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Evaluating the Food Web and Ecosystem Function of a Large, Shallow, Eutrophic Lake Dominated by Non-Native Fishes

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Abstract

Utah Lake, Utah, USA, has undergone an anthropogenic ecosystem shift from clearwater to a turbid state in less than 150 years. There is now strong citizen support for its restoration, including its native fishes. However, no effort has been made to understand its food web or ecosystem function, essential for scientifically based restoration. Consequently, a representative food web model was urgently needed. We present the first-ever food web-based, ecosystem function model of Utah Lake using EcoPath. Biomasses, diets, and production/biomass ratios of eighty-one taxonomic groups were modeled. Results showed an impaired Utah Lake ecosystem dominated by only a handful of taxa, including invasive carp, other invasive fishes, and pollution-tolerant chironomids. Lake energy sources were co-dominated by water column primary production and detritus, mostly as detrital snow with negligible benthic photosynthetic production. Utah Lake has low robustness (e.g., resistance), is below optimal trophic functioning, and is trapped in an 'immature' early succession stage primarily because of chronic wave action that disturbs unconsolidated sediments, thus preventing system maturation, maintaining the lake in a 'bloom' susceptible eutrophic state that underutilizes available nutrients. Carp reduction had positive mixed-level trophic impacts on several groups, indicating the need for an improved reduction program. Increased monitoring and research are essential, including ecosystem network analyses needed to predict future changes to Utah Lake's ecosystem, including directing restorative actions.

Keywords: Restoration; Ecopath; Food Web Model; Ecosystem Function; Ecosystem Network Analysis; Utah Lake; *Cyprinus Carpio*

INTRODUCTION

Utah Lake (40°12'59.96"N, 111°48'28.20"W), Utah, USA, a remnant of Late Pleistocene Lake Bonneville, is a large (≈380 km^2), shallow (mean ≈3 m depth), turbid, eutrophic, slightly saline, and highly regulated lake managed as a reservoir. Its ecosystem has been severely degraded since first settlement by Americans of European descent over 150 years ago [1]. Primary production in Utah Lake has been almost completely dominated by water column phytoplankton (algae) for more than 50 years. In a healthy state, the lake should have relatively equal contributions from water column and benthic primary production given its shallow nature. Algal blooms, including potentially harmful cyanobacteria blooms (HABs), occasionally occur during some summer months. Submerged and emergent aquatic macrophytes (plants) were abundant throughout much of its once extensive littoral zone but are now near absent. Mollusk (mussels, clams, and snails) diversity and abundance peak in the Utah Lake-Jordan River drainage and the surrounding areas in the molluskan depauperate western USA [2,3]. Unfortunately, Utah Lake's keystone native mollusk community has been near extirpated. The lake's once diverse benthic invertebrate assemblage is now mostly dominated by only two or three pollution tolerant chironomid (midge) and oligochaete (segmented worm) taxa [1]. Utah Lake once supported 13 species of native fish, ten of which have been extirpated or are extinct, including the keystone species Bonneville Cutthroat Trout (Oncorhynchus virginalis utah). The lake currently only supports three native species including Threatened June Sucker (Chasmistes liorus), Utah Sucker (Catastomus ardens), and Utah Chub (Gila artraria) that account for less than 2% relative abundance whereas, twelve non-native and highly invasive species now account for 98% relative abundance, including over dominance by Common Carp (Cyprinus carpio) (S2). By most standards the lake has lost its ecological integrity and is in poor health. Utah Lake's resilience to future perturbation and its resistance to improvement (restoration) appears to be compromised [1].

Given its degraded state, there is much concern by citizens and managers as to the future of Utah Lake and what can be done to improve its condition (i.e., health, integrity), including the reduction of algal blooms and restoring native fish populations. However, the focus of concern has been almost exclusively on external nutrient input reduction and to a lesser extent invasive carp control. There has been little to no effort expended to examine or understand the importance of direct and indirect interactions within the lake's food web or how top-down, trophic cascades directly and indirectly effect and respond to current conditions. Managers are just now considering how biomanipulation may help restore its ecosystem functions. Restoring Utah Lake's ecosystem function and native fisheries cannot proceed without this understanding. Hence, a representative food web- based, ecosystem function model was urgently needed.

Presented here is the first trophic- level, mass- balanced food web model of Utah Lake. This model along with subsequent iterations and improvements will allow researchers and managers to understand and better manage this important ecosystem. A food web reference point is now established for Utah Lake for comparisons with future scenarios. Describing the food web structure and trophic interactions among the lakes' biological groups will vastly improve our current knowledge on the role of key ecosystem processes and development of decision support

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tools necessary for effective management [4-6].

