similar estimate of egg mortality is possible from the field populations. Of the total number, an additional 64% died within 9 days. Twenty-three days was the length of time it took to complete the first

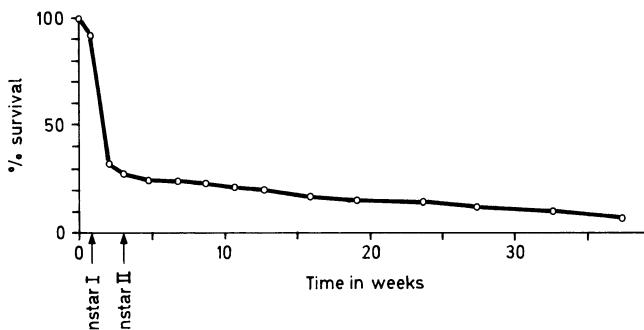


Fig. 8.4. Survivorship curve for *Hydropsyche siltalai* from the egg stage to Instar V in 257 days of laboratory culture

instar. This implies that the mortality occurred during the first half of the first instar and was not connected with the moulting from instar I to II. It has been suggested that one reason for mortality in insects is damage suffered during the molt (Wigglesworth 1965) which may lead to secondary pathogen invasion (Cummins and Wilzbach 1987). From day 9 through day 257 an additional 22% died.

The mortality observed in the laboratory population occurred in a synchronized cohort, all hatching within 24 h of each other, and closely approximated the type IV survivorship curve shown in Fig. 8.1. This differs from the type III survivorship observed in the field population of the same species. The cause of this discrepancy could be that the field data is not from a synchronized cohort. First instar individuals were being recruited into the Lerbäcken population over a 45-day period (Petersen and Petersen 1988). This means that the mortality rate measured with the field data underestimates the actual mortality, since new individuals were entering the population during the time between samples and essentially replacing some of those who had died.

There was little effect of the toxicants on the survival of the eggs. Egg mortality was not significantly different from the control at all concentrations of arsenite and 4,5,6-TCG except at 3920 µg As/L as arsenite. The egg stage in most aquatic insects seems to be resistant and in aquatic populations, in general, egg mortality tends to be low. Petersen (1974) observed an 8% mortality in the egg stage of *Nigronia serricornis* which could be attributed to death by failure of the egg to hatch (lack of fitness or pathogens) or egg predation. While hymenopteran parasites have been indicated in egg mortality (Azam and Anderson 1969; Pritchard and Leischner 1973) parasites in general are rare among aquatic insects (Hynes 1970). In a review of toxicity tests with 410 chemicals and 66 species of freshwater animals, Mayer and Ellersieck (1986) concluded that the eyed-egg stage of fish was the least sensitive life stage.

In all 12 laboratory cultures of *H. siltalai* (see above) regardless of toxicant or concentration there occurred a sharp decrease in the number of larvae during the first 9 days after hatching which was followed by a much longer and lower rate of mortality (Fig. 8.5 A,B). The mortality curve was then divided into

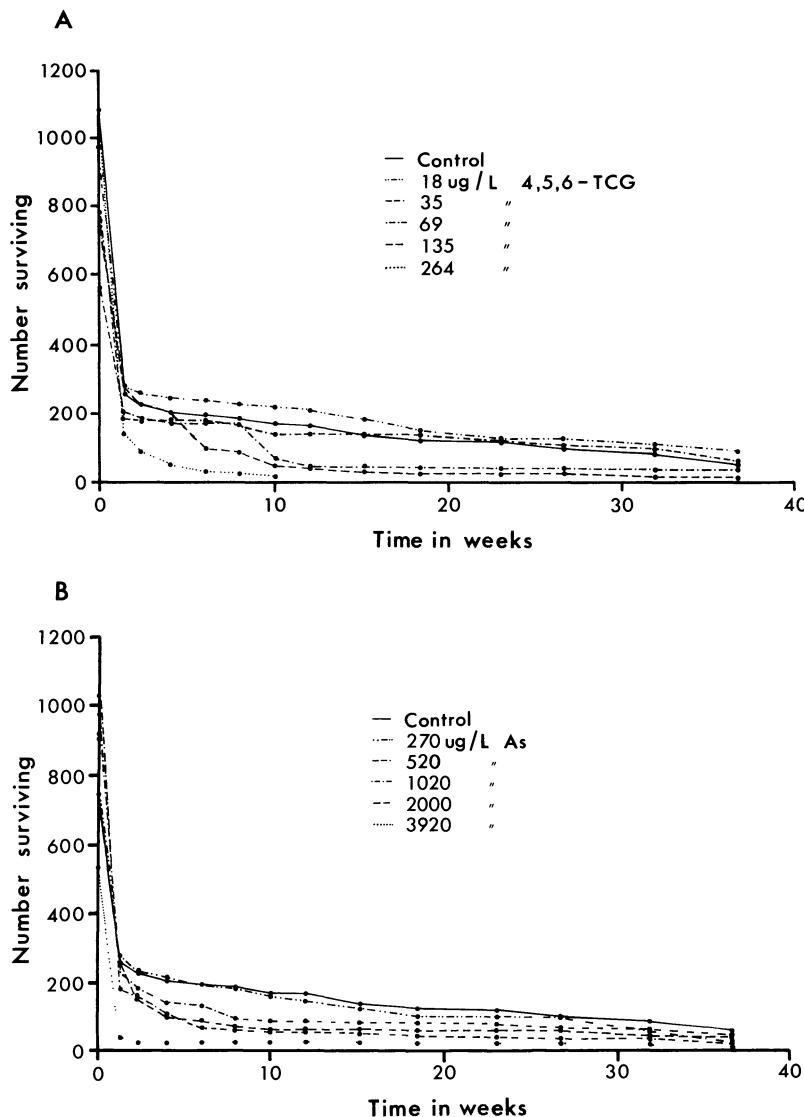


Fig. 8.5 A,B. Survivorship curve for *Hydropsyche siltalai* larvae from 24 h old through instar V and 257 days of laboratory culture. **A** Survival under 5 concentrations of 4,5,6-TCG; **B** Survival under 5 concentrations of sodium metaarsenite

two sections one consisting of the first 9 days and the second from 9 days to the end of the experiment, day 257. When the mortality rates during the initial 9-day period were analyzed for dependence on toxicant concentration there was no significant effect of either 4,5,6-TCG or arsenite (Fig. 8.6). Mortality rates during these first 9 days calculated using the negative exponential model ranged from 7.6%/day in the control to 19.9%/day at 3920 µg As/L (Table 8.1).

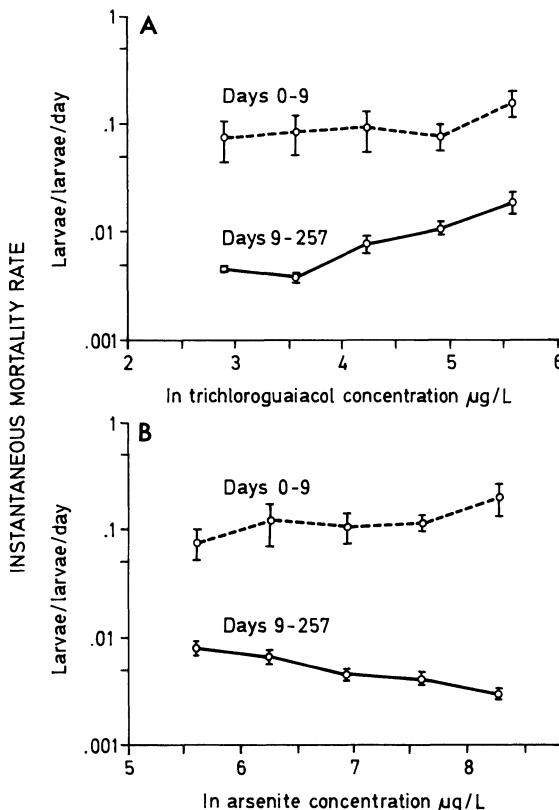


Fig. 8.6 A,B. Mortality rate of *Hydropsyche siltalai* during the first 9 days of life compared to the remaining 248 days while under toxic stress. **A** Mortality rate under 5 concentrations of 4,5,6 trichloroguaiacol; **B** Mortality rate under 5 concentrations of arsenite. Vertical error bars around each mortality rate are one standard error of the fit to the negative exponential model

However, as shown in Fig. 8.6 the dose response curve for both 4,5,6-TCG and arsenite during the first 9 days was flat ($P=0.075$ for arsenite and $P=0.162$ for 4,5,6-TCG). When the data were recalculated using probits with Abbott's correction (Finney 1947) there was no significant dose response for either toxicant.

Survivorship during the period day 9 through 257, however, was dependent on both 4,5,6-TCG and arsenite concentration (Fig. 8.6). Instantaneous mortality rates ranged from 0.5 to 1.3%/day and were correlated with concentration. Complete elimination of all larvae occurred at a concentration of 264 $\mu\text{g/L}$ 4,5,6-TCG after 75 days. Larval death at high 4,5,6-TCG concentrations was associated with abdominal gill deterioration and an increased sensitivity to low oxygen concentrations. The 4,5,6-TCG concentrations used stimulated the myxobacteria *Sphaerotilus* which at low levels can be used as food by *Hydropsyche* but at high densities lowered the oxygen concentration.

