A mechanistic sub-model predicting the influence of potassium on radiocesium uptake in aquatic biota

Lars Håkanson\textsuperscript{a,*}, José A. Fernandez\textsuperscript{b}

\textsuperscript{a} Institute of Earth Sciences, Uppsala University, Villav. 16, 756 53 Uppsala, Sweden
\textsuperscript{b} Plant Biology, University of Málaga, Campus de Teatinos S/N. 29071, Málaga, Spain

Received 15 April 2000; received in revised form 16 August 2000; accepted 21 August 2000

Abstract

It is often argued that the quality of science is related to the possibilities of making accurate predictions. It has also long been argued that due to the complex nature of ecosystems, it will never be possible to predict important target variables, especially with more comprehensive dynamic models. New results in radioecology have, however, demonstrated that those arguments are no longer valid. The key to the predictive success lies in the structuring of the model. The accident at Chernobyl has, in fact, provided science with an intriguing opportunity to study how the pulse of $^{137}\text{Cs}$ is transported through ecosystem pathways, thus revealing the basic structure of these ecosystems, i.e. which are the key and the less-important pathways. It is paradoxical to conclude that the Chernobyl accident is, perhaps, the most important factor behind the revolution in predictive ecosystem modelling which lies behind the decrease in the uncertainty factor from 10 to 0.25–0.5. The sub-model for the potassium moderator presented in this paper is an example of a mechanistically based sub-model used within the framework of a more comprehensive lake model for $^{137}\text{Cs}$. The K-moderator presented is derived from the existing knowledge on ion transport in biological membranes and takes into account ion equilibria modelled by the Nernst equation and the uptake kinetics quantified by the Michaelis–Menten model. It provides the type of structure to this overall lake model that helps to explain the excellent predictive power of this model. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Aquatic systems; Potassium; Radiocesium; Bio-uptake; Modelling; Validations; Predictive power

*Corresponding author. Tel.: +46-18-471-3897; fax: +46-18-471-2737.
E-mail addresses: lars.hakanson@natgeog.uu.se (L. Håkanson), ja_fernandez@uma.es (J.A. Fernandez).
1. Introduction and aim

The effects on aquatic organisms of ionising radiation concern both individual and population levels and the variables of interest include mortality rate, fertility rate and mutation rate (see Whicker & Schultz, 1982; Jimenez & Gallego, 1998). There are major differences between different organisms in sensitivity to ionising radiation and there are major differences for one and the same organisms living in different environments. Bio-uptake is a central issue in radioecology and the focus of this paper is on the mechanisms regulating uptake and accumulation of $^{137}$Cs, thus determining the concentration capacity of the organisms with respect to the activity in the environment, expressed as the concentration factor. Many of the principles discussed for $^{137}$Cs in this paper would also be valid for other radionuclides and heavy metals.

Predictive models are fundamental tools for forecasting the consequences of different contaminations and remedial actions (see IAEA, 2000). The term “predictive model” is used to indicate models where one or a few important $y$-variables are predicted from a few readily available $x$-variables. This goal is often very difficult to achieve. Practically useful models in radioecology must satisfy some categorical features that make them reliable tools for environmental management:

- they must be characterised by a relevant and simple structure, i.e. involve the smallest possible number of driving variables;
- the values of the necessary driving variables should be easy to access and/or to measure;
- the models must be validated for a variety of circumstances showing a wide range of environmental characteristics.

The requirements set out for the overall lake model for $^{137}$Cs discussed in this work are that it should:

- be mechanistically sound, i.e. whenever possible be based on fundamental scientific principles;
- include key processes regulating the bio-uptake of $^{137}$Cs in aquatic systems.

