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ABAM, a Model for Bioaccumulation of POPs in Birds: Validation for Adult Herring Gulls and Their Eggs in Lake Ontario

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An Avian BioAccumulation Model (ABAM) of persistent organic pollutant (POP) uptake and elimination in adult life-stage of birds was validated by simulation of concentrations of DDE, dieldrin, mirex, and HCB in herring gull eggs in Lake Ontario for the years 1985, 1990, and 1992. These chemicals represented a range of whole-body half-lives of 82−265 days in the gull. Dietary intake of POPs by a female gull was simulated by a dynamic bioenergetics model which included dependence on temperature, photoperiod, egg production, and feeding chicks. Concentrations in the two main prey fish of the gull in Lake Ontario were used for POP exposure. Clearance from the female was based on a two compartment toxicokinetic model. Egg concentrations were estimated from egg/whole body female concentration ratios. Simulated concentrations were compared to measured concentrations in gull eggs from 4 different colonies in the northern part of Lake Ontario. Simulations using a diet of 81% fish and 19% uncontaminated food resulted in the best fit with least variance among predicted and measured data. The mean ratio of predicted to measured concentrations in eggs was 1.0 ± 0.27 among chemicals, years, and colonies for this exposure scenario. This result was in excellent agreement with field assessments of herring gull diet composition in Lake Ontario of 80−82% fish. The ability to perform accurate *a priori* simulations for the range of test conditions employed in the validation constituted a rigorous test of the soundness of the model's structure and parameterization. With species-specific adjustments, ABAM can be regarded as a general model for lipophilic POPs bioaccumulation in birds.

Introduction

Models of bioaccumulation of POPs in organisms or food webs lie somewhere along an empirical−mechanistic spectrum (*1*). Highly empirical bioaccumulation models may give good predictions within certain constraints, but there is considerable uncertainty that they are capable of adequate prediction "outside the box" in the real environment. Highly mechanistic bioaccumulation models may be more universally applicable than empirical models because the independent variables to which the model output is most sensitive have been identified and incorporated in the model, but may be very difficult to parameterize. The ideal model strikes a balance by having sufficient detail to simulate processes influencing bioaccumulation while minimizing the number of parameters that must be obtained. Mackay and Fraser (*1*) noted that the direction in bioaccumulation modeling is toward more mechanistic models because our understanding of the underlying processes is improving. Kelly et al. (*2*) compared four different mechanistic models of gastrointestinal absorption of POPs in fish, wildlife, and humans and concluded that there were considerable equivalencies despite fundamental differences in the assumed underlying mechanisms in the models. This emphasizes the danger in deriving mechanisms from models rather than the other way around.

Environmental realism of models of POPs bioaccumulation frequently suffers from having been developed in a laboratory context. Most models fail to incorporate the gamut of ecological, climatic, and physiological variables which may be influential in bioaccumulation of POPs by wild species (*3*). Ambient temperature is probably foremost among these important environmental variables because of its influence on metabolic rate and therefore feeding rate. Temperature may also affect POP excretion rate by modifying lipid content of the animal. Ambient temperature is particularly important in metabolic rate of poikilotherms (fish and reptiles), but also has some influence on metabolic rate in homeotherms (birds and mammals). Some models of bioaccumulation of POPs in fish and food webs take into account ambient temperature for this reason (*4*). However, most models simply use average values of temperature-dependent parameters and ignore temperature altogether.

The lifetime exposure history of birds to POPs is poorly understood, but is expected to be decidedly different from that of mammals. In birds, exposure to POPs appears to peak at hatching (*5*), whereas peak exposure in mammals probably occurs during the nursing period. Birds experience whole body biomagnification factors (on a wet weight basis) of recalcitrant POPs as high as 100 (*6*) due to a high ratio of metabolic rate to body weight.

Compared to aquatic food webs and fish, there has been little effort to develop models of bioaccumulation of POPs in wild birds. Glaser and Connolly (*7*) reported a model for DDE and PCB accumulation in three bird species. Field metabolic rates (FMR) of the species were estimated from empirical equations to determine feeding rates and therefore dietary uptake of contaminant by the birds. However, clearance rates were adjusted to fit the model to field data, so the model was more empirical than mechanistic. Nichols et al. (*8*) developed a bioenergetic model for bioaccumulation

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of PCBs in nestling tree swallows which was adapted for accumulation of brominated flame retardants in nestling great tits (*9*). These models were only concerned with the period from hatching to fledging. Debruyn et al. (*10*) developed a bioenergetic biomagnification model of POPs bioaccumulation in animals, including birds. The model predicts maximum biomagnification factor (BMF). Over a broad range of taxa the modeled and measured BMF_{max} values were highly correlated, but predictions for individual species of birds were frequently a factor of 2 too high or low. Drouillard et al. (*5*) reported an empirical toxicokinetic model for uptake of PCBs by herring gull embryos from egg yolk. None of these models attempted to simulate the temporal changes in bioaccumulation of POPs experienced by a wild adult bird. A full life-history model taking into account relevant environmental factors would be very helpful in understanding the unique features of POPs bioaccumulation in birds.

The present study documents the validation of the adult life-stage of an Avian BioAccumulation Model (ABAM) using the herring gull (*Larus argentatus*) in Lake Ontario as the test species. ABAM is a deterministic model of bioaccumulation of lipophilic POPs in an average individual, free-living bird divided into three life-stages (embryo, chick, and breeding adult) developed sporadically over a 25 year period in the Canadian Wildlife Service (*5, 6, 11*−*18*). Lake Ontario was chosen for validation of the model because excellent data for concentrations of contaminants in both diet and gull eggs were available. Furthermore, the birds remain on the lake year-round in Lake Ontario, allowing better assessment of year-round diet (*16*). POPs concentrations and biomass data were available for the two principal species eaten by herring gulls in Lake Ontario, alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) (*19*), allowing various diet scenarios to be tested.

