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Test of the suitability of ECOPATH/ ECOSIM modelling software as a compliment to estimate flows of carbon, C-14 and radionuclides in the Öregrundsgrepen area

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Abstract

In this study it was evaluated whether the ECOPATH with ECOSIM software could be used as a standard platform to facilitate for radioecologists to construct and study transport and accumulation of radionuclides in aquatic food webs. The evaluation was based upon: 1) a previously published food web model of carbon/carbon-14 flow for the Öregrundsgrepen area, Baltic Sea, 2) a generic model, 3) an ECOSIM model and 4) an ECOTRACE model. The results presented clearly shows that there is great potential for a successful development of this scientific approach in the future.

The original carbon flows and assumptions was easily incorporated into the ECOPATH with ECOSIM modelling environment. The carbon flows differed only negligible between the two models, except for the benthic flows, which was more accurately described in this study. Further, by using ECOPATH it was easily discovered that the growth efficiencies used in the original model was quite high, being 47% for most of the heterotrophs, which are high from an ecological point of view. However, that is probably due to differences in how the carbon flows have been estimated in the original versus the present study. It is likely, however that the carbon demand has been underestimated in the original model.

The generic model was parameterised from data available through the software as well from the diets and assumptions used in the original carbon model. The use of these parameters resulted in carbon flows, which was between 0.7 to 11 times the flows estimated by the ECOPATH model. The difference was greatest for primary producers being 3.7 to 11 times the original flows. Thus, depending on the question one is addressing it was suggested that the use of generic parameters is best for making test models of carbon and radionuclide flows in ecosystems, where the data set for validation is limited.

Finally, the ECOPATH and ECOSIM model was well suited to drive a C-14 flow model, such as ECOTRACER for each of the organisms included in the model. ECOTRACER estimated steady state concentrations of C-14 that were between 73–142% of the original flows. The differences found are probably due to the adjustment of the benthic carbon flows and the water retention in the system. To conclude, the present models show that the ECOPATH with ECOSIM software is well suited for integrating scientific knowledge about food webs and radioecological models for aquatic systems.

Sammanfattning

I den här studien undersöktes fördelar och nackdelar med modelleringsprogrammet ECOPATH-ECOSIM med avseende på fördelning och ackumulation av radionuklider i akvatiska näringsvävar. Analysen baserades på en tidigare publicerad modell av kol/radionuklidflöden för ett kustområde i Öregrundsgrepen, Östersjön för att; 1) reproducera original kolflödesmodellen, 2) göra en generell modell, 3) göra en dynamisk kolflödesmodell och 4) en radionuklidflödesmodell.

Resultaten visar att det var fullt möjligt att återskapa den ursprungliga modellens kolflöden samt radionuklidflöden med hjälp av ECOPATH-ECOSIM. Däremot, så skiljde sig de bentiska kolflödena jämfört med den tidigare kolflödesmodellen. Vidare så framkom det att tillväxteffektiviteten var ca 47 % för de flesta heterotrofer, vilket är något högt ur ekologisk synvinkel. Detta resultat beror troligen på skillnader i hur de grundläggande kolflödena har uträknats i den ursprungliga modellen jämfört med den här studien. Förmodligen så har den tidigare modellen underskattat kolbehovet hos dessa heterotrofer.

Den generella kolmodellen, parameteriserades utifrån data tillgängliga från ECOPATH-ECOSIM, medan den underliggande näringsvävsstrukturen, dieten och övriga antaganden baserades på original kolflödesmodellen. Dessa antaganden och uppskattningar resulterade i en kolflödesmodell där flödena var mellan en faktor 0,7–11 av original flödena. Skillnaden var störst för primär producenterna, vilka var 3,7 till 11 gånger större än vad som uppskattats i original modellen. Utifrån dessa resultat konstateras att användandet av generella data bäst lämpar sig för preliminära test modeller av kol och radionuklidflöden där det finns begränsad mängd data för validering.

Slutligen, kolflödesmodellen i jämvikt användes för att driva en dynamisk kolflödesmodell och parallellt med denna en radionuklidflödesmodell. Dessa radionuklidflödesberäkningar resulterade i jämviktskoncentrationer av kol-14 jämförbara med de värden som uppskattas i den ursprungliga modellen. För varje organismgrupp påvisades koncentrationer av kol-14 mellan 73 till 142 % av den ursprungliga modellen. Orsaken till dessa skillnader kan bero på skillnader i uppskattningar av bentiska kolflöden och/eller möjligheten att implementera vattenutbyte för kustekosystemet med hjälp av ECOPATH. Sammanfattningsvis är det tydligt att forskning där man länkar samman kunskaper inom marin ekologi och radioekologi har potential till betydande utveckling i framtiden.

Contents

1 Introduction

Generally, models describing the dispersion of radionuclides in aquatic environments can be divided into: 1) water circulation and transport models, 2) sediment transport models and 3) biological transport models /Aldridge et al, 2003; Smith et al, 2003; Thiessen et al, 1999/. The latter types of models are generally simple descriptions of radionuclide transport through biotic part of aquatic system, such as simple trophic interactions in food webs /Sazykina, 2000; Wang et al, 2000/ or for single organisms such as fish /Sundbom et al, 2003/ or groups of organism in benthic and pelagic habitats /Smith et al, 2000/. Models describing the accumulation of radionuclides by organisms in biological communities are often based on concentration- (CF) and transfer factors (TF) /Blust, 2001/. These types of factors describe the concentration of a radionuclide in an organism, either relative to the water surrounding it (CF) or relative to the concentration in their prey (TF) /Blust, 2001; Ryan, 2002/. From an ecological perspective these factors might not fully include all the complexity whereby radionuclides are transferred in ecosystems, since these factors depend on the environmental conditions and influences of physical and biological interaction occurring in the system studied. The type of radionuclides studied as well as the specific conditions prevailing during experimentation might also be of importance /Ryan, 2002/.

In the Baltic Sea, Öregrundsgrepen area, /Kumblad et al, 2003/ have presented a model describing the flows of radionuclides through a coastal food web in greater detail. The study is part of the “SAFE” project (Safety Assessment of the Final Repository for Radioactive Operational Waste, SFR-1). The repository is used for waste management of low and intermediate radioactive materials. The model describes the aquatic ecosystem adjacent to Forsmark nuclear power plant (Northern Uppland, Sweden) and right above the repository separated by the seabed and the bedrock. The environment surrounding SFR-1, have previously been addressed in a number of studies, in terms of historic- and future shoreline displacement, future changes in sedimentation, lake dynamics as well as the phytobenthic habitat and water circulation /all cited in Kumblad, 1999/. The radionuclide flow (RF) model was estimated by constructing a carbon flow (CF) model for the coastal food web. From the CF model additional parameters and assumptions were made in order to estimate radionuclide flows. From this approach Kumblads CF model gave a reasonable scenario of both the ecological processes in the area as well as how a radioactive discharge of carbon-14 would be absorbed and transferred within the ecosystem.

