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Uncertainty assessment of trophic flows in Hamilton Harbour: A linear inverse modelling analysis

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Ecopath with Ecosim has been extensively used to examine ecosystem attributes and the effects of management actions. One of the main limitations in using Ecopath to credibly guide management decisions lies in the quality and quantity of the data used. Linear Inverse Modelling treats the problem of ecosystem characterization in a rigorous mathematical way in which the foodweb is described as a (linear) function of the flows and model parameters are (inversely) derived from observed data. In this study, our thesis is that Linear Inverse Modelling can be used as a complement to Ecopath applications to evaluate our confidence in typically reported ecosystem characterizations. Based on a simplified version of a previously published foodweb topology (Hossain et al., 2012), we demonstrate that there is considerable uncertainty associated with the predicted energy flows within the ecosystem of Hamilton Harbour, Lake Ontario, Canada. Uncertainty related to external flows (e.g. respiratory and detrital flows) appears to be much higher than for internal flows associated with predator-prey relationships. Our Linear Inverse Modelling analysis reinforces earlier findings that most of the trophic flows are concentrated within the first two trophic levels, while mass fluxes at the higher trophic levels are significantly lower. The intermediate ecotrophic efficiency for zooplankton suggests that planktivorous fishes do not fully capitalize upon the available food in the system. Our model estimates that a substantial amount of the detrital material is being recycled by the microbial community within the system. Taken together with the significant detrital pool directly supporting zooplankton and oligochaetes/chironomids, this prediction is consistent with recent empirical evidence that particulate organic matter from various allochthonous or autochthonous origins constitute important components of the energy transferred to higher trophic levels. Overall, our Linear Inverse Modelling analysis offers meaningful insights that should contribute towards the development of a reliable ecosystem model for Hamilton Harbour.

Keywords: Ecopath Modelling, Areas of Concern

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Introduction

Ecopath with Ecosim (EwE) is a popular modelling tool to elucidate the relative importance of different ecological processes and project how ecosystems will respond to external perturbations (climate warming, invasive species) or alternative management practices (biomanipulations, nutrient loading reductions) (Christensen and Pauly, 1992; Pauly et al., 2000; Walters et al., 2000). In this regard, Hossain et al. (2012) have recently undertaken an Ecopath exercise to shed light on the trophodynamics underlying the Hamilton Harbour ecosystem. A conceptual model, comprising all the essential foodweb components of the system, was parameterized using empirical evidence, field data, and literature-based information. Among the trophic relationships considered by the Hamilton Harbour ecosystem model, Hossain et al. (2012) highlighted the broader implications of Round Goby (*Neogobius melanostomus*) on a number of functional groups at both higher and lower trophic levels. Several ecosystem attributes (e.g. primary production/biomass, biomass/total throughput, system omnivory index, amount of recycled throughput, and Finn's cycling index) provided evidence that Hamilton Harbour is an immature and fairly simple system with linear food chain structure. Based on the internal redundancy and system overhead values, Hossain et al. (2012) also predicted that the Harbour possesses substantial reserves to overcome external perturbations. The aggregation of the ecosystem into discrete trophic levels suggested that most of the energy flows are concentrated within the first two trophic levels, while flows at the higher foodweb were comparatively minor.

One of the main limitations in using Ecopath to guide management decisions lies in the quality and quantity of the data used. In the Hamilton Harbour ecosystem model, one major knowledge gap involved the dietary compositions, as the corresponding data were available for only a few of the functional groups considered and the taxonomic resolution is typically low in the stomach analyses carried out. Hossain et al. (2012) achieved mass-balance by iteratively changing the entries of the diet matrix, while the values assigned to biological rates (e.g. production and consumption rates) were predominantly based on estimates from other Ecopath modelling studies, literature values, or assumptions made from neighbouring systems (e.g. Bay of Quinte). The original study did not provide any formal sensitivity analyses to test the effect of input parameters and various *ad hoc* adjustments made to achieve mass balance on the inference drawn by the model. In addition, some of the contradictory findings regarding the characterization of the relative importance of ecosystem processes or the overall ecosystem conceptualization may stem from erroneous model assumptions and questionable data quality (Hossain et al., 2012).

A recent advancement in our efforts to achieve ecosystem-scale quantitative mapping is Linear Inverse Modelling (LIM), in which the problem of foodweb reconstruction is formulated in a rigorous mathematical way, the available foodweb data are parsed into a matrix equation, and the unknown flows are obtained by solving the linear equation system (Soetaert and van Oevelen, 2009; van Oevelen et al., 2010). LIM is founded on universal mass-balance principles and trophic flows are typically estimated using an objective least-squares criterion (Savenkoff et al., 2007). LIM is designed to directly compute a balanced network, if it is existent, conditional upon the constraints imposed by the available data and prior system knowledge (Vézina and Platt, 1988; Savenkoff et al., 2004). Furthermore, LIM may also be combined with Markov Chain Monte Carlo (MCMC) to obtain a set of acceptable solutions and ultimately select the optimal one out of an infinite number of foodweb structures. LIM is capable of utilizing multiple currency input parameters and retain the entire vector of acceptable solutions for further analysis. Recent investigation has demonstrated the similarities in the solutions obtained by Ecopath and LIM (Hossain et al., in prep. 2017), but little work has been done to illustrate how LIM can offer a complement to an existing ecosystem model; particularly in assessing uncertainties of EwE model estimates.

In this study, our main objective is to demonstrate how LIM can be used as a complement to existing Ecopath applications in order to evaluate the credibility of the derived flow quantities. To do so, we first simplify the topology of the Hossain et al. (2012) Ecopath model. Using the input parameters of the newly balanced Ecopath model, we parameterize a LIM configuration in R (R Development Core Team, 2015). With the current LIM, we retain all the Ecopath flows (i.e. feeding, respiratory, cannibalism and flow to detritus) and present a comprehensive overview of the trophic linkages that regulate the energy flows within the

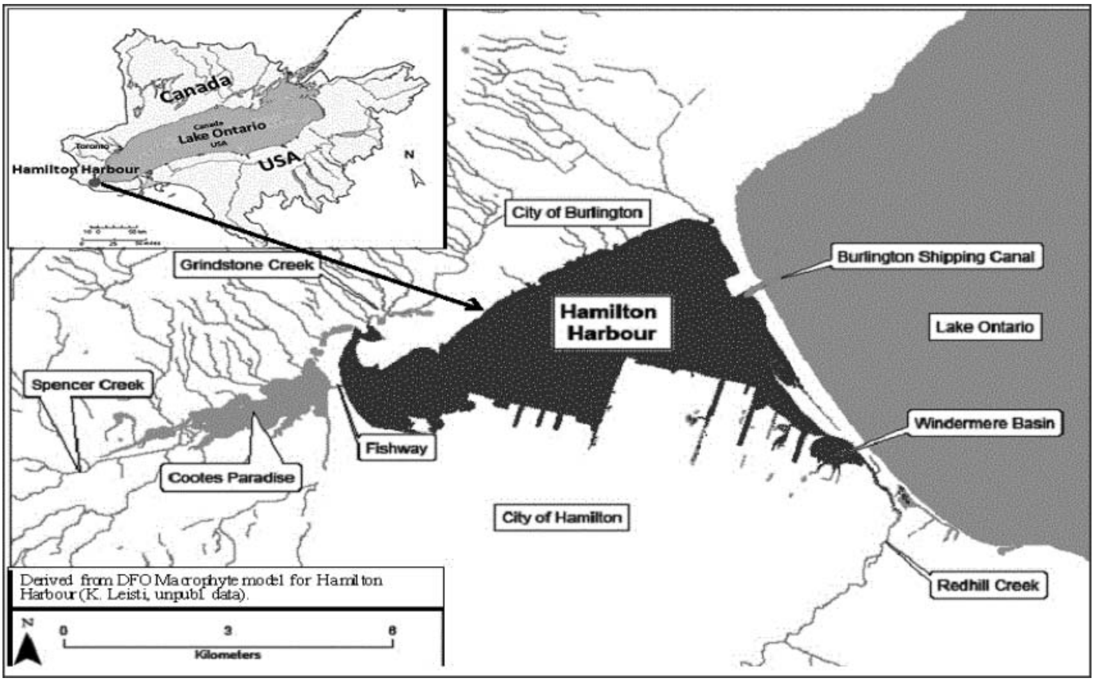
Hamilton Harbour ecosystem. Our objective is to offer insights that should contribute towards the development of a credible ecosystem model for the management of Hamilton Harbour.

Materials and methods

Hamilton Harbour Ecopath Model

Hamilton Harbour is a cone-shaped embayment (20.97 km^2, maximum depth of 24 m, and mean depth of 13.0 m) located at the western tip of Lake Ontario (Figure 1). For several decades, waste discharges from industrial and municipal activities had converted this scenic water body into one of the most polluted sites in the Laurentian Great Lakes (Hiriart-Baer et al. 2009; Long et al., 2015). Moreover, elimination of the vegetated littoral zone and disappearance of essential wetlands and fish nursery habitats, due to infilling for industrial activities as well as for railway or highway constructions along the south and east shores of the harbour, posed major threats to the integrity of the native fish community. Recognizing the broader repercussions of pollution to ecosystem functioning, the International Joint Commission (IJC) designated Hamilton Harbour as one of 17 Canadian Areas of Concern (AOC). Several of the Beneficial Use Impairments (BUIs) refer directly to fish, such as "Restrictions on Fish and Wildlife Consumption," "Tainting of Fish and Wildlife Flavour," "Degradation of Fish and Wildlife Populations," "Fish Tumours or other Deformities" and "Loss of Fish and Wildlife Habitat" (Bowlby et al., 2007).