The Model

General Characteristics. ABAM consists of two submodels; a bioenergetics submodel to predict the bird's exposure to contaminants, and a toxicokinetics submodel to predict clearance of contaminants from the birds. While the basic structure is fixed, the model is highly flexible and interactive. All of the equations and parameters can be altered during a run, and there are alternate ways of inputting data (see Supporting Information for description). The bioenergetic submodel for an adult female herring gull calculates rate of food consumption from the sum of daily existence energy requirement (minimal activity, non-foraging) of a non-passerine bird, production costs (eggs and lipid), the cost of foraging to meet these requirements, and the cost of feeding chicks (*17*). The rate of food consumption determines the POP ingestion rate from dietary concentrations. Rate of POP uptake by the bird is assumed to be a simple proportion of the ingestion rate (*12*). The toxicokinetics submodel is based on the two-compartment (blood and whole-body lipid pool) model of disposition and clearance of POPs in herring gulls developed by Clark et al. (*11*). POP concentrations in eggs are based on concentration ratios of egg to female whole body, which are about 0.5 for species such as the herring gull which use primarily exogenous resources for egg formation (*6*), and about 1 for species such as waterfowl which use primarily endogenous lipids in eggs (*14*).

Bioenergetics Submodel. The bioenergetics submodel of an adult bird considered four contributions to total daily energy expenditure (Q_g in this model, DEE in avian bioenergetics literature) that determine feeding rate: daily existence metabolic rate (Q_{em}, minimal, non-foraging activity plus basal metabolism), cost/benefit of production/utilization of adipose tissue lipids ($\pm Q_L$), energy required to produce eggs for females (Q_{egg}), and energy expenditure for foraging (Q_{for}).

$$Q_g = (Q_{em} + Q_L + Q_{egg} + Q_{for})/F_d \quad (kJ{\cdot}d^{-1}) \qquad (1)$$

where F_d is efficiency of assimilation of energy from the diet.

Foraging costs were calculated as a proportion of the sum of the individual's own energy requirement for maintenance, egg production, lipid production/utilization, plus costs for rearing a chick (Q_{ch}) times number of chicks, prorated 50% to each parent.

Q_{em} was calculated as a continuous allometric function of body weight, photoperiod, and ambient temperature based on an equation derived for non-passerine birds (*17*)

$$Q_{em} = (14.2 + 0.22PP)W_b^{0.54} - (0.59 + 0.025PP)T_{am}W_b^{0.30} \quad (kJ{\cdot}d^{-1}) \quad (2)$$

where PP is photoperiod (h daylight), W_b is body weight (g), and T_{am} is ambient temperature (°C). The photoperiod term serves to take into account seasonal temperature acclimation. The effect is to decrease the response to temperature changes in winter (short photoperiod) compared to summer (long photoperiod).

The average body weight minus lipid weight (i.e., fat-free wet weight, W_{b-f}) was fixed at 856 g for the adult female herring gull (*17*). Whole body lipid content of herring gulls fluctuates in response to changing ambient temperature (*17*). This has an effect on bioenergetics due to costs/benefits of production/loss of adipose lipid, as well as effects on metabolic rate due to weight fluctuations. Whole body clearance of POPs has also been shown to be inversely proportional to whole body lipid content (*11*). There is an inverse linear relationship between fraction lipid (F_L) in whole body weight of adult herring gulls and ambient temperature (T_{am}) (*17*)

$$F_L = 0.136 - 0.0027T_{am} \qquad (3)$$

From eq 3, and W_{b-f}, adult whole body weight (W_b) as a function of ambient temperature can be estimated as

$$W_b = W_{b-f}/(1 - F_L) = W_{b-f}/(0.864 - 0.0027T_{am}) \quad (g) \qquad (4)$$

W_b calculated from eq 4 was substituted into eq 2 to calculate Q_{em}.

Lipid production cost/benefit contribution was calculated from daily lipid weight increments driven by eq 4, and the energy density of lipid (E_L, $kJ{\cdot}g^{-1}$)

$$Q_L = E_L \Delta W_b \quad (kJ{\cdot}d^{-1}) \qquad (5a)$$

The dependence of ΔW_b on ΔT_{am} can be estimated from the first derivative of eq 4. Substituting this derivative into eq 5a, the dependence of Q_L on daily temperature change is

$$Q_L = -0.0027E_L W_{b-f}(0.864 - 0.0027T_{am})^{-2}\Delta T_{am} \quad (kJ{\cdot}d^{-1}) \qquad (5b)$$

where ΔT_{am} is daily temperature increment. In the model, monthly mean temperatures were used, which were linearly interpolated between months, and Q_L was calculated directly from eq 5a, not 5b.

The total cost to the female for forming the first egg was assumed to be spread evenly over the 15 day period prior to laying. Because herring gull eggs are normally laid 2 days apart, the cost of each subsequent egg was added beginning 2 days after the previous one until the total number of eggs were included. This results in a step function which spreads the total energy cost (Q_{egg}) over varying lengths of

TABLE 1. Fixed Model Parameter Values in the Validation Simulations for a Female Herring Gull

parameter	value[a]	units	description
W_{b-f}	856	g	lipid-free whole body weight
E_{egg}	602	kJ	energy content of one egg
E_L	39.3	kJ·g^{-1}	energy cost/benefit per g lipid weight increase/decrease
N_{egg}	3		number of eggs laid
N_{ch}	3		number of chicks reared
F_{con}	0.75		efficiency of energy conversion to egg energy (mass)
F_{for}	0.28		ratio of foraging to sum of other energy requirements
F_d	0.85		efficiency of energy uptake from the diet
F_{in}	0.9		efficiency of POP uptake from the diet
V_p	0.039W_b	mL	volume of plasma (W_b in g)
k'_{pc}	0.11	mL·g^{-1}·d^{-1}	HCB plasma clearance rate
	0.28	mL·g^{-1}·d^{-1}	dieldrin plasma clearance rate
	0.041	mL·g^{-1}·d^{-1}	mirex plasma clearance rate
	0.070	mL·g^{-1}·d^{-1}	DDE plasma clearance rate
K_{pf}	0.0061	mL·g^{-1}	HCB plasma/body lipid distribution coefficient
	0.0059	mL·g^{-1}	dieldrin plasma/body lipid distribution coefficient
	0.0067	mL·g^{-1}	mirex plasma/body lipid distribution coefficient
	0.0039	mL·g^{-1}	DDE plasma/body lipid distribution coefficient

[a] Derivation of bioenergetic parameter values except F_{in} is described in ref *17*. F_{in} is an average value for PCB accumulation in ringed doves (*Streptopelia risoria*) taken from ref *12*. Clearance parameters (k'_{pc} and K_{pf}) were taken from ref *11* with the following modifications: An error (factor 2 too low) was discovered in the calculation of k'_{pc} for dieldrin in ref *11*. The value of k'_{pc} for DDE in ref *11* was 0.035. The predicted half-life of DDE in an adult herring gull using this value was 418 d, compared to the field-measured value of 265 d (*18*). The value of k'_{pc} for DDE given in the table was therefore derived from the field half-life.

time depending on the number of eggs. Thus, for 3 eggs, the total energy cost was spread over 19 days

$$\Sigma Q_{egg} = E_{egg} N_{egg} / F_{con} \quad \text{(kJ)} \tag{6}$$

where N_{egg} is the number of eggs, E_{egg} is the total energy content of an egg, and F_{con} corrected for the efficiency of energy conversion to body mass. Using E_{egg} = 602 kJ and F_{con} = 0.75 (Table 1), the net cost of producing 3 eggs was 2408 kJ.