The concentrations used in this long term chronic study were selected based on prior tests of the sensitivity of *Hydropsyche* to arsenite and 4,5,6-TCG. Petersen and Petersen (1984) have shown that the EC₅₀ for instar V *H. angustipennis*, a species similar but slightly more tolerant to metals than *H. siltalai*

Table 8.1. Instantaneous mortality rates (%/day) \pm standard errors of laboratory populations of *H. siltalai* during the first 9 days following eclosion and for the remaining 248 days at 5 concentrations of 4,5,6-trichloroguaiacol and arsenite. Average initial population density of cultures were 1000

Condition	Instantaneous Mortality Rates	
	Days 0–9	Days 9–257
Control	7.6 \pm 2.9	0.53 \pm 0.03
4,5,6-Trichloroguaiacol		
18 $\mu\text{g/L}$	7.4 \pm 3.4	0.45 \pm 0.02
35 $\mu\text{g/L}$	8.6 \pm 3.6	0.38 \pm 0.04
69 $\mu\text{g/L}$	9.2 \pm 3.8	0.78 \pm 0.15
135 $\mu\text{g/L}$	7.7 \pm 2.2	1.09 \pm 0.15
264 $\mu\text{g/L}$	16.0 \pm 4.5	1.90 \pm 0.44
Sodium metaarsenite		
270 $\mu\text{g/L}$	7.6 \pm 2.4	0.79 \pm 0.08
520 $\mu\text{g/L}$	12.0 \pm 5.1	0.66 \pm 0.08
1020 $\mu\text{g/L}$	10.8 \pm 3.4	0.45 \pm 0.06
2000 $\mu\text{g/L}$	11.5 \pm 1.8	0.41 \pm 0.07
3920 $\mu\text{g/L}$	19.8 \pm 6.6	0.30 \pm 0.02

(Petersen 1986), is 135 $\mu\text{g/L}$ TCG. In the present test with first instar *H. siltalai*, no effect of 135 $\mu\text{g/L}$ TCG was seen during the first 9 days of exposure. This can be interpreted as a contradiction of the general idea that early life stages are more sensitive than more mature forms. However, the lack of sensitivity was not due to any greater tolerance at the individual level but rather the tolerance of the population to absorb the effect of the toxicant within the already high mortality. The two sources of mortality, that due to the toxicant and that already occurring, were not additive. If they had been, then Abbott's correction, in the probit analysis, would have separated the two sources, and revealed that mortality due to the toxicant alone. This could not be done since even after Abbott's correction, there still was no dose response relationship during the first 9 days.

In standardized short-term toxicity tests, high mortality in the control is viewed as an error in the experimental design since it is important to measure the effect of the toxicant. However, it may not be an error if the response to the toxicant by a natural population is being questioned. In the present study the high background mortality is viewed as an appropriate model for assessing the impact of these two toxicants on a natural population. From this it can be concluded that hydropsychid larvae up to 9 days old are not particularly sensitive to toxic stress due to either 4,5,6-TCG or arsenite. This lack of sensitivity occurred only because of the compensatory population mechanism involved and had little to do with an actual toxicant tolerance.

A central theme in the relatively new discipline of ecotoxicology is the greater degree of scientific sophistication and knowledge that is required. An example of this is the recognition that the effect of a toxicant on population processes over a life cycle, not just mortality, is an important consideration.

Unfortunately, the organisms most commonly used, *Daphnia* and *Ceriodaphnia*, have mortality distributions quite different from most other aquatic invertebrates and fish. While bioassays such as the 21-day or 7-day *Daphnia* tests may be an improvement over short-term acute bioassays, it is not certain that these data will be enough to predict the effect on natural populations. In the preceding discussion we have tried to go beyond the count-the-bodies approach that dominates research in this area and suggest that the distribution of deaths over a life cycle can affect our interpretation of the effect of toxic substances. While there have been several thoughtful discussions by population ecologists on death (Slobodkin 1961; Hutchinson 1978) there are no similar discussions by toxicologists or ecotoxicologists.

8.2.3 The Survivor Effect at the Population Level

It is generally accepted that individuals that exist in an environment with toxic chemicals will have a greater tolerance to those chemicals, even though most of the evidence for this view has come from field observations of metal tolerance in plants and pesticide resistance in insects (Moriarty 1983). Tolerance to toxic chemicals can be explained in two ways depending on the time scale that is used. Over the short term only the hardier individuals in a stressed environment will survive. These will be more tolerant, more hardy than individuals from an unstressed population. Over a longer time interval, in terms of generations, tolerance occurs through selection of genotypes (see Sect. 2.7).

An example of the survivor effect was observed in the chronic study of *H. siltalai* exposed to arsenite. At 3920 µg/L arsenite, 93% of the first instar larvae died after 9 days of exposure, having an instantaneous mortality rate of 20%/day. However, over the following 248 days, the 37 larvae that survived the initial 9 day exposure had an average instantaneous mortality of 0.30%/day (Fig. 8.6, Table 8.1) which was slightly less than that in the control. Also the slope of the curve of mortality rate on ln arsenite concentration for day 9 through 257 was negative ($P=0.003$) not positive. The negative slope means that those that survived the highest concentration, and there were few who did, were resistant to arsenite during the remainder of the experiment. Those that survived the initial 9 day period were exhibiting the "survivor effect" (Stewart 1985).

The survivor effect was coined to describe the statistical impact of collecting data on the human survivors of the Hiroshima atomic explosion in 1945 where only a small number of very fit individuals survived (Stewart 1985). Follow-up studies of those that survived the blast have shown that the incidence of radiation-related disease such as leukemia is statistically lower in this group than in the normal population at large, exposed to the same conditions. Stewart (1985) also pointed out how this was misused to set standards of exposure. The survivors of Hiroshima had a low incidence of radiation disease not because of a low hazard but because the study group which survived was exceptionally resistant to radiation disease.

In the study of the caddisflies, the high dosages of arsenite eliminated all but a small group of very fit, and tolerant larvae. There was no indication of a survivor effect among the larvae that survived the highest concentration of 4,5,6-TCG (Fig. 8.6). At 264 µg/L TCG 87% of the larvae died during the first 9 days. But of the 141 larvae that survived the initial 9 day exposure all were dead after an additional 75 days, having a mortality rate of 1.9%/day. This contrasts with not only the survivorship of the larvae at the highest arsenite concentration, but with the arsenic survivors having reduced sensitivity. This may indicate a significant difference in the toxic mechanism at the population level of the two chemicals.

It is already known that physiologically the two chemicals have very different toxic mechanisms. Arsenite is highly water soluble and as with arsenicals in general, is able to combine with essential mercapto-groups also called sulphhydryl-groups, thiol-groups or SH-groups, by the formation of a covalent As-S bond (Albert 1985). Enzymes such as lipoic acid dehydrogenase and pyruvate oxidase which have cysteine thiol-groups are then particularly sensitive to arsenic poisoning. The 4,5,6-TCG is mildly hydrophobic and an uncoupler of mitochondrial oxidative phosphorylation (Lundberg et al. 1980). Uncoupling occurs by the transport of hydrogen ions across the inner mitochondrial membrane until its resting potential is discharged (Albert 1985). Albert (1985) in his treatise on selective toxicity recognizes only one class of substances that are not highly sensitive to small changes in structure. These are the biological depressants which include the hypnotics, general anaesthetics and volatile insecticides. These substances tend to be, like 4,5,6-TCG, soluble in lipids and particularly active in cells rich in lipids. They tend to depress many cellular functions in most forms of life, which is probably due to their lipid solubility. However, biological toxicity tends to be parabolic not linear with lipid solubility. A substance that has no solubility in water will be bound to the first lipid site it encounters (Hansch et al. 1968). This is important when considering the toxicity of 4,5,6-TCG which is only moderately lipid soluble, but is about three orders of magnitude more toxic to caddis-fly larvae than arsenite. Arsenite then may be classed as a selective toxicant since it tends to be specific towards sulfur containing enzymes while 4,5,6-TCG is relatively non-selective in that it disturbs membrane resting potential.

The reason that the hydropsychid larvae continued to die in the 4,5,6-TCG but became resistant to arsenic was most likely due to how this physiological difference acted at the population level. In the arsenic cultures those individuals that survived were able to cope with the attack on their thiol-group containing enzymes either by switching to other enzymes to perform the same function, producing more of the affected enzymes, producing thiol containing compounds or a combination of these and other mechanisms. In other words, there are most likely several ways to overcome a specific toxicant. However, in the 4,5,6-TCG cultures a much more complicated physiological attack, encompassing a general class of cellular functions involving lipid membranes, had to be overcome.