METHODS

Food web models are widely used to investigate complex interactions at the ecosystem level by providing simplified representations based on trophic structure. One of the most popular approaches to determine aquatic food web dynamics is the temporal dynamic modeling approach used in EcoPath with EcoSim (EwE) [7,8]. EwE models have been shown to provide valuable forecasts [9-11]. The EwE modelling approach is based on modelling energy flow and provides several well documented flow-based indicators [8-13]. EwE has been applied to hundreds of ecosystems around the world [14,15], with over 500 unique models documented in EcoBase, so far (see website at http://sirs.agrocampus-ouest.fr/EcoBase/). EwE has been used for large lake food web modelling including extensively throughout the Great Lakes, USA [16-23]. Derivations of EwE are detailed in Christensen and Pauly and Walters et al.; software and documentation are available at http://www.EcoPath.org/. EwE version 6.6.7 was used for our Utah Lake food web model.

Two master equations must be satisfied to correctly parameterize the EcoPath model. The first equation describes the production of each functional group as a set of n linear equations for n groups:

$$\left(\frac{P_i}{B_i}\right) \cdot B_i \cdot EE_i - \sum_{j=1}^{n} B_j \cdot \left(\frac{Q_j}{B_j}\right) \cdot DC_{ji} - Y_i - E_i - BA_i = 0$$

where (P_i/B_i) is the production to biomass ratio for group i (which is equal to the coefficient of total mortality Z under steady-state conditions [24], EEi is the ecotrophic efficiency (the proportion of production used in the system), B_i and B_j are the biomasses of the prey and predators respectively, (Q_j/B_j) is the consumption to biomass ratio, DC_{ji} is the fraction of prey i in predator j's diet, Yi is catch rate for the fishery for group i, E_i is the net migration rate, and B_{ai} is the biomass accumulation for group i. The EcoPath model assumes conservation of mass over a year.

Energy balance within each group is ensured with the second master equation:

Consumption = production + respiration + unassimilated energy

where production can be described as:

Production = predation mortality + catches + net migration + biomass accumulation + other mortality

$$P_i = \sum_{l} Q_j \cdot DC_{ji} + (F_i + NM_i + BA_i + MO_i) \cdot B_i$$

where P_i is the production of prey group i, Q_j is the consumption of predator j, DC_{ji} is the diet composition contribution of i to j's diet, F_i is the instantaneous rate of fishing mortality, NM_i is the net migration rate of prey group i, BA_i is the biomass accumulation rate for i, $M0_i$ is the other mortality rate for i (non-predation, non-fishery), and B_i is the biomass of i.

Data Used

Eighty-one taxa groups were used in the model (Table 1a, 1b). Phytoplankton, zooplankton, and benthic invertebrate biomass and diets were derived from Richards and Miller [25-28], Richards [1-32], Wasatch Front Water Quality Council, and Utah Division of Water Quality databases. Fish biomass and diets were derived from Walsworth, Landom, and Gaeta [33], Walsworth and Landom [34], Walsworth, Wallace, and Landom [35], University of Utah unpublished diet estimates, and Utah Division of Wildlife Resources survey data. Fish taxa biomass other than carp biomass estimates were derived from reported carp biomass estimates [34], relative abundances, and length/weight relations presented in S1 and S2. Fish diet data were cross referenced using FishBase (https://www.fishbase.se/home.htm). Fish taxa were separated into several ontogenetic groups based on University of Utah unpublished diet study size classes (Table 1b). Zooplankton and benthic invertebrate ontogenetic groups were not used in this model but can be in future models.

Basic estimates of the food web inputs are in Table 2. Production to biomass ratio (P/B) estimates were generated from literature values. Most of the phytoplankton, zooplankton, and benthic invertebrate P/B values (Table 2) were estimated on the high end of reported values because Utah Lake is highly eutrophic and productive. For example, phytoplankton P/B was consistent with Mutsert et al. [36], where P/B = 182 in nutrient rich waters of the Gulf of Mexico that had high primary production [37]. Benthic invertebrate P/B was modeled based on Richards unpublished data and freshwater benthic invertebrate authorities Benke et al., and Hauer and Benke who documented that chironomid P/B > 100 is common [38].

Several diet estimates had to be adjusted incrementally to balance the model because EcoPath is a mass balance model, and all diet proportions must add to 1.00. Utah Lake mean annual temperature of 16.7 ^{0}C [1], was used to help generate and verify several benthic invertebrate production values using Brey [39], associated computational spreadsheets, empirical models, and the Brey [40] model.

Model Parameters

The model was based on yearly averages using data from 1995 to 2021, although seasonal averages can be modeled in future iterations when adequate data are compiled, and the need arises. The currency unit used was wet weight (tons/km2). The model was developed as a mostly quasi-closed system, i.e., little or no migration but can be modeled as an open system (e.g., transfer of mass and energy in and out of the system) in future iterations. Utah Lake ecosystem was not separated into subregions for this model but can be in future scenarios.