Because chick rearing increases the energy requirement of each parent gull by about 33% during peak chick requirements to near the parents' maximum sustainable daily metabolic rate (*17*), it is important to include this cost in the model. The proportion of a chick's existence energy requirement met by the parents (Q_{ch}) as a function of the chick's age (A_{ch}) was estimated in three divisions of the chick's life from hatching (A_{ch} = 0) to 100 days of age, when the chick was assumed to be independent of the parents (*17*). See Supporting Information for details. Foraging by each parent to feed chicks is usually shared equally, therefore the total chick energy requirement assigned to the foraging energy budget of each parent (Q_{cf}) was

$$Q_{cf} = N_{ch} \cdot Q_{ch} / 2 \quad \text{(kJ·d}^{-1}\text{)} \tag{7}$$

where N_{ch} is number of chicks reared to independence. The model was validated assuming 3 chicks reared. Thus, requirement for extra foraging cost to the female was based on Q_{cf} = 1.5Q_{ch}. Q_{cf} was calculated as outlined in the Supporting Information and added to the female energy budget from Julian day 144 (hatching in late May) to 244 (self-foraging chick beginning of September).

Average ratio of foraging costs to sum of all other energy requirements, including feeding chicks, was estimated to be 0.28 (range 0.12−0.46) from a time-activity budget for two male and two female adult herring gulls (all from different nests) feeding chicks in an eastern Lake Erie colony (*17*). This is designated as foraging efficiency (F_{for}) in the model. Thus, foraging cost (Q_{for}) is $F_{for}/(1 - F_{for})$ times the sum of all non-foraging energy requirements

$$Q_{for} = (F_{for}/1 - F_{for}) \cdot (Q_{em} + Q_L + Q_{egg} + Q_{cf}) \quad \text{(kJ·d}^{-1}\text{)} \tag{8}$$

For F_{for} = 0.28, foraging costs are 39% of all other energy expenditures.

From eqs 1, 2, 5b, and 6−8, and energy density (caloric content) of the diet (E_d, kJ·g^{-1}), the total daily diet consumption rate of an adult female (R_d, g·d^{-1}) calculated by the model at each time point can be represented by eq 9

$$\begin{aligned} R_d = (F_d E_d)^{-1} \{ (1 - F_{for})^{-1} [& (14.2 + 0.22\text{PP}) (W_{b-f} (0.864 - 0.0027 T_{am})^{-1})^{0.54} - (0.59 + 0.025\text{PP}) T_{am} (W_{b-f} (0.864 - \\ & 0.0027 T_{am})^{-1})^{0.30} - 0.0027 E_L W_{b-f} (0.864 - 0.0027 T_{am})^{-2} \Delta T_{am} + E_{egg} N_{egg} F_{con}^{-1}] + \\ & Q_{cf} F_{for} (1 - F_{for})^{-1} \} \quad \text{(g·d}^{-1}\text{)} \end{aligned} \tag{9}$$

The main time-dependent variables are T_{am}, PP, E_{egg}, and Q_{cf}. Note that temperature changes affect food consumption in two ways. Existence metabolism (first two lines of eq 9) has a complex inverse allometric dependence on ambient temperature through body weight increases and decreases due to lipid changes, but the overall tendency is to decrease with increasing temperature. Lipid production or utilization is negatively related to temperature changes (ΔT_{am} term on third line of eq 9), that is, a temperature increase results in reduction of food requirement, a temperature decrease increases feeding rate, and if there are no temperature changes, the term drops out.

Toxicokinetics Submodel. The toxicokinetics submodel follows the two-compartment model given in Clark et al. (*11*), developed from experimental data for toxicokinetics of ten common chlorinated POP compounds in caged, fully grown chicks kept at ambient temperature in Ottawa, Canada through the winter. Net daily POP intake rate from the gut (R_{in}, μg·d^{-1}) was calculated from the total daily diet consumption rate of an adult female (R_d) as represented by eq 10, the concentration of POP in the diet (C_d, μg·g^{-1}) and the efficiency of uptake of chemical (F_{in})

$$R_{in} = F_{in} R_d C_d \quad (\mu\text{g·d}^{-1}\text{, whole bird}) \tag{10}$$

The model assumes that POPs are taken up from the diet into a central compartment (blood plasma) and rapidly equilibrated between plasma lipids and whole body lipid pool (W_L, g) which includes *all* extractable neutral lipids in

the bird (in adipose tissue, muscle, liver, bone, skin, etc.). The distribution coefficient between plasma ($\mu g \cdot mL^{-1}$ wet weight) and whole body lipid ($\mu g \cdot g^{-1}$ lipid weight) compartments was designated as K_{pf} (*11*). Wet weight rather than lipid weight basis for concentration in plasma was chosen because plasma lipid content may vary with the method used to determine it, leading to incomparability among studies. Nevertheless, it was found that K_{pf} values were independent of log K_{ow} and close to the total lipid content (including lipoproteins) of plasma indicating that there was thermodynamic equilibrium distribution between lipids in plasma and whole body (*11*). Similar lack of variation in K_{pf} has also been found for PCB congeners in the American kestrel (*Falco sparverius*) (*14*). The whole body lipid pool in herring gulls is seasonally dependent on ambient temperature according to eq 3 (*17*). Whole body lipid pool size is inversely proportional to POPs concentrations in plasma and therefore affects clearance rates (*11*).