A graphical illustration of a typical compartmental model is given in Fig. 1A. The figure illustrates top predator (like pike or large perch), small fish 1 and 2 (e.g. small perch and roach), zooplankton, phytoplankton, algae and benthos, and abiotic compartments (like water and active and passive sediments) and the processes regulating the fluxes between these compartments. The figure also gives the fluxes to the lake (direct lake load and river input related to catchment load) and from the lake (outflow and sediment transport from the active to the passive sediment layer). This is a general and traditional modelling set-up applicable for any substance X in a lake. The concentration of X in any biological compartment is defined as the ratio between the amount of X in the compartment (in g or Bq) divided by the biomass of the species (e.g. kg pike in the lake). One needs bio-uptake rates and excretion rates for all biological compartments, variables to describe the compartments (like age, sex, organ or weight of the fish) and the biomasses of the species in the lake. All these
model variables are difficult and expensive to access, they vary seasonally and are often just guessed. This means that models of this kind generally provide poor predictions. Better predictions can often be obtained for models structured in such a way that one uses a dynamic model for all important abiotic processes, which are relatively easy to handle compared to biological processes. This means that the concentration of X in water and/or sediments can be predicted accurately. Then one would use the bioconcentration factor (BCF) approach and another set of differential equations to model the fluxes per mass-units, i.e. direct modelling of
concentrations without having to estimate biomasses. Often there is knowledge about the factors influencing the bio-uptake, like a lower bio-uptake for radiocesium in lakes with high concentrations of potassium, or lower bio-uptake of Hg in lakes with high concentrations of selenium. This knowledge can be expressed by dimensionless moderators operating on the BCF-values (see Fig. 1B).

The crucial point in practical lake ecosystem modelling is the structuring of the model (Håkanson, 1999). The model structure should include all important processes regulating the transport and bio-uptake of X; no more, no less. The most important water chemical variable regulating the bio-uptake of $^{137}$Cs is the lake K concentration — the more ions similar to Cs, like K, the lower the uptake of $^{137}$Cs, a case of “chemical dilution” (Black, 1957; Fleishman, 1963; Carlsson, 1978). Uptake of ions, including radionuclides, takes place through different kinds of membrane proteins that allow the transfer of the ions from one side of the membrane to the other. These proteins have been developed for the uptake of essential nutrients for biomass maintenance and growth, but many of them are sensitive to artificial radionuclides, heavy metals or other types of xenobiotics (Clements, 2000). Thus, the potassium transport systems in plants and animals are sensitive to $^{137}$Cs and both channels and carriers elicit the uptake of cesium into living cells. The transport of potassium and cesium through channels is diffusive, exhibits a linear kinetic, and allows the distribution of these ions according to the difference in electrical potential, diffusion potential ($E_D$), to both sides of the membranes (Smith, Smith & Walker, 1987). The concentration distribution can be predicted from $E_D$ by the Nernst equation. In contrast, carriers do transport potassium and cesium actively. Carrier transport exhibits saturation as given by the Michaelis–Menten kinetic and accumulates ions inside the cells well above the predictions of the Nernst equation for conditions of equilibrium (Blatt, Rodriguez-Navarro & Slayman, 1987).

Potassium channels and carriers have a universal distribution in membranes of living cells and, over the ecological range of potassium concentrations, one often finds dual uptake kinetics (Benlloch, Moreno & Rodriguez-Navarro, 1989). A similar uptake kinetic pattern has been described for $^{137}$Cs in the freshwater plant Riccia fluitans (Fernandez et al., 1997). This study indicates that $^{137}$Cs is incorporated and accumulated inside plant cells through the same mechanisms as those for potassium. A number of genes, encoding potassium channels and carriers, have been recently cloned and expressed in heterologous systems, and in some cases it has been demonstrated that cesium can be transported by these systems (for a review see Rodriguez-Navarro, 2000).

From this general background, the aims of this study were:

1. To develop a new algorithm describing how potassium influences bio-uptake of $^{137}$Cs.
2. To put this algorithm into the framework of a new lake model for $^{137}$Cs (see Håkanson, 2000, for a more thorough description of the overall lake model).
3. To demonstrate how the modelling approach actually works by means of a model validation.
2. The potassium moderator

The potassium moderator, $Y_K$, expresses the influence of lake K concentrations on the bio-uptake for animals and plants, i.e. for all types of cells. The critical limit between sufficiency and deficiency is generally (see Fernandez et al., 1997) set at $C_K = 0.1\text{ mM} = 3.91\text{ mg K/l}$. In natural lakes, one can expect $C_K$ to vary from about 0.2 to 40 mg/l (see Desmet et al., 1997). This dimensionless moderator is based on physiological mechanistic models for the bioconcentration factor for both sufficiency ($C_K > 0.1\text{ mM}$) using the Nernst equation and deficiency ($C_K < 0.1\text{ mM}$) using the Michaelis–Menten model (see Fig. 2).