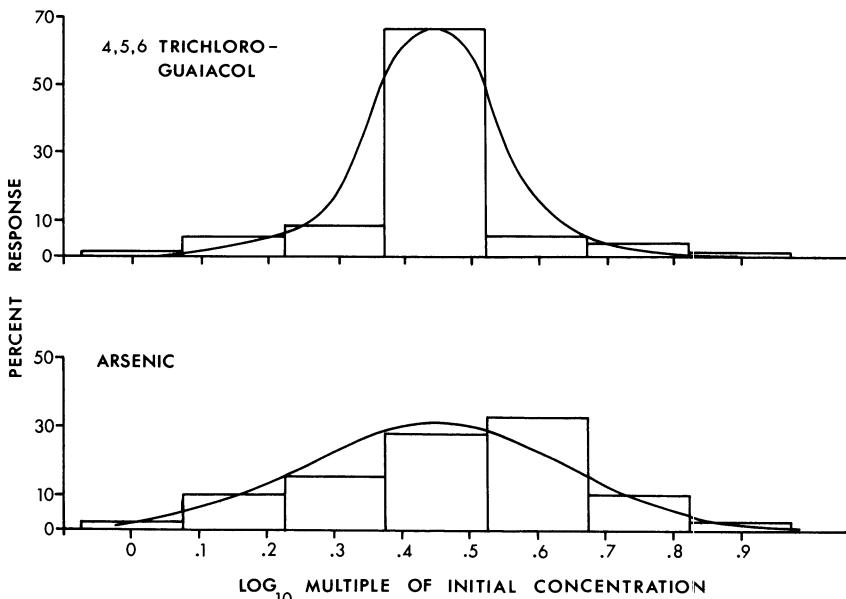


Fig. 8.7. Comparison of the population response of *Hydropsyche siltalai* to lethal concentrations of sodium metaarsenite and 4,5,6 trichloroguaiacol. The abscissa shows the log multiples of the no-effect concentrations for each toxicant. The curves are the least squares solution of the proportion of the total population responding within a concentration range to a normal distribution

A further indication of the difference between a specific versus a non-specific toxicant is the lower variation in the percent responding to the non-specific than the specific toxicant. This is illustrated in Fig. 8.7 where the toxicity of arsenite and 4,5,6-TCG to *H. siltalai* in an acute 96-h test are compared. The concentrations for both toxicants were standardized multiples from the no-effect concentration to 100% responding. The proportion responding at each concentration was expressed as the proportion responding within each concentration by subtraction. The percent responding was then fit to a log-normal distribution. The width of the bell shaped curve, i. e. the variance of the normal distribution, also represents the inverse of the slope of the ln dose response curve (Finney 1947). In Fig. 8.7 4,5,6-TCG had a significantly lower response variance ($\log F$ -test, $P < 0.05$) than arsenite. The narrow response range for 4,5,6-TCG indicates that it was acting on individuals in a more uniform manner. If it is assumed that this uniformity of response is a measure of the genetic variability within the population to survive in the presence of a toxic substance then there was greater genetic variation among individuals to withstand toxic poisoning caused by arsenite than by 4,5,6-TCG.

8.3 Assessment of Toxic Effects at the Community Level

8.3.1 *Community Analysis*

Analysis of communities generally falls into three major types, consisting of (a) an expected relationship between species and abundances described by an index of diversity, such as the Shannon (Shannon 1949) and Margalef (Margalef 1957) index, (b) an expected presence or absence of indicator species expressed as an index such as the Saprobiec (Sladecek 1973), Chandler (Chandler 1970), or Trent (Woodiwiss 1978) index, and (c) a comparison of communities between locations with such measures as the Sørensen (Sørensen 1948) or Czekanowski Percentage Similarity Index (Goodall 1978). Regardless of the technique used, assessment of effects at the community level usually involves the counting of species just as most assessment approaches at the population level involves counting bodies.

The most serious drawback to community analysis in the aquatic environment, as in other habitats, is the lack of objective criteria. These are criteria which define a community when not in the presence of an environmental disturbance. While this problem can be lessened with control locations and preimpact studies, the normal variation in community structure presents a problem in determining toxic action at the community level. In addition, community techniques are unable to measure changes in the ecological interactions between species caused by a toxicant. While the importance of these interactions to community structure is one of the most controversial topics in community ecology today (Lewin 1983) understanding the effects of toxic substances on biotic interactions is an area which remains to be explored in environmental hazard assessment.

Regardless of the technical drawbacks, the analysis of whole communities, i. e. species lists, is of limited use in hazard assessment since it is difficult to attach biological meaning to changes in the available indices (Moriarity 1983). Woodiwiss (1978) described the shortcomings of community indices when he said his Trent Index, one of most widely used indices in western Europe, should not replace the detailed knowledge of the biologist on the organisms present. This warning should also apply to diversity indices which are widely used in the United States, and the saprobic index widely used in eastern Europe.

In the following sections we will illustrate how 4 areas of community ecology can be used in effect assessment. However, community ecology as a subdiscipline of ecology, is going through a period of development and considerable controversy exists concerning the underlying principles (Lewin 1983; Strong et al. 1984; Salt 1984).

8.3.2 *The Guild: A Community Tool for Complex Ecological Interactions*

The advantages of the detailed specificity of single species toxicity testing and the holistic benefits of community analysis can be combined in an analysis of a

small group of ecologically related species, a guild (Petersen 1986). This is essentially the approach of using mesocosms (*sensu* Odum 1984 also referred to as microcosms see Giesey 1980, see also Chap. 10) where a reduced number of species are investigated and is the approach suggested here.

The term guild as originally defined (Root 1967) refers to a group of species that use resources in a similar way. This term has become popular in the ecological literature and its original definition, correctly or incorrectly, has been broadened to refer to taxonomically related species found in the same habitat with little regard to similarity of niche requirements (Jaksic 1981).

Guilds that are to be used in assessment of ecological effects should be selected with some practical considerations in mind (Table 8.2). The net-spinning caddisfly larvae of the genus *Hydropsyche* are a guild of aquatic insects which demonstrate these practical considerations and have been used in toxicological studies in Sweden (Petersen and Petersen 1983, 1984; Petersen 1986).

For a guild to be a useful tool it must be a fairly well known and common member of the community, found in a variety of habitats, from clean to polluted, and over a wide geographical area. Taxonomically the Hydropsychidae are well known in Scandinavia (Svensson and Tjeder 1975; Petersen 1981), Europe (Tobias 1972a,b; Schmid 1968) and North America (Wiggins 1977). There are more species of hydropsychids than of any other family of Trichoptera with 779 recognized species and 55 genera in 4 subfamilies (Higler 1981; Fischer 1973). The family is pandemic, known from all biogeographical areas. Members of the family tend to be one of the most common groups of stream benthic invertebrates (Wiggins 1977). As a family the hydropsychids are classified as "indeterminant" in most indicator species indices (Chandler 1970; Woodiwiss 1978). This is because within the family there are some tolerant species and some sensitive species. For example, *H. saxonica* is a rare species in Sweden and is restricted to pristine, small woodland streams. It has been reported as having become extinct in England (Badcock 1976). *H. angustipennis* by comparison is probably the most tolerant species among the Scandinavian

Table 8.2. Practical considerations for the selection of guilds to be used in the assessment of the effects of toxic effluents on natural communities

Consideration	Definition
Taxonomic simplicity	Choose a group of species for which the taxonomy is either simple or well known.
Commonness	Choose a group of species which are common in both pristine and disturbed environments.
Sensitivity	The guild should exhibit a wide range of sensitivities within its members
Available literature	There must be a considerable depth of published knowledge concerning all aspects of the biology
Lab/field practicality	The group of species must be practical to study under both field and laboratory conditions.

Table 8.3. Downstream change in the density of hydropsychid larvae (number/m²) below Vassen, an eutrophic pond in southern Sweden. The Shannon diversity is calculated for all benthic macroinvertebrates found

Species	Distance Below Pond (m)			
	10	100	500	1500
	Number/m ²			
<i>H. angustipennis</i>	7000	1000	100	50
<i>H. siltalai</i>	0	10	200	100
<i>H. pellucidula</i>	0	0	40	50
Shannon diversity	.	1	2	3

Table 8.4. Diversity measures of the macroinvertebrate fauna at the 5 study locations on the Kolbäcksån river in central Sweden (data recalculated from Wiederholm et al. 1983)

Location	Diversity Measures			
	N	S	H	J
5 Smedjebacken	268	10	1.01	0.43
4 Fagersta	18,802	12	0.55	0.22
3 Trångfors	6004	21	1.40	0.46
2 Sörstafors	957	17	1.52	0.54
1 Strömsholm	616	26	2.34	0.72

N the number of individuals observed on 4 multiplate samplers; S the number of taxa; H Shannon diversity; J evenness.

and northern European species (Badcock 1976). In Sweden it can be found in large numbers under polluted conditions being joined by *H. siltalai* and *H. pellucidula* in order of sensitivity as conditions improve (Table 8.3).

The *Hydropsyche* were used to compare the guild concept to more commonly used community analysis techniques in the Kolbäcksån, a river located in central Sweden with a history of heavy metal pollution (Ahl 1980; Wiederholm et al. 1983; Bengtsson and Lithner 1981; Håkanson 1981; Petersen 1986). The community methods included several measures of diversity (Table 8.4). The guild analysis consisted of the individual size and instars of the hydropsychid species (Fig. 8.8). Both were examined at 5 locations downstream the major source of heavy metal pollution.