In this context, Hossain et al. (2012) developed an Ecopath model to examine the relative importance of the underlying trophic relationships of the Hamilton Harbour foodweb. There were 26 functional groups in the model, consisting of the detritus compartment (pelagic detritus and sedimented detritus), primary producers (generic phytoplankton, epiphytes, autotrophic picoplankton, and macrophytes), zooplankton (carnivorous and herbivorous cladocerans, calanoid and cyclopoid copepods, and micro-zooplankton), benthic invertebrates (Oligochaetes and Chironomids, miscellaneous Benthos, Gastropods and Bivalves, and Dreissenids). The fish assemblage of the model was primarily designed to depict the interplay between the current eutrophic fish community and the "desired" one that is expected to emerge if the restoration efforts are successful. Northern Pike (*Esox lucius*) and largemouth bass (*Micropterus*



Derived from DFO Macrophyte model for Hamilton Harbour (K. Leisti, unpubl. data).

Figure 1. Hamilton Harbour located at the western tip of Lake Ontario, Canada.

salmoides) were represented as independent groups to evaluate their current ecological state; exotic species, common carp (*Cyprinus carpio*) and Round Goby, were retained as independent groups to allow assessment of their impacts on the foodweb of the Harbour; Channel Catfish (*Ictalurus punctatus*) and brown bullhead (*Ameiurus nebulosus*) were combined together into a group labelled as "toxic-tolerant" fish; Yellow Perch (*Perca flavescens*) and White Bass (*Morone chrysops*) were labelled as "desired-forage" fish; Bluegills (*Lepomis macrochirus*), Pumpkinseed (*Lepomis gibbosus*), and Rock Bass (*Ambloplites rupestris*) represented the "centrarchids"; Alewife (*Alosa pseudoharengus*), White Perch (*Morone Americana*), Gizzard Shad (*Dorosoma cepedianum*), and White Sucker (*Catostomus commersonii*) formed a functional group called "other forage" fish; Emerald Shiner (*Notropis atherinoides*), Spottail Shiner (*Notropis hudsonius*), and Golden Shiner (*Notemigonus crysoleucas*) were lumped together and labeled as "small pelagic" fish. Finally, fish-eating birds were represented by the Cormorants (*Phalacrocorax auritus*). The model aimed to represent the average ecosystem state for the period 2004–2008. The currency used was the wet weight biomass per year, and the proxy for ecosystem functioning was the flow of mass from one component to another. The model was not spatially explicit, i.e. horizontally or vertically resolved. Detailed information about the Hamilton Harbour Ecopath model can be found in Hossain et al. (2012).

Linear Inverse Model (LIM)

LIM was originally developed for a situation where many flows among biological groups are very difficult to directly measure and data sets remain incomplete or uncertain (Woodward et al., 2005; van Oevelen et al., 2010). The LIM strategy is considered a rigorous mathematical process to formulate the problem of foodweb quantification. It directly deals with the underdetermined matrix equation and solves multiple mass balances simultaneously (Klepper and Van de Kamer, 1987; Vézina and Platt, 1988). It is worth noting that Ecopath is essentially a linear inverse exercise. LIM integrates the mass balance(s) of each compartment with a set of qualitative or quantitative constraints. The overall LIM structure is formed by two matrix equations:

$$\text{Equality equation: } E * x = f \qquad (1)$$

where $\boldsymbol{E}$ is the matrix of coefficients for equality relationships, $\boldsymbol{x}$ is the vector that contains all the unknown flows (that is, $\boldsymbol{x_1}, \ldots, \boldsymbol{x_n}$) while each element ($\boldsymbol{x_i}$) represents a flow, $\boldsymbol{f}$ is the vector of equality results. Each row in the equality equation (Equation (1)) enforces a hard constraint: a linear combination of the flows that must match the corresponding value in the vector $\boldsymbol{f}$. Therefore, the equality constraints are utilized to include high-grade data (empirical evidence) in LIM.

$$\text{Inequality equation: } G * x \geq h \qquad (2)$$

where $\boldsymbol{G}$ is the matrix of coefficients inequality relationships, $\boldsymbol{x}$ is the vector that contains the all unknown flows (that is, $\boldsymbol{x_1}, \ldots, \boldsymbol{x_n}$) while each element ($\boldsymbol{x_i}$) represents a flow, and $\boldsymbol{h}$ is the vector of inequality values. Relatively less strict data constraints are included through the inequality equation (Equation (2)), where each row applies a lower bound value on a linear combination of the flows. This criteria is used for soft data constraints that are typically obtained from literature sources on similar foodweb studies.

Inequality Equation (2) accepts only lower bounds while upper bound constraints can be implemented after converting them to the lower bound constraints by multiplying the left- and right-hand side with -1. A default set of inequalities is that $\boldsymbol{x} \geq \boldsymbol{0}$, which forces the flows to have direction consistent with the foodweb topology (i.e. predators can consume prey, but the prey cannot consume the predators). The principle of mass conservation assumes that if a group is not predated upon, then the ingested food items are either respired, defecated, or will serve as a biomass increase due to growth (van Oevelen et al., 2010). Then, the mass balance for each group on a daily basis can be expressed as:

$$\begin{aligned}\text{Growth} = dB/dt = {} & \text{ingestion/production} \\ & - \text{predation mortality} - \text{defecation} \\ & - \text{respiration} \qquad (3)\end{aligned}$$

where $\boldsymbol{B}$ is the biomass of the group, and $\boldsymbol{dB/dt}$ is growth (i.e. the rate at which biomass changes over time). Detailed description along with illustrative examples of LIM is given in Soetaert and Van Oevelen (2009).

LIM implementation in Hamilton Harbour

We simplified the original topology of the Ecopath model for Hamilton Harbour to a new one with 12 functional groups (Table 1). Specifically, we retained the aquatic birds, large predators (Northern Pike and Largemouth Bass), and Round Goby from the original model. The simplified fish community also considered the insectivores (Yellow Perch, White Bass, Bluegills, Pumpkinseed and Rock Bass), littoral (Common Carp, Channel Catfish and Brown Bullhead), and pelagic (Alewife, White Perch, Gizzard Shad, White Sucker, Emerald Shiner, Spottail Shiner and Golden Shiner) assemblages. The benthic community was split into two major groups comprising Oligochaetes/Chironomids (Benthos-OC) and Dreissenids (Benthos-DBG). Zooplankton were represented by one single group as was detritus. The autotrophic community was classified into two groups; namely, the large (or aquatic vegetation) and small (or phytoplankton dominated)

Table 1. Functional groups of the Hamilton Harbour LIM. Former Groups column presents the compartments included in the original Hossain et al. (2012) Ecopath model. Simplified Groups presents the aggregated functional groups used in the current LIM.

Former Groups	Simplified Groups	Code	Group Name	Description
1	1	Cor	Aquatic Birds	*Phalacrocorax auritus*
2, 3, 4 and 5	2	Lpr	Large Predators	*Esox lucius, Micropterus salmoides*
7 and 8	3	Ins	Insectivores	*Perca flavescens, Morone chrysops, Lepomis macrochirus, Lepomis gibbosus and Ambloplites rupestris*
6 and 12	4	Lif	Littoral Fishes	*Cyprinus carpio, Ictalurus punctatus and Ameiurus nebulosus*
9 and 11	5	Pdf	Pelagic-dominated Fishes	*Alosa pseudoharengus, Morone Americana, Dorosoma cepedianum,Catostomus commersonii, Notropis atherinoides, Notropis hudsonius and Notemigonus crysoleucas*
10	6	Rgb	Round Goby	*Neogobius melanostomus*
13 and 14	7	Boc	Benthos-OC	Oligochaeta, Chironomidae, Hydrachnids, Amphipods and Isopods (Diptera)
15 and 16	8	Bdb	Benthos-DBG	*Dreissena polymorpha, Dreissena bugensis,* Sphaeriids., *Pisidium* sp., and *Physella* sp.
17-20	9	Zoo	Zooplankton	Calanoid, copepodids, calanoid nauplii, *Leptodiaptomus siciloides*, cyclopoid nauplii, cyclopoid copepodids, *Diacyclops thomasi, Mesocyclops edax, Bosmina longirostris, Eubosmina coregoni, Daphnia retrocurva, Chydorus sphaericu, Heterotrophic nanoflagellates* and *ciliates*
21 and 22	10	Lpp	Large Primary Producers	*Myriophyllm spicatum, Vallisneria americana,* and aquatic vegetation between 20 and 500 μm
23 and 24	11	Spp	Small Primary Producers	Cyanophytes, Chlorophytes, Cryptophytes, Chrysophytes, Diatoms, Dinophytes, Bacteria and autotrophic picoplankton
25 and 26	12	Det	Detritus	Suspended organic matter in the water column, and decomposed organic matter deposited on benthic sediments

primary producers. Our practice during the model reconfiguration can be summarized as follows: (i) functional groups retained from the Hossain et al. (2012) model were based on the originally assigned production and consumption rates; (ii) newly designed functional groups, derived from the aggregation of multiple original groups, were based on weighted averages of the individual group rates reported by Hossain et al. (2012).