Fleets: There is only one semi-commercial fishing fleet in Utah Lake, the carp removal project. Estimates of tons km^{-2} $year^{-1}$ of carp removal vary and were tentatively modeled at 3 t km^{-2} $year^{-1}$ based on Walsworth, Wallace, and Landom [35]. Unfortunately, the carp removal project was put on hold starting in 2024. Recreational sports fisheries are popular on Utah Lake. However, no estimates of 'take' (i.e., creel census data) have been collected by fisheries managers therefore, we estimated harvest as 5% of harvestable larger size class game fish biomass, excluding two non-game fish, Fathead Minnow and June Sucker.

Exports, Immigration and Emigration rates: Export estimates were made for two Chironomidae taxa, Chironominae and Tanypodinae as adults leaving the system. We assumed that about half of the adult population biomass of these two taxa did not return to lake based on several assumptions, 1) males were half the adult population biomass and did not return as did females to deposit eggs, 2) wind events forced a portion of the population away from the lake, 3) an unknown proportion of the adult population was lost to predation (e.g., spiders, birds, dragonflies, etc.), and 4) artificial urban lights attracted adults away from the lake and that portion of the population was unable to return to the lake. Subsequently net migration was estimated at 1.70 t km^2 y^{-1} for Chironominae and 0.52 t km^2 y^{-1} for Tanypodinae. We estimated immigration for detritus at 1% that mostly occurs during high water spring runoff. As far as we know, no empirical data has ever been collected for immigration of other biota into Utah Lake and was assumed to be negligible given our knowledge of the ecosystem. Certainly, some plankton, drifting invertebrates, and fishes leave (emigrate) the system downstream via the Jordan River. Emigration in Utah Lake occurs 'naturally' when water levels are higher than the

Table 1a: Non-fish taxonomic groups used in model including taxon functional group used and representative dominant taxa.

Taxon Functional Group Used	Dominant taxa in Utah Lake
Bacillariophyta	*Melosira granulata* var. angustissima, *Fragilaria crotonensis*, *Nitzschia acicularis*, *Stephanodiscus niagarae*, centric diatoms, pennate diatoms
Chlorophyta	*Chlamydomonas* spp., *Oocystis* sp., *Kirchneriella* spp., *Pediastrum* duplex, *Pediastrum* spp., *Monoraphidium arcuatum*, *Acutidesmus pectinatus*, *Willea rectangularis*, *Ankistrodesmus falcatus*, *Closteriopsis longissima* var. tropica, *Scenedesmus* quadricauda, Lagerheimia spp.
Cryptophyta	*Cryptomonas* sp.
Cyanophyta	*Dolichospermum crassum*, *Aphanizomenon flosaquae, Planktothrix agardhii, Phormidium* sp.
Dinophyta	*Ceratium hirudinella*
Euglenophyta	*Euglena* spp., *Phacus* spp., *Lepocinclis* spp., *Trachellomonas* spp.
Benthic Algae	*Oedogonium* sp., *Cladophora* sp., *Mougeotia* sp. *Stigeoclonium* sp. *Microspora* sp., and *Spirogyra* sp.
Macrophytes	*Bolboschoenus maritimus, Typha latifolia, Ceratophyllum demersum, Rumex crispus, Lemna minor, Schenoplectus acutus, Phragmites australis, Stuckenia* sp., others
Epiphytes	*Oedogonium* sp., *Cladophora* sp., *Mougeotia* sp. *Stigeoclonium* sp. *Microspora* sp., and *Spirogyra* sp.
Protozoa	Flagellates, ciliates, ameboids, etc.
Asplanchnidae	*Asplanchna* sp.
Bosminidae	*Bosmina longirostris, Bosmina liederi, Bosmina* sp.
Brachionidae	*Brachionus calyciflorus, B. plicatilis, B. quadridentatus, B. variabilis, Brachionus spp. Almenara* sp., *Keratella* sp.
Canthocamptidae	*Attheyella* sp., *Cletocamptus sp.*
Ceriodaphnia	*Ceriodaphnia cf. acanthine, C. dubia, C. quadrangula*
Chydoridae	*Chydorus brevilabrus, C. sphaericus, Kurzia media, Leberis c.f. davidi, Leydigia leydigi, L. lousi, Pleuroxus aduncus, P. denticulatus, P. striatus*
Cyclopidae	*Acanthocyclops americanus, A. robustus, Eucyclops agilis, Microcyclops rubellus*
Daphniadae	*Daphnia ambigua, D. exilis D. galeata, D. magna, D. mendotae, D. pulex, D. retrocurva, Scapholeberis mucronate, S. vetulus, S. mixtus, S. c.f. punctatus*
Diaptomidae	*Leptodiaptomus sicilis*
Ilyocryptidae	*Ilyocryptus* sp.
Laophontidae	NA
Leptodoridae	*Leptodora kindtii*
Macrothricidae	*Macrothrix* sp.
Moinidae	*Moina cf. micrura, M. macrocopa*
Sididae	*Diaphanosoma cf. Heberti, D. brachyurum*
Acari	*Lebertia* sp.