All diversity indices showed the same general trend: namely an increase in diversity going downstream the major effluent of heavy metals at Smedjebacken (location 5) towards Strömsholm (location 1) (Table 8.4). The downstream increase in community species diversity away from a toxic source has been commonly observed in streams (Sheehan and Winner 1984) and is commonly referred to as recovery (Hynes 1970). When the species lists for the 5 locations were compared using both the Sørensen index and the Czekanowski index, both indices gave identical clusters of community similarity and similar information about the relative differences between locations (Petersen

1986). This information was also similar to that provided by the community indices. There was an increase in similarity of species occurrences in a downstream direction below the source.

Using the whole community indices it is difficult to conclude more than there was a change in the benthic community downstream Smedjebacken. There is no possibility to analyze changes in individual growth rates, alterations in competitive interactions nor how extensive the recovery was. In contrast, it is possible to discuss changes in the hydropsychid guild structure and relate these changes to the degree of heavy metal pollution.

Starting at location 1 and going upstream towards the pollution source at location 5 there was a loss of one species of hydropsychid, *H. pellucidula*, and a reduction from 10 to 6 species-specific instar size-classes for the entire guild (Fig. 8.8). *H. siltalai* was the most responsive species in that it demonstrated the greatest variation in abundance going from 887 larvae per 4 samples at Trångfors to 7 at Fagersta. The variation in abundance over the 5 locations was significantly higher ($F > 200$; $P < 0.001$) for *H. siltalai* than for either of the other two species.

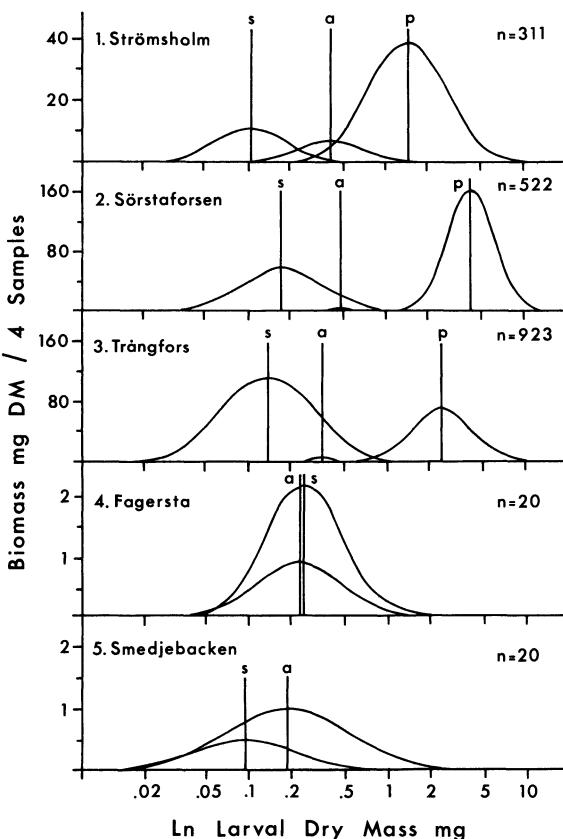


Fig. 8.8. Biomass (mg dry weight/4 multiple plate samples within each larval instar for the three coexisting species of *Hydropsyche* at the five locations on the Kolbäcksån River. Data has been fitted to a log-normal curve. Each vertical bar indicates the mode of each normal distribution for *H. siltalai* (s), *H. angustipennis* (a) and *H. pellucidula* (p), n refers to the total number of larvae found at each location (from Petersen 1986 with permission)

H. siltalai seemed to benefit most from the reduction in abundance of the other species, while demonstrating greater tolerance to the metal stress. Going upstream towards the pollution *H. siltalai* first increased in abundance reaching a maximum at Trångfors. It then became reduced at Fagersta and Smedjebacken. Its life cycle was also advanced at locations closer to the pollution as there were more mature larvae at the more upstream locations. No instar V larvae were found at the downstream Strömsholm location while approximately 2% of the population consisted of instar V at both Fagersta and Smedjebacken. This tends to support the idea that *H. siltalai* experienced faster growth rates, as competing species were eliminated.

H. angustipennis seemed to be the most indifferent of the three species. It was found at all 5 locations with an abundance that ranged from 11 larvae at Fagersta to 62 at Strömsholm. There was no statistical difference in the abundance over the 5 locations for *H. angustipennis* (Kruskal-Wallis ANOVA; $P > 0.05$).

For each population the distribution of larval biomass over its instars reflects that population's ability to exploit resources. Hydropsychids, with a smaller average size, will exploit smaller sized food particles than a population of larger sized individuals. This follows from the mechanisms of niche separation between coexisting species and assumes that the utilization functions for several closely related species can be approximated from information on the size of the organisms (May and MacArthur 1972).

The biomass distribution of larval hydropsychids at each location in the Kolbäcksån was calculated by multiplying the number of larvae in each instar by its weight, fitted to a normal curve (Kolb 1982) and plotted for the 5 locations (Fig. 8.8). The mode of each distribution is the size of the average individual in each population and is presented in Fig. 8.8 as a vertical bar. At Strömsholm the modes of the normal curves for the three populations are separated by distances along the log-transformed weight axis by distances of 1.3 between *H. angustipennis* and *H. pellucidula* and 1.3 between *H. siltalai* and *H. angustipennis*. These distances are indices of species packing and conform to the theoretical expectations of niche separation (May and MacArthur 1972) as to how similar two species can be to coexist. Niche overlap is measured by the ratio of the separation of the modes and the variance about each mode. Graphically this can be seen in Fig. 8.8 as the distance between the mode lines and the width of each normal curve. Moving upstream with increasing pollution, niche separation distance between *H. siltalai* and *H. angustipennis* was reduced as overlap increased. At Fagersta, with the elimination of *H. pellucidula*, there is complete overlap between the two remaining species *H. angustipennis* and *H. siltalai*. This also occurs at Smedjebacken but the modes are slightly separated. Also at Smedjebacken *H. angustipennis* is the dominant species. It is both the most numerous and physically the larger. At all other locations *H. angustipennis* was larger but not more numerous.

The reduction in abundance that occurred in *H. pellucidula* resulted in more resources becoming available for *H. siltalai* larvae. The fact that at the most polluted locations, Fagersta and Smedjebacken, the abundance of *H. siltalai*

was reduced while *H. pellucidula* was eliminated supports the suggestion that tolerance differences to metal pollution between species changed the level and outcome of interspecific interactions.

8.3.3 The Specialist-Generalist Concept Applied to Hazard Assessment

The terms specialist and generalist are commonly used in a relative sense to indicate that a particular species specializes in a particular niche dimension relative to another species. In general, natural selection will favor specialists when resources are abundant and generalists when resource are scarce (Mayr 1942; MacArthur and Wilson 1967; Maynard-Smith 1974; Pianka 1983).

At the community level, the broader niche of the generalist translates into greater tolerance to environmental disturbance. Woodwell (1970) has suggested that the changes in natural ecosystems caused by different types of disturbances are similar, predictable, and includes the survival of species which occur under a wide range of conditions, the generalists. This is because the disturbance, whether it be man made or natural, effects organisms in similar ways and allows species that have evolved the ability to survive under diverse conditions to survive even if the perturbation has never been observed. Levins (1968) gives the example of tolerance to heat death. Part of the cause of heat death is anoxia. A species may resist high temperature by some tolerance to anoxia, by, for example, evolving additional or alternate enzymes of the cytochrome system. It would then also be tolerant to anoxia caused by specific poisons of the cytochrome system which it has never met before. Generalists would be more likely to have these alternate systems.

One probable reason for the difference between specialist and generalist species is that generalist species should possess a greater genetic heterogeneity compared to specialist species. Confirmation of this assumption comes from studies of the cheetah, *Acinonyx jubatus*, a specialist now restricted to two populations in southern and eastern Africa. A genetic survey of over 200 structural loci revealed that the cheetah has 10 to 100 times less genetic variation than other mammalian species (O'Brien et al. 1985). The low genetic diversity seems to be related to the overall sensitivity of this species. In 1983 a breeding colony of cheetah was decimated when a coronavirus-associated feline infectious peritonitis broke out in the colony. By comparison the common house cat has a morbidity of approximately 1 percent when exposed to the coronavirus (O'Brien et al. 1985).

Petersen (1986) has documented that within the genus *Hydropsyche* specialized species with a narrow niche width are more sensitive to toxicants than generalists. In laboratory studies on the toxicity of copper to two species of *Hydropsyche*, damage to the anal papillae, the ion regulatory organs, was used as a measure of sublethal effect. In 96-h static bioassays for copper under conditions of 100 mg CaCO₃/L and 18 °C, the EC50 for *H. saxonica* was 18 mg/L and for *H. angustipennis* it was 27 mg/L as calculated according to the probit method (Finney 1947; Litchfield and Wilcoxon 1949). The results of the dupli-

cated runs for the 8 test concentrations were reconfigured to represent the percent of the test population responding in each interval of copper and plotted as the normal distribution (Fig. 8.9). The modes of the two distributions are the same as the estimated EC₅₀ values for each species. In addition, the width of each bell shaped curve in Fig. 8.9 is a measure of the variance within each population of sensitivity to copper. The variance about the mode of the distribution was wider for the more tolerant species. The ecologically more sensitive species, *H. saxonica*, not only had a lower tolerance to copper than its congener with which it occurs but there was a lower variation within the population to copper stress. In a sense we can refer to generalist species which have a broad tolerance to toxic substances as eurytoxic species and specialists with a narrow tolerance as stenotoxic as illustrated graphically in Fig. 8.9.