Following the parameter estimation of the simplified 12 group Ecopath model, a similar LIM structure was designed with the additional representation of respiratory and export flows (Figure 2). We used the exact input data from the newly balanced Ecopath model, but converted to units of wet weight mass per day (g ww m^{-2} d^{-1}). We removed the fixed diet constraints of the Ecopath model, which were implemented as inequalities in LIM. The complete LIM consists of 77 flows, 18 mass balances, and 86 inequalities. We used three R-packages (LIM [Soetaert and Van Oevelen, 2008], limSolve [Soetaert et al., 2008] and splus2R [Constantine et al., 2013]) that run in R (R Development Core Team, 2015). The

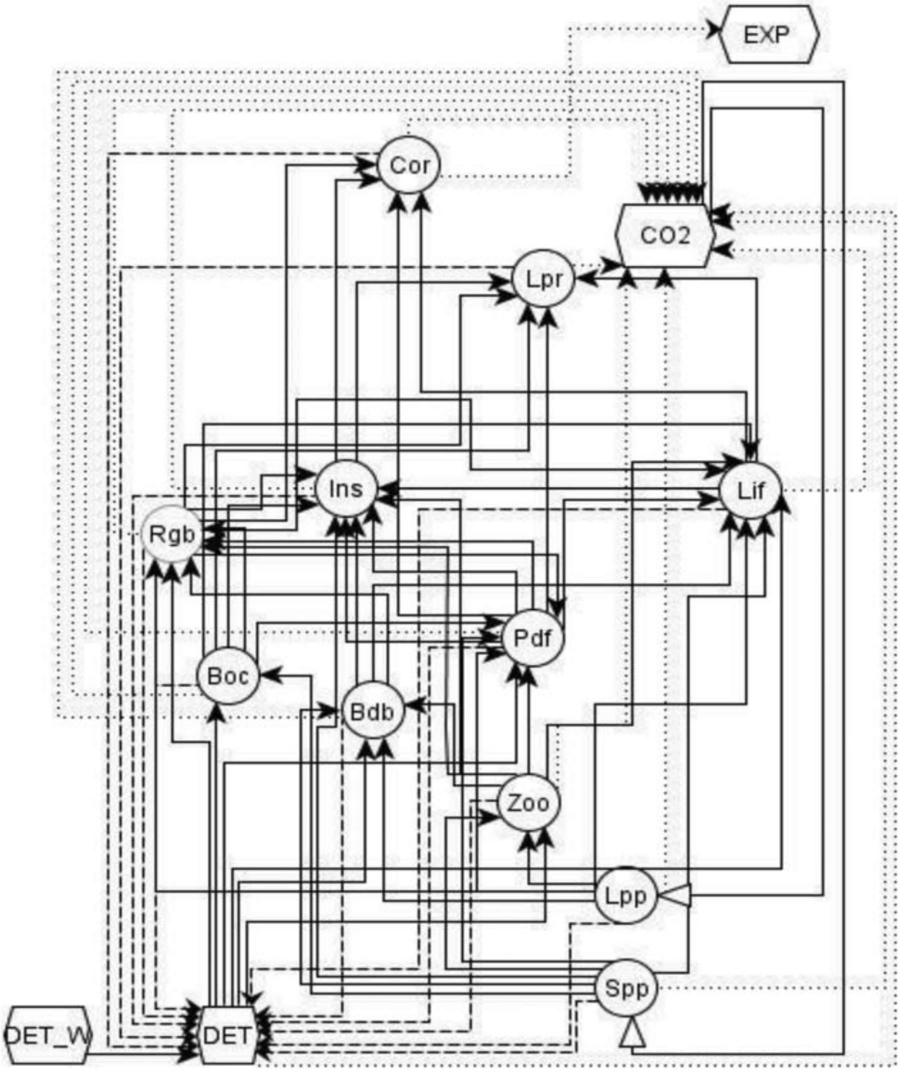


Figure 2. Food web topology of the Hamilton Harbour LIM. Solid lines represent predator-prey relationships and dotted lines represent respiration and fluxes to detritus.

second package allowed us to obtain an acceptable LIM solution using least-squares fitting.

The uncertainty for each foodweb pathway was calculated by perturbing (randomly sampling) both production and consumption rates within ±10% of their Ecopath values and then quantifying the marginal probability distributions of the flows along with the correlations between flows (Klepper and Van de Kamer, 1987; Stone et al., 1993; van Oevelen et al., 2006). This analysis generates an uncertainty envelope around each flow, which reflects the potential range that a flow can span (i.e. lower and upper extremes) given the data used and the equality/constraint equations specified (i.e. minimize or maximize x_i, under the LIM equality and inequality conditions). Finally, we retrieved the distribution of flow values in the solution set to quantify the uncertainty of the foodweb characterization as a complement to Ecopath model. The R codes related to the Hamilton Harbour LIM (Appendix 1.r and Appendix 2(Hamilton_Harbour).r) are provided in the online supplemental information (SI).

Results

An initial attempt to solve the model failed as a result of uncertainty in the representation of respiration for primary producers and unrealistic outgoing flows (exports) from Cormorants. To achieve ecologically acceptable solutions, we had to specify the photosynthetic rates of the two autotrophic functional groups, $CO_2 \rightarrow Lpp$, $CO_2 \rightarrow Spp$, and the inflows of particulate organic matter from external sources to the detritus pool of the system, Det_W→Det (Table 1 in the SI). The core ecological indices obtained from the Hamilton Harbour LIM are shown in Table 2. We obtained the ratios of production to respiration (*P/R*) for all the groups along with the corresponding Ecotrophic Efficiency (*EE*) values. Among the fish functional groups considered, the large predators that represent the desired fish community are the biotic component with the lowest production to respiration ratio in the Harbour (Table 2). The calculated ratio of primary production to respiration was greater than one, 1.69 for large and 3.33 for small primary producers, which is on par with the value (3.46) derived from the original Ecopath model (see Table 6 in Hossain et al., 2012).

Our modelling results were influenced by several sources of uncertainty related to specification of the twelve functional groups at various trophic levels. The uncertainty in external flows (e.g. respiratory and detrital flows) was generally much larger than the internal flows associated with predator-prey relationships. Due to large differences in the flow values, the results are shown in multiple figures, classified according to the corresponding magnitudes (Figure 3; Table 1 and Figures 1–2 in the SI). The largest internal flow values (and associated ranges) stemmed from the trophic interactions between phytoplankton and zooplankton or

Table 2. Ecosystem indices predicted from the Hamilton Harbour LIM.

Code	Group Name	Production (tww/km^2/year)	Consumption (tww/km^2/year)	Ecotrophic Efficiency	Production/ Respiration
Cor	Cormorants	0.231	0.0	0.00	0.213
Lpr	Large Predators	0.300	0.283	0.94	0.011
Lif	Littoral Fishes	0.788	0.458	0.58	0.662
Ins	Insectivores	0.177	0.019	0.11	0.229
Pdf	Pelagic Dominated Fishes	0.991	0.327	0.33	0.331
Rgb	Round Goby	1.620	0.748	0.46	0.448
Boc	Benthos OC	53.332	29.729	0.55	0.604
Bdb	Benthos DGB	1.406	0.596	0.42	0.407
Zoo	Zooplankton	168.017	81.952	0.48	0.502
Lpp	Large Primary Producers	66.88	17.496	0.26	1.692
Spp	Small Primary Producers	668.85	349.45	0.52	3.333
Det	Detritus	536.35	208.58	—	—

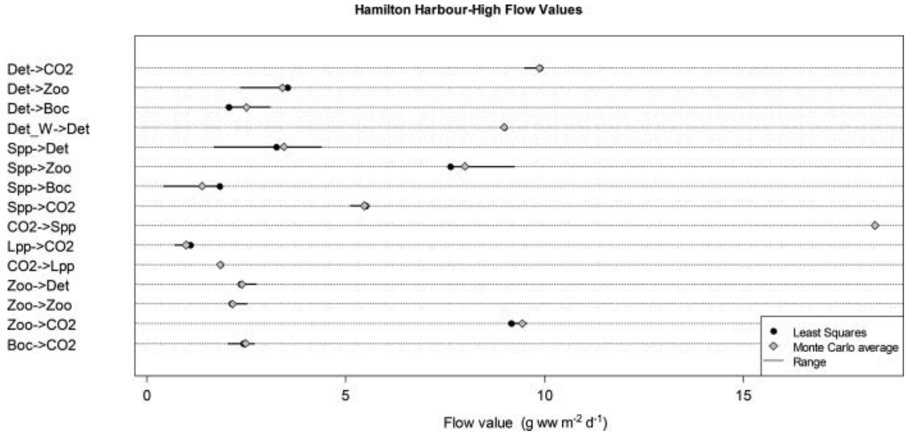


Figure 3. High flow food web pathways (and associated uncertainty zones) as predicted by the least-squares and Monte Carlo averaged LIM.

benthic organisms (oligochaetes and chironomids) (Table 1 in the SI); namely, the internal flows originating from small primary producers to zooplankton (flow #68; Spp → Zoo; 7.6 g ww m^{-2} d^{-1} with a range between 7.5 and 9.2 g ww m^{-2} d^{-1}) and the benthic community (flow #66; Spp → Boc; 1.82 g ww m^{-2} d^{-1} varying from 0.40 to 1.82 g ww m^{-2} d^{-1}) (Figure 3; Table 1 in the SI). Among the external flows, the largest one was the inputs of unconsumed phytoplankton to the detritus pool (flow #69; Spp → Det; 3.25 g ww m^{-2} d^{-1} varying from 1.6 to 4.3 g ww m^{-2} d^{-1}). In addition, ecological pathways related to the role of zooplankton and oligochaetes/chironomids had relatively high flow values, such as detritus ingestion by zooplankton and oligochaetes/chironomids with estimated fluxes of 2.36 g ww m^{-2} d^{-1} (flow #76; Det → Zoo) and 2.05 g ww m^{-2} d^{-1} (flow #74; Det → Boc), respectively (Figure 3; Table 1 in the SI). The same biotic compartments were characterized by the highest respiratory fluxes of 9.16 g ww m^{-2} d^{-1} (flow #47; Zoo → CO2) and 2.42 g ww m^{-2} d^{-1} (flow #35; Boc → CO_2), respectively. Our model estimates that approximately 9.88 g ww m^{-2} d^{-1} of the detrital material is subject to bacterial aerobic respiration within the system (flow #77; Det → CO_2). The remaining mass fluxes related to the trophodynamics of the Harbour were <1 g ww m^{-2} d^{-1} (Figures 1–2 and Table 1 in the SI). Interestingly, the degree of identification of the LIM fluxes, as expressed by the range: average ratio, suggests that the simplified foodweb topology is still not fully constrained by the existing empirical evidence and literature information (Table 1 in the SI).

The pair-wise sets of solutions for all the flows obtained by the Monte Carlo sampling are also shown in multiple figures (Figures 4 and Figure 3S). The histograms on the diagonal reflect the marginal probability distributions of the fluxes associated with each foodweb pathway. The dashed line in the histograms denotes the least-squares solution, and the solid line is the mean of the complete set of valid Monte Carlo solutions. The shapes of the distributions vary among the different flows considered. A few flows have a bell-shaped distribution (e.g. Pdf → CO_2; Bdb → Rgb; Spp → Pdf; Spp → Bdb), while some are strongly skewed toward their left or right limits (e.g. Rgb → Cor; Boc → Rgb; Zoo → Rgb; Rgb → CO_2). The latter pattern suggests that the acceptable range assigned to these fluxes can be marginally realized by the production and consumption rates postulated by our LIM exercise. A number of flows had uniform distributions (e.g. Lif → Lpr; Lif → Ins; Ins → Lpr), indicating that the available data did not offer any insights with respect to the most likely values of these pathways. Another meaningful presentation of the acceptable solutions is the paired plots that allow us to infer correlation patterns between flow pairs, which directly stem from their ecological role, e.g. increase respiratory flows decrease the fluxes to the detritus pool, but also pinpoint processes that are poorly defined even in the context of the simplified LIM foodweb structure.