Clearance rate of POPs (R_{cl}) from the bird by all mechanisms (metabolism and excretion unchanged in feces primarily, possibly respiratory loss in the case of HCB) except deposition in eggs was determined to be first order in concentration in plasma concentration, C_p ($\mu g \cdot mL^{-1}$). Thus, daily clearance rate from the bird was

$$R_{cl} = k_{cl} C_p V_p \quad (\mu g \cdot d^{-1}) \tag{11}$$

where k_{cl} (d^{-1}) is the first-order clearance rate constant and $V_p$is plasma volume (mL). In order to represent first-order clearance rates independent of body weight to be able to compare clearance rates among species, a modified first-order rate constant multiplied by plasma volume to body weight ratio (k'_{pc}, $mL \cdot g^{-1} \cdot d^{-1}$) was used (*11*). This was converted to k_{cl} by dividing by the volume of plasma per unit weight of the bird (V_p/W_b). Substituting k'_{pc} into eq 11,

$$R_{cl} = k'_{pc} C_p W_b \quad (\mu g \cdot d^{-1}, \text{ whole bird}) \tag{12}$$

Concentration in plasma can be estimated from the total amount of POP in the bird X_b (μg), fraction lipid in the bird F_L, and K_{pf}, assuming that a negligible amount of the total body burden was in plasma

$$C_p = (X_b/F_L W_b) K_{pf} \quad (\mu g \cdot mL^{-1}) \tag{13}$$

Combining eqs 12 and 13, clearance from the bird becomes

$$R_{cl} = k'_{pc} K_{pf} X_b / F_L \quad (\mu g \cdot d^{-1}, \text{ whole bird}) \tag{14}$$

Thus, clearance is inversely proportional to fraction lipid content of the bird. The order of calculation in the model took mass of contaminant in the bird from the previous day ($X_{b(t-1)}$) added the amount accumulated from the diet on that day (R_{in}) from eq 11 to obtain $X_{b(t)}$, distributed this new mass of contaminant between plasma and body lipids according to K_{pf}, calculated various POP outputs (e.g., concentration in lipid, whole body, and plasma), then applied eq 14 to calculate $X_{b(t+1)} = X_{b(t)} - R_{cl}$.

Deposition of POPs in eggs was based on the ratio of whole egg (yolk plus albumin) to whole body concentration (K_{eb}) given in Braune and Norstrom (*6*) times the concentration in whole body (C_b) calculated by the model. The chronology of deposition to egg was the same as for egg formation, that is, beginning 15 days before date of first egg laid, the mass of POP deposited in eggs was calculated from mass of egg ($W_{egg(t)}$) formed that day and continued for 15 days until the egg was formed

$$X_{egg(t)} = C_b K_{eb} W_{egg(t)} \quad (\mu g, \text{ time } (t)) \tag{15}$$

Deposition of POP in each subsequent egg began 2 days after the previous egg until total mass per egg times number of eggs specified in the model had been laid down. For 3 eggs, the resulting form of the POP excretion curve in eggs was a step pyramid-shaped function over 21 days. Amount of POPs cleared from the bird each day, $X_{egg(t)}$, was subtracted from $X_{b(t)}$ prior to clearance modeled by eq 15 to maintain mass balance.

Although the model could account for concentrations in individual eggs, it was decided not to build this capability in, since body burdens of POPs are unlikely to change significantly in the 21 day period of laying down 3 eggs unless there is a sudden increase in POP uptake due to highly contaminated diet. There is good experimental evidence that concentrations of POPs are statistically indistinguishable in A, B, and C eggs from 3-egg clutches for both herring gulls (*21*) and glaucous gulls (*22*). This assumption would not be valid for some bird species for which females lay a high proportion of body weight in eggs. For herring gulls, POP concentration in all eggs laid was assumed to be the total mass of contaminant excreted in eggs divided by the total weight of eggs

$$C_{egg} = \sum X_{egg(t)} / N_{egg} W_{egg} \quad (\mu g \cdot g^{-1}) \tag{16}$$

Effectively, $C_{egg} = \hat{C}_b K_{eb}$, where $\hat{C}_b$ is the average concentration of POP in the bird over the period eggs are laid down.

Validation of the Model for Lake Ontario Herring Gulls and Eggs

General Approach. Four different scenarios of fish composition in the diet were tested: all alewife, all smelt, a mixture of alewife and smelt based on their relative abundance in the lake, and a mixture of alewife and smelt based on their relative biomass in the years of simulation.

Choice of POPs to include in the validation required that experimental whole body clearance data and POP concentrations in both fish and gull eggs be available. In order to test the model over a range of POP clearance rates, the following POPs were chosen (with estimated half-life in an adult herring gull (*11, 18*)): HCB (107 d), dieldrin (82 d), mirex (231 d), and DDE (265 d). Simulations were carried out for 3 years (1985, 1990, and 1992) for which there were prey abundance data and a representative collection of alewife and smelt to determine concentrations of mirex, DDE, dieldrin, and HCB in the diet. The fish were sampled from different areas of Lake Ontario in different years. DDT was ca. 10% of DDE in Lake Ontario alewife and smelt in 1985−1992. The possible contribution of DDT to DDE accumulation in the gull was therefore small and was ignored.

Parameterization of the Model. For validation, the model was run for a female, laying 3 eggs, sharing half the rearing of costs of 3 chicks with its mate, assuming constant POP concentration in the diet for each diet scenario. Herring gull females typically do not lay eggs before 4 years of age. Model-simulated egg concentrations were slightly higher in females laying their first clutch of eggs than in other years and remained stable thereafter at constant concentrations in the diet, showing that steady state between uptake and excretion was reached within a year after first breeding. Thus, validation was based on predicted POP concentrations in eggs of females in their second year of breeding (age 5). POPs concentrations in fish throughout the female's life were assumed to be the same as the concentrations in the year the eggs were laid. This was a reasonable assumption since POPs concentrations in Lake Ontario herring gull eggs were changing slowly in the late 1980s and early 1990s compared to whole body clearance rates in the gull (*24*−*26*). For small annual changes, approach to near steady-state would be achieved rapidly.