In order to test whether generalists within a community are the ones best able to survive under pollution stress the benthic invertebrate data from 16 locations in the Kolbäcksån River system (Wiederholm et al. 1983) was reanalyzed. For each taxon found, the number of locations at which that taxon occurred was determined and the frequency distribution of number of taxa found at 1 through 16 locations plotted (Fig. 8.10 A). The terms generalist and specialist were then arbitrarily defined: the generalist as a taxon found at many locations and the specialist as one found at few. A taxon found at only one location out of 16 is more specialized than a taxon found at all 16 locations. In Fig. 8.10A there are many more specialist taxa within the Kolbäcksån system than generalist. The number of locations at which a taxon occurred was then used to assign each taxon a specialist-generalist score which had a range from 1 to 16. These scores were then used to determine if the species present at a polluted location (Fig. 8.10 B) and a recovered location (Fig. 8.10 C) were specialists or generalists. The polluted location was Smedjebacken (Table 8.4), a location polluted with heavy metal discharges (see Sect. 8.3.2) which not only had a reduction in the number of species but those species remaining tended to be

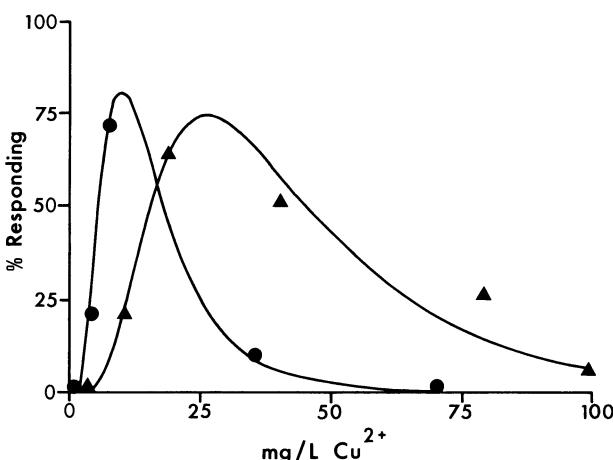


Fig. 8.9. Comparison of the population response as measured as the percent showing anal papillae damage to copper. The narrow bell-shaped curve is for the specialist *H. saxonica* which can be referred to as a stenotoxic species. The wider bell-shaped curve is for a population of the generalist *H. angustipennis* and can be referred to as a eurytoxic species (from Petersen 1986 with permission)

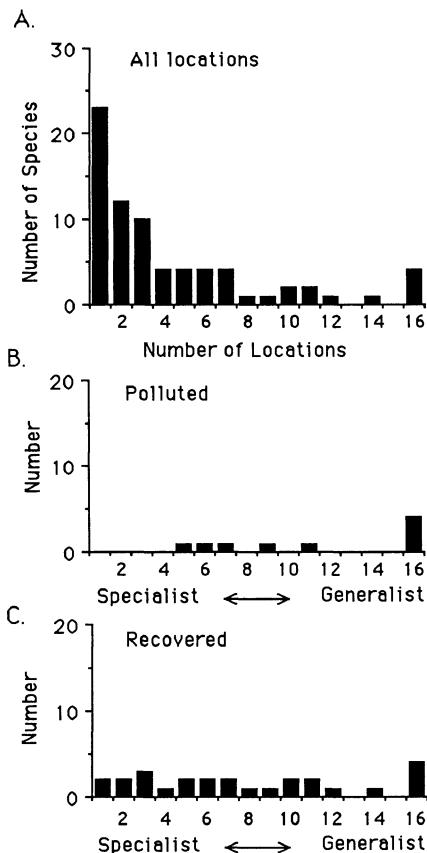


Fig. 8.10. A Frequency distribution of habitat specialists and generalists in the benthic fauna of 16 locations in the Kolbäcksån river system. Each taxon was then assigned a score equal to the number of locations out of 16 at which it occurred. B The benthic fauna at a polluted location, Smedjebacken, consisted only of species which occurred at many locations, generalists. C The recovered location, Strömsholm, had both specialist and generalist species present

generalists. The recovered location, Strömsholm, showed a much more even distribution between specialist and generalist species. The major difference between the locations is the lack of specialist taxa. Generalist taxa occur just as frequently at polluted as clean locations.

8.3.4 Role of Keystone Species in Effect Assessment

The term keystone species was first used by Paine (1969) to describe the importance of the starfish (*Pisaster ochraceus*) in structuring the rocky intertidal community on the Pacific Northwest of the United States. Paine physically removed the starfish, an abundant carnivore, at low tide and observed that significant changes occurred in the community such as increased population density of a few species, a general reduction in species richness, and a change in the overall physical appearance of the community. Additional evidence suggested that equivalent changes did not occur in communities where the starfish

were not removed. Paine's idea was that this one species had a disproportionate role in structuring the entire community and was similar to the keystone in a roman arch. Removal of this one stone and the entire arch would collapse.

When Paine first reported this observation it was somewhat counter to the prevailing ecological doctrine of the time, which focused on the pyramidal nature of ecological communities in which energy flowed to the top carnivore (McIntosh 1985). Now, here was a carnivore which maintained the high diversity and structure of the community. The perception of the ecological function of predators changed dramatically.

Similar observations have been made in other ecosystems. Morin (1986, 1987) and Wilbur et al. (1984) have studied the effect of predation on structuring pond communities using mesocosms. Morin (1987) demonstrated that the pond dwelling salamander *Notophthalmus viridescens*, a predator of tadpoles, will facilitate the growth and survivorship of the tree frog tadpole, *Hyla crucifer*. *Hyla* is a poor competitor and when embedded in frog tadpole guilds tends to grow poorly and to be rare and reclusive. When Morin (1987) compared the success of *Hyla* in the presence of several tadpole species, with and without the predator *Notophthalmus*, *Hyla* did best in mesocosms with the predator present. The reclusive behavior and small size of *Hyla* gave the tadpole a certain measure of protection against *Notophthalmus*. *Notophthalmus* functioned as a keystone species structuring the tadpole guild.

Sometimes humans are directly responsible for the removal of a keystone species and the rather dramatic ecological shifts that follow. The sea otter (*Enhydra lutris*) of the Pacific Northwest coast feeds preferentially on the sea urchin (*Strongylocentrotus polyacanthus*). During the period 1741 to 1911 it was hunted to extinction by man for its fur. When the sea otter disappeared, its main food item, the sea urchin, increased in abundance and reduced the abundance of its main food species, the macroalgae *Laminaria* spp. and *Agarum cibrosum*. Elimination of the macroalgae in the coastal waters reduced the spatial complexity of the benthos and caused the collapse of the entire benthic community. Diversity and abundance of almost all species decreased dramatically. Estes et al. (1978) have followed the effect of the reintroduction of the sea otter to the Aleutian Islands, Alaska and report that even a small number of sea otters have been able to decrease the sea urchin population with a parallel increase in benthic community diversity.

In addition to direct human interference with natural communities such as hunting, environmental disturbance on a global scale can affect keystone species and thus change the structure of ecological communities. In Swedish oligotrophic lakes well established fish populations can control both the abundance and distribution of the invertebrate predators (Stenson and Oscarson 1985; Henrikson and Oscarson 1978). Predator species such as the phantom midge, *Chaoborus* (Neill 1981), water beetles in the family Dytiscidae (Arts et al. 1981) and water boatmen in the family Corixidae (Nyman et al. 1985) have been named as important predators of zooplankton. In acidified lakes, which experience a reduced fish population, these macroinvertebrate predators

can increase in number due to reduced predation pressure which then alters the zooplankton population.

Not only are certain species important to the structure of entire aquatic communities but within sub-communities, guilds, certain species can have an important role through competitive interactions on other species. In the preceding discussion of the guild analysis, Petersen (1986) has shown that heavy metal pollution in the Kolbäcksån River not only reduces the number of species present and alters community diversity but also alters species packing of the community. This can be accomplished by removing some species which are more sensitive to metal pollution than others. The more resistant species are then released from the competitive pressure by intolerant species. In the Kolbäcksån example, *H. pellucidula* emerges early and attains the instar V class before the rest of the guild. It is physically larger than the other species as the guild enters the fall. Throughout the winter this species functions as the dominant with the other two species essentially having to wait for *H. pellucidula* to emerge.

Within the hydropsychid guild *H. pellucidula* is the keystone species to guild structure. Its removal by metal pollution changed the structure of the guild which at Fagersta resulted in; (1) an increase in abundance of *H. siltalai*, (2) a reduction in niche separation between *H. siltalai* and *H. angustipennis*, (3) an increase in growth rate and advancement of the life cycle of *H. siltalai* and (4) an increase in the niche overlap between *H. siltalai* and *H. angustipennis*. Heavy metal pollution in the Kolbäcksån River not only removed species but eliminated a keystone species, *H. pellucidula*, which further altered community structure.