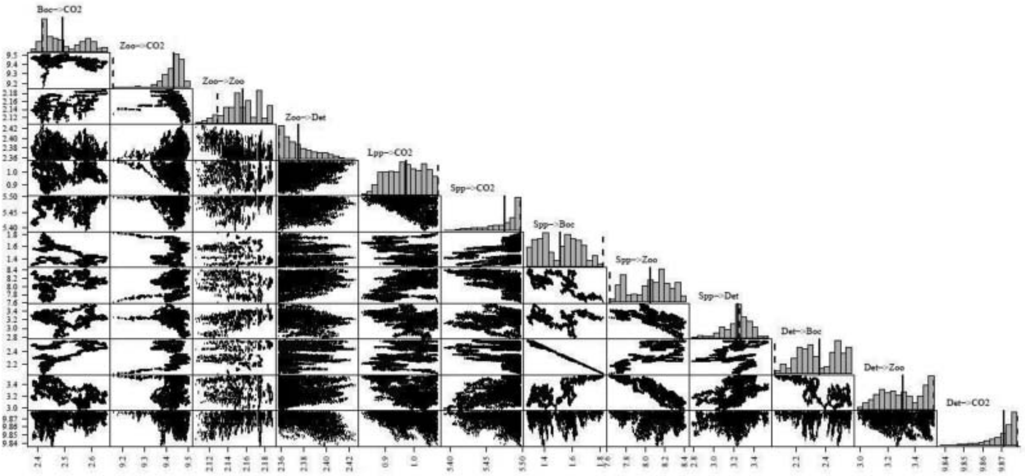


Figure 4. The pair-wise set of solutions of high flow values obtained by Monte Carlo sampling of the Hamilton Harbour LIM; each dot is a valid flow value. The histograms on the diagonal represent the marginal distributions of the flows of each food web pathway (g ww m^{-2} d^{-1}) as derived from the sampled set of valid solutions. The x- and y-axes are scaled to the pre-specified flow ranges. The dashed line in the histograms denotes the LIM solution obtained by least-squares fitting and the solid line is the mean of the complete set of valid Monte Carlo solutions.

Discussion

Ecopath models have most frequently been used as a popular tool for (i) heuristic applications, where their use is intended to elucidate trophic inter-relationships and to pinpoint unexpected implications of management actions; and (ii) predictive uses aiming to offer a formal examination of policy-relevant responses of the fish community, e.g. stock biomass, maximum sustainable yield (Kitchell et al., 2000; Plagányi, 2007; Christensen and Walters, 2011; Jorgensen, 2011). But increasingly, Ecopath models are being used to examine the effects of nutrient loads, invasive species, and habitat quality (Blukacz-Richards and Koops, 2012; Kao et al., 2014; Christensen et al., 2014). Because these types of models require the collection of a considerable amount of information, and therefore the credibility of the inference drawn largely depends on the data quality and underlying assumptions (Essington, 2007; Hossain et al., 2010, 2013). Another problematic aspect of the typical EwE modelling practice is that the usual methods to achieve a mass-balance solution do not address the well-known equifinality (poor model identifiability), where several distinct choices of model inputs lead to the same model outputs (many sets of parameters fit the data about equally well; Essington, 2007). A main reason for the equifinality problem is that the ecological processes/trophic interactions considered for understanding how the system works internally is of substantially higher order than what can realistically be monitored (Arhonditsis et al., 2007). However, having a model that captures the food-web dynamics is particularly important when the model is intended for making predictions in the extrapolation domain, i.e. predict future conditions significantly different from those used to calibrate the model (Savenkoff et al., 2004).

Along the same line of thinking, Hossain et al. (2012) cautioned that although the Hamilton Harbour ecosystem model could ultimately be used for predictive purposes, the substantial uncertainty associated with several critical inputs (biomass estimates, diet compositions) poses limitations on its use and also invites a rigorous assessment of some of the assumptions made during its development. In this regard, our exercise aims to offer a proof of the concept that LIM could be used as a complementary tool to critically assess the uncertainty of Ecopath models and impartially distinguish between real knowledge gained and existing gaps in our ecosystem understanding.

In terms of the ecosystem characterization, our LIM analysis projects that 9.88 g ww m^{-2} d^{-1} of the detrital material is being recycled within the system. Combined with the substantial fluxes directly supporting zooplankton and oligochaetes/ chironomids ($\approx$4.40 g ww m^{-2} d^{-1}), this prediction is on par with recent empirical evidence that the interplay between particulate organic matter and the microbial community (bacteria, autotrophic picoplankton, heterotrophic nanoflagellates, and ciliates) of Hamilton Harbour constitutes an important contributor of the energy transferred to higher trophic levels (Munawar et al., 2005, Fitzpatrick et al., 2007). Furthermore, microbially-mediated mineralization is likely to be an important supplier of bioavailable nutrients in the mixed layer of the system and may significantly modulate epilimnetic phytoplankton dynamics (Gudimov et al., 2010, 2011).

Although higher than the values reported by Hossain et al. (2012), the modest ecotrophic efficiency estimate (0.48) for zooplankton suggests that planktivorous fish does not fully capitalize upon the available food in the system. According to the derived flow estimates, zooplankton contributes 0.007 g ww m^{-2} d^{-1} to insectivores, 0.048 g ww m^{-2} d^{-1} to pelagic fish, and 0.073 g ww m^{-2} d^{-1} to Round Goby. Empirical evidence of the moderate zooplankton control by planktivorous fishes was also the smaller mean length of cladocerans (320–425 μm) recorded in the system relative to neighboring systems (i.e. Bay of Quinte), as fish preferentially consume larger zooplankton individuals and the mean zooplankton community length can reflect the balance between piscivores and planktivores within the fish community (Mills et al., 1987; Gudimov et al., 2010, 2011). On the other hand, the significant flux associated with zooplankton mortality (flow #53; Zoo$\rightarrow$Zoo = 2.11 g ww m^{-2} d^{-1}) may support Hossain et al. (2012) assertion that carnivorous zooplankton (*Leptodora kindtii, Polyphemus pediculus, Cercopagis pengoi*) has the strongest direct association with herbivorous zooplankton and therefore dominates the flows of mass/energy in the third trophic level of Hamilton Harbour. The likelihood of carnivorous zooplankton to be a primary regulatory factor was also proposed by Munawar and Fitzpatrick (2007), who noted that the proportion of carnivorous to herbivorous zooplankton is relatively high, frequently accounting for 25–50% of the zooplankton biomass.

One of the key findings of Hossain et al. (2012) Ecopath modelling work was the relative importance of Round Goby with a wide range of trophic interactions with a number of functional groups at different trophic levels. Round Goby became established in the Harbour in 1998 and have been detected in higher numbers at various locations in Hamilton Harbour (Balshine et al., 2005; Vélez-Espino et al., 2010; McCallum et al., 2014). Rapid proliferation and aggressive behaviour of Round Goby can alter benthic communities and nutrient cycles (Janssen and Jude, 2001), displace native species through shelter monopolization (Balshine et al., 2005), and voraciously consume eggs of native fishes (Jude, 2001). Likewise, our LIM analysis highlights the importance of their predation pressure on the benthic community, i.e. Oligochaetes/Chironomids (0.032 g ww m^{-2} d^{-1}), and Dreissenids (0.009 g ww m^{-2} d^{-1}).

The negligible fluxes associated with predation pressure by piscivores (<0.001 g ww m^{-2} d^{-1}) is consistent with the existing empirical evidence that their numbers are still fairly low in Hamilton Harbour (Bowlby et al., 2007). In particular, piscivores should contribute at least 20% of the total biomass in a balanced system (Minns et al., 1999), whereas the average biomass of piscivores is less than 10% in this system (Brousseau and Randall, 2008). Degraded water quality conditions and lack of high quality habitat (fine substrates and dense macrophytes) in Hamilton Harbour appear to be the major impediment to the establishment of a diverse fish community that can effectively support top predators and subsequently mitigate the impact of invasive species (LaPointe et al., 2007) or induce other desirable “top-down” water quality controls (Gudimov et al., 2011). It is also worth noting the extremely high ecotrophic efficiency of 0.98 derived by our LIM analysis for large predators, which deviates from the low EE values (0.04–0.20) reported by Hossain et al. (2012). The main difference between the original model and the present LIM approach has to do with the assumptions made regarding the relative contribution of the large predators to the detritus pool and the losses due to cannibalism in Northern Pike and Largemouth Bass young-of-the-year. The original model downplayed the latter process (see Table 2 in Hossain et al., 2012), whereas the present model assigns a distinctly higher value to this path (0.00774 g ww m^{-2} d^{-1}) relative to the flow that replenishes the detritus pool (0.00048 g ww m^{-2} d^{-1}). Although Northern Pike are quite cannibalistic, Largemouth Bass are much less so and thus the specified value may be somewhat inflated. Nonetheless, a plausible explanation could be that the elevated losses due to cannibalism partly account for the emigration of top predators from the Hamilton Harbour.

In this analysis, even though a simplified foodweb configuration was used, we found that the existing input data and qualitative constraints were still not adequate to identify all the modelled fluxes. If we also consider that the uncertainty band examined was fairly conservative (±10% of the Ecopath estimates of production and consumption rates), it stands to reason that strategies basing ecosystem descriptions on single solutions can be misleading and may undermine the value of foodweb modelling for management purposes. Recognizing the problem of incomplete data and mathematical indeterminacy as well as quantifying the uncertainties associated with our foodweb reconstruction exercise is certainly a way forward. An important step with the next iteration of our LIM development is the use of available stable isotope data (^{13}C and ^{15}N) to provide important constraints on diet composition and trophic position of organisms in the Hamilton Harbour foodweb (Ryman, 2009).