The entire realistic range for $C_K$ has been tested in the derivation of the $K$-moderator (see Fig. 3). The curve marked $\text{CF}/\text{CF}_{\text{norm}}(\text{MM}&\text{N})$ is the ratio between the actual calculated concentration factor (CF) and the reference, or norm CF-value ($\text{CF}_{\text{norm}} = 40$; the ratio is used to get a dimensionless expression). This is the theoretical dimensionless moderator as calculated from the Michaelis–Menten model for deficiency and the Nernst equation for sufficiency according to the presuppositions given in Fig. 2. The curve marked $\text{CF}/\text{CF}_{\text{norm}}(N)$ is obtained by using just the Nernst equation. The half-life for Cs in plants is set to 0.55 days, the default temperatures to 20°C, the default Cs concentration in water to 0.001 μM, the maximum uptake rate in cells is set to 46,560 μmol/g dw d, the affinity constant of the active transport system for Cs ($K_{sCs}$) is set to 27.5 μM, the affinity constant of the active transport system for potassium to 23.2 μM and the diffusion potential ($E_D$) for K to 105 mV (Eq. (3)). There is also an empirical constant in the Nernst equation for radiocesium. The constant 0.73 comes from a linear fitting of CF in *Riccia fluitans*, submitted to potassium sufficiency, as a function of the external potassium concentration. This parameter modifies the capacity of plants to accumulate Cs versus K, i.e. it is a selectivity coefficient. It agrees roughly with the relative permeability of Cs over K (0.6) obtained from controlled physiological experiments.

From Fig. 3, one can note:

(1) the smooth transition from sufficiency to deficiency when using both the Michaelis–Menten model and the Nernst equation, which indicates that the model is well calibrated,

(2) that by using only the Nernst equation one obtains data that deviate more and more from the two other curves with lower $C_K$-values, and

(3) that the calculated curve $\text{CF}/\text{CF}_{\text{norm}}(\text{MM}&\text{N})$ can, in fact, be described very well by a the new dimensionless moderator, $Y_K$, expressed as:

$$Y_K = 300/(4.5 + C_K^{0.75}).$$

(1)

This is meant to be a general moderator applicable for plants and animals. Instead of writing $C_K/1$, where 1 is a reference concentration, Eq. (1) is written in the simplified form. All the equations and presuppositions given in Fig. 2 are fundamental for the modelling and understanding of the mechanisms regulating...
the bio-uptake process of $^{137}$Cs. However, if the focus is set not on these processes but on other targets, e.g. at predicting the $^{137}$Cs concentrations in fish, many of the details in Fig. 2 are redundant. Then, the new algorithm (Eq. (1)) captures (see Fig. 3) the essentials of the Nernst equation and the Michaelis–Menten model.
Eq. (1) does not depend on temperature or on the Cs activity in the water, as illustrated in Fig. 4, which gives predicted CF/CF$_{norm}$ ratios for the default conditions and for a temperature of 10°C and a $^{137}$Cs concentration 1000 times higher than the default value. Note that in this model $C_K$ must be given in $\mu$eq/l ($=(mg/l)/0.0391$).

Fig. 3. A comparison between model-predicted values for the CF/CF$_{norm}$-ratio using (1) the Michaelis–Menten model and the Nernst equation (the curve marked M&N), (2) only the Nernst equation (curve marked N) and (3) the new dimensionless moderator for potassium ($Y_K$).

Fig. 4. A comparison between model-predicted values for the CF/CF$_{norm}$-ratio using the Michaelis–Menten model and the Nernst equation, and the new dimensionless moderator for potassium ($Y_K$) for two temperatures (10 and 20°C) and two Cs concentrations (default = 0.001 and 1 $\mu$M).

Eq. (1) does not depend on temperature or on the Cs activity in the water, as illustrated in Fig. 4, which gives predicted CF/CF$_{norm}$ ratios for the default conditions and for a temperature of 10°C and a $^{137}$Cs concentration 1000 times higher than the default value. Note that in this model $C_K$ must be given in $\mu$eq/l ($=(mg/l)/0.0391$).
However, the uptake of $^{137}\text{Cs}$ is not only a problem of chemical dilution. Firstly for plants, the potassium concentration in the lake water determines the kind of transport system in the membranes that will be relevant for both the potassium and cesium uptake. In the case of low $K$ concentrations in lake water, plants will be subjected to potassium deficiency. Under these conditions, plant cells will close potassium channels to avoid passive $K$ leakage. At the same time, the plants will express genes encoding high-affinity transport systems for $K$. Carriers that can extract $K$ (and Cs) from diluted environments will concentrate internal $K$ and Cs several orders of magnitude with respect to the levels in the environment. Under $K$ sufficiency, $K$ is transported inside plant cells passively, through $K$ channels and is accumulated inside the cells in equilibrium with $E_D$, as predicted by the Nernst equation (Fernandez et al., 1997). Secondly, both potassium and cesium compete for potassium channels and carriers. Thus, the higher the potassium concentration in the water the lower will be the uptake rate and accumulation of cesium. In the model presented in this paper (Fig. 2), the relationship between potassium concentration in the water and the uptake rate of cesium is not empirical but is based on the physiological mechanisms of ion transport.