Amphipoda	*Hyalella* sp.
Chironominae	*Chironomus crassicaudatus, Chironomus decorus* grp. spp., *Glyptotendipes* sp., *Cladotanytarsus* sp.
Coleoptera	*Oreodytes* sp., other Dytscidae
Corbicula sp. (bivalves)	*Corbicula* sp.
Corixidae	*Corisella decolor, C. tarsalis*
Decopoda	*Faxonius virilis (?), Procambarus clarkii(?)*
Glossiphoniidae	Hirudinea, *Helobdella stagnalis*
Isopoda	*Caecidotea sp.*
Lymnaeidae	*Stagnicola* sp.
Physidae	*Physa* sp.
Odonata	Misc. Zygoptera, Anisoptera
Oligochaetes	*Eiseniella* sp.
Ostracod	*Ostracoda* sp.
Tanypodinae	*Tanypus neopunctipenis*
Bacteria	Unknown
Detrital snow	All dead water column micro-organisms settling onto benthic detritus
Detritus	Dead organic matter

Table 1b: Fish taxa ontogenetic groups and size classes used in model.

		Size classes (mm)	
Common Name	Scientific Name	Min	Max
Black Bullhead 1	*Ameiurus melas*	5	36
Black Bullhead 2	*Ameiurus melas*	37	197
Black Bullhead 3	*Ameiurus melas*	207	360
Black Crappie 1	*Pomoxis nigromaculatus*	5	40
Black Crappie 2	*Pomoxis nigromaculatus*	41	156
Black Crappie 3	*Pomoxis nigromaculatus*	160	288
Bluegill 1	*Lepomis macrochirus*	5	26
Bluegill 2	*Lepomis macrochirus*	27	137
Bluegill 3	*Lepomis macrochirus*	141	228
Green Sunfish 1	*Lepomis cyanellus*	5	131
Green Sunfish 2	*Lepomis cyanellus*	132	195
Green Sunfish 3	*Lepomis cyanellus*	223	499
Channel Catfish 1	*Ictalurus punctatus*	503	746
Channel Catfish 2	*Ictalurus punctatus*	5	76
Channel Catfish 3	*Ictalurus punctatus*	77	104
Channel Catfish 4	*Ictalurus punctatus*	110	145
Common Carp 1	*Cyprinus carpio*	5	21
Common Carp 2	*Cyprinus carpio*	22	294

Common Carp 3	*Cyprinus carpio*	300	725
Fathead Minnow 1	*Pimephales promelas*	5	46
Fathead Minnow 2	*Pimephales promelas*	47	48
Fathead Minnow 3	*Pimephales promelas*	51	63
June Sucker 1	*Chasmistes liorus*	5	313
June Sucker2	*Chasmistes liorus*	314	391
June Sucker 3	*Chasmistes liorus*	401	576
Northern Pike 1	*Esox lucius*	5	81
Northern Pike 2	*Esox lucius*	82	299
Northern Pike 3	*Esox lucius*	302	594
Northern Pike 4	*Esox lucius*	608	892
Walleye 1	*Sander vitreus*	5	80
Walley 2	*Sander vitreus*	81	145
Walleye 3	*Sander vitreus*	255	420
Walley 4	*Sander vitreus*	460	721
White Bass 1	*Morone chrysops*	5	34
White Bass 2	*Morone chrysops*	35	128
White Bass 3	*Morone chrysops*	133	298
White Bass 4	*Morone chrysops*	303	412
Yellow Perch 1	*Perca flavescens*	5	47
Yellow Perch 2	*Perca flavescens*	48	145
Yellow Perch 3	*Perca flavescens*	160	251

Table 2: Basic estimates of Utah Lake food web. Biomass (tons/km2), Production/biomass (/year) and Production/consumption(/year) were estimated by authors to mass balance the model. Consumption/biomass(/year) and Ecotrophic efficiency were estimated by the EcoPath model.

Group name (taxon)	Trophic level	Biomass (t/km^2)	Production/ biomass	Consumption/ biomass	Ecotrophic Efficiency	Production/ consumption
1. Bacillariophyta	1.00	1.30	150.00		0.99	
2. Chlorophyta	1.00	1.70	130.00		0.88	
3. Cryptophyta	1.00	0.50	120.00		0.71	
4. Cyanophyta	1.00	2.10	120.00		0.47	
5, Dinophyta	1.00	0.75	110.00		0.30	
6. Euglenophyta	1.00	0.50	110.00		0.42	
7. Benthic Algae	1.00	0.08	120.00		0.94	
8. Macrophytes	1.00	0.06	40.00		0.10	
9. Epiphytes	1.00	0.05	140.00		0.97	
10. Protozoa	2.00	2.25	100.00	200.00	0.88	0.50
11. Asplanchnidae	2.74	0.70	79.00	158.00	0.47	0.50
12. Bosminidae	2.30	0.70	78.00	156.00	0.32	0.50
13. Brachionidae	2.20	1.00	78.00	156.00	0.23	0.50
14. Canthocamptidae	2.20	0.17	110.00	220.00	0.81	0.50
15. Ceriodaphnia	2.20	0.60	85.00	170.00	0.70	0.50