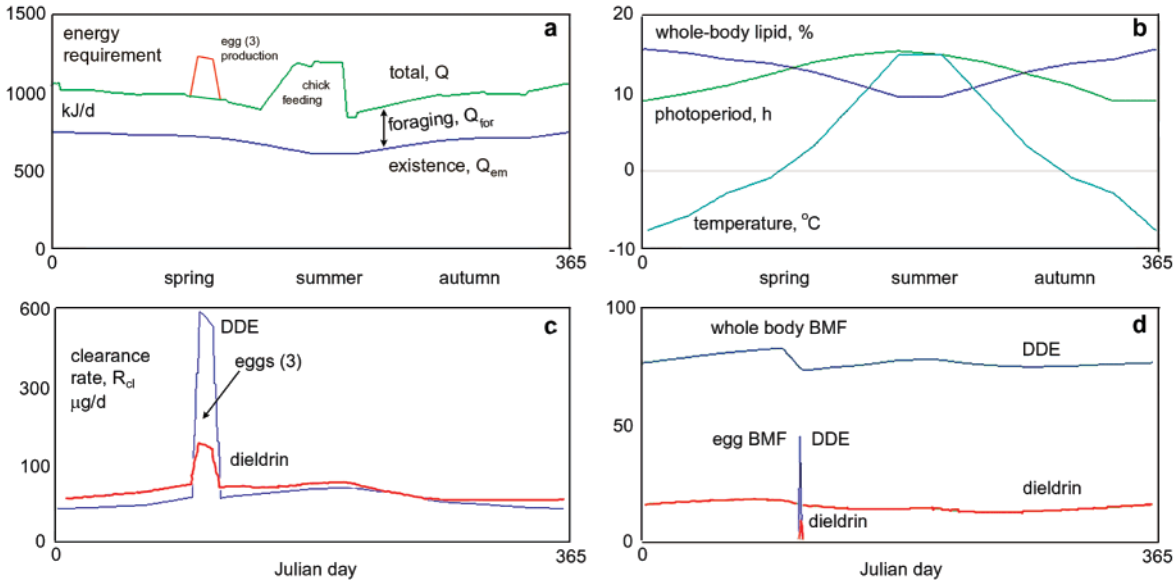

FIGURE 1. Model output, January 1 to December 31, 1992, female herring gull in Lake Ontario laying 3 eggs, sharing half the cost of raising 3 chicks, feeding on 100% fish (92% alewife and 8% smelt): (a) major components of daily energy requirement (lipid production/utilization is not identified); (b) seasonal changes in ambient temperature, photoperiod for northern Lake Ontario (Toronto) and whole body lipid content; (c) whole-body DDE (blue line) and dieldrin (red line) daily clearance rate; (d) egg/diet and whole body/diet BMF, wet weight basis, for DDE (blue) and dieldrin (red).

Values of the constant parameters that were used in the model (apart from those given as coefficients or exponents in eqs 2−9 above) are listed in Table 1. Derivation of other parameters in the model specific to Lake Ontario, including mean monthly ambient temperature and photoperiod, alewife and smelt energy density, fish collection methods, abundance and biomass of alewife and smelt in each year, POPs concentrations in fish, and POPs concentrations in herring gull eggs for comparison to model predictions are available in the Supporting Information.

Sensitivity to Seasonal Fish Energy Density and Local Temperature Regimes. Alewife energy density fluctuates seasonally according to a well-defined trend (*27*, *28*). This fluctuation affected amount of food required to meet model bioenergetic requirements and thus POP uptake rate. For chemicals with fast clearance rates, significant change in energy density of diet, even for a relatively short period of time, could have an influence on predicted whole body concentrations. The model predicted that seasonal fluctuation in energy density would have a negligible influence on concentrations of POPs in gull eggs using any of the four diet scenarios for any of the chemicals: mean −3.2 ± 0.7% compared to annual average energy density. Therefore, mean annual energy densities were used for the validation simulations.

Similarly, different temperature regimes in the Lake Ontario basin theoretically could affect clearance and therefore predicted egg concentrations. Kingston and Toronto mean monthly temperature regimes were used to evaluate the affect of temperature on predicted egg concentrations. It was found that regional differences in temperature could contribute a mean 5.1 ± 1.1% change in predicted egg concentration. Because Herring gulls are known to travel throughout the Lake Ontario basin during the winter, never isolated to one microclimate, this estimate was considered to be the upper limit of the ambient temperature affect on egg concentrations. Therefore mean monthly temperatures at Toronto were considered sufficiently accurate for simulation.

A Priori Simulations, 100% Fish in the Diet, Four Diet Scenarios. Concentrations of POPs in female whole body and eggs were simulated from POPs concentrations in alewife and smelt in 1985, 1990, and 1992. The major components of the energy budget for 1992 generated by the model are shown in Figure 1a. Mean monthly temperature and photoperiod were the same for all diet scenarios in each year as shown in Figure 1b. Annual energy density and POP chemical concentrations in the diet changed with simulation year according to proportional species contribution in each diet scenario.

For 1992, using a POP exposure from alewife and smelt based on their relative biomass, the DDE and dieldrin clearance to 3 eggs represented 16% and 4% of the total annual DDE and dieldrin clearance, respectively, from a female herring gull (Figure 1c). Predicted whole body BMFs were seasonally variable due to lipid content and metabolic rate changes (Figure 1d). Predicted wet weight egg/fish BMFs were 9.7 for dieldrin and 45 for DDE (Figure 1d). Note that predicted BMFs are independent of POP concentration in diet and bird and are therefore not affected by changes in fish consumption used to calibrate the model in the next section.

Individual values of the ratio of predicted to measured POPs concentrations were generally in the 0.7−1.5 range (Table 2). The exception was 100% smelt in the diet. In 1985, the ratio of predicted to measured concentrations of mirex and DDE for this scenario was 0.2−0.3, while only dieldrin gave a ratio above 1. On the other hand, the 1992 100% smelt diet simulations gave ratios above 2 for mirex and DDE. The coefficient of variation of the grand mean ratio for the 100% smelt diet simulations was by far the highest of all the scenarios, 61.7%. The larger over-prediction, much higher variance, and inconsistency in ratios (greater and less than 1) suggested that 100% smelt was a poor representation of the diet of herring gulls in Lake Ontario. This was the expected result based on the generally smaller population of this species compared to alewife in Lake Ontario (abundance ca. 1:2, biomass ca. 1:10, smelt:alewife) (*29*).