Under potassium sufficiency, CF for cesium has been predicted by using the Nernst equation as a simple relationship between ionic asymmetry and the diffusion potential $E_D$. Potassium exerts a double influence on plant cells subjected to potassium sufficiency. On the one hand, $E_D$ depends dramatically on the external concentration of potassium (Hope, 1971) and on the other potassium channels exhibit different permeability for cesium compared to potassium. Under potassium sufficiency, i.e. potassium concentration in the water higher than 0.1 mM, we predicted CF for radiocesium from the Nernst equation accordingly:

$$ CF = \frac{1}{\exp(\text{Emp. constant } \ln(C_K\cdot0.001)+E_0 F/(R(Tem+273)))}, $$

where $F$ is Faraday’s constant, $R$ is the gas constant, $T$ the temperature ($^\circ$C) and the empirical constant is 0.73. This value was obtained experimentally by using the freshwater plant *Riccia fluitans* L. as a model and assuming that the internal concentration of potassium was constant (Fernandez, Garcia-Sanchez & Felle, 1999). This means that $E_D$ is expressed as a function of the concentration of potassium in the water

$$ E_D = E_0 + p \cdot RT/F \ln(C_K), $$

where $E_0$ is $E_D$ for a $C_K$ equal to 1 mM and $p$ is a constant that represents the overall relative permeability of membranes for Cs over K.

$E_D$ was recorded continuously at the same time that external concentration of potassium was changed from 0.1 to 10 mM. Fitting of the data to the equation gave $E_D= -105 + 18.5\ln(C_K)$ ($r^2 = 0.96, n = 23$). One important assumption here is that the effect of $K$ on $E_D$ prevails on different chemical conditions.

Under potassium deficiency, i.e. $C_K$ below 0.1 mM, uptake of cesium takes place through $K$ carriers (high-affinity $K$ transporters). They exhibit Michaelis–Menten kinetics and Cs and K exhibit competitive inhibition for these transport systems
Thus the uptake rate of cesium can be expressed as a function of the concentration of total cesium and potassium in the water

\[
UR = \frac{V_{\text{max}}}{K_{S\text{Cs}} (1 + (C_K / K_{S\text{K}})) + C_{\text{Cs}}},
\]  

where \( UR \) and \( V_{\text{max}} \) are the uptake rate and the maximum uptake rate, respectively. \( K_{S\text{Cs}} \) and \( K_{S\text{K}} \) are the cesium and potassium concentrations in the water that yields an uptake rate of Cs or K half of \( V_{\text{max}} \). \( C_{\text{K}} \) and \( C_{\text{Cs}} \) are the concentration of K and Cs in the water.

Fig. 5 illustrates how the K-moderator actually works. If the \( Y_{\text{K}} \)-value is set higher than the default value, the bio-uptake increases, and hence also the Cs-concentrations in biota, in this example, 500 g pike in Lake Flatsjön, Sweden (see Håkanson, 1999). Fig. 5 shows that in this particular case there was a very good correspondence between empirical data and modelled values and that the model predictions are sensitive to the \( Y_{\text{K}} \)-values. The following model validations will demonstrate how the models predicts Cs concentrations in many different species of fish in many different lakes.

Since activity in plants has a great influence at other levels in the trophic chain, the K-moderator can be applied in whole ecosystem modelling to improve the predictions of CF both in plants and animals. An example of this will be given in the following fish model.