Conclusions

LIM can be used as a complement to Ecopath applications to evaluate the credibility of the typically reported ecosystem characterizations. In this study, using a simplified version of a previously published foodweb topology (Hossain et al., 2012), we were able to demonstrate the considerable uncertainty associated with the derived flow quantities. In particular, the uncertainty of external flows (e.g. respiratory and detrital flows) tended to be much higher than the internal flows associated with predator-prey relationships. The benefit of this type of uncertainty assessment is that it can provide a solid ground to guide future monitoring and research activities. Our LIM analysis reinforces earlier findings that most of the energy flows are concentrated within the first two trophic levels of Hamilton Harbour, while flows at higher foodweb levels were distinctly lower. Although higher than previously reported values, the intermediate ecotrophic efficiency for zooplankton suggests that planktivorous fishes do not fully capitalize upon the available food in the system. Our model estimates that approximately 9.88 g ww m^{-2} d^{-1} of the detrital material is being recycled by the microbial community within the system. Taken together with the substantial fluxes directly supporting zooplankton and oligochaetes/chironomids ($\approx$4.40 g ww m^{-2} d^{-1}), this prediction is on par with recent empirical evidence that the particulate organic matter collectively constitutes an important contributor of energy that gets transferred to higher trophic levels. Overall, our LIM analysis offers meaningful insights that should contribute towards the development of a reliable ecosystem model for Hamilton Harbour.

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Supplemental material

Supplemental data for this article can be accessed on the publisher's website.

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Uncertainty Assessment of Trophic Flows in Hamilton Harbour: A Linear Inverse Modelling Analysis

Supporting Information

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Table 1 SI: Predicted flows and associated uncertainty ranges (g ww m^{-2} d^{-1}) from the Hamilton Harbour LIM. Standardized Variability (StVar) of each flow is calculated as the range divided by the corresponding least-squares mean value. Flow names are composed of the three-letter code from the compartment of origin to the three-letter code of the destination compartment.

		Flow			
Number	**Name**	**Values**	**Ranges**		**StVar**
			Minimum	**Maximum**	
1	Cor→CO2	0.02980	0.00000	0.02990	>100%
2	Cor→Det	0.00602	0.00602	0.03593	>100%
3	Cor→Exp	0.00032	0.00022	0.00032	33%
4	Lpr→CO2	0.74295	0.08493	0.74767	89%
5	Lpr→Cor	0.00002	0.00001	0.00002	33%
6	Lpr→Lpr	0.00774	0.00774	0.01161	50%
7	Lpr→Det	0.00048	0.00048	0.38700	>100%
8	Lif→CO2	0.03265	0.00000	0.03265	100%
9	Lif→Cor	0.01207	0.01183	0.01836	54%
10	Lif→Lpr	0.00004	0.00004	0.00006	50%
11	Lif→Lif	0.00045	0.00045	0.00068	50%
12	Lif→Ins	0.00000	0.00000	0.00000	33%
13	Lif→Det	0.00904	0.00904	0.04169	>100%
14	Ins→CO2	0.02119	0.00000	0.02119	100%
15	Ins→Cor	0.00048	0.00046	0.00075	58%
16	Ins→Lpr	0.00001	0.00001	0.00001	50%
17	Ins→Lif	0.00003	0.00003	0.00004	50%
18	Ins→Ins	0.00001	0.00001	0.00001	50%
19	Ins→Det	0.00434	0.00434	0.02554	>100%
20	Pdf→CO2	0.08202	0.00000	0.08319	>100%
21	Pdf→Cor	0.00336	0.00000	0.00609	>100%
22	Pdf→Lpr	0.00083	0.00083	0.00125	50%
23	Pdf→Lif	0.00250	0.00250	0.00374	50%
24	Pdf→Ins	0.00132	0.00132	0.00198	50%
25	Pdf→Pdf	0.00095	0.00095	0.00142	50%
26	Pdf→Rgb	0.00001	0.00001	0.00001	50%
27	Pdf→Det	0.01820	0.01820	0.10138	>100%
28	Rgb→CO2	0.09887	0.00000	0.10377	>100%
29	Rgb→Cor	0.02021	0.01527	0.02319	39%
30	Rgb→Lpr	0.00003	0.00003	0.00004	50%
31	Rgb→Lif	0.00005	0.00005	0.00007	50%
32	Rgb→Ins	0.00022	0.00015	0.00022	33%
33	Rgb→Pdf	0.00001	0.00001	0.00001	50%
34	Rgb→Det	0.02388	0.02388	0.12765	>100%
35	Boc→CO2	2.41892	2.03240	2.69041	27%

Table 1 SI (Cont): Predicted flows and associated uncertainty ranges (g ww m^{-2} d^{-1}) from the Hamilton Harbour LIM. Standardized Variability (StVar) of each flow is calculated as the range divided by the corresponding least-squares mean value. Flow names are composed of the three-letter code from the compartment of origin to the three-letter code of the destination compartment.

Flow					
Number	**Name**	**Values**	**Ranges**		
			Minimum	**Maximum**	**StVar**
36	Boc→Lpr	0.74195	0.44057	0.74621	41%
37	Boc→Lif	0.01107	0.01107	0.01660	50%
38	Boc→Ins	0.01278	0.00852	0.01278	33%
39	Boc→Pdf	0.01689	0.01689	0.02533	50%
40	Boc→Rgb	0.03180	0.03180	0.04771	50%
41	Boc→Det	0.64668	0.64668	1.03320	60%
42	Bdb→CO2	0.09465	0.00000	0.09550	>100%
43	Bdb→Lif	0.00344	0.00344	0.00515	50%
44	Bdb→Ins	0.00431	0.00000	0.01112	>100%
45	Bdb→Rgb	0.00860	0.00860	0.01289	50%
46	Bdb→Det	0.02220	0.02220	0.11770	>100%
47	Zoo→CO2	9.15788	9.15788	9.54439	4%
48	Zoo→Lpr	0.00059	0.00039	0.00059	33%
49	Zoo→Lif	0.00526	0.00526	0.00789	50%
50	Zoo→Ins	0.00741	0.00494	0.00741	33%
51	Zoo→Pdf	0.04418	0.04418	0.06627	50%
52	Zoo→Rgb	0.07325	0.00000	0.07325	>100%
53	Zoo→Zoo	2.11458	2.08986	2.51552	20%
54	Zoo→Det	2.35793	2.35793	2.74445	16%
55	CO2→Lpp	1.83247			
56	Lpp→CO2	1.08248	0.69596	1.08248	36%
57	Lpp→Lif	0.00416	0.00416	0.00624	50%
58	Lpp→Rgb	0.00096	0.00096	0.00143	50%
59	Lpp→Bdb	0.00266	0.00266	0.00400	50%
60	Lpp→Zoo	0.47159	0.47159	0.70738	50%
61	Lpp→Det	0.27062	0.22268	0.65714	>100%
62	CO2→Spp	18.32466			
63	Spp→CO2	5.49730	5.11088	5.49740	7%
64	Spp→Lif	0.02170	0.00000	0.02170	100%
65	Spp→Pdf	0.03930	0.00000	0.03930	100%
66	Spp→Boc	1.82364	0.40890	1.82364	78%
67	Spp→Bdb	0.06571	0.00000	0.06571	100%
68	Spp→Zoo	7.62360	7.57644	9.22822	22%
69	Spp→Det	3.25321	1.67340	4.36852	83%
70	Det_W→Det	8.98000			

Table 1 SI (Cont): Predicted flows and associated uncertainty ranges (g ww m^{-2} d^{-1}) from the Hamilton Harbour LIM. Standardized Variability (StVar) of each flow is calculated as the range divided by the corresponding least-squares mean value. Flow names are composed of the three-letter code from the compartment of origin to the three-letter code of the destination compartment.

Flow					
Number	**Name**	**Values**	**Ranges**		
			Minimum	**Maximum**	**StVar**
71	Det→Lif	0.00561	0.00561	0.00841	50%
72	Det→Pdf	0.00786	0.00786	0.01179	50%
73	Det→Rgb	0.02865	0.02865	0.04298	33%
74	Det→Boc	2.05645	2.05645	3.08467	50%
75	Det→Bdb	0.06482	0.06482	0.09723	50%
76	Det→Zoo	2.35793	2.35793	3.53690	33%
77	Det→CO2	9.87800	9.49148	9.87800	4%

Figure 1 SI: Medium flow food web pathways (and associated uncertainty zones) as predicted by the least-squares and Monte Carlo averaged LIM.