The 100% alewife diet scenario gave a much more consistent predicted/measured ratio (range 1.3−1.67, both for DDE) than 100% smelt diet (Table 2). Variances for the 100% alewife diet were also more uniform, CVs ranging from 15% for all chemicals (except mirex) and colonies in 1992 to 36% for mirex for all years and colonies. The grand mean

TABLE 2. Ratio of Model-Predicted (*a priori* Simulations) to Measured Concentrations of Mirex, DDE, Dieldrin, and HCB in Herring Gull Eggs from Lake Ontario Colonies in Three Areas: the Eastern Part of the Lake near Kingston (Snake Island), near the Outlet of the Lake in the St. Lawrence River (Strachan Island), and near the City of Toronto (Muggs Island and Leslie St. Spit), in 1985, 1990, and 1992, Employing 100% Fish in the Diet and Four Scenarios of Alewife and Smelt Composition of the Diet[a]

simulation scenario	year	colony	mirex	DDE	dieldrin	HCB	mean colony	mean by colony, year
biomass[b]	1985	Snake Isl.[d]	1.01	1.00	1.07	1.50	1.15 (21.0)	
	1985	Snake Isl.[e]	1.22	1.32	1.62	1.17	1.33 (15.1)	1.36 (21.8)
	1985	Muggs Isl.[d]	1.35	1.46	1.56	2.02	1.60 (18.4)	
	1990	Snake Isl.[f]	0.90	0.85	0.94	1.00	0.92 (7.2)	
	1990	Snake Isl.[g]	0.92	1.01	1.26	1.77	1.24 (30.7)	
	1990	Leslie St. Spit[f]	0.79	0.85	0.99	1.33	0.99 (24.3)	1.01 (26.0)
	1990	Strachan Isl.[f]	0.71	0.76	0.94	1.10	0.88 (20.1)	
	1992	Snake Isl.[f]	1.92	1.43			1.68 (21.0)	
	1992	Leslie St. Spit[f]	1.80	1.43			1.62 (16.0)	1.62 (13.7)
	1992	Strachan Isl.[f]	1.73	1.43			1.58 (13.7)	
	mean by chemical		1.24 (36.0)	1.15 (24.7)	1.20 (24.3)	1.41 (26.4)		
	grand mean for all years, colonies and chemicals							**1.24 (28.6)**
abundance[c]	1985	Snake Isl.[d]	0.71	0.71	1.12	1.17	0.93 (27.5)	
	1985	Snake Isl.[e]	0.85	0.94	1.70	0.92	1.10 (36.5)	1.11 (31.5)
	1985	Muggs Isl.[d]	0.94	1.03	1.63	1.58	1.30 (27.7)	
	1990	Snake Isl.[f]	1.03	1.06	1.14	1.45	1.17 (16.2)	
	1990	Snake Isl.[g]	1.07	1.26	1.53	2.55	1.60 (41.2)	
	1990	Leslie St. Spit[f]	0.91	1.07	1.20	1.91	1.27 (34.8)	1.29 (34.0)
	1990	Strachan Isl.[f]	0.82	0.95	1.15	1.58	1.12 (29.5)	
	1992	Snake Isl.[f]	2.08	1.62			1.85 (17.4)	
	1992	Leslie St. Spit[f]	1.94	1.63			1.79 (12.3)	1.79 (10.9)
	1992	Strachan Isl.[f]	1.87	1.62			1.74 (10.0)	
	mean by chemical		1.22 (42.8)	1.19 (27.9)	1.35 (18.9)	1.59 (33.1)		
	grand mean for all years, colonies and chemicals							**1.32 (33.3)**
alewife	1985	Snake Isl.[d]	1.12	1.10	1.05	1.62	1.22 (21.8)	
	1985	Snake Isl.[e]	1.35	1.46	1.60	1.27	1.42 (10.0)	1.45 (21.3)
	1985	Muggs Isl.[d]	1.50	1.60	1.53	2.17	1.70 (18.7)	
	1990	Snake Isl.[f]	0.83	0.75	0.85	0.80	0.81 (5.2)	
	1990	Snake Isl.[g]	0.86	0.89	1.14	1.41	1.08 (23.9)	
	1990	Leslie St. Spit[f]	0.73	0.76	0.89	1.06	0.86 (17.5)	0.88 (21.6)
	1990	Strachan Isl.[f]	0.66	0.67	0.85	0.88	0.77 (14.7)	
	1992	Snake Isl.[f]	1.86	1.34			1.60 (22.9)	
	1992	Leslie St. Spit[f]	1.74	1.35			1.54 (17.9)	1.55 (15.1)
	1992	Strachan Isl.[f]	1.67	1.34			1.50 (15.6)	
	mean by chemical		1.23 (36.3)	1.13 (29.8)	1.13 (28.0)	1.32 (36.3)		
	grand mean for all years, colonies and chemicals							**1.20 (32.5)**
smelt	1985	Snake Isl.[d]	0.19	0.22	1.21	0.62	0.56 (85.0)	
	1985	Snake Isl.[e]	0.23	0.29	1.83	0.48	0.71 (107)	0.69 (87.4)
	1985	Muggs Isl.[d]	0.25	0.32	1.76	0.83	0.79 (87.9)	
	1990	Snake Isl.[f]	1.38	1.58	1.65	2.52	1.78 (28.4)	
	1990	Snake Isl.[g]	1.42	1.89	2.21	4.45	2.49 (54.0)	
	1990	Leslie St. Spit[f]	1.21	1.60	1.73	3.33	1.97 (47.6)	1.99 (44.6)
	1990	Strachan Isl.[f]	1.10	1.41	1.65	2.76	1.73 (41.6)	
	1992	Snake Isl.[f]	2.66	2.38			2.52 (7.9)	
	1992	Leslie St. Spit[f]	2.49	2.40			2.44 (2.8)	2.45 (4.6)
	1992	Strachan Isl.[f]	2.40	2.38			2.39 (0.5)	
	mean by chemical		1.33 (70.8)	1.45 (61.0)	1.72 (17.3)	2.14 (71.5)		
	grand mean for all years, colonies and chemicals							**1.61 (61.7)**

[a] Mean ratios of simulated to actual concentrations (CV in parentheses) are given for each diet scenario, by chemical without regard to year or colony, by colony and year without regard to chemical, and by year without regard to colony or chemical. A grand mean ratio (CV) for all colonies, chemicals, and years is also given for each diet scenario. [b] Biomass diet for 1985 and 1990 was 89% alewife and 11% smelt; for 1992, 92% alewife and 8% smelt. [c] Abundance diet for 1985 was 57% alewife and 43% smelt; for 1990, 64.6% alewife and 35.4% smelt; and for 1992, 74% alewife and 26% smelt. [d] Gull egg data from ref *24*. [e] Gull egg data from ref *6*. [f] Gull egg data from ref *26*. [g] Canadian Wildlife Service unpublished data.

ratio indicated a 20% over-prediction by the model based on this diet, and the CV of the grand mean was half that of the 100% smelt diet.