However, even if the Kumblad RF models represent a relatively realistic approach to model radionuclide flows, the transparency of these kinds models to other researchers, as well as the possibility to extrapolate the structure and assumptions of the model to other environmental areas are not straightforward. One way to facilitate for others scientists to evaluate existing RF and construct new models could be to use the ECOPATH with ECOSIM software as a modelling platform. The ECOPATH with ECOSIM software represents a user-friendly interface to calculate mass balanced models for energy related elements, through a food web. These so called mass balance models, which describe the flows of matter, or elements in a system rely on the first law of thermodynamics. This law states that: “energy in a system can not be created or destroyed, it can only be transformed from one form to another”. Accordingly, for any given system the total amount of energy supplied to the system and total outputs from the system should balance by definition. Traditionally, energy related currencies have been used to describe the flows of matter in ecosystems /see Lindemann, 1942/. Nowadays, it is more common to use carbon or other elements instead of energy to describe processes occurring in an ecosystem. The assumption of mass balance for each compartment in a system can be used to confront field data on radionuclide concentration factors and transfer factors with theoretical assumptions on carbon flow and radionuclide accumulation for a given area, such as Öregrundsgrepen. Accordingly, the structure of the ECOPATH with ECOSIM program and evaluation facilities might thus be beneficial to test whether the models have been well parameterised /see Christensen, 1992; Christensen & Pauly, 1995/.

1.1 Aim of this study

In this study the aim is to evaluate whether the ECOPATH with ECOSIM approach could be used as a standard platform to facilitate for radioecology scientist to construct and study transport and accumulation of radionuclides in aquatic food webs. In order to evaluate the suitability of the software for this purpose we used the data available in Kumblad et al 2003 to: 1) parameterise a carbon budget for the Öregrundsgrepen area, 2) construct a generic model, where biomass, diets and structure of the model remained the same, but the carbon flow parameters where taken from a generic model available in the software, 3) evaluate how the ECOPATH carbon budget behave in ECOSIM and the implications of the additional parameters used to create dynamics in the model, 4) parameterise an ECOTRACE C-14-flow model for the Öregrundsgrepen area. Thus, for each step in the modelling process the suitability of using ECOPATH and ECOSIM could be evaluated as well as the possibilities to go to the next step in the evaluation scheme (Figure 1-1).

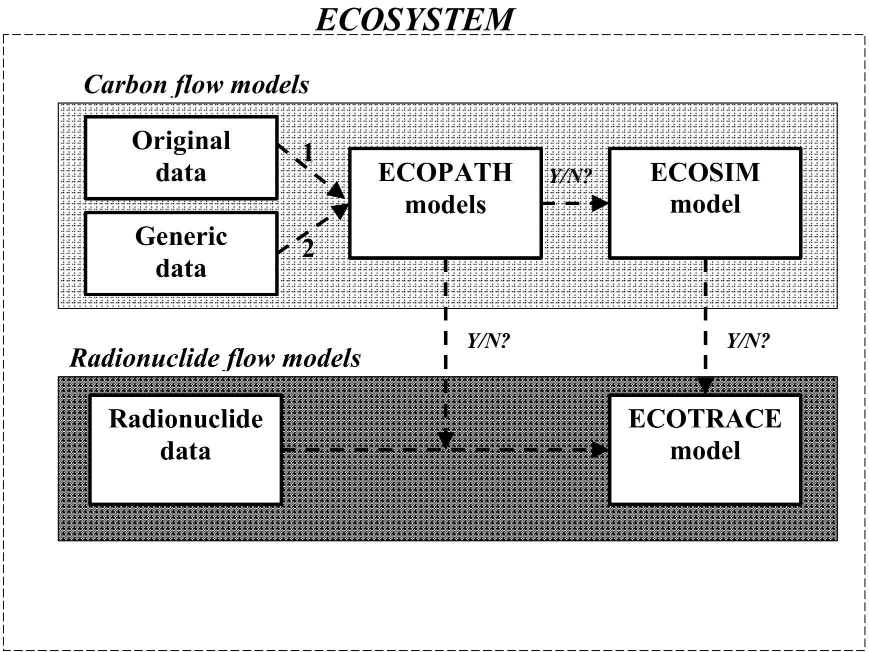

Figure 1-1. Description of the connections between different model types in ECOPATH with ECOSIM and modelling of carbon flows versus radionuclide flows. Each model type is further dependent on a successful parameterisation of a model at a lower hierarchical level (e.g. ECOSIM dependent on a ECOPATH model etc).

2 Estimating carbon flows using ECOPATH with ECOSIM version 5

The ECOPATH with ECOSIM software (version 5, available at www.ECOPATH.org) is well documented in the literature and have been used frequently in food web and fishery ecology. The basic equations used in the ECOPATH software is based on the theory of mass balance modelling, which requires the model to be in steady state. Therefore, for each compartment (i), input must equal output, i.e.

Consumption by (i) = all production of (i) (1)

\+ Un-assimilated part of consumption by (i)

\+ Respiration of (i)

Equation (1) is used in ECOPATH to balance each compartment in the model by adjusting the respiration term. The production is further calculated from a set of simultaneous linear equations, one for each group (i) in the system:

Production by (i) – all predation on (i) – non predatory losses of (i) – export of (i) = 0, for all i. (2)

Equation (2) can be expressed as:

$$P_i - B_i \cdot M2_i - P_i \cdot (1 - EE_i) - EX_i = 0$$

where: P_i is the production of (i), B_i is the biomass of (i) $M2_i$ is the predation mortality of (i), EE_i is the ecotrophic efficiency of (i) (the fraction of the production that is passed up through the food web or exported out of it), $(1\text{-}EE_i)$ is all other mortality and EX_i is the export of (i).

In the calculations Equation (2) is used in the form:

$$B_i \cdot (P/B)_i - \sum_{j=1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji} - (P/B)_i \cdot (1 - EE_i) - EX_i = 0$$

Or (3)

$$B_i \cdot (P/B)_i \cdot EE_i - \sum_{j=0}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji} - EX_i = 0$$

where. $(P/B)_i$ is the production / biomass ratio, and $(Q/B)_i$ is the consumption / biomass ratio of i. DC_{ji} is the fraction of prey (i) in the average diet of predator (j). Thus in ECOPATH modelling you need the parameters B_i, $(P/B)_i$, $(Q/B)_i$, DC_{ji}, EX_i and the fraction of consumption that is not assimilated for each living compartment, in order to calculate a mass balance model. The $(P/B)_i$ and $(Q/B)_i$, ratios can be derived from empirical regressions which can be used together with known biomass data. By definition all flows are calculated from the input parameters and the organism respiration is calculated as a rest term.

2.1 ECOPATH model

2.1.1 Data and definitions

In this study the aggregated carbon flows for the benthos compartment was individually addressed so that the model included a total of 15 compartments. The input data and parameters are given in Tables 1–3 (Appendix) and all data with a few exceptions mirrors those given in /Kumblad et al, 2003/. The biomass data, primary production, respiration, and total carbon demand were taken from /Kumblad et al, 2003/, whereas the predatory carbon demand was calculated from Figure 4a in /Kumblad et al, 2003/, respectively. The human-compartment was modelled for one person only, assuming a weight of 85 kg and a carbon content of 10%. The fraction of consumption that becomes egested by each group was not explicitly described in /Kumblad et al, 2003/, but was assumed to be 20% for all organisms. The original carbon flow data was recalculated in order to be in accordance to the parameters required in ECOPATH such as: P/B_i- and Q/B_i- and unassimilated food/consumption-ratios (see Appendix Table 1). Still, there are some issues that need to be clarified. For instance, in ECOPATH the uptake of carbon dioxide (DIC) by primary producers are by default not included. In order to include the inorganic carbon uptake by pelagic- and benthic primary producers one possibility could be to define these two compartments as partly heterotrophs and partly autotrophs. We made preliminary calculations, where we let the primary producers act as a consumer of its resource e.g. a DIC compartment. Through this procedure it was possible to estimate all carbon flows in the same way as originally described in /Kumblad et al, 2003/. However, when the ECOPATH model was run in ECOSIM (see Figure 1-1) the model behaved unrealistically over time. The estimated biomass increased to 100 times the original biomass for all groups. A well parameterised model would not change at all over time in ECOSIM e.g. be in steady state. Therefore, the uptake of DIC by primary producers was in these preliminary investigations omitted from the analysis. Respiration was therefore calculated by difference according to the ECOPATH equations.