3. The overall fish model

The aim of this section is to put the new K-moderator into its context, the overall fish model for radiocesium (Fig. 6; see Håkanson, 1999, 2000 for detailed model descriptions). Technically, the biotic processes are treated separately from the biotic fluxes in the overall radiocesium model and the two pathways are linked by means of a bioconcentration factor (Fig. 1B). This is, as already stressed, a simplification with many advantages for predictive modelling:

1. One can then predict the target concentrations in biota directly without data on biomasses, which are generally extremely hard to access. The basic aim is to predict the concentration of \( X \) (here \(^{137}\text{Cs} \)) in fish for human consumption. This model uses compartments of one mass unit: \(^{137}\text{Cs} \) is transported from one mass unit of lake water to one mass unit of biota. This means that the model automatically yields concentrations. Most mass-balance models use the lake or a given part of the lake as the unit of size and calculate the concentration of a substance in water as the ratio between the total amount (g or kg) of material in the total volume. Such models can be extended to the populations of pike or perch by treating the fish as summed volumes (e.g., \( V_1 \) or \( V_2 \) in 1 = dm³). If the density = \( d(\text{kg}/\text{l} = \text{g}/\text{cm}^3) \), and if \( X_1 \) and \( X_2 \) are the amounts of contaminant (in g), then the concentrations of \( X \) in pike and perch are \( X_1 / V_1 d \) and \( X_2 / V_2 d \), respectively, in the two species.

2. Models of this type can be relatively easily tested (calibrated and validated), since concentrations in biota are easily measured. This model structure generally gives better predictive success than traditional models using connected or parallel
biotic compartments (like phytoplankton, zooplankton, benthos, prey fish and predator fish models of the type illustrated in Fig. 1A). The uptake of $^{137}$Cs from water to biota is still modelled dynamically.

Fig. 5. A comparison (sensitivity test) between empirical data and modelled values for $^{137}$Cs concentrations in 500g pike in Lake Flatsjön, Sweden, when the K-moderator is changed from the empirical default value (1 mg K/l in this lake) to 1.1def and 1.5def.

Fig. 6. An outline of the biotic (fish) part of the model for radiocesium (modified from Hákanson, 2000).
In the fish model (Fig. 6), the bioconcentration factor is modified by factors known to influence the bio-uptake of $^{137}$Cs:

- The potassium concentration in lake water.
- The amount of radiocesium in dissolved and particulate phases.
- The feeding habits of the fish.
- The weight of the fish.
- The trophic characteristics of the lake.
- The water temperature.

Approaches like this are most relevant in cases when the biotic fluxes of the chemical are much smaller than the abiotic fluxes. This is the case for the majority of metals and radionuclides in most lakes (see Håkanson, 1999).

The differential equation for the concentration (i.e. $C_{\text{fish}}$ in Bq $^{137}$Cs/kg ww):

$$C_{\text{fish}}(t) = C_{\text{fish}}(t-\text{dt}) + (F_{\text{IF}} - F_{\text{FO}})\text{dt},$$

(5)

where $F_{\text{IF}}$ is the bio-uptake (Bq/month kg), $F_{\text{FO}}$ the excretion (Bq/month kg).

The calculation time, $\text{dt}$, is set to 1 month to obtain seasonal variations. The bio-uptake is given by

$$F_{\text{IF}} = Y_{\text{AL}} \cdot Y_{\text{AU}} \cdot Y_{\text{K}} \cdot \text{BMF} \cdot \text{SMTH}(C_{\text{diss}} + C_{\text{parT}} + \text{BUD}, C_{\text{diss}} + C_{\text{parT}}),$$

(6)

where $Y_{\text{AL}}$ is a dimensionless moderator for allochthonous lake bioproduction driven by C and N from tributary inflows; the more bacteria, zooplankton and fish, the lower the Cs concentration in such groups, if all else is constant; this is often referred to as “biological dilution”, $Y_{\text{AU}}$ a dimensionless moderator for autochthonous production; the higher the lake production of phytoplankton (driven by phosphorus), zooplankton and fish, the lower the Cs concentration in such groups, if all else is constant; this is also a case of “biological dilution”, $Y_{\text{K}}$ the new dimensionless potassium moderator presented in Eq. (1), BMF a biomagnification factor related to feeding habits; if all else is comparable, Cs concentrations differ significantly between planktivores, benthivores, omnivores and piscivores, SMTH a smoothing function based on the concentration of $^{137}$Cs in the dissolved phase in lake waters, $C_{\text{diss}}$, the total amount in particulate phase in lake waters and sediments, $C_{\text{parT}}$, and a bio-uptake delay factor (BUD); for example, small planktivores reach dynamic steady-state concentrations relative to the concentration of $^{137}$Cs in water more quickly than large benthivores.