Of the two mixed-species diet scenarios, relative abundance (numbers of individual fish) was not quite as good at predicting concentrations as relative fish biomass in lake Ontario, based on grand mean over-prediction (32% vs 24%) and variance (33% vs 29%), respectively. The relative biomass and 100% alewife diet scenarios gave similar results.

Ratios of predicted to measured POP concentrations higher than 1 could result from one or a combination of three factors: the model overestimated the rate of uptake (bioenergetics), underestimated rate of clearance (toxicokinetics), or the concentration in the diet was too high. The herring gull in Lake Ontario is known to eat insects, small birds, small mammals, plants, and garbage (*19*, *23*). These terrestrial dietary items are expected to have lower concentrations of POPs than fish. The most reasonable hypothesis for the *a priori* simulation over-prediction was a too-high proportion of alewife and smelt in the diet.

Calibration by Adjusting Percent Fish in the Diet. The inverse of the grand mean model-predicted to measured

TABLE 3. Mean Ratio of Model-Predicted to Measured Lake Ontario Egg Concentrations (from 2−3 Colonies Each Year)[a], Simulated by Year and Chemical, Calibrated by Assuming Percent Fish in the Diet Was the Inverse of Each Diet Scenario's Grand Mean Ratio of Predicted to Measured Concentration Eggs for the 100% Fish Diet Simulations (Table 2)

simulation	year	mean mirex	mean DDE	mean dieldrin	mean HCB	mean year	grand mean ratio (CV)
biomass, 81% fish[b]	1985	0.97	1.02	1.15	1.27	1.10 (21.8)	
	1990	0.67	0.70	0.84	1.05	0.82 (26.0)	
	1992	1.47	1.16			1.32 (13.7)	1.00 (27.4)
abundance, 76% fish[b]	1985	0.63	0.68	1.13	0.93	0.84 (31.5)	
	1990	0.73	0.82	0.95	1.42	0.98 (34.0)	
	1992	1.49	1.23			1.36 (11.0)	0.98 (32.5)
alewife, 83% fish	1985	1.10	1.15	1.16	1.40	1.20 (21.3)	
	1990	0.64	0.64	0.77	0.86	0.73 (21.6)	
	1992	1.46	1.11			1.28 (15.2)	0.99 (31.5)
smelt, 62% fish	1985	0.14	0.17	0.99	0.40	0.42 (87.4)	
	1990	0.79	1.00	1.12	2.03	1.24 (44.6)	
	1992	1.56	1.48			1.52 (4.6)	
							0.97 (63.4)

[a] Mean of concentrations in eggs from all Lake Ontario colonies were used in the calculation. [b] Alewife and smelt composition for each year was the same as in Table 2.

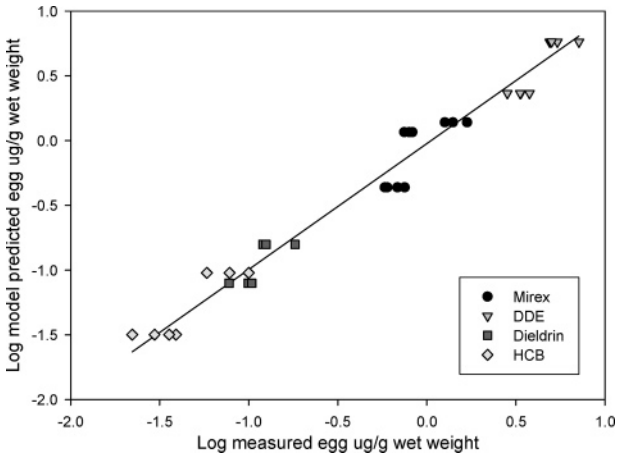

FIGURE 2. Relationship between log transformed measured and model-predicted concentrations (μg/g wet weight) in herring gull eggs using 19% uncontaminated food and 81% alewife + smelt in diet. The species composition was based on relative biomass in the lake for each simulation year. Line represents the linear regression fit to the data: Log_{10}[predicted] = −0.021 (±0.02) + 0.97 (±0.03) × Log_{10}[measured]; R^2 = 0.9758 (SE = 0.12).

concentrations from the fish-only simulations in Table 2, 0.62−0.83, was assumed to represent the fraction fish in the diet for each species composition scenario, and the simulations were rerun with no other changes to parameters, assuming that the non-fish diet was uncontaminated (Table 3).

The all-smelt diet had much higher variance (CV 63%) in predicted/measured concentrations among chemicals, years, and colonies than the other three diets. The relative abundance and all alewife diets, had intermediate variance (CV = 32−33), and the alewife and smelt relative biomass diet had the lowest overall variance (CV = 27%). Note that variances for all except all-smelt were well within the range of those for measured concentrations of POPs in individual eggs in any colony and year (30−40%, Table 3 in the Supporting Information). The biomass, abundance, and alewife diets produced similar results because alewife dominated in these diets. All three had good predictive power with minor modifications in percent fish in the diet (76−83%). The species composition of the relative biomass diet (smelt/alewife, 1:8 to 1:12, footnotes, Table 2) agreed with the field studies (*19*, *23*) better than relative abundance (smelt/alewife, 1:1 to 1:3) and was therefore the most probable of the four diet scenarios. Other species, such as perch, would undoubtedly be present in the diet, but were adequately represented by alewife and smelt. The relative biomass diet was composed of 81% fish. If there was contaminant input from the 19% non-fish diet, concentrations in eggs were not sensitive to this, since input from sources other than fish was assumed to be zero. Using the aggregate data for all chemicals, years, and colonies, the relative biomass diet predicted concentrations in eggs which had a strong and significant ($r^2 = 0.9758$; $p > 0.95$) correlation with measured Lake Ontario egg concentrations (Figure 2). The slope was not significantly different from 1 (t test; $p > 0.17$) with a standard error of 0.03. That is, statistically, the predicted and actual concentrations were the same over a broad range of chemical, geographical, and temporal conditions.