16. Chydoridae	2.13	0.16	100.00	200.00	0.79	0.50
17. Cyclopidae	2.81	0.76	100.00	200.00	0.93	0.50
18. Daphnia	2.15	0.37	115.00	230.00	0.86	0.50
19. Diaptomidae	2.00	0.44	100.00	200.00	0.77	0.50
20. Ilyocryptidae	2.15	0.12	110.00	220.00	0.96	0.50
21. Laophontidae	2.04	0.12	110.00	220.00	0.84	0.50
22. Leptodoridae	2.08	0.10	100.00	200.00	0.43	0.50
23. Macrothricidae	2.00	0.10	100.00	200.00	0.91	0.50
24. Moinidae	2.14	0.10	100.00	200.00	0.98	0.50
25. Sididae	2.00	0.12	100.00	200.00	0.93	0.50
26. Acari	2.00	0.04	90.00	180.00	0.84	0.50
27. Amphipoda	2.00	0.32	57.00	142.50	0.91	0.40
28. Chironominae	2.00	3.37	40.00	100.00	0.85	0.40
29. Coleoptera	3.03	0.15	40.00	88.89	0.69	0.45
30. Corbicula sp.	2.05	0.50	40.00	100.00	0.18	0.40
31. Corixidae	2.34	0.17	40.00	100.00	0.87	0.40
32. Decapoda	2.48	0.04	37.00	92.50	0.94	0.40
33. Glossiphoniidae	2.00	0.10	40.00	100.00	0.86	0.40
34. Isopoda	2.00	0.11	40.00	100.00	0.97	0.40
35. Lymnaeidae	2.00	0.04	45.00	112.50	0.97	0.40
36. Physa sp.	2.00	0.04	45.00	112.50	0.95	0.40
37. Odonata	3.35	0.13	47.00	104.44	0.99	0.45
38. Oligochaetes	2.00	0.55	40.00	100.00	0.36	0.40
39. Ostracod	2.22	0.06	47.00	117.50	0.95	0.40
40. Tanypodinae	2.22	1.10	40.00	88.89	0.94	0.45
41. BlackBullhead1	3.43	0.50	20.00	42.55	0.96	0.47
42. BlackBullhead2	3.06	1.40	7.00	17.50	0.95	0.40
43. BlackBullhead3	4.37	6.49	0.15	1.50	0.33	0.10
44. BlackCrappie1	3.43	0.20	22.00	45.83	0.98	0.48
45. BlackCrappie2	3.37	0.28	6.00	15.00	0.84	0.40
46. BlackCrappie3	4.59	4.69	0.20	2.00	0.25	0.10
47. Bluegill1	3.43	0.09	25.00	53.19	0.96	0.47
48. Bluegill2	3.06	0.70	7.00	17.50	0.88	0.40
49. Bluegill 3	3.08	5.06	0.20	2.00	0.25	0.10
50. GreenSunfish1	3.05	0.08	22.00	55.00	0.97	0.40
51. GreenSunfish 2	3.06	0.25	5.00	12.50	0.52	0.40
52. GreenSunfish 3	3.06	0.50	0.20	2.00	0.25	0.10
53. ChannelCatfish1	3.58	0.27	26.00	55.32	0.89	0.47
54. ChannelCatfish2	3.26	3.00	2.00	5.00	0.79	0.40
55. ChannelCatfish3	3.87	5.00	0.22	2.20	0.99	0.10

56. Channel Catfish 4	4.14	0.10	0.10	2.00	0.50	0.05
57. CommonCarp1	3.20	0.50	16.00	34.04	0.62	0.47
58. CommonCarp2	3.00	15.00	2.00	5.00	0.44	0.40
59. CommonCarp3	2.87	88.00	0.08	1.10	0.91	0.07
60. Fathead Minnow1	3.43	0.07	26.00	52.00	0.96	0.50
61. Fathead Minnow2	3.55	0.50	12.00	30.00	0.31	0.40
62. Fathead Minnow 3	3.33	0.50	0.15	1.50	0.79	0.10
63. June Sucker 1	3.30	0.29	25.00	62.50	0.31	0.40
64. JuneSucker2	3.27	1.00	12.00	30.00	0.88	0.40
65. JuneSucker 3	3.27	0.61	0.10	2.00	0.00	0.05
66. NorthernPike1	3.09	0.00	14.00	35.00	0.24	0.40
67. NorthernPike2	3.96	0.00	2.00	5.00	0.72	0.40
68. NorthernPike3	4.51	0.00	0.42	2.10	0.84	0.20
69. Northern Pike 4	4.76	0.00	0.05	1.18	0.96	0.04
70. Walleye1	3.05	0.07	20.00	40.00	0.79	0.50
71. Walley2	4.69	0.60	10.00	25.00	0.90	0.40
72. Walleye3	4.62	0.21	1.00	10.00	0.05	0.10
73. Walley 4	4.69	0.01	0.10	1.25	0.50	0.08
74. WhiteBass1	3.38	1.40	20.00	40.00	0.95	0.50
75. WhiteBass2	4.15	1.50	11.00	22.00	0.92	0.50
76. WhiteBass3	4.41	11.00	0.30	3.00	0.17	0.10
77. White Bass 4	4.42	1.10	0.08	1.25	0.67	0.06
78. YellowPerch1	3.43	0.20	10.00	25.00	0.05	0.40
79. YellowPerch2	3.32	0.40	3.00	7.50	0.91	0.40
80. YellowPerch3	4.14	0.46	0.15	1.50	0.33	0.10
81. Bacteria	1.00	3.00	300.00		0.77	
82. Detrital Snow	1.00	4.00	80.00		0.83	
83. Detritus	1.00	5.00			0.84	