These factors affecting bio-uptake have been examined in detail by Håkanson (1999, 2000).

4. Validations

The ultimate model testing is validation, i.e. critical testing against independent data. This modelling approach for bio-uptake of $^{137}$Cs in fish using the K-moderator has been validated for a broad set of lakes for $^{137}$Cs concentrations in lake fish (see Håkanson, 2000). The validation lakes cover a wide range of lake characteristics,
although they are all European. Their sizes vary from 0.041 to 1147 km², mean depth \((D_m)\) from 2.9 to 90 m, characteristic pH from 5.1 to 8.5, trophic status ranges from oligotrophic \((\text{TP from } 10 \mu g/l)\) to hypertrophic \((\text{TP = } 60 \mu g/l)\), and cesium fallout ranges from 2 to 130 kBq/m² (Table 1).

Note that the validation lakes cover a very wide domain in terms of potential K-influences on bio-uptake. The characteristic lake K concentration varies from 0.37 mg/l for the small Swedish lake, Lill-Selasjön (2214) to 7 mg/l for Lake IJsselmeer, the Netherlands, which is very large (1147 km²) and shallow.

The validation of the biotic (=fish) part of the \(^{137}\text{Cs}\) model has been done in the following manner.

Firstly, empirical data were directly compared to modelled values. Fig. 7A exemplifies this with empirical data for Cs concentration in 500 g pike in Lake Siggefora on the \(y\)-axis, Sweden, and the corresponding modelled values on the \(x\)-axis. These data were then regressed against one another, as illustrated in Fig. 7B. The \(r^2\)-value in this case was 0.5 \((r = \text{correlation coefficient})\), and the number of fish was 22. This regression only covers one lake and one type of fish and, hence, has a limited range. The modelled data are also not independent of one another and there are large empirical uncertainties for Cs concentrations in fish \((\text{CV} \approx 0.22; \text{see } \text{Håkanson, 2000})\). This is illustrated by the uncertainty bands in Fig. 7B.

Then, the complete data series like the one for 500 g pike in Lake Siggefora were modelled for all species of fish and all the selected lakes (Table 1), see Fig. 8. The data set comprised 185 values for seven species of fish covering a very wide range, from 2 to over 30,000 Bq/kg ww.

There are three typical outliers in Fig. 8. If these three outliers are omitted, the \(r^2\)-value was 0.98. This is almost like an analytical solution. If the three outliers were included, the \(r^2\)-value is 0.95. The slope approaches 1 \((= 1.027)\). The \(r^2\)-value for the actual (non-transformed) data is 0.86. This demonstrates that the structuring of this model is very good. If excellent predictions can be obtained for \(^{137}\text{Cs}\) for fish in lakes, this holds great promise for other types of contaminants in future models. It also means that models of this type in the future are likely to become widely used and excellent tools in remedial contexts.

5. Conclusions

There has been a rapid development in predictive ecosystem modelling over the last decade. The BIOMOV project \((\text{BIOSpheric MOdel Validation Study}; \text{BIOMOV, 1990})\) played a major role in disclosing the fact that many old, traditional ecosystem models in radioecology had low predictive power, while the VAMP project \((\text{Validation of Model Predictions, IAEA, Vienna})\) demonstrated new methods to test and increase predictive power in ecosystem models \((\text{IAEA, 2000})\).

This work has presented a potassium moderator that takes into account the different mechanisms regulating the competition between K and Cs for the bio-uptake transport systems. The new K-moderator is based on existing and well-proven principles of membrane transport and makes it relatively easy to identify and
## Table 1
Data on the lakes used for validating the radiocesium model