Discussion

Fox et al. (*19*) found that alewife and smelt composed 80% of the fish species eaten by herring gulls in Lake Ontario during the breeding season, 1977−1983. It is probable that POPs concentrations in the remaining 20% of the species (e.g., perch) were adequately represented by those in alewife and smelt. Ewins et al. (*23*) noted that the herring gull diet in the lower Great Lakes throughout the rest of the year is broadly similar to that during the breeding season. Die-offs of alewife probably account for a significant part of the diet of Lake Ontario gulls during winter. Ewins et al. (*23*) classified the herring gull in the lower Great Lakes as an opportunistic piscivore. None of the published data can be used to calculate the percentage of the gull's energy that is met by various diet items, since all the data are reported as frequency of occurrence rather than volume or weight. However, energy intake from fish is likely to be similar to or higher than the frequency of occurrence of fish in the diet, which is in the order of 82% (*19*, *23*), since most of the other items are either small (e.g., insects, plants, and garbage) or are highly seasonal (migrating birds, small rodents).

The mixed alewife/smelt diet which achieved best fit of the model-predicted to measured concentrations of POPs in eggs was 81% fish on an energy content basis; remarkably close to the field estimates of percent fish in the diet of the herring gull in this lake. Considering that no adjustments of any parameters other than percent fish in the diet were made to achieve a close fit of predicted to measured data, the validation process was not subject to a common concern about complex environmental models: that compensatory

adjustment of several parameters may achieve a fit, but leave doubts whether the model structure and parameters truly represent underlying mechanisms assumed in its formulation. In this instance, the range of clearance rates of chemicals, chemical concentrations, years, and colonies employed in the validation constituted a rigorous test of the model's structure and parameterization as well as its validity under a particular set of conditions.

The strength of the validation of the ABAM adult life phase model is the extensive research and high quality data sets that lie behind it: bioenergetics and feeding ecology data, experimental clearance rate studies, prey abundance, concentrations in prey, concentrations in the gull, and egg/female concentration ratios. ABAM can be considered valid for the herring gull in any environment, since there is nothing in the model which is specific to the environment in which it was validated (Lake Ontario) or which cannot be adjusted for any other environment. This includes toxicokinetic parameters.

How applicable is ABAM likely to be for other species of birds? Because of its flexibility (see Supporting Information), we believe the structure of the toxicokinetics submodel of ABAM (*11*) is applicable for modeling bioaccumulation of lipophilic POPs in any bird after suitable species-specific modifications.

It is likely that the bioenergetics submodel of ABAM will be valid for closely related larid species, such as the ringed-bill gull (*Larus delawarensis*) and the glaucous gull (*Larus glaucuscens*) with little or no modification except body size. Of course, migration will affect many of the environmental parameters for these species, and this must be taken into account. It may also be very difficult to determine what these species are eating even during breeding. Ringed-bill gulls are considerably more terrestrial-feeding than herring gulls in inland environments, and are migratory in the Great Lakes, for example. As a first approximation, clearance rate parameters could be scaled allometrically to body weight (glaucous gulls are bigger and ringed-bill gulls are smaller than herring gulls) as discussed previously.

The core of the bioenergetics submodel is existence metabolism (EM) of a non-passerine bird as a function of ambient temperature and photoperiod. This part of ABAM is applicable to any non-passerine species without modification (and to passerines with appropriate changes). To existence metabolism must be added some estimate of foraging cost. Ellis and Gabrielsen (*30*) recommend abandoning existence metabolism in favor of field metabolic rate (FMR) for birds, which is now the most commonly used measure of daily energy expenditure (DEE) in birds. FMR is measured directly by doubly labeled water techniques. The problem with FMR for modeling DEE of a bird is that it can only be measured realistically at limited periods in a bird's annual cycle, typically during breeding, because it requires capture and recapture of the bird. Therefore, while there are good empirical relationships for FMR as a function of body weight for birds (*31*), there are none that account for variation of FMR with temperature or estimate costs of feeding young. Because of the more extensive empirical relationships available between EM and temperature, EM is more useful than FMR for the modeling feeding rate of a bird throughout the year.

The approach taken in ABAM of adding an estimate of foraging costs to the energy budget as a fraction of all other costs (foraging efficiency, F_{for}, (*17*)) is nonstandard in avian bioenergetics, but produced an estimate of DEE (Q_g) which is in excellent agreement with predictions from FMR equations. Mean annual DEE from ABAM was 1100 kJ·d^{-1} (e.g., Figure 1a). The range of FMR calculated for a 997 g female bird from empirical equations of FMR as an allometric function of body weight (*31*) is 1093 kJ·d^{-1} (based on 40 species of non-passerine birds) to 1143 kJ·d^{-1} (based on 62 species of birds, no categorization).

The most herring-gull-specific part of the bioenergetics submodel in ABAM is the temperature dependence of whole-body lipid content. Knowledge of how lipid varies through the year is extremely important to the modeling toxicokinetics of POPs, less important in the energy budget. It is probable that other cold-temperate climate larid species will demonstrate a dependence similar to that of herring gulls, but specific information for each species would be desirable. Average annual lipid content could be used in the absence of more detailed information.

The bioenergetics submodel is capable of handling species which lay much larger proportion of body weight in eggs, such as waterfowl. Adjustment may need to be made in the model for use of endogenous lipid reserves (possibly also protein) in the female for egg production. On the other hand, cost of feeding chicks would be excluded for precocial species such as waterfowl. In the absence of information on foraging costs for a species, FMR could be substituted for existence metabolism (Q_{em}) and foraging efficiency (F_{for}) could be set to 1.

A simple model was developed by Glaser and Connolly (*7*) for bioaccumulation of DDE by peregrine falcons, bald eagles, and double-crested cormorants. Excretion rates were chosen to fit modeled egg/prey BMFs to field BMFs, and compared to those from an empirical relationship of whole body DDE elimination rates in seven species of birds and $(W_b)^{0.7}$. It was found that the fitted excretion rates followed the expected allometric relationship with body weight. Thus, it may be possible to scale whole-body clearance rate constants (k_{pc}) of POPs in herring gulls allometrically to body weight among avian species. To some extent this is already accommodated in ABAM by use of k'_{pc}, which is relatively independent of body size. However more research is needed to test this method, especially for chemicals where biotransformation is involved in clearance. The ratio of POPs concentrations in total blood lipids and whole body lipids was close to 1. Thus K_{pf}, the other clearance parameter, can be approximated from fraction of total lipid in plasma.

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Supporting Information Available

General description of the model, alewife and smelt energy density, fish collection and POP concentrations, POP concentrations in herring gull eggs for comparison to model predictions, relative abundance and biomass of alewife and smelt in Lake Ontario, additional references, and data tables. This material is available free of charge via the Internet at http://pubs.acs.org.

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