dam typically during spring runoff but is becoming more uncommon. Emigration occurs during lower water levels thorough out much of the remainder of the year via a pump station for water users downstream. There were no empirical data available for estimation of these exports for any of the groups used in this model. Therefore, we estimated emigration rates of 10% for phytoplankton, zooplankton, detrital bacteria, and detrital snow. We assumed emigration of other taxa was negligible.

RESULTS

Diets and metrics

S2 contains diet estimates for all taxa groups. In addition to these taxa diets, two frog species, Boreal Chorus Frog (Pseudacris maculata) (native) and the American Bullfrog (Lithobates catesbeianus) (invasive) occur in Utah Lake but there was no available biomass data consequently, they were not used in the model. However, one American Bullfrog was found in a Northern Pike stomach sample. Table 2 provides EcoPath's basic estimates of Utah Lake food web including estimated biomass (ton km^{-2}), production/biomass ($year^{-1}$) and production/consumption ($year^{-1}$). Consumption/biomasses ($year^{-1}$) and ecotrophic efficiencies (EE) were estimated by the EcoPath model. Figures 1, 2 and 3 show trophic level flows within the food web based on biomass and production, respectively. Table 3 provides three key indices, flow to detritus (tons km^2 $year^{-1}$), net efficiency, and omnivory index from the EcoPath model. Our model estimated that unconsumed cyanophytes could contribute more than 100 tons km^{-2} yr^{-1} to detritus whereas bacillariophytes (diatoms) contributed about 2 tons km^{-2} yr^{-1} (Figure 4).

EcoPath's, pedigree index P, and measure of fit t* were used to estimate the overall quality of our data. Pedigree, P for our Utah Lake model = 0.23 and t* = 2.08 showing that our model was in the range of other models used worldwide and was moderately robust [6-45].

Table 4 provides several respiration related results for each taxonomic group. These metrics include respiration, assimilation, respiration/assimilation, production/respiration, and respiration/biomass.

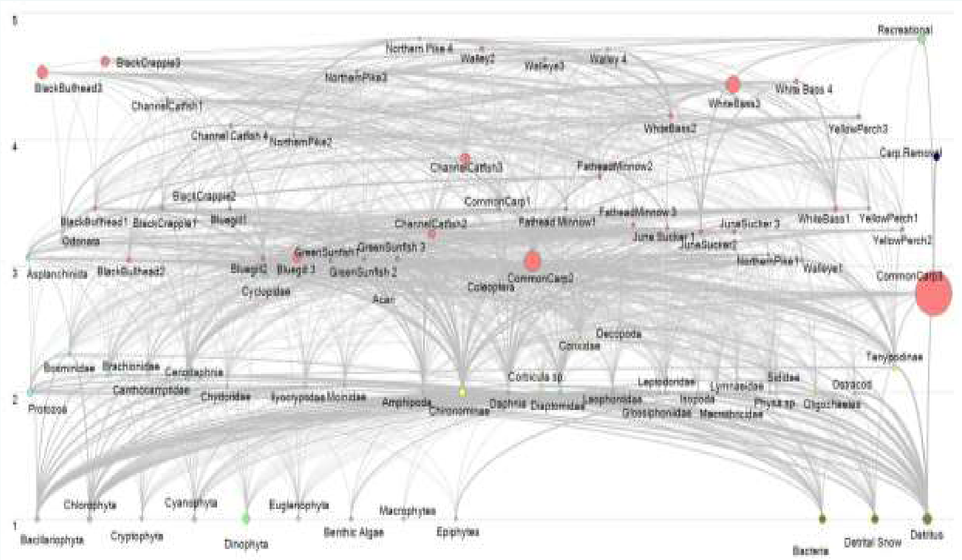

Figure 1: Trophic level flow diagram of Utah Lake food web based on biomass (tons km^{-2})