<table>
<thead>
<tr>
<th>Lake</th>
<th>County</th>
<th>Fallout (kBq/m²)</th>
<th>Area (km²)</th>
<th>Dm (m)</th>
<th>K (mg/l)</th>
<th>pH</th>
<th>TP (µg/l)</th>
<th>Tw (yr)</th>
<th>Trophic status</th>
<th>Fish species</th>
<th>Abiotic variable</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>IJsselmeer</td>
<td>Netherl.</td>
<td>2.2</td>
<td>1147</td>
<td>4.3</td>
<td>7</td>
<td>8.5</td>
<td>60</td>
<td>0.41</td>
<td>Hypertr.</td>
<td>Roach, smelt, perch</td>
<td>Water 2</td>
<td>2</td>
</tr>
<tr>
<td>Iso Valkjärvi</td>
<td>Finland</td>
<td>70</td>
<td>0.042</td>
<td>3.1</td>
<td>0.4</td>
<td>5.1</td>
<td>11</td>
<td>3.0</td>
<td>Oligotr.</td>
<td>Pike, whitef., perch</td>
<td>Water 2</td>
<td>2</td>
</tr>
<tr>
<td>Ø. Heimdalsvatn</td>
<td>Norway</td>
<td>130</td>
<td>0.78</td>
<td>4.7</td>
<td>0.4</td>
<td>6.8</td>
<td>10</td>
<td>0.17</td>
<td>Oligotr.</td>
<td>Minnow, trout</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>Esthwaite</td>
<td>England</td>
<td>2</td>
<td>1</td>
<td>6.4</td>
<td>1.09</td>
<td>8</td>
<td>25</td>
<td>0.19</td>
<td>Eutr.</td>
<td>—</td>
<td>Water 3</td>
<td>2</td>
</tr>
<tr>
<td>Siggeforsa</td>
<td>Sweden</td>
<td>30</td>
<td>0.73</td>
<td>4.2</td>
<td>0.6</td>
<td>7.2</td>
<td>10</td>
<td>0.78</td>
<td>Oligotr.</td>
<td>Pike, roach, perch</td>
<td>SPM 1</td>
<td>1</td>
</tr>
<tr>
<td>Hamstasjon (2217)</td>
<td>Sweden</td>
<td>50</td>
<td>0.18</td>
<td>3.8</td>
<td>1.43</td>
<td>6.6</td>
<td>22.9</td>
<td>0.21</td>
<td>Mesotr.</td>
<td>Perch</td>
<td>Water 4</td>
<td>4</td>
</tr>
<tr>
<td>Lill-Selasjon (2214)</td>
<td>Sweden</td>
<td>70</td>
<td>0.07</td>
<td>2.9</td>
<td>0.37</td>
<td>5.1</td>
<td>10.9</td>
<td>0.02</td>
<td>Oligotr.</td>
<td>—</td>
<td>Water 4</td>
<td>4</td>
</tr>
<tr>
<td>Zürich</td>
<td>Switzerland</td>
<td>5.9</td>
<td>537.4</td>
<td>90</td>
<td>1.49</td>
<td>7</td>
<td>10</td>
<td>4.2</td>
<td>Oligotr.</td>
<td>—</td>
<td>Water 3</td>
<td>3</td>
</tr>
</tbody>
</table>

*a 1, Marcus Sundbom (pers. comm.); 2, IAEA (2000); 3, Jim Smith (pers. comm.); 4, Håkanson (1991). Dm = mean depth; TP = total phosphorus.*
quantify the effect of other chemical, physiological or ecological variables influencing the bio-uptake of $^{137}$Cs.

The new model for $^{137}$Cs incorporating the potassium moderator has been validated against an independent set of data covering a wide range of lake characteristics. The data set for the validation for the Cs concentrations in lake fish

![Illustration of the relationship between empirical data and modelled values for 500 g pike in Lake Siggefora, Sweden.](image)

**Fig. 7.** Illustration of the relationship between empirical data and modelled values for 500 g pike in Lake Siggefora, Sweden. (A) gives a direct comparison on a time scale; (B) gives the corresponding regression and also the empirical uncertainties using a standard characteristic CV of 0.22 for lake fish (or rather $2\sigma = 95\%$ confidence interval for empirical values; $CV = \text{coefficient of variation}; CV = SD/MV; SD = \text{standard deviation}; MV = \text{mean value}$). The two co-ordinates marked $\times 20$ and $\times 21$ from Lake Siggefora (upper figure) are also marked in the lower figure.
comprises 185 monthly data for seven species of fish covering a very wide range of contamination. There is an excellent fit between empirical data and model predictions ($r^2 = 0.98$; slope $\approx 1$). The K-moderator provides the type of generality to the overall lake model needed to produce excellent predictive power.

**Acknowledgements**

The work presented in this paper has been carried out in the ECOPRAQ-project (an EU-project co-ordinated by Dr. Rob Comans). We would like to express our gratitude to our colleagues in this project, especially to Rudie Heling who has given valuable input on the use of the Nernst equation.

**References**