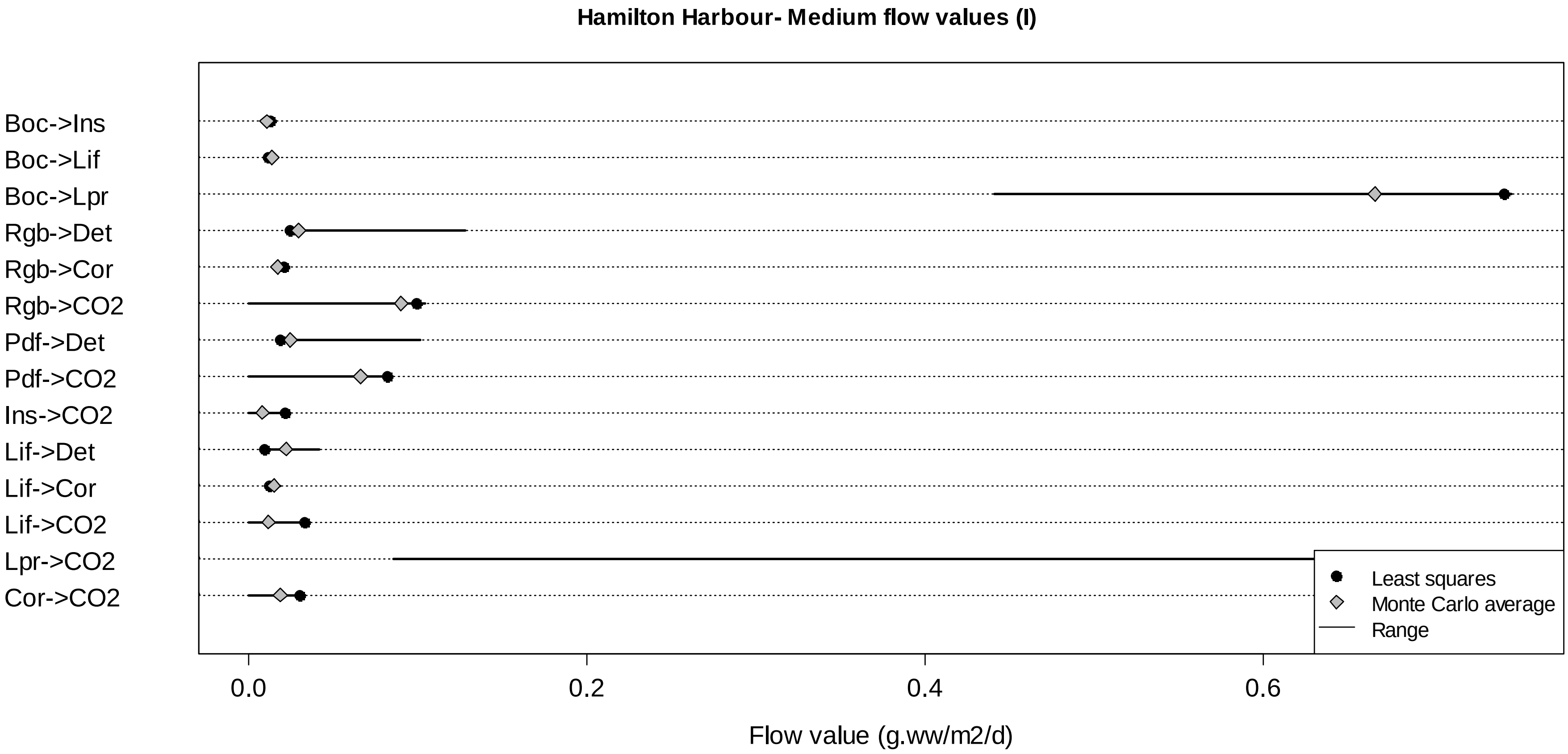

Figure 1 SI (Cont): Medium flow food web pathways (and associated uncertainty zones) as predicted by the least-squares and Monte Carlo averaged LIM.

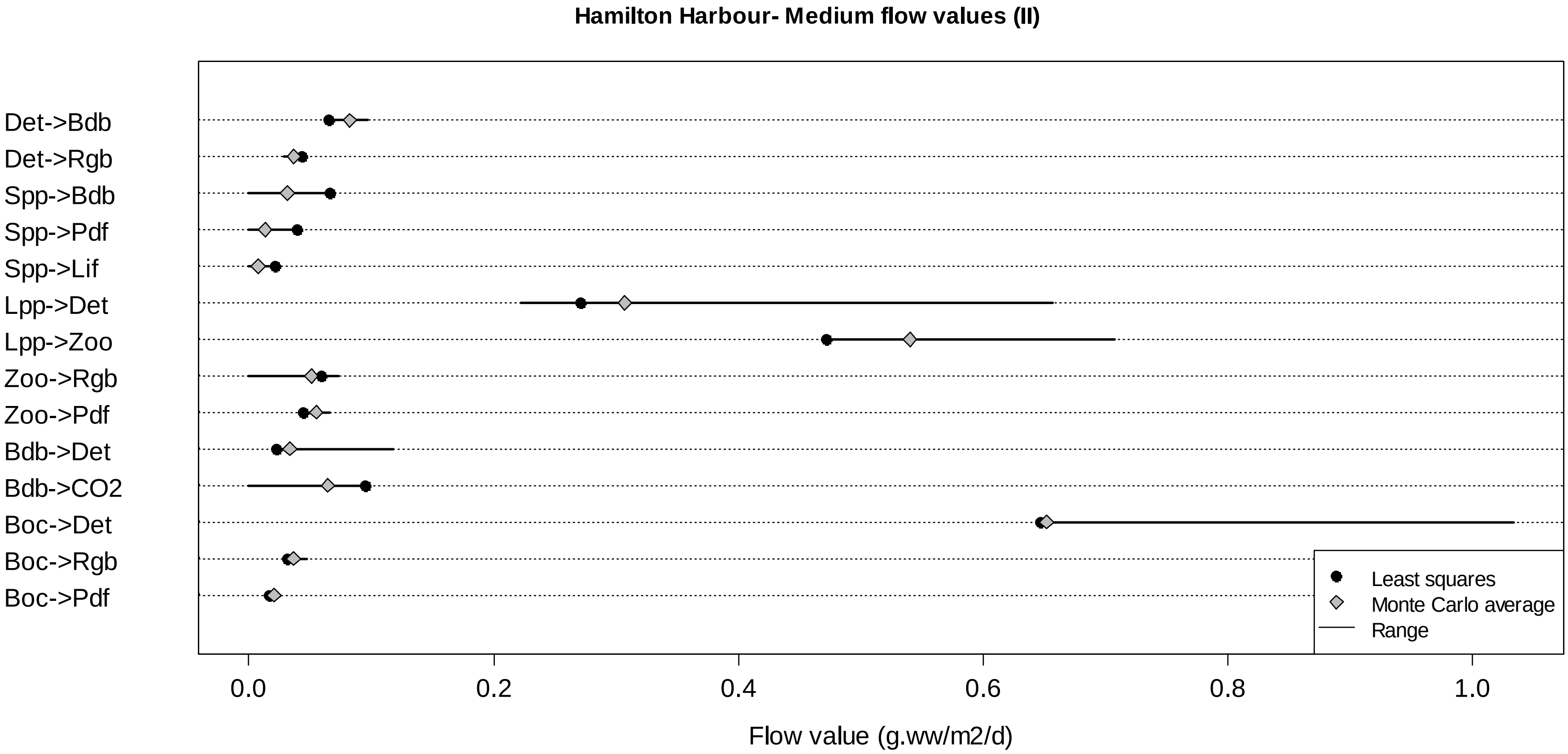

Figure 2 SI: Low flow food web pathways (and associated uncertainty zones) as predicted by the least-squares and Monte Carlo averaged LIM.

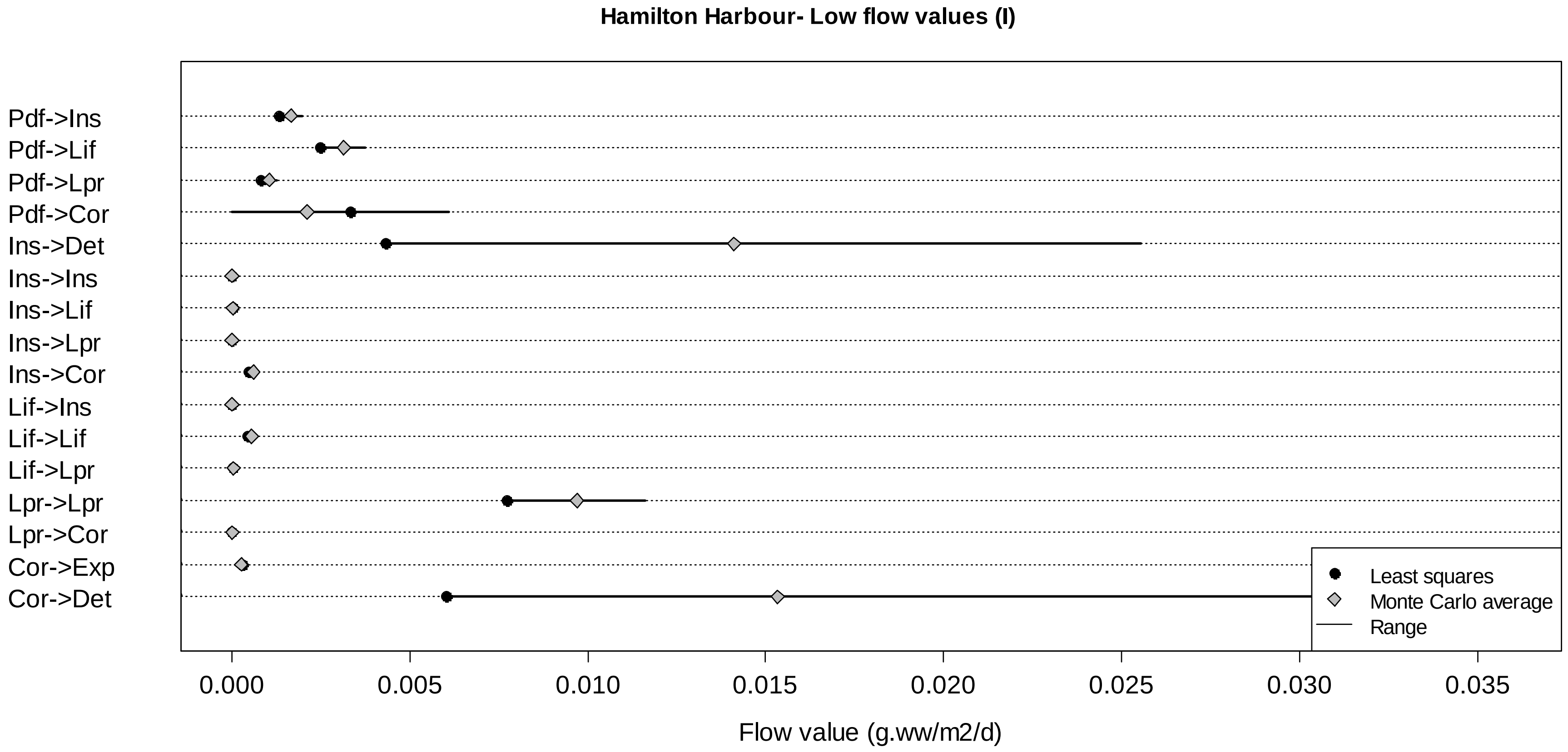

Figure 2 SI (Cont): Low flow food web pathways (and associated uncertainty zones) as predicted by the least-squares and Monte Carlo averaged LIM.