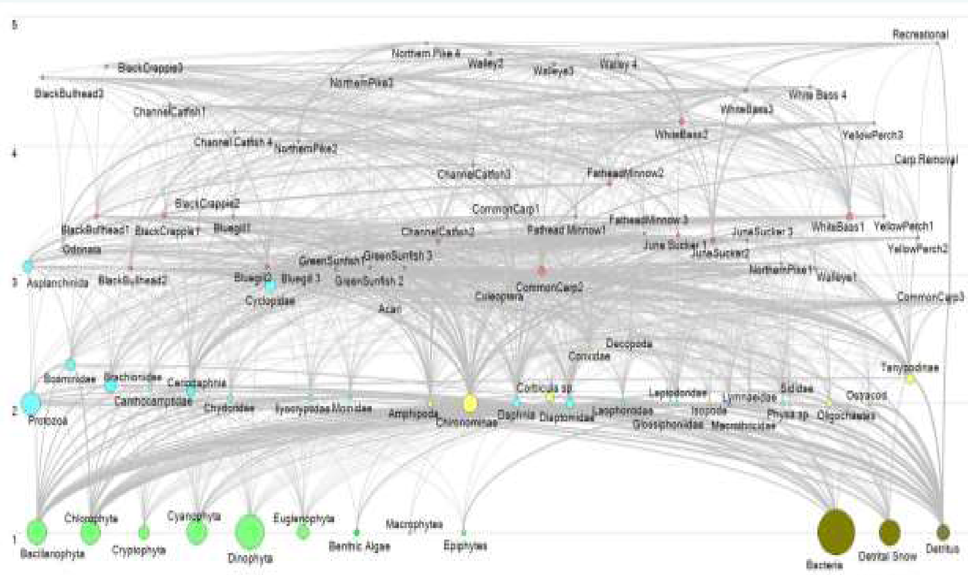

Figure 2: Trophic level flow diagram of Utah Lake food web based on production (tons km^{-2} $year^{-1}$)

Table 3: Flow to detritus, net efficiency, and omnivory index

Group (taxon)	Net migration (t/km²/year)	Flow To Detritus (t/km²/year)	Net efficiency	Omnivory index
Bacillariophyta	0.14	2.47		0.00
Chlorophyta	0.12	24.39		0.00
Cryptophyta	0.05	15.52		0.00
Cyanophyta	0.15	121.09		0.00
Dinophyta	0.37	51.88		0.00

Euglenophyta	0.07	28.59		0.00
Benthic Algae	0.01	0.47		0.00
Macrophytes	0.00	1.79		0.00
Epiphytes	0.01	0.21		0.00
Protozoa	0.20	185.77	0.83	0.00
Asplanchinida	0.07	66.21	0.83	0.29
Bosminidae	0.07	72.88	0.83	0.21
Brachionidae	0.10	109.94	0.83	0.16
Canthocamptidae	0.02	16.53	0.83	0.16
Ceriodaphnia	0.05	50.33	0.83	0.16
Chydoridae	0.02	14.59	0.83	0.11
Cyclopidae	0.07	59.26	0.83	0.33
Daphnia	0.04	35.63	0.83	0.13
Diaptomidae	0.04	40.87	0.83	0.00
Ilyocryptidae	0.01	9.93	0.83	0.13
Laophontidae	0.01	11.37	0.83	0.04
Leptodoridae	0.01	12.32	0.83	0.07
Macrothricidae	0.01	8.02	0.83	0.00
Moinidae	0.01	7.35	0.83	0.12
Sididae	0.01	9.38	0.83	0.00
Acari	0.00	1.60	0.63	0.00
Amphipoda	0.00	10.29	0.50	0.00
Chironominae	1.69	83.78	0.50	0.00
Coleoptera	0.00	4.33	0.56	0.24
Corbicula sp.	0.00	26.32	0.50	0.05
Corixidae	0.00	4.27	0.50	0.42
Decopoda	0.00	0.73	0.50	0.28
Glossiphoniidae	0.00	2.54	0.50	0.00
Isopoda	0.00	2.32	0.50	0.00
Lymnaeidae	0.00	0.96	0.50	0.00
Physa sp.	0.00	0.98	0.50	0.00
Odonata	0.00	2.68	0.56	0.23
Oligochaetes	0.00	24.96	0.50	0.00
Ostracod	0.00	1.55	0.50	0.22
Tanypodinae	0.52	22.04	0.56	0.22
BlackBullhead1	0.00	8.87	0.78	0.12
BlackBullhead2	0.00	2.93	0.44	0.01
BlackBullhead3	0.00	1.13	0.11	0.12
BlackCrappie1	0.00	2.75	0.69	0.12
BlackCrappie2	0.00	0.70	0.44	0.19