For benthic microfauna, meiofauna and macrofauna the original data given in /Kumblad et al, 2003/ for consumption, respiration and excess carbon flow was inconsistent. The group specific carbon demand was lower than the sum of respiration, predatory loss and excess flow. Thus, in accordance with the original assumptions on carbon demand the benthic carbon demand should be three (or two for microfauna) times the respiration and that the excess flow then should equal the consumption minus the respiration and predatory loss /Kumblad et al, 2003/. The diets of each heterotrophic compartment are shown in Appendix Table 2. The diets follow the assumptions made by /Kumblad et al, 2003/, except for the benthic compartment for which it was assumed that fish predated only on benthic macrofauna due to their biomass dominance. The three other benthic groups included were assumed to have negligible predation loss. The four-benthic compartments as parameterised were subsequently aggregated so that the whole model was equivalent to that presented by /Kumblad et al, 2003/.

2.1.2 Resulting carbon flows in ECOPATH vs the original model

The ECOPATH carbon budget based on the original carbon flows /Kumblad et al, 2003/ worked well in ECOPATH without any major flaws. The carbon flows was more or less the same as originally presented (Table 2-1). The only difference was that the benthic compartmental carbon flows differed slightly compared to those presented in /Kumblad et al, 2003/.

The main experience in the process of translating the original data into the ECOPATH software environment was related to differences in how the original carbon flows were estimated. For instance, /Kumblad et al, 2003/ estimates respiration from organism specific biomass, a conversion factor and the number of degree-days per year. From the estimated respiration carbon demand and excess flow (e.g. egested POC plus non-predated productivity) of carbon was calculated. Accordingly, in /Kumblad et al, 2003/ the main focus was on estimating respiration and the other flows were estimated as a consequence of the respiratory flows. The carbon flows for individual compartments will thus balance by definition; whereas the aggregated carbon flows (total input, respiration and other loss) need to be considered in order to balance the model. On the other hand, in ECOPATH productivity and carbon demand are estimated from biomasses of the organisms and assumed P/B- and Q/B-ratios. The assimilation efficiency of individual organism groups is further used to estimate the unassimilated part of food consumption. Respiration is estimated by difference from the other carbon flows. Thus, in ECOPATH the least reliable process is the respiratory flows, whereas in Kumblads CF model the estimated loss flow (non predated production) is less reliable. Still, in ECOPATH it is possible to use the same assumptions as used in /Kumblad et al, 2003/ and bioenergetic relationships between consumption, production, respiration and fecal loss processes to calculate the specific parameters necessary in ECOPATH.

Accordingly, what comes out from this exercise is that one really needs to be clear on how the flows have been calculated and what the flows really estimates. For instance, the output from ECOPATH easily revealed that the individual growth efficiencies for all heterotrophs (excluding microfauna) were exceedingly high (47%) except fish (24%) and the top-predators, which were assumed lower (10%). Usually, GE centres around 20–40% for pelagic zooplankton /Straile, 1997/, which means that benthic organisms, which are dependent on organic material of lower quality, might process food with similar or even lower efficiency. However, the exact value of the GEs as found here relates to how the two model types have been defined. Generally, the ECOPATH approach aims at estimating carbon flows with rather high detail, whereas the Kumblad model did not emphasise on estimating biomass productivity exactly. Therefore, for those occasions when the aim is to clearly estimate each carbon flow process accurately the parameterisation of these processes needs to be more carefully considered.

Table 2-1. ECOPATH carbon demand and flows to POC (10^6 gC /year).

#	Prey \ Predator	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Plankton	51	–	–	–	–	–	–	–	–	–	–	92	–
2	Bentophytes	–	57	–	–	–	–	2.5	–	–	–	–	321	–
3	Zooplankton	–	–	–	–	–	–	19.9	–	–	–	–	14	–
4	Macro Grazers	–	–	–	–	–	–	1.2	–	–	–	–	37	–
5	Filter feeders	–	–	–	–	–	–	–	–	–	–	–	8	–
6	Bent. microf	–	–	–	–	–	–	–	–	–	–	–	98	–
7	Bent. meiof	–	–	–	–	–	–	–	–	–	–	–	156	–
8	Bent. Macrof	–	–	–	–	–	–	1.2	–	1.3	–	–	489	–
9	Fish	–	–	–	–	–	–	–	0.19	–	0.005	0.12	11	–
10	Seal	–	–	–	–	–	–	–	–	–	–	–	0.04	–
11	Eider duck	–	–	–	–	–	–	–	–	–	–	–	0.26	–
12	Eagle	–	–	–	–	–	–	–	–	–	–	–	0.001	–
13	Humans	–	–	–	–	–	–	–	–	–	–	–	0.02	–
14	POC	–	–	12.6	196	234	738	–	–	–	–	–	–	–
15	DIC	–	–	–	–	–	–	–	–	–	–	–	–	–
16	Import	–	–	–	–	–	–	–	–	–	–	–	–47.2	48
17	Sum	51	57	12.6	196	234	738	24.9	0.19	1.3	0.005	0.11	1181	48

Table 2-2. Same as Table 2-1 but the benthos flows have been aggregated.

#	Prey \ Predator	3	4	5	6	7	8	9	10	11	12
1	Plankton	51	–	–	–	–	–	–	–	92	–
2	Bentophytes	–	57	–	2.5	–	–	–	–	321	–
3	Zooplankton	–	–	–	19.9	–	–	–	–	14	–
4	Macro Grazers	–	–	–	1.2	–	–	–	–	37	–
5	Filter feeders / Ben / Bent. Macrof	–	–	–	1.2	–	1.3	–	–	752	–
6	Fish	–	–	–	–	0.19	–	0.005	0.12	11	–
7	Seal	–	–	–	–	–	–	–	–	0.04	–
8	Eider duck	–	–	–	–	–	–	–	–	0.26	–
9	Eagle	–	–	–	–	–	–	–	–	0.001	–
10	Humans	–	–	–	–	–	–	–	–	0.02	–
11	POC	–	–	1181	–	–	–	–	–	–	–
12	DIC	–	–	–	–	–	–	–	–	–	–
13	Import	–	–	–	–	–	–	–	–	–47.2	48
	Sum	51	57	1181	24.9	0.19	1.3	0.005	0.11	1181	48

2.2 Generic model

Detailed models of radioactive flows of elements in aquatic food webs are to our knowledge not readily available in the literature. The ECOPATH software could represent an approach in which assumptions and basic food web structure from published models (e.g. Kumblads CF model) could be used as a standard platform to develop new radioecological models. Such an approach could facilitate for radioecologists with limited background in constructing aquatic food web models to estimate models for new areas. We hypothesise that the structure and the assumptions available for a coastal system as given in /Kumblad et al, 2003/ could serve as a test model. The approach was to investigate whether the default parameters as given in the generic model 37 in the ECOPATH software program and the model structure as given in /Kumblad et al, 2003/ would results in realistic carbon flow estimations. Deviations in major carbon flows in the original Kumblad model and the Generic model would pinpoint differences in the parameters used. If the "default" parameters would result in realistic carbon flows it might suggest that such parameters could be used to estimate preliminary models in other environments as well.