8.3.5 The Survivor Effect at the Community Level

It is well established that aquatic populations can increase their tolerance to toxicants (Jensen et al. 1974; Brown 1976; Fraser et al. 1978; Stokes 1981, 1986). This may be due to selection of hardy genotypes, or survival of hardy individuals, the survivor effect. However, there is also evidence that communities, through a change in species composition also increase their tolerance to toxicant stress. In analogy to the idea of the survivor effect for a population where individuals are selected, an entire community may demonstrate the survivor effect by the selection of more tolerant species. In the CEPEX program, Thomas and Seibert (1977) added copper to enclosed pelagic communities and found a replacement of centric diatoms by microflagellates and pennate diatoms. Photosynthesis of the new plankton community had a higher copper tolerance and was related to the preexposure concentration (Harrison et al. 1977). Blanck et al. (1988) have shown that a toxicant that exerts selection pressure on a periphyton community will restructure it and give rise to Pollution-Induced Community Tolerance (PICT). The tolerance increase was assessed by a short-term test system measuring the inhibition of periphyton photosynthesis. Furthermore the tolerance increase was fairly specific, with significant co-tolerance only for toxicants that were closely related chemically or by mode of action (see further discussion in Chap. 10).

8.4 Assessment of Effects at the Ecosystem Level

8.4.1 Stress and Ecosystems

For the moment, let us consider a general framework for determining the effect of toxic substances on biological systems. In most toxicological studies this centers on the toxic substance in question and results in experiments to measure the effects on the system. For determining the effect on a community this approach requires experiments using microcosms or mesocosms depending on the chosen scale (cf. Chap. 10). However, it can be suggested that this approach may be impractical when large-scale systems, i. e. communities, ecosystems, biomes, are under consideration or when the ecological realism of the test system is in question.

As an alternative, the system response by itself and not the stimulus to the system can be considered. This is essentially the approach when one considers ecosystem behavior under stress. The study of stress in ecology seeks to determine the response of a biological component to a stress. The biological component may be the individual (Selye 1973, 1974) or the ecosystem (Rapport et al. 1985). Fortunately, the study of the stress response at the individual level is directly analogous to the study of stress at the higher order organization level (hierarchy) of the ecosystem. It can therefore be suggested that the ecological concept of stress is related to effect assessment and both can be viewed hierarchically.

Not all symptoms of ecological dysfunction occur or are detectable under every instance of toxic chemical contamination. Detection is a practical limitation and may be due to lack of technology, theory, money or all three. Screening for effects should not be based on any single parameter or even a group of parameters from one level of organization. Instead, a set of parameters spanning several levels of system structure should be developed. This approach has been suggested for determining ecosystem damage (Rapport et al. 1985). Odum and Cooley (1980) suggest that for ecosystem damage a group of indicators be formed into a profile based on normal values. These values are dependent on the type and age of the system similar to the profiles used by hospitals for patients. Just as doctors routinely screen patients by examining a battery of physiological parameters, the determination of ecosystem health requires screening for a group of indicators rather than reliance on a single indicator. It is recognized in both cases that the direction of deviation is less important than the magnitude (Rapport et al. 1985).

8.4.2 Cumulative Environmental Effects

The current approach to assessment of chemicals by both researchers and government agencies focuses primarily on the environmental effects of single events and spends little time considering cumulative effects (National Research Council 1986). A cumulative effect in this context is the sum of several inde-

pendent or interrelated insults to a biological system. Odum (1982) has borrowed the idea of cumulative effects from economists who refer to this as the "tyranny of small decisions" where the sum effect of many small, independently made decisions does not take into consideration the effect on the whole. In the assessment of chemicals in the environment, cumulative effects should refer to both the effect of all toxic chemicals present and the combined effects of changes in ecological structure at the population, community and ecosystem level. The effect of toxic mixtures has received considerable attention (Marking 1985), but the biological effects are still poorly understood (Moriarty 1983) and the cumulative effect of both chemical and biological perturbation is still to be investigated.

Acidification of inland waterways is a prime example of the problem of cumulative effects. In 1981, 18,000 lakes and 90,000 kilometers of running waters in Sweden were reported to have pH values so low that damage could be expected (Dickson 1985). The source of the acid rain comes primarily from sulfur deposition from 11 countries, combined with a 10% contribution from Sweden itself. This has resulted in, over the last 20-year period, a decrease in the pH of surface waters ranging from 0.6 pH units in southern Norway (Økland 1980) to 0.35 pH units in Sweden (Andersson 1980). This reduction has been linked to reduced fish populations and decreased forest productivity as well as many other smaller ecological changes (Drablos and Tollan 1980; Swedish Environmental Protection Board 1986). In addition to the direct effects of a lowered pH on soil and surface waters there is also a growing list of secondary effects. Recently Petersen and colleagues (Petersen and Kullberg 1985; Petersen et al. 1986, 1987; Petersen and Persson 1987) have suggested that the acidification of surface waters can lead to the biological mobilization of both naturally occurring dissolved organic compounds and xenobiotics.

The impact of cumulative effects are difficult and expensive to study but will be of increasing importance in the area of effect assessment. In the foregoing discussion the effect of removing the sea otter, starfish or salamander from a community was enough to cause large changes in community structure. In the three examples given, a predator by its presence was allowing a greater number of species to coexist than when it was not present. However, in the example of the metal polluted Kolbäcksån River, there was at the benthic community level a cumulative effect of both the toxicity of the discharged heavy metals and the ecological damage due to the loss of a keystone species. Add to these ecological and chemical effects, the reduction in pH of surface waters, and problem of cumulative effects takes on a new meaning.

8.5 Decision Rules for Interpreting the Effects of Chemicals

We can conclude this discussion with a series of recommendations or decision rules to help in the interpretation of chemical effects data on aquatic systems. The primary use of these rules should be as a series of ecological warnings when the effect of a chemical on a natural system has to be established and the

main source of data comes from a limited set of controlled laboratory experiments. A central theme in all the rules is that there are no short cuts in the understanding and interpretation of chemical effects data and that detailed knowledge of the organisms under question has to be available. Even though there is considerable disagreement within the discipline of ecology as to the relative importance of different ecological processes there is a central agreement that these processes can be studied and all contribute to the ecological system we observe.

Rule 1. Natural population mortality should be considered since it may mask the effect of a toxic chemical through compensatory mechanisms.

As shown in the above, density dependent or self-regulating mechanisms are important processes in population ecology and can not be overlooked when chemical effects are being assessed. The major consideration must be to know the type of mortality that the population normally experiences and when the major number of deaths occur. As was suggested, even though juvenile individuals may be more sensitive per se to a toxic chemical, this may or may not be important to the population or to the effect of a chemical on it.

Rule 2. Guilds of ecologically related species will provide more information on toxic effects than whole communities.

This recommendation is primarily a practical suggestion stemming from the belief that in order to be able to interpret the effect of a chemical on a biological system, ecological information has to be available at more than one level of organization. This was illustrated with the hydropsychid caddis-flies where information on individual species sensitivity was combined with knowledge of how several species coexisted and this provided greater insight to the level of environmental disturbance.

Rule 3. Species with broad ecological niches (generalists) will be more tolerant to toxic stress (eurytoxic) than species with narrow specialized niches.

This recommendation can be used both to detect changes in community organization and to predict which species will be affected most by a level of disturbance. It is assumed that specialized species are operating with a genome with relatively lower genetic heterogeneity than a generalist and, while this may be beneficial when resources are plentiful and the environment is hospitable, it puts these species at a disadvantage in disturbed and toxic environments. Proof for this assumption is fragmentary with the best example to date coming from the African cheetah. However, determining which species are specialists in a particular system is not difficult and may be useful for the interpretation of chemical effects.

Rule 4. The keystone species and the effect of a toxic chemical on it is important to identify in an aquatic system.

The point of this rule is that not all species are of equal ecological value to the existing community structure. In a practical sense it reinforces the need for detailed ecological knowledge of individual species. While there have been sev-

eral rather interesting and recent ecological studies of the role of keystone species in ecological systems, this concept has not been adapted for use in assessment protocols. It can be recommended that the identification of keystone species in either guilds or communities may be a useful addition to effects assessment.

Rule 5. Structural properties (i. e., diversity) of communities are less conservative (homeostatic, resistant, resilient) and will be affected first and to a greater extent by a toxic agent than functional properties (i. e., community metabolism)

At the community level, a change in structure, the loss of species, tends to occur before a change in function. This is primarily because system function is a process performed by several if not many species. Loss of some of these species will not change the ability of the remaining species to carry out the function, it may actually improve the ability of the remaining species to exploit a particular resource. The evidence for this generality comes from many studies of ecosystems under stress (Rapport et al. 1985) and most notably by the work done in Canada (Schindler and Turner 1982, Schindler et al. 1985). In several studies with the addition of either acid or nutrients to lakes, Schindler and co-workers have shown that system function such as community metabolism was relatively unchanged even though the species composition of plankton and fish were changed to a large extent.

Rule No. 5 has been entered last but forms the basis for much of this entire chapter which has concentrated on the effects of pollutants on the ecology of species, their niche, and the nature of their interaction and competitive coexistence in the community. This as defined at the beginning of the chapter as the goal of ecotoxicology.