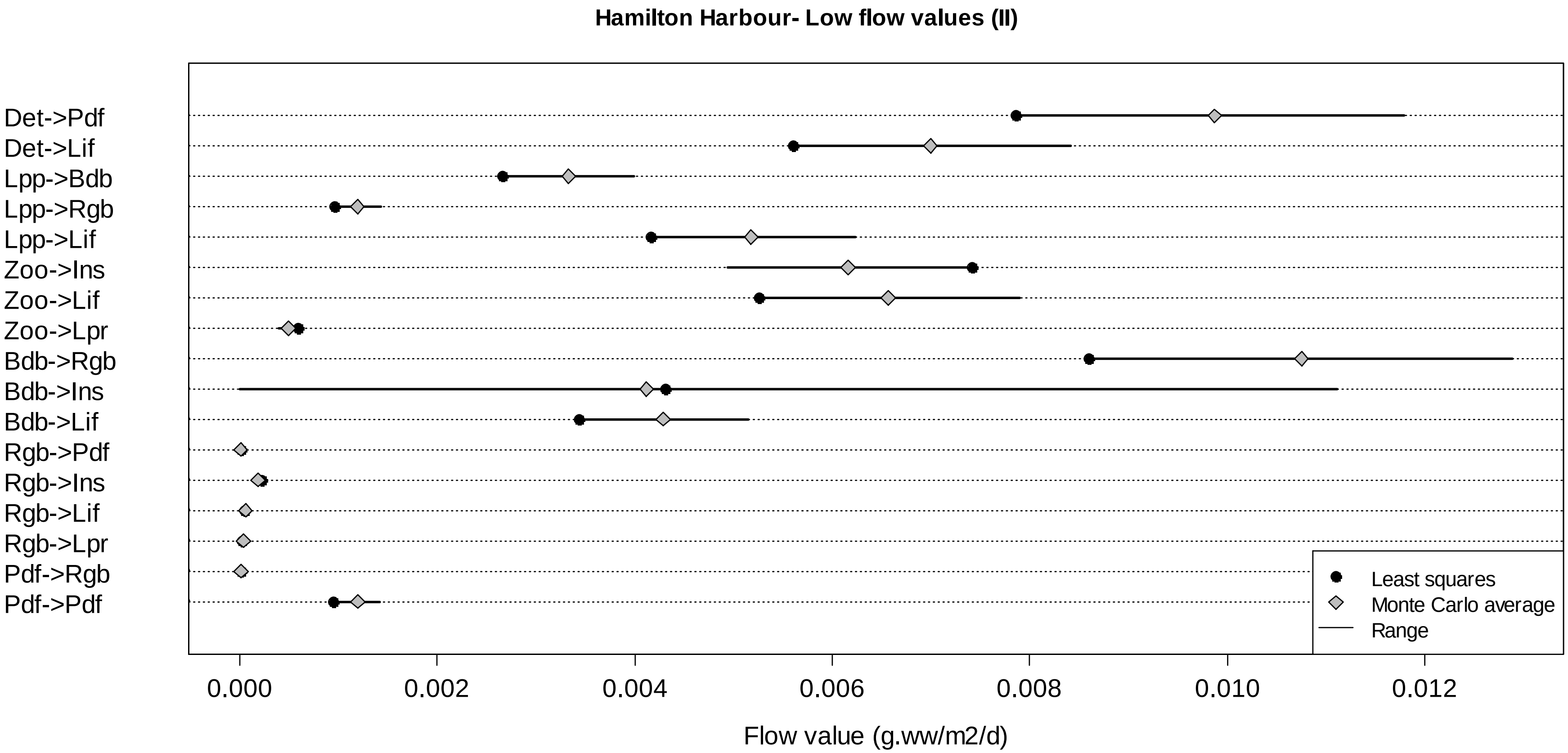

Figure 3 SI: The pair-wise set of flow solutions obtained by Monte Carlo sampling of the Hamilton Harbour LIM; each dot is a valid flow value. The histograms on the diagonal represent the marginal distributions of the flows of each food web pathway (g ww/m^2/d) as derived from the sampled set of valid solutions. Flow numbers 1-15 from Table 1 SI are shown.

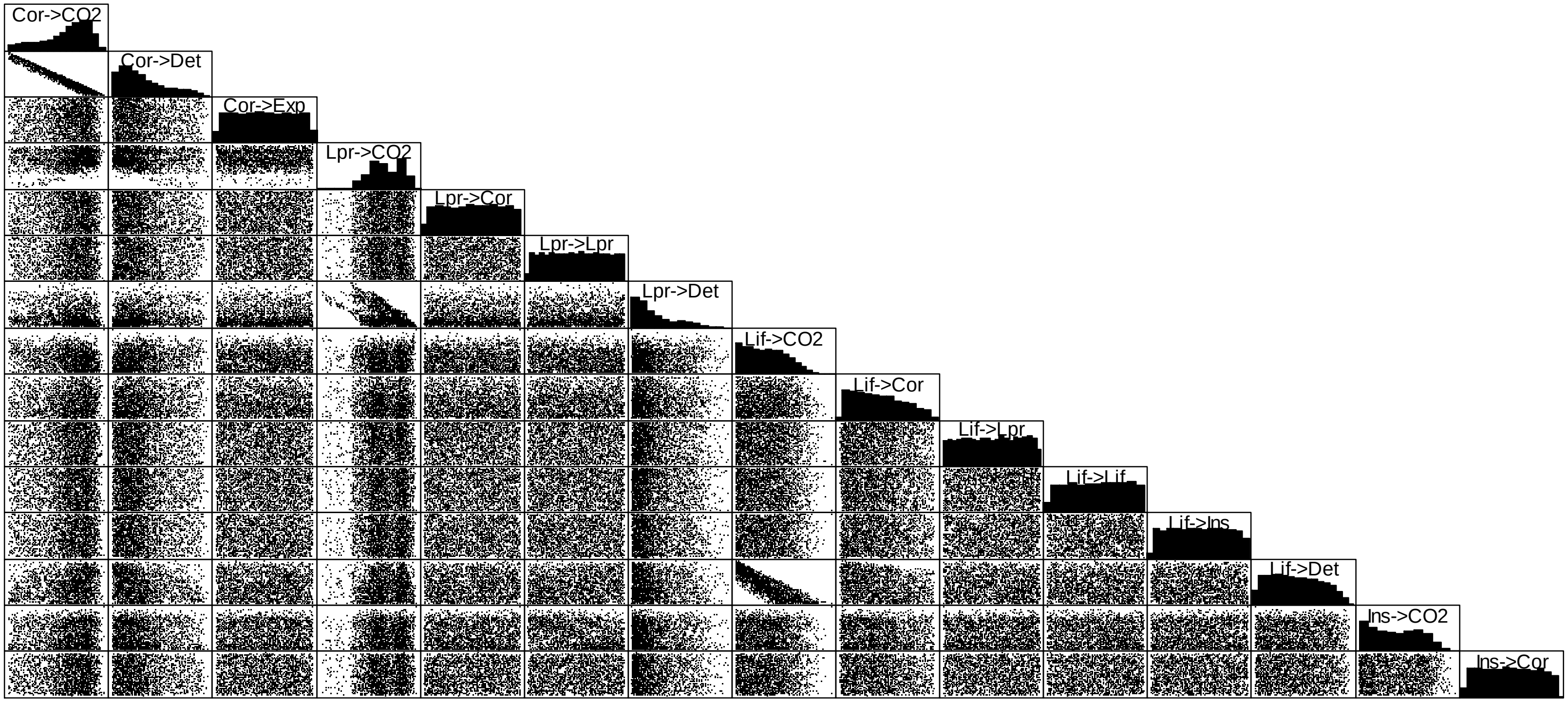

Figure 3 SI (Cont): The pair-wise set of flow solutions obtained by Monte Carlo sampling of the Hamilton Harbour LIM; each dot is a valid flow value. The histograms on the diagonal represent the marginal distributions of the flows of each food web pathway (g ww/m^2/d) as derived from the sampled set of valid solutions. Flow numbers 16-30 from Table 1 SI are shown.