2.2.1 Model structure and data

The generic model was based on the same number of compartments, biomass and diets as in the original CF model. Input parameters, such as P/B- and Q/B-ratios and growth efficiencies (GE) were taken from the generic model (37) as given in the ECOPATH software. The P/B-, Q/B-ratios and GE used are shown in Table 2-3.

Table 2-3. Parameters used in the generic model.

Original group	Generic group	P/B (year–1)	Q/B (year–1)	GE (%)
Plankton	Phytoplankton	150		
Bentophytes	Benthic plants	10		
Zooplankton	Zooplankton, other	30		0.25
Macro Grazers	Krill	5		0.25
Benthos	Macrobenthos	2		0.3
Fish	Benthopelagics, small medium	0.6		0.25
Seal	Seals	0.07	50	0.0014
Eider duck	Birds	0.1	100	0.001
Eagle	Birds	0.1	100	0.001
Humans	Seals	0.07	50	0.0014

2.2.2 Generic model vs the original CF model

The resulting carbon flows in the Generic and the original CF model were shown to differ most for the autotrophic carbon flows. The planktonic- and phytobenthic primary production was estimated 11 and 3.4 times higher in the generic model as compared to the original CF model (Table 2-4). Thus the P/B–ratio for primary production as given in the generic model 37 was higher than that estimated through losses via generic P/B- and Q/B-ratios for the heterotrophic compartments. Thus, sedimentation of carbon via primary producers was much higher than originally estimated and higher than the estimated heterotrophic demand for autotrophic production. However, the carbon flows for the heterotrophic compartments were in reasonable agreement with those estimated by /Kumblad et al, 2003/. They deviated between 0.7–3.7 of the original carbon flows. The flows of carbon to the POC pool were in the same order of magnitude, between 0.6–4 times the original carbon flows, except for the loss from pelagic and phytobenthic primary producers, which was 16 and 4 times the original flows, respectively. In the generic model the amount POC flowing from primary producers was 90 and 93% compared to 64 and 85% in the original CF model. Thus, there is a large discrepancy in the balance between inputs of carbon to the system and the demands from the heterotrophic community. Accordingly it is not straightforward to use parameters that have not been adjusted to the specific environment one is describing. The variation in carbon flows are expected to be large and a generic ECOPATH model as the present one does not seem to be suitable to use in analysis of radionuclide flows from an ecological point of view. Therefore, in order to present better estimations of carbon flow it is necessary to know, at the least, the quantity of primary production introduced to the area you are studying. If the goal is to estimate realistic carbon flows and consequently realistic radionuclide flows for a specific environment, one would also need realistic assumptions on carbon demand for the predators included in the model. However, since it is common that estimations of radionuclides in the environment show greater variation than presented in this study it is still useful to use the present approach for making preliminary test models of CF and RF flows.

Table 2-4. Carbon flows for the Generic model (10^6 gC /year).

#	Prey \ Predator	1	2	3	4	5	6	7	8	9	10
1	Plankton	156	–	–	–	–	–	–	–	1419	–
2	Bentophytes	–	90	–	2.0	–	–	–	–	1218	–
3	Zooplankton	–	–	–	15.9	–	–	–	–	54.2	–
4	Macro Grazers	–	–	–	1.0	–	–	–	–	39.5	–
5	Filter feeders / Ben / Bent. Macrof	–	–	–	1.0	–	6.8	–	–	389	–
6	Fish	–	–	–	–	1	–	0.051	2.5	5.4	–
7	Seal	–	–	–	–	–	–	–	–	0.1	–
8	Eider duck	–	–	–	–	–	–	–	–	0.9	–
9	Eagle	–	–	–	–	–	–	–	–	0.005	–
10	Humans	–	–	–	–	–	–	–	–	0.25	–
11	POC	–	–	794	–	–	–	–	–	–	–
12	DIC	–	–	–	–	–	–	–	–	–	–
13	Import	–	–	–	–	–	–	–	–	–48	48
	Sum	156	90	794	19.92	1	6.8	0.051	2.5	3078	48

2.3 ECOSIM model

In order to describe biomass dynamics in a food web over time a well-balanced ECOPATH carbon flow model can be transferred to ECOSIM for further analysis (Figure 1-1). A reasonable ECOSIM model is also a prerequisite for using the ECOTRACER routine to estimate flows of a contaminant/tracer (Figure 1-1). Thus, since we would like to use the Kumblad model to estimate radionuclide flows in the Öregrundsgrepen area, we need to construct an ECOSIM model (e.g. a dynamic CF model) based on the present CF model. Accordingly, the element flows in ECOSIM is based on the output variables and parameters computed in ECOPATH. The basic equations describing biomass changes are:

$$dB_i/dt = g_i \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i)B_i \qquad (6)$$

where dB_i represents the growth rate in terms of its biomass (B_i) during the time interval dt of group (i), g_i is growth efficiency, C_{ji} represents the fraction of js consumption of prey i, M_i the non-predation (“other”) natural mortality rate, F_i is fishing mortality rate, e_i is emigration rate, I_i is immigration rate (and $e_i - I_i$ is the net migration rate). C_{ij} represents the fraction of the production by i that is consumed by a predator j. C_{ij} is calculated from:

$$C_{ij} = v_{ij}a_{ij}B_iB_j/(v_{ij} + v'_{ij} + a_{ij}B_j) \qquad (7)$$

where a_{ij} is a rate of effective search for prey type i by predator j. The other parameters v_{ij} and v'_{ij} are prey vulnerability parameters with default setting $v_{ij} = v'_{ij}$. Thus a_{ij} estimate predator related behaviour, whereas v_{ij} represent the effect that the behaviour of prey have on the availability of prey biomass to consumers (Figure 2-1). Low values of v_{ij} imply bottom-up control, e.g. available prey biomass control predator biomass production, whereas high values of v_{ij} imply top-down control, e.g. predators are able to control prey biomass.