References

- Ahl T (1980) Investigations of the Kolbäcksån River drainage system: investigations of 1979. PM 1287. Swed Natl Environ Protect Bd, Solna, Sweden (in Swedish)
- Albert A (1985) Selective toxicity, 7th ed. Cambridge Univ Press
- Allen KR (1949) Some aspects of the production and cropping of fresh waters. Trans R Soc N Z 77: 222-228
- Anderson RM, May RM (1982) Population biology of infectious diseases. Springer Berlin Heidelberg New York
- Andersson G (1980) Long term changes in basic water chemistry in some Swedish lake regions. PhD Thesis, Inst Limnol, Univ Lund, Sweden
- Arts MT, Maly EJ, Pastschniak M (1981) The influence of *Acilius* (Dytiscidae) predation on *Daphnia* in a small pond. Limnol Oceanogr 26: 1172-1175
- Azam KM, Anderson NH (1969) Life history and habits of *Sialis rotunda* and *Sialis californica* in western Oregon. Ann Entomol Soc Am 62: 549-558
- Badcock RM (1976) The distribution of Hydropsychidae in Great Britain. In: Malicky H (ed) Proc 1st Int Symp Trichoptera. Junk, The Hague, pp 49-58
- Begon M, Townsend C, Harper J (1986) Ecology: individuals, populations and communities. Blackwell, Oxford
- Bengtsson Å, Lithner G (1981) Aquatic moss (*Fontinalis*) as a measurement of metal pollution. PM 1391. Swed Natl Environ Protect Bd, Solna, Sweden (in Swedish)

- Benke AC (1984) Secondary production of aquatic insects. In: Resh VH, Rosenberg DM (eds) *The ecology of aquatic insects*. Praeger, New York, pp 289–322
- Blanck H, Wängberg S-Å, Molander S (1988) Pollution induced community tolerance (PICT) – a new ecotoxicological tool. In: Cairns J, Jr., Pratt J (eds) *Functional testing of aquatic biota for estimating hazards of chemicals*. ASTM STP 988. Am Soc Test Mat, Philadelphia, pp 219–230
- Brown BE (1976) Observations on the tolerance of the isopod *Asellus meridianus* Rac. to copper and lead. *Water Res* 10: 555–559
- Burnham KP, Anderson DR (1984) Tests of compensatory vs. additive hypotheses of mortality in Mallards. *Ecology* 65: 105–112
- Butler GC (1978) *Principles of ecotoxicology*, Scope 12. John Wiley & Sons, New York
- Chandler JR (1970) A biological approach to water quality management. *Water Pollut Control* 69: 415–422
- Connell JH, Tracey JG, Webb LJ (1984) Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecol Monogr* 54: 141–164
- Cuffney TF, Minshall GW (1981) Life history and bionomics of *Arctopsyche grandis* (Trichoptera) in a Central Idaho stream. *Holarct Ecol* 4: 252–262
- Cummins KW, Wilzbach MA (1988) Do pathogens regulate stream invertebrate populations. *Verh Int Verein Limnol* 23: 1232–1243
- Deevey ES (1947) Life tables for natural populations of animals. *Q Rev Biol* 22: 283–314
- Dickson W (1985) Liming acidic waters: environmental and policy concerns. *Proc Conf, Center Environ Inf*, Rochester, N Y, pp 29–40
- Drablos D, Tolland A (eds) (1980) *Ecological impact of acid precipitation*. Proc Int Conf, SNSF Proj, Ås-NLH, Norway
- Estes JA, Smith NS, Palmisano JF (1978) Sea otter predation and community organization in the western Aleutian Islands Alaska. *Ecology* 59: 822–833
- Finney DJ (1947) *Probit analysis. A statistical treatment of the Sigmoid response curve*. Cambridge Univ Press
- Fischer FCJ (1973) *Trichopterorum catalogus*. Index vol I–XI, NEV Adam
- Fraser J, Parkin DT, Verspoor E (1978) Tolerance to lead in the freshwater isopod *Asellus aquaticus*. *Water Res* 12: 637–641
- Gieger J G, Buikema AL, Cairns J (1980) A tentative seven day test for predicting effects of stress on populations of *Daphnia pulex*. In: Eaton JG, Parish PR, Hendricks AC (eds) *Aquatic toxicology*, ASTM 707. Am Soc Test Mat, Philadelphia, pp 13–26
- Gieseck JB (1980) *Microcosms in ecological research*. DOE Symp Ser 52 CONF-781101. Natl Tech Inf Serv, Springfield
- Gillespie DM, Benke AC (1979) Methods of calculating cohort production from field data – some relationships. *Limnol Oceanogr* 24: 171–176
- Goodall DW (1978) Simple similarity and species correlation. In: RH Whittaker (ed) *Ordination of plant communities*. Junk, The Hague, pp 99–141
- Håkanson L (1981) Investigation of the Kolbäcksån River drainage system. XIII. Metals in fish and sediment. PM 1408. Swed Natl Environ Prot Bd, Solna, Sweden (in Swedish)
- Hansch C, Steward AR, Anderson SM and Bentley D (1968) The parabolic dependence of drug action upon lipophilic character as revealed by a study of hyponotics. *J Med Pharm Chem* 11: 1–11
- Harrison WG, Eppley RW, Renger EH (1977) Phytoplankton nitrogen metabolisms, nitrogen budgets, and observations on copper toxicity: controlled ecosystem pollution experiment. *Bull Mar Sci* 27: 44–57
- Henrikson L, Oscarsson HG (1978) Fish predation limiting the abundance and distribution of *Glaenocoris p. propinquua* (Hemiptera). *Oikos* 31: 102–105
- Higler LWG (1981) Caddis fly systematics up to 1960 and a review of the genera (Insecta: Trichoptera). In: Moretti G (ed) 3rd Int Symp Trichoptera. Junk, The Hague, pp 117–126
- Hutchinson GE (1978) *An introduction to population ecology*. Yale Univ Press, New Haven
- Hynes HBN (1970) *The ecology of running waters*. Univ Toronto Press
- Jaksic FM (1981) Abuse and misuse of the term “guild” in ecological studies. *Oikos* 37: 397–400

- Jensen A, Rystad B, Melsom S (1974) Heavy metal tolerance of marine phytoplankton. I. The tolerance of three algal species to zinc in coastal sea water. *J Exp Mar Biol Ecol* 15: 145–157
- Kolb WE (1982) Curve fitting for programmable calculators. Marlboro, Maryland
- Levins R (1968) Evolution in changing environments. Monographs in population biology, vol 2. Princeton Univ Press
- Lewin R (1983) Santa Rosalia was a goat. *Science* 221: 636–639
- Litchfield JT, Wilcoxon F (1949) A simplified method of evaluating dose-effect experiments. *J Pharmac Exp Ther* 96: 99–113
- Lundberg P, Renberg L, Arrhenius E, Sundström G (1980) Detoxication disturbances and uncoupling effects in vitro of some chlorinated guaiacols, catechols and quinones. *Chem Biol Interact* 32: 281–290
- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton Univ Press
- Margalef R (1957) La teoria de la informacion en ecologia. *Mem R Acad Barcelona* 32: 373–449
- Marking LL (1985) Toxicity of chemical mixtures. In: Rand GM, Petrocelli SR (eds) Fundamentals of aquatic toxicology. McGraw-Hill, New York
- May RM (1983) Parasitic infections as regulators of animal populations. *Am Sci* 71: 36–45
- May RM (1985) Regulation of populations with nonoverlapping generations by microparasites: a purely chaotic system. *Am Nat* 125: 573–584
- May RM, MacArthur RH (1972) Niche overlap as a function of environmental variability. *Proc Natl Acad Sci USA* 69: 1109–1113
- Mayer FL, Ellersieck MR (1986) Manual of acute toxicity: interpretation and data base for 410 chemicals and 66 species of freshwater animals. *Resour Publ* 160, US Dep Inter, Fish Wild Serv, Washington DC
- Maynard-Smith J (1974) Models in ecology. Cambridge Univ Press
- Mayr E (1942) Systematics and the origin of species. Columbia Univ Press, New York
- McIntosh RP (1985) The background of ecology: concept and theory. Cambridge Univ Press
- McKim JM (1977) Evaluation of tests with early life stages of fish for predicting long-term toxicity. *J Fish Res Bd Can* 34: 1148–1154
- McKim JM (1985) Early stage toxicity tests. In: Rand GM, Petrocelli SR (eds) Fundamentals of aquatic toxicology. McGraw-Hill, New York, pp 58–95
- Moriarty F (1983) Ecotoxicology. The study of pollutants in ecosystems. Academic Press, New York London
- Morin PJ (1986) Interactions between intraspecific competition and predation in an amphibian predator-prey system. *Ecology* 67: 713–720
- Morin PJ (1987) Predation, breeding asynchrony, and the outcome of competition among tree-frog tadpoles. *Ecology* 68: 675–683
- Mortensen E (1977) Density dependent mortality of trout fry (*Salmo trutta* L.) and its relationship to the management of small streams. *J Fish Biol* 11: 613–617
- Murton RK, Westwood NJ, Isaacson AJ (1974) A study of wood-pigeon shooting: the exploitation of a natural animal population. *J Appl Ecol* 11: 61–81
- National Research Council (ed) (1986) Ecological knowledge and environmental problem-solving. Natl Acad Press, Washington DC
- Neese J, Dugdale RC (1959) Computation of production for populations of aquatic midge larvae. *Ecology* 40: 425–430
- Neill WE (1981) Impact of *Chaoborus* predation upon the structure and dynamics of a crustacean zooplankton community. *Oecologia* 48: 164–177
- Nyman HG, Oscarson HG, Stenson JAE (1985) Impact of invertebrate predators on the zooplankton composition in acid forest lakes. *Ecol Bull* 37: 239–243
- O'Brien SJ, Roelke ME, Marker L, Newman A, Winkler CA, Meltzer D, Colly L, Evermann JF, Bush M, Wildt DE (1985) Genetic basis for species vulnerability in the cheetah. *Science* 227: 1428–1434
- Odum EP (1984) The mesocosm. *BioScience* 34: 558–562
- Odum EP, Cooley JL (1980) Ecosystem profile analysis and performance curves as tools for