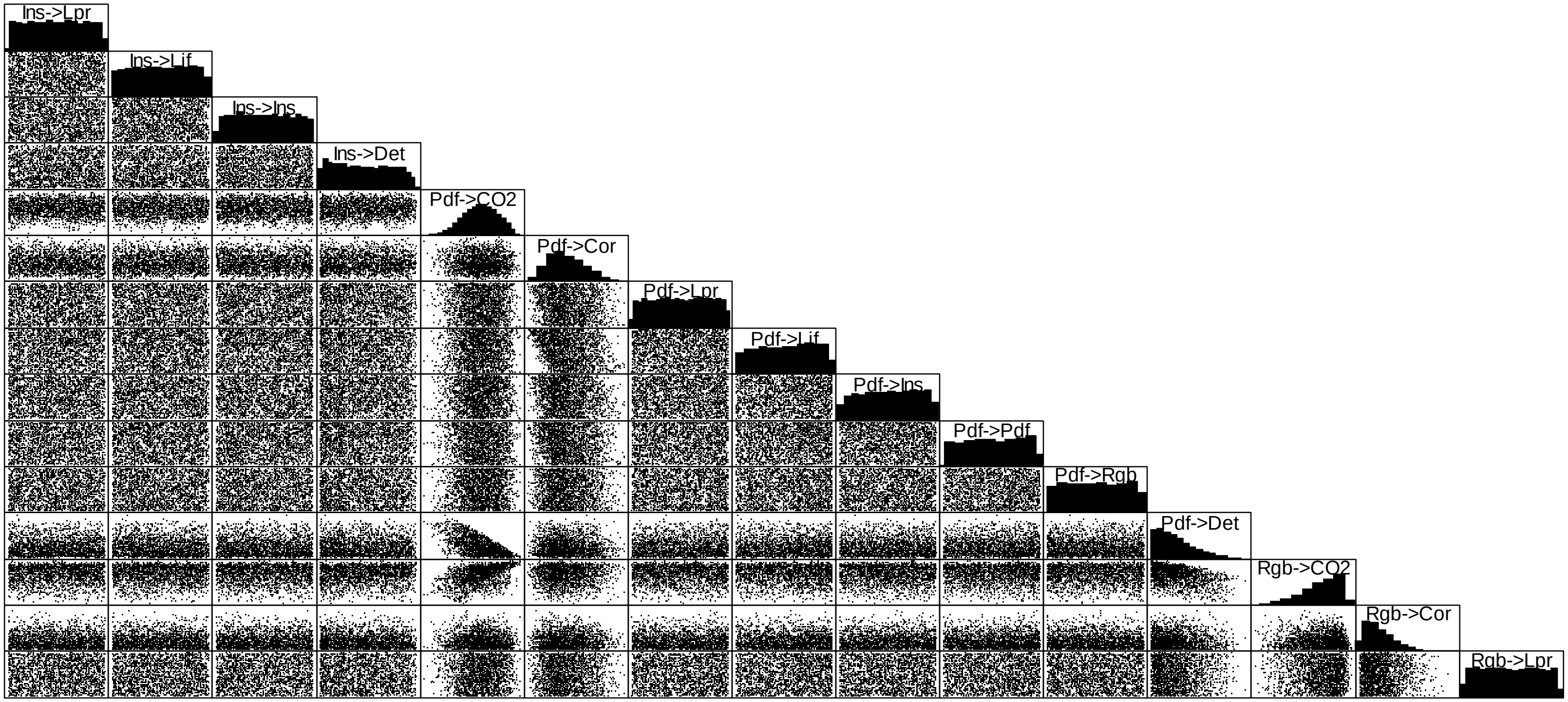

Figure 3 SI (Cont): The pair-wise set of flow solutions obtained by Monte Carlo sampling of the Hamilton Harbour LIM; each dot is a valid flow value. The histograms on the diagonal represent the marginal distributions of the flows of each food web pathway (g ww/m^2/d) as derived from the sampled set of valid solutions. Flow numbers 31-45 from Table 1 SI are shown.

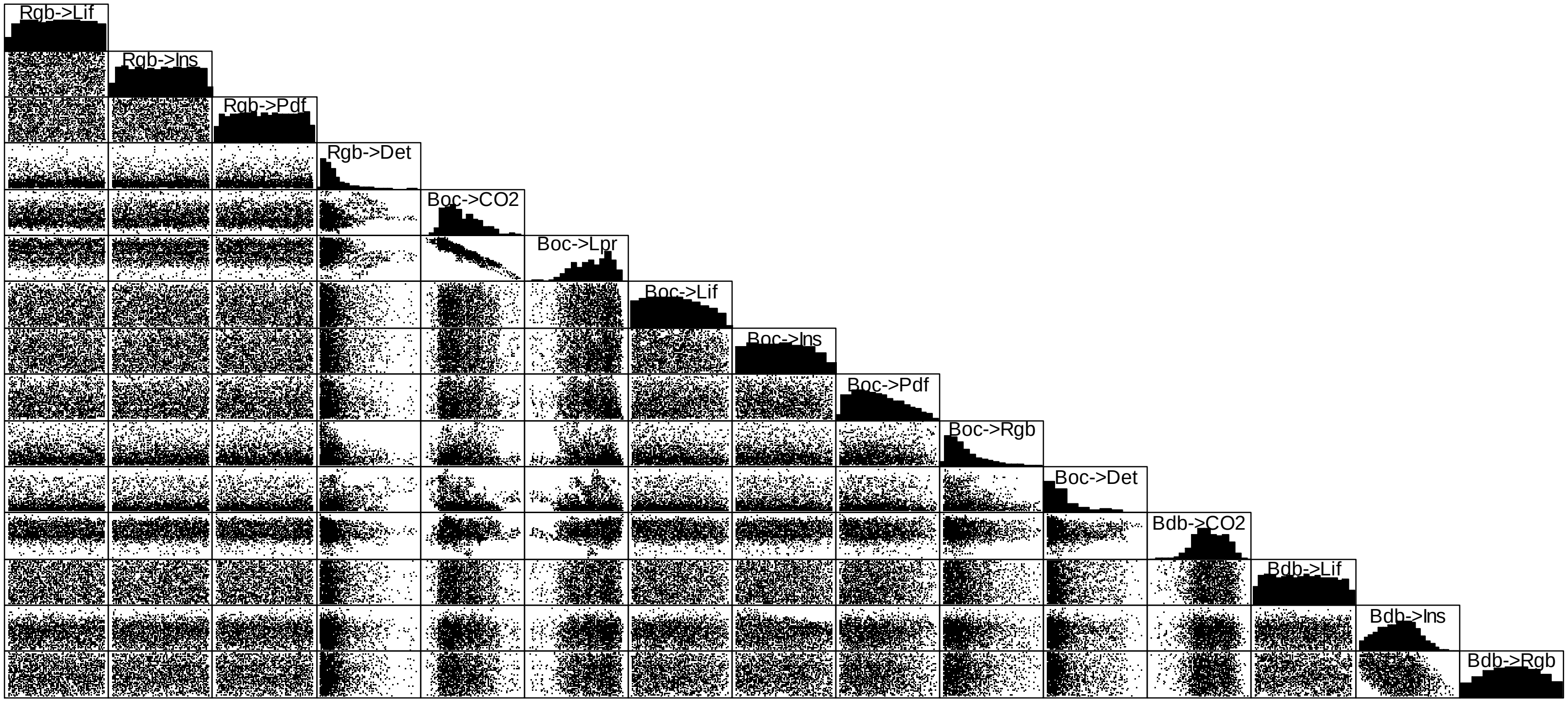

Figure 3 SI (Cont): The pair-wise set of flow solutions obtained by Monte Carlo sampling of the Hamilton Harbour LIM; each dot is a valid flow value. The histograms on the diagonal represent the marginal distributions of the flows of each food web pathway (g·ww/m^2/d) as derived from the sampled set of valid solutions. Flow numbers 46-60 from Table 1 SI are shown.

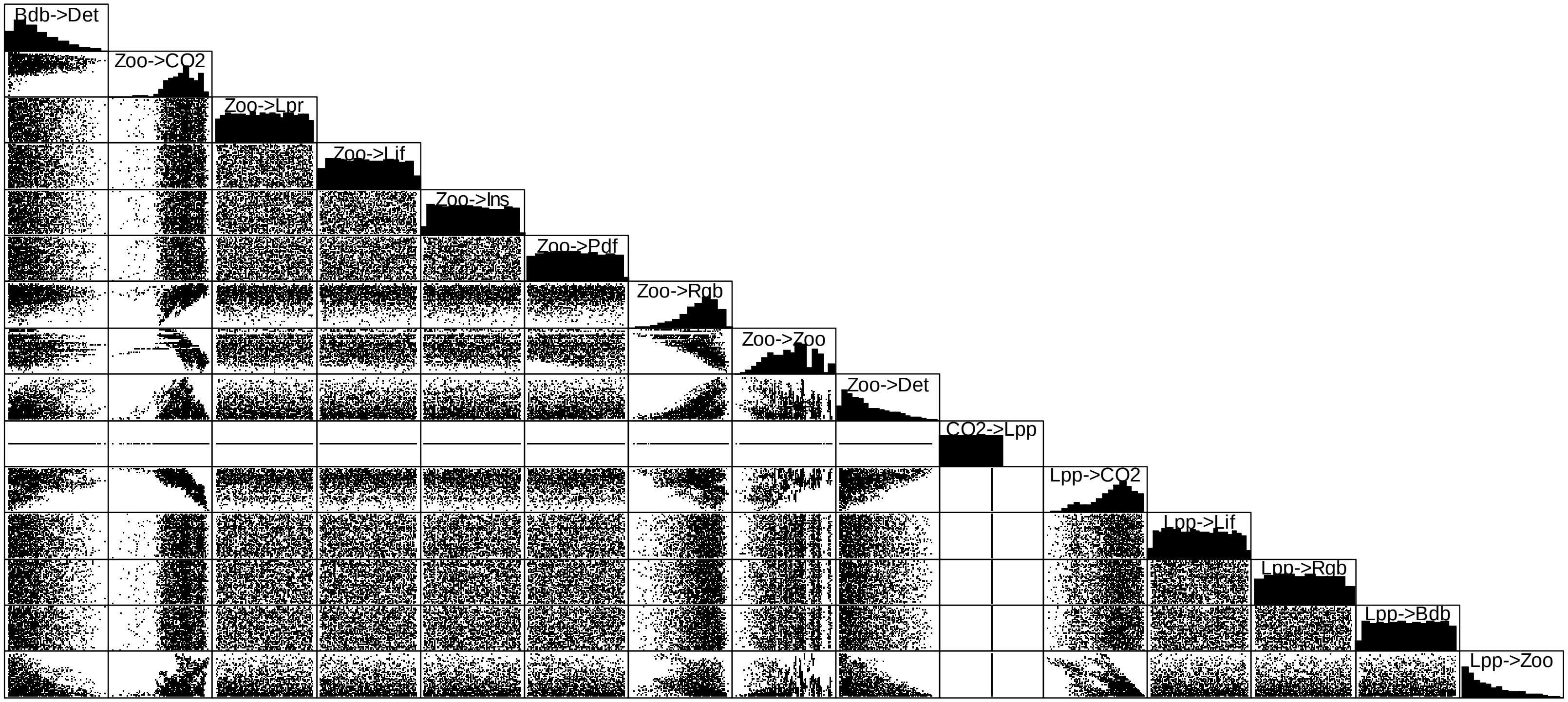

Figure 3 SI (Cont): The pair-wise set of flow solutions obtained by Monte Carlo sampling of the Hamilton Harbour LIM; each dot is a valid flow value. The histograms on the diagonal represent the marginal distributions of the flows of each food web pathway (g·ww/m^2/d) as derived from the sampled set of valid solutions. Flow numbers 61-77 from Table 1 SI are shown.