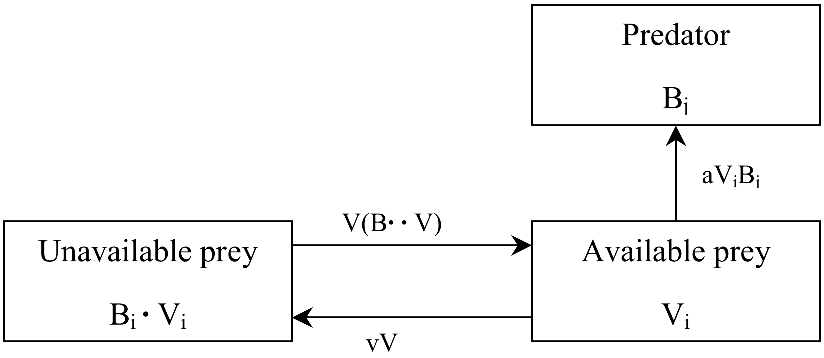

Figure 2-1. *Schematic relationship between unavailable and available prey in ECOSIM. The rate of transfer from one state to another is determined by the rate coefficients: V, v and a.*

Consequently, since the dynamics in organism biomass is based on Equation 6 it can be easily deduced that the parameters $a_{ij \text{ and}}$ v_{ij} directly influence the behaviour of prey and predators. Variation in these two parameters may thus determine most of the variation in organism biomass. The software does however provide many possibilities to test how the estimated consumption reacts to changes in these parameters. The user can constrain the maximum possible production and consumption so that unrealistic dynamics in the model is avoided. For instance, for primary producers it is optional to define a maximum relative P/B-ratio that can be achieved by the producers. There are also several options in which the effective search rate of predators can be constrained, but the tuning of these parameters are not easily overviewed and are neither clearly described in the software.

2.3.1 What determines stability in an ECOSIM model

A prerequisite for running a dynamic CF model in ECOSIM is that it is based on a balanced steady state CF model constructed in ECOPATH. In the preliminary version of the CF model used in ECOSIM the biomass fluctuated slightly for some organisms. The model was also found to be sensitive to changes in vulnerability settings. In these analysis's it was discovered that there was a slight imbalance in the net flow of POC for the system. Therefore the export of POC from the system was adjusted slightly compared to the original CF model in ECOPATH, so that the model was completely balanced. After that adjustment the instability of the dynamic CF model disappeared. For instance, when the model was run in ECOSIM for a 100-year period, changes in the vulnerabilities did not affect the dynamics in the model at all. The resulting biomass dynamics was more or less constant for the whole time period. This means that the model was in complete balance and there was no dynamics in the model.

A conclusion from the above analysis is that there are several advanced possibilities to include complex interaction in the analysis of carbon flows in aquatic food webs through either vulnerability settings or group specifications of feeding time etc. However, since the present model has been defined to balance, the model does not respond to changes in these parameters. It can be hypothesised that for a more complicated model the evaluation of different parameters would be more complicated if the bioenergetic parameters used would differ more between groups of organisms than assumed. Nevertheless, in this study the main purpose was to use the steady state and dynamic CF models to make a RF model by using ECOTRACER in the ECOPATH with ECOSIM program. From that perspective it is easier to work with a less complicated model that facilitates the evaluation of the software and the consequences of introducing a tracer into an aquatic system.

3 Estimating radionuclide flows using ECOTRACER

3.1 ECOTRACE model

In parallel with the estimations of biomass changes per time (ECOSIM) it is possible to use the ECOTRACE routine to predict movements and accumulation of a contaminant or a tracer in a food web. The differential equations used in ECOTRACE are linear dynamic equations with time-varying rate coefficient that depend on the carbon biomass flow rates estimated. Accordingly, along with the ECOSIM simulations the body burdens or total amounts of a radionuclide per organism/compartment are simulated (see Figures 1-1 and 3-1).

In the modelling program it is possible to specify the specific conditions of radionuclide flow one would like to describe. Initially it is possible to specify the amounts of tracers already present in the system, being part of either an environmental fraction or one or several biotic compartments. Direct input of a radionuclide from outside the system can be set to enter the system either to the environmental fraction (see Figure 3-1) or via immigration of organism biomass. Direct output of a radionuclide from a system can likewise be set to occur via emigration of organism biomass or decay rate of individual compartments biomass. The latter process describes all loss processes, such as organism respiration of C-14 and additional losses from biomass pools one need to include in the model. The tracer/contaminant is assumed to flow between different pools at instant rates equal to the probabilities of being sampled as part of the biomass flows (instantaneous rate = (flow)/(biomass in prey pool). Eventual absorption/uptake of the tracer/contaminant need also to be defined for each organism group. The basic equations that are solved along with the ECOSIM equations are:

1. Uptake from food (assimilated contaminant):

$$\mathrm{Cj\ GCi\ Qji/Bj} \tag{8}$$

where Cj = conc. in food j, GCi = proportion of food assimilated by type i organisms; Qji = biomass flow rate from j to i (estimated in ECOPATH as Bi(Q/B)i DCij)i, Bj = food j biomass.

2. Direct uptake from the environment:

$$\mathrm{ui\ Bi\ Co} \tag{9}$$

where ui = parameter representing uptake per biomass per time, per unit environmental concentration, Bi = biomass, Co = environmental concentration.

3. Conc. in immigrating organisms:

$$\mathrm{ci\ Li} \tag{10}$$

where ci = parameter (tracer per unit biomass in immigrating biomass), Ii = biomass of pool i immigrants per time, which can be defined in the ECOPATH model.

4. Predation:

$$Ci\ Qij/Bi \tag{11}$$

where Ci = concentration in pool I, Qij = consumption rate of type i organisms by predator type j, Bi = biomass in pool i.

5. Detritus:

$$Ci\ Moi+(1–GCi)\ SjCjQji/Bj) \tag{12}$$

where Moi = non-predation death type i (per year), GCi = fraction of food intake assimilated, Qji = intake rate of type j biomass by type i, all taken from ECOPATH

6. Emigration:

$$ei\ Ci \tag{13}$$

where ei = emigration rate (per year). Unfortunately calculations of ei is not clearly described in the ECOPATH manual, but is probably estimated from the amount biomass per compartment immigrated and emigrated as defined in ECOPATH.

7. Metabolism:

$$di\ Ci \tag{14}$$

where di = metabolism + decay rate for the material while in pool i. Thus, the combined loss of a radionuclide via respiration and decay per biomass should be estimated.

Thus, along with the data taken from the ECOPATH input data, it is necessary to specify the following parameters.

- Initial pool concentrations Ci, including environmental concentration Co.
- Direct uptake rate parameters ui as rates per time per biomass per unit Co.
- Concentrations per biomass Ci in immigrating organisms.
- Metabolism/decay rates.

According to the above Equations (8-14) it is obvious that an ECOTRACER model is constrained by the initial parameterisation and balancing of the ECOPATH model (Figure 1-1), the dynamic ECOSIM model (Figure 1-1) as well as the additional assumptions and specific input data necessary to describe the radionuclide flows.