- assessing environmental impact. In: Biological evaluation of environmental impacts. US Fish Wildl Serv, Washington DC, pp 94–102
- Odum WE (1982) Environmental degradation and the tyranny of small decisions. BioScience 32: 728–729
- Økland J (1980) Acidification in 50 Norwegian lakes. Nordic Hydrol 11: 25–32
- Paine RT (1969) A note on trophic complexity and community stability. Am Nat 103: 91–93
- Pennak R W (1953) Freshwater invertebrates of the United States. Ronald, New York
- Petersen LB-M (1981) Taxonomy, biology and ecology of the Hydropsychidae literature study. Pre-Doc Thesis, Inst Limnol, Univ Lund, Sweden [U Lund Libr coden LUNBDS/(NBLI-3046)]
- Petersen L B-M (1989) Resource utilization of coexisting species of Hydropsychidae. Arch Hydrobiol Suppl. 83, 1: 83–119
- Petersen LB-M, Petersen RC, Jr. (1983) Anomalies in hydropsychid capture nets from polluted streams. Freshwater Biol 13: 185–191
- Petersen LB-M, Petersen RC, Jr. (1984) Effect of kraft pulp mill effluent and 4,5,6-trichloroguaiacol on net spinning behavior of *Hydropsyche angustipennis*. Ecol Bull 36: 68–74
- Petersen RC, Jr. (1974) Life History and Bionomics of *Nigronia serricornis* (Say) (Megaloptera: Corydalidae). PhD Thesis, Michigan State Univ, East Lansing
- Petersen RC, Jr. (1986) Population and guild analysis for interpretation of heavy metal pollution in streams. In : Cairns J, Jr. (ed) Community toxicity testing, ASTM STP 920. Am Soc Test Mat, Philadelphia, pp 180–198
- Petersen RC, Jr., Kullberg A (1985) The octanol: water partition coefficient of humic material and its dependence on hydrogen ion activity. Vatten 41: 236–239
- Petersen RC, Jr., Persson U (1987) Comparison of the biological effects of humic materials under acidified conditions. Sci Total Environ 6: 387–398
- Petersen RC, Jr., Petersen L B-M (1988) Compensatory mortality in aquatic populations: its importance for interpretation of toxicant effects. Ambio 17: 381–386.
- Petersen RC, Jr., Petersen L B-M, Persson U, Kullberg A, Hargeby A, Paarlberg A (1986) Health aspects of humic compounds in acid environments. Water Qual Bull 11: 44–52
- Petersen RC, Jr., Hargeby A, Kullberg A (1987) Biological effect of humic material in acidified waters. SNV PM 3388. Swedish Environ Protect Bd, Solna, Sweden
- Pianka ER (1983) Evolutionary ecology. Harper & Row, New York
- Pritchard G, Leischner TG (1973) The life history and feeding habits of *Sialis cornuta* Ross is a series of abandoned beaver ponds (Insecta: Megaloptera). Can J Zool 51: 121–131
- Rand GM, Petrocelli SR (1985) Fundamentals of aquatic toxicology. McGraw-Hill, New York
- Rapport DJ, Regier HA, Hutchinson TC (1985) Ecosystem behavior under stress. Am Nat 125: 617–640
- Ricker WE (1946) Production and utilization of fish populations. Ecol Monogr 16: 373–391
- Ricker WE (1954) Effects of compensatory mortality upon population balance. J Wildl Manag 18: 45–51
- Ricklefs R (1973) Ecology. Chiron, Portland
- Roland J, Hannon SJ, Smith MA (1986) Foraging pattern of pine siskins and its influence on winter moth survival in an apple orchard. Oecologia 69: 47–52
- Root RB (1967) The niche exploitation pattern of the bluegray gnatcatcher. Ecol Monogr 37: 317–350
- Salt GE (1984) Ecology and evolutionary biology. Univ Chicago Press
- Schindler DW, Turner MA (1982) Biological, chemical and physical responses of lakes to experimental acidification. Water Air Soil Pollut 18: 259–271
- Schindler DW, Mills KH, Malley DF, Findlay DL, Shearer J A, Davies I J, Turner M A, Lindsey GA, Cruikshank DR (1985) Long-term ecosystem stress: the effects of years of experimental acidification on a small lake. Science 228: 1395–1401
- Schmid F (1968) La famille des arctopsychidae. Mem Soc Ent Quebec 1: 1–84
- Selye H (1973) The evolution of the stress concept. Am Sci 61: 692–699
- Selye H (1974) Stress without distress. Lippincott, New York
- Shannon CE (1949) The mathematical theory of communication. In: Shannon CE, Weaver W (eds) The mathematical theory of communication. Univ Illinois Press, Urbana, pp 29–125

- Sheehan PJ, Winner RW (1984) Comparison of gradient studies in heavy-metal-polluted streams. In: Sheehan PJ, Miller GC, Butler GC, Bourdeau Ph (eds) Effects of pollutants at the ecosystem level. SCOPE 22. John Wiley & Sons, New York, pp 255–271
- Sheehan PJ, Miller GC, Butler GC, Bourdeau Ph (eds) (1984) Effects of pollutants at the ecosystem level. Scope 22. John Wiley & Sons, New York
- Sladeczek V (1973) System of water quality from the biological point of view. Arch Hydrobiol Beih Ergebn Limnol 7: 1–218
- Slobodkin LB (1961) Growth and regulation of animal populations. Holt, Rinehart & Winston, New York
- Sørensen T (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. Biol Skr 5: 1–34
- Stenson JAE, Oscarsen HG (1985) Crustacean zooplankton in the acidified Lake Gårdsjön system. Ecol Bull 37: 224–231
- Stewart A (1985) Detection of late effects of ionizing radiation: why deaths of A-bomb survivors are so misleading. Int J Epidem 14: 52–56
- Stokes PM (1981) Benthic algal communities in acid lakes. In: Singer R (ed) Effects of acid precipitation on benthos. N Am Benthol Soc, Hamilton, New York, pp 119–138
- Stokes PM (1986) Ecological effects of acidification on primary producers in aquatic systems. Water Air Soil Pollut 30: 421–438
- Strong DR, Jr., Simberloff D, Alele LG, Thistle AB (1984) Ecological communities: conceptual issues and the evidence. Princeton Univ Press
- Svensson BW, Tjeder B (1975) Check-list of the trichoptera of north-western Europe. Ent Scand 6: 261–274
- Swedish Environmental Protection Board (ed) (1986) Air pollution and acidification: monitoring and research in Sweden concerning the effects and measures for mitigating them. Swed Natl Environ Protect Bd, Solna, Sweden
- Thomas WH, Seibert LR (1977) Effects of copper on the dominance and the diversity of algae: controlled ecosystem pollution experiment. Bull Mar Sci 27: 23–33
- Tobias W (1972a) Zur Kenntnis europäischer Hydropsychidae. I. Senckenberg Biol 53: 59–89
- Tobias W (1972b) Zur Kenntnis europäischer Hydropsychidae. II. Senckenberg Biol 53: 245–268
- Truhaut R (1977) Ecotoxicology: objectives, principles and perspectives. Ecotoxicol Environ Saf 1: 151–173
- Waters TF (1969) The turnover ratio in production ecology of freshwater invertebrates. Am Nat 103: 173–185
- Waters TF, Crawford GW (1973) Annual production of a stream mayfly population: a comparison of methods. Limnol Oceanogr 18: 286–296
- Wiederholm T, Ekström C, Fritzon A, Johansson C, Petersen RC, Jr., Svensson B, Söderström O (1983) Biological methods for recipient investigations in running waters. PM 1574. Swed Natl Environ Protect Bd, Solna, Sweden (in Swedish)
- Wiggins GB (1977) Larvae of the North American caddisfly genera (Trichoptera). Univ Toronto Press, Toronto Buffalo
- Wigglesworth GB (1965) The principles of insect physiology. Methuen, London
- Wilbur H, Morin PJ, Harris RN (1984) Anuran responses to salamander predation. Bio Science 34: 257
- Woodiwiss FS (1978) The Trent biotic index, macroinvertebrates in biological surveillance. Rep 1st UK/USSR Sem, Valkai, USSR, pp 58–81
- Woodwell GM (1970) Effects of pollution on the structure and physiology of ecosystems. Science 168: 429–433
- Zar TM (1980) Predation and freshwater communities. Yale Univ Press, New Haven