3.2 ECOTRACER input data

Beside a fully balanced ECOPATH CF model to be used in ECOSIM for estimating radionuclide flows in ECOTRACER, it is necessary to specify how the radionuclide is introduced into the system. The original CF model introduces the radionuclide to the benthic water environment (e.g. to the DIC pool). Since, we do not have included an active uptake of DIC primary producers in the CF model it is assumed that the radionuclide is introduced to the biological pathways via the “environmental” compartment. The total annual input of C-14 was $5.13x10^6$ Bq/year, which result in about $1.4x10^5$ Bq per area,

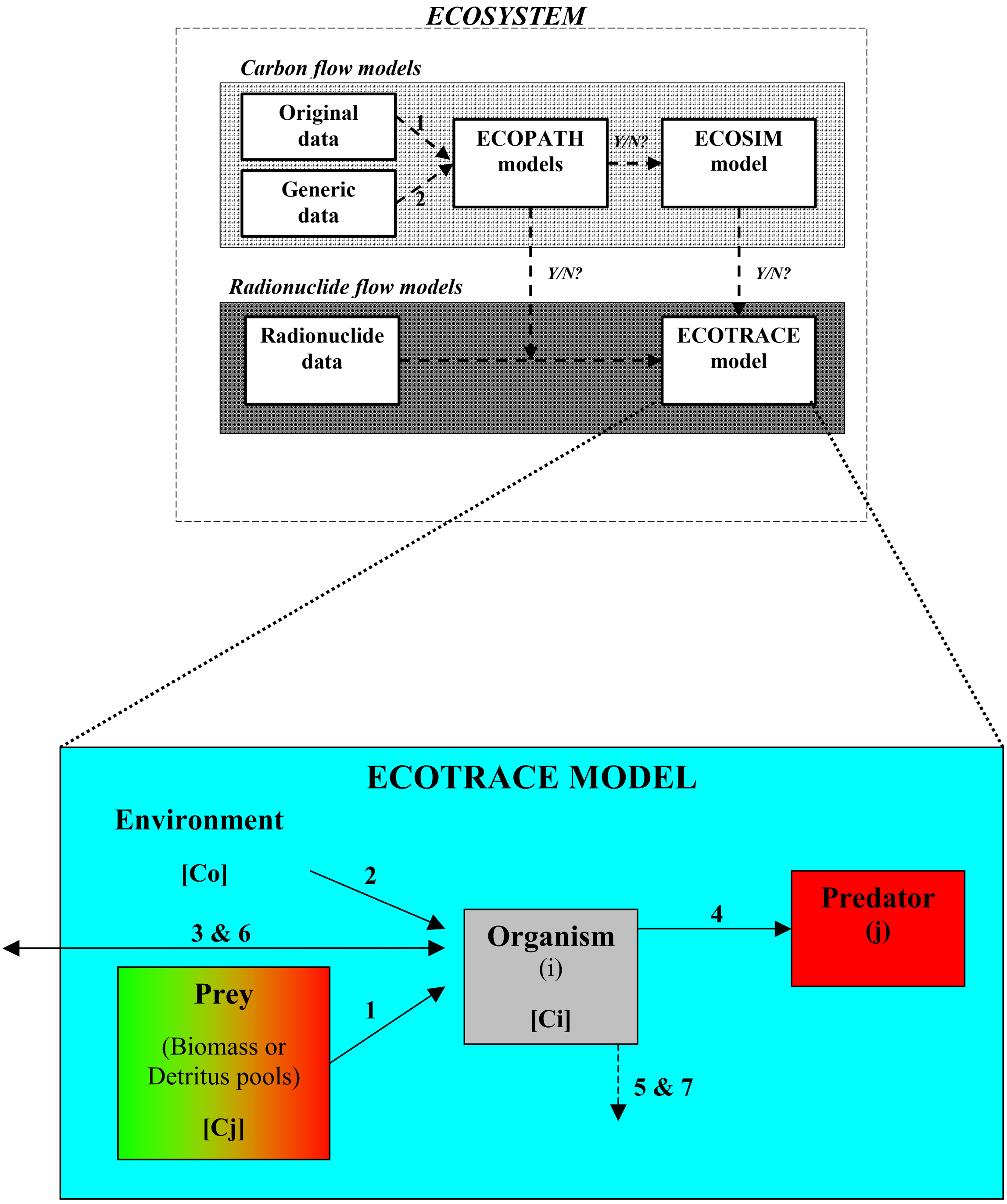

Figure 3-1. *Input and loss processes of a contaminant/tracer through: uptake from food (1), direct uptake from the environment (2), immigration and emigration (3 and 6, respectively), predation (4) and detritus and metabolism/decay loss (5 and 7, respectively).*

Table 3-1. ECOTRACER input data.

#	Group Name	Initial conc. (gC/m²)	Conc. in immigrating biomass (t/t)	Direct absorption rate (t/t/t/year)	Decay rate (per year)
1	Environment	0			0
2	Plankton	0	0	0	0
3	Bentophytes	0	0	0.000273	0
4	Zooplankton	0	0	0.001175	13.077
5	Macro Grazers	0	0	0	4.223
6	Benthos	0	0	0	3.579
7	Fish	0	0	0	1.687
8	Seal	0	0	0	3.167
9	Eider duck	0	0	0	6.372
10	Eagle	0	0	0	3.529
11	Human	0	0	0	0.037
12	POC	0	0	0	365.000
13	DIC	0	0	0	0.000

given that the total water in the system is exchanged 365 times each year. From the environmental compartment the two producer compartments, plankton and phytobenthos are assumed to "adsorb" the radionuclide in an amount equivalent to the autochthonous inorganic carbon uptake (e.g. ui). For the present RF model it is sufficient to use the radioactivity C-14 uptake for plankton (400 Bq) and phytobenthos (22000 Bq) per biomass and environmental concentration as specified in the original CF model. Accordingly, from this procedure ui could be calculated for plankton and phytobenthos, respectively.
It was further necessary to consider the effect of water exchange on plankton, zooplankton and POC in the system. However, since the planktonic C-14 uptake (ui) is linked to the environmental compartment, which already is set to be exchanged 365 times each year, it is only the other compartments that need to be considered. For zooplankton the water exchange was estimating by setting the amount of biomass immigrated and emigrated from/to the system each year equal to the per area biomass times the water exchange. For POC the water exchange was considered by assuming a decay rate of biomass of 365 (di). Thus, though these adjustments it was possible to account for water exchange for the plankton, environment, POC and zooplankton compartments

3.3 ECOTRACER result

The resulting steady state radionuclide concentrations estimated by ECOTRACER were in the same order of magnitude as the original CF model (Table 3-2). The difference between the two modelling approaches ranged between 100 and 109% for environment, plankton, bentophytes and zooplankton compartments. For the other compartments the difference was larger, being between 73–142% of the original radionuclide concentrations. Analytically, it was not straightforward to identify the causes of these differences, since the input and output flows as calculated by the ECOTRACER programme is not available through the software. Still, it is most likely that the differences found are due to a combination of several factors. First of all, the carbon flows for the benthic compartments different slightly as compared to the original CF model due to inconsistent data presented in /Kumblad et al, 2003/. That resulted in estimates of excess carbon flow being 123, 93, and 94% of the original carbon flow estimations. Thus, it is possible that some of the differences in radionuclide concentrations could be a result of differences between the present and original CF models. On the other hand the water exchange of POC was not satisfactory considered in the ECOPATH program. It was only possible to account for the radionuclide part of POC (C-14) that is lost from the system by setting the decay rate of this material to 365 times each year, whereas the simultaneous input of POC to the system was omitted. The input of non-radioactive POC carbon was therefore not possible to include in the model. Further, it was neither possible to include re-circulation of radionuclides via heterotrophic respiration and thereby loss of radionuclides within the system. Still, a rough estimation of the importance of that radionuclide flow suggest that only about 0.2% of the annual input to the system depend on respiration and would thus not result in such a high differences between the two RF models.

To conclude, it is possible to reproduce the original C-14 flows by using ECOTRACER, but the possibilities to consider water exchange for all compartments are limited. Further, since the resulting model only show steady state concentrations it is difficult to check the accuracy of the modelled flows. Hopefully, these drawbacks will be improved in future developments of the software. In the case of C-14 estimations it was difficult to account for recycling of the radionuclides through respiratory processes since there is no possibility for including that in the programme at the moment.

Table 3-2. ECOTRACER output. Comparative results from original model and ECOTRACER model in percent.

#	Group Name	Original conc (gC/m^2)	Ecotracer conc. (gC/m^2)	Original/ Ecotracer (%)
1	Environment	1.40E+05	1.40E+05	100%
2	Plankton	30	30	100%
3	Bentophytes	7900	7814	99%
4	Zooplankton	0.29	0.29	100%
5	Macro Grazers	240	262	109%
6	Benthos	280	230	82%
7	Fish	54	75	139%
8	Seal	0.13	0.18	138%
9	Eider duck	0.16	0.13	88%
10	Eagle	0.0033	0.0047	142%
11	Human	–	0.14	
12	POC	77	56	73%
13	DIC	0	0	0

4 Discussion

ECOPATH with ECOSIM /Pauly et al, 2000; Walters et al, 1999/ have proven to be widely used in traditional food web and fisheries science, ranging from reef ecosystems /Gribble, 2003/, estuaries /Harvey et al, 2003; Rybarczyk and Elkaim, 2003; Sandberg et al, 2000/, terrestrial ecosystems /Krebs et al, 2003; Ruesink et al, 2002/, lakes /Kitchell et al, 2000/, mangroves /Vega-Cendejas and Arreguin-Sanchez, 2001/ and ocean ecosystems /Cox et al, 2002; Shannon et al, 2000/. Even existing carbon flow models /Carrer and Opitz, 1999/ have been combined with an ecotoxicological approach to model dioxins in a lagoon system /Carrer et al, 2000/. Nowadays, the inclusion of ECOTRACE in the modelling program have enhanced the possibilities to integrate traditional mass balance modelling of carbon in food webs /sensu Lindemann, 1942/ with that of contaminant fate models of aquatic ecosystems.

In this study, the results presented clearly show that there is potential for a successful development of this scientific approach in the future. The parallel modelling of carbon flow in ECOPATH and ECOSIM, with C-14 flows in ECOTRACER resulted in steady state concentrations of C-14 between 72–142% of the original model. By considering that the carbon flows differed slightly between the present and original CF model, these differences are negligible. Thus, the present approach puts the data and assumptions of the original CF model in a methodological environment that facilitate for others scientists to test and develop new radioecological models for other ecosystems and environmental regimes. However, it must be realised that the specific scale at which food relationships are described defines each food web, and constrains the specific questions one seeks to answer from them /cf Peters, 1988/. This statement can be exemplified from the present CF and RF models. For instance, by using ECOPATH it was discovered that the bioenergetic relationships used by /Kumblad et al, 2003/, such as the relation between respiration and consumption and assimilation efficiency resulted in unrealistically high growth efficiencies for all heterotrophs in the system (47%), except fish. Normally, the relation between biomass growth and consumption of food, i.e. growth efficiency, range between 10–40% for planktonic heterotrophs. However, in the original CF model the main focus was to estimate respiration and calculate all the other processes from that estimate. Thus, if /Kumblad et al, 2003/ have estimated respiration accurately it is likely that they have underestimated carbon consumption in the system, since higher carbon consumption would lead to lower growth efficiencies. Further, in the case of C-14 flow estimations it would be preferable to include phytoplanktonic uptake of dissolved inorganic carbon in the model. Hopefully, it will be possible to include that in future development of the program. Further, the generic model obviously showed that it is difficult to generalise biological parameters from one environmental regime to another. The site-specific organism biomass and biological factors, such as P/B and Q/B-ratios are necessary to connect to the specific environment, which the model is to describe. Thus, differences in carbon flows between the generic model and the present CF model ranging between factors 3 to 10 are not surprising. However, if one is interested to make preliminary estimations of carbon and radionuclide flows it is worthwhile to use the present approach to perform such tests. However, that would require some field data useful for validation.

Still, one of the major drawbacks with the present approach is that the ECOPATH with ECOSIM program represent a model environment, which is fixed. This means that the possibilities to make adjustment of the model or additional tests of the model that have not been originally considered in the program are small. For instance, we discovered that the recycling of C-14 was not possible to account for in ECOTRACER and thereby the RF model. However, it was estimated that the respiratory flows should be less than 0.2%, of the annual input to the system, which really do not affect the overall flow rates. However, this process might be of importance in models describing other systems or other radionuclide substances. Further, it was not straightforward to include the effect of water exchange on radionuclide concentrations in the system. Even though we could include the radionuclides exchanged through water circulation, the methodology used was not optional and rather robust. One further thing that could be improved in ECOTRACER is that the input/output of radionuclides causing a certain steady state concentration of the radionuclide in the model ought to be available as a separate output data sheet. Obviously, that would make the model more easily to analyse and the cause of a certain steady state concentration as estimated through ECOTRACER.

Currently, it seems that most models describing the fate of radionuclides in aquatic systems focus on estimating dispersion of the radionuclide in the aquatic environment and rarely include detailed estimates of the complex pathways by which a radionuclide can be transferred through biotic compartments /Thiessen et al, 1999/. The traditional use of concentration and transfer factors in estimates of radionuclide flow through biological compartments can be used successfully to a certain extent, but the coupling between food web dynamics and processing of radionuclides by different groups of organism can be misleading. Therefore, radioecologists could gain a lot of insights by combining knowledge of uptake mechanism of contaminants, decay rates in the system and biological interactions occurring in food webs by following the approach as outlined in this study.

To conclude even though there are some issues that need to be considered more carefully in the future development of the program in order to strengthen the ECOTRACER routine in ECOPATH. The basic carbon flow models (e.g. ECOPATH) are quite straightforward to construct for any given ecosystem. The main bottlenecks are the availability of data for the system one would like to describe. The main argument for using ECOPATH with ECOSIM is that both the basic structure of the program and the increasing number of ECOPATH models available from various ecosystems around the world makes it a suitable platform for interactions between scientist with competence in food web modelling and those dealing with contaminant modelling, such as radioecology.

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6 References

Aldridge J N, Kershaw P, Brown J, McCubbin D, Leonard K S, Young E F, 2003. Transport of plutonium (Pu-239/240) and caesium (Cs-137) in the Irish Sea: comparison between observations and results from sediment and contaminant transport modelling. Continental Shelf Research 23, 869–899.

Blust R, 2001. Radionuclide accumulation in freshwater organisms: Concepts and Models. In Radioecology, Radioactivity and Ecosystems, pp 275–307. Edited by E. Van der Stricht & R. Kirchmann. Liége: Fortemps.

Carrer S, Opitz S, 1999. Trophic network model of a shallow water area in the northern part of the Lagoon of Venice. Ecological Modelling 124, 193–219.

Carrer S, Halling-Sorensen B, Bendoricchio G, 2000. Modelling the fate of dioxins in a trophic network by coupling an ecotoxicological and an Ecopath model. Ecological Modelling 126, 201–223.

Christensen V, 1992. Network Analysis of Trophic Interactions in aquatic Ecosystems. In Department of General Chemistry. Copenhagen: Department of General Chemistry.

Christensen V, Pauly D, 1995. Fish production, Catches and the Carrying Capacity of the World Oceans. NAGA the ICLARM Quartely 18, 34–40.

Cox S P, Essington T E, Kitchell J F, Martell S J D, Walters C J, Boggs C, Kaplan I, 2002. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics. Canadian Journal of Fisheries and Aquatic Sciences 59, 1736–1747.

Gribble N A, 2003. GBR-prawn: modelling ecosystem impacts of changes in fisheries management of the commercial prawn (shrimp) trawl fishery in the far northern Great Barrier Reef. Fisheries Research 65, 493–506.

Harvey C J, Cox S P, Essington T E, Hansson S, Kitchell J F, 2003. An ecosystem model of food web and fisheries interactions in the Baltic Sea. Ices Journal of Marine Science 60, 939–950.

Kitchell J F, Cox S P, Harvey C J, Johnson T B, Mason D M, Schoen K K, Aydin K, Bronte C, Ebener M, Hansen M, Hoff M, Schram S, Schreiner D, Walters C J, 2000. Sustainability of the Lake Superior fish community: Interactions in a food web context. Ecosystems 3, 545–560.

Krebs C J, Danell K, Angerbjorn A, Agrell J, Berteaux D, Brathen K A, Danell O, Erlinge S, Fedorov V, Fredga K, Hjalten J, Hogstedt G, Jonsdottir I S, Kenney A J, Kjellen N, Nordin T, Roininen H, Svensson M, Tannerfeldt M, Wiklund C, 2003. Terrestrial trophic dynamics in the Canadian Arctic. Canadian Journal of Zoology-Revue Canadienne De Zoologie 81, 827–843.

Kumblad L, 1999. A carbon budget for the Aquatic Ecosystem above SFR in Öregrundsgrepen, pp 1–36. Stockholm University: Department of Systems Ecology.

Kumblad L, Gilek M, Naeslund B, Kautsky U, 2003. An ecosystem model of the environmental transport and fate of carbon-14 in a bay of the Baltic Sea, Sweden. Ecological Modelling 166, 193–210.

Lindemann R, 1942. The trophic-dynamic aspect of ecology. Ecology 23, 399–418.

Pauly D, Christensen V, Walters C, 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. Ices Journal of Marine Science 57, 697–706.

Peters R H, 1988. Some general problems for ecology illustrated by food web theory. Ecology 69, 1673–1676.

Ruesink J L, Hodges K E, Krebs C J, 2002. Mass-balance analyses of boreal forest population cycles: Merging demographic and ecosystem approaches. Ecosystems 5, 138–158.

Ryan T P, 2002. Transuranic biokinetic parameters for marine invertebrates – a review. Environment International 28, 83–96.

Rybarczyk H, Elkaim B, 2003. An analysis of the trophic network of a macrotidal estuary: the Seine Estuary (Eastern Channel, Normandy, France). Estuarine Coastal and Shelf Science 58, 775–791.

Sandberg J, Elmgren R, Wulff F, 2000. Carbon flows in Baltic Sea food webs – a re-evaluation using a mass balance approach. Journal of Marine Systems [J. Mar. Syst.] 25, 249–260.

Sazykina T G, 2000. ECOMOD – An ecological approach to radioecological modelling. Journal of Environmental Radioactivity 50, 207–220.

Shannon L J, Cury P M, Jarre A, 2000. Modelling effects of fishing in the Southern Benguela ecosystem. Ices Journal of Marine Science 57, 720–722.

Smith C N, Clarke S, McDonald P, Goshawk J A, Jones S R, 2000. Reconstructing historical radionuclide concentrations along the east coast of Ireland using a compartmental model. Science of the Total Environment 254, 17–30.

Smith, C N, Goshawk J A, Charles K, McDonald P, Leonard K S, McCubbin D, 2003. MEAD (part II) – Predictions of radioactivity concentrations in the Irish Sea. Journal of Environmental Radioactivity 68, 193–214.

Straile D, 1997. Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator-prey weight ratio and taxonomic group. Limnology and Oceanography 42, 1375–1385.

Sundbom M, Meili M, Andersson E, Ostlund M, Broberg A, 2003. Long-term dynamics of Chernobyl Cs-137 in freshwater fish: quantifying the effect of body size and trophic level. Journal of Applied Ecology 40, 228–240.

Thiessen K M, Thorne M C, Maul P R, Pröhl G, Wheater H S, 1999. Modelling radionuclide distribution and transport in the environment. Environmental Pollution 100, 151–177.

Walters C, Pauly D, Christensen V, 1999. Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems 2, 539–554.

Wang W X, Ke C H, Yu K N, Lam P K S, 2000. Modelling radiocesium bioaccumulation in a marine food chain. Marine Ecology-Progress Series 208, 41–50.

Vega-Cendejas M E, Arreguin-Sanchez F, 2001. Energy fluxes in a mangrove ecosystem from a coastal lagoon in Yucatan Peninsula, Mexico. Ecological Modelling 137, 119–133.

Appendix

Table 1. Basic input parameters.

#	Group Name	Habitat	B	P/B	Q/B	EE	P/Q	Biom. Acc	Un.assim	Import
1	Plankton	1	10.5	13.619				0.00	0	
2	Bentophytes	1	131	2.908				0.00	0	
3	Zooplankton	1	1.3	18.308	39.231			0.00	0.2	
4	Macro Grazers	1	4.5	5.911	12.667			0.00	0.2	
5	Filter feeders		1.7	3.459	7.412			0.00	0.2	
6	Bent. microf		12	8.167	16.333			0.00	0.2	
7	Bent. meiof		6.4	17.063	36.563			0.00	0.2	
8	Bent. Macrof	1	99	3.479	7.455			0.00	0.2	
9	Fish	1	8.3	0.713	3.000			0.00	0.2	
10	Seal	1	0.02	0.950	9.500			0.00	0.2	
11	Eider duck	1	0.068	1.912	19.118			0.00	0.2	
12	Eagle	1	0.00051	1.059	10.588			0.00	0.2	
13	Human	1	0.00900	6.039	12.941			0.00	0.2	
14	POC	1	29							–47.2
15	DIC	1	1780							48

Table 2. Diet composition of the food web.

#	Prey/Predator	3	4	5	6	7	8	9	10	11	12	13
1	Plankton	1										
2	Bentophytes		1					0.1				
3	Zooplankton							0.8				
4	Macro Grazers							0.05				
5	Filter feeders											
6	Bent. microf											
7	Bent. meiof											
8	Bent. Macrof							0.05		1		
9	Fish								1		1	1
10	Seal											
11	Eider duck											
12	Eagle											
13	Human											
14	POC			1	1	1	1					
15	DIC											
16	Import											
17	Sum	1	1	1	1	1	1	1	1	1	1	1

Table 3. Detritus fate of the compartments.

#	Prey/Predator	POC	DIC	Export	Sum (must = 1)
1	Plankton	1	0	0	1
2	Bentophytes	1	0	0	1
3	Zooplankton	1	0	0	1
4	Macro Grazers	1	0	0	1
5	Filter feeders	1	0	0	1
6	Bent. microf	1	0	0	1
7	Bent. meiof	1	0	0	1
8	Bent. Macrof	1	0	0	1
9	Fish	1	0	0	1
10	Seal	1	0	0	1
11	Eider duck	1	0	0	1
12	Eagle	1	0	0	1
13	Human	1	0	0	1
14	POC	1	0	0	1
15	DIC	0	1	0	1