BlackCrappie3	0.00	2.57	0.13	0.43
Bluegill1	0.00	1.45	0.67	0.12
Bluegill2	0.00	1.80	0.44	0.02
Bluegill 3	0.00	1.77	0.11	0.04
GreenSunfish1	0.00	1.37	0.57	0.01
GreenSunfish 2	0.00	0.91	0.44	0.03
GreenSunfish 3	0.00	0.21	0.12	0.02
ChannelCatfish1	0.00	5.21	0.67	1.00
ChannelCatfish2	0.00	4.27	0.50	0.10
ChannelCatfish3	0.00	1.11	0.11	0.39
Channel Catfish 4	0.00	0.06	0.07	0.15
CommonCarp1	0.00	8.09	0.67	0.26
CommonCarp2	1.00	46.69	0.67	0.47
CommonCarp3	2.00	39.34	0.11	0.51
Fathead Minnow1	0.00	1.15	0.71	0.12
FatheadMinnow2	0.00	8.62	0.57	0.07
FatheadMinnow 3	0.00	0.09	0.11	0.07
June Sucker 1	0.00	10.75	0.59	0.10
JuneSucker2	0.00	4.42	0.44	0.10
JuneSucker 3	0.00	0.43	0.07	0.10
NorthernPike1	0.00	0.01	0.47	0.02
NorthernPike2	0.00	0.00	0.44	0.36
NorthernPike3	0.00	0.00	0.25	0.28
Northern Pike 4	0.00	0.00	0.05	0.15
Walleye1	0.00	1.00	0.67	0.01
Walley2	0.00	1.32	0.42	0.22
Walleye3	0.00	0.30	0.11	0.25
Walley 4	0.00	0.00	0.08	0.23
WhiteBass1	0.00	15.25	0.67	0.12
WhiteBass2	0.00	7.91	0.63	0.30
WhiteBass3	0.00	9.33	0.13	0.24
White Bass 4	0.00	0.10	0.06	0.10
YellowPerch1	0.00	2.64	0.47	0.12
YellowPerch2	0.00	0.41	0.44	0.25
YellowPerch3	0.00	0.18	0.13	0.04
Bacteria	0.20	80.97	0.00	0.57
Detrital Snow	0.30	72.21	0.00	0.38
Detritus	-0.01	0.00	0.00	0.66

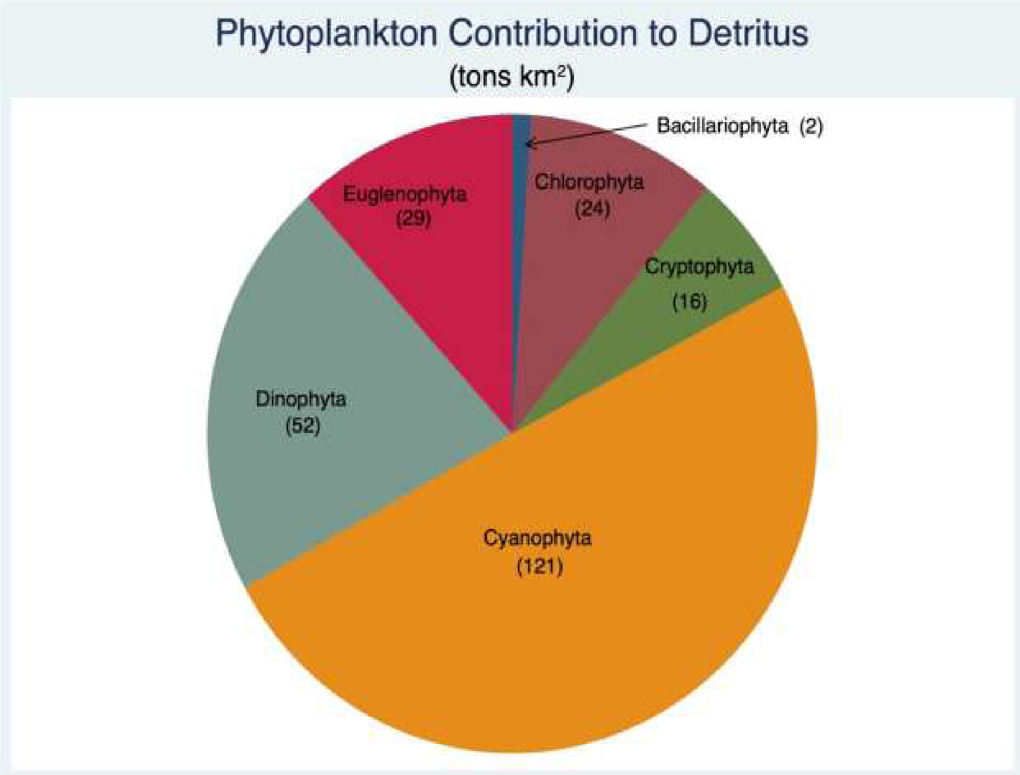

Figure 3: Estimated flow of phytoplankton division biomass to detritus. Values in parentheses are tons km^{-2} yr^{-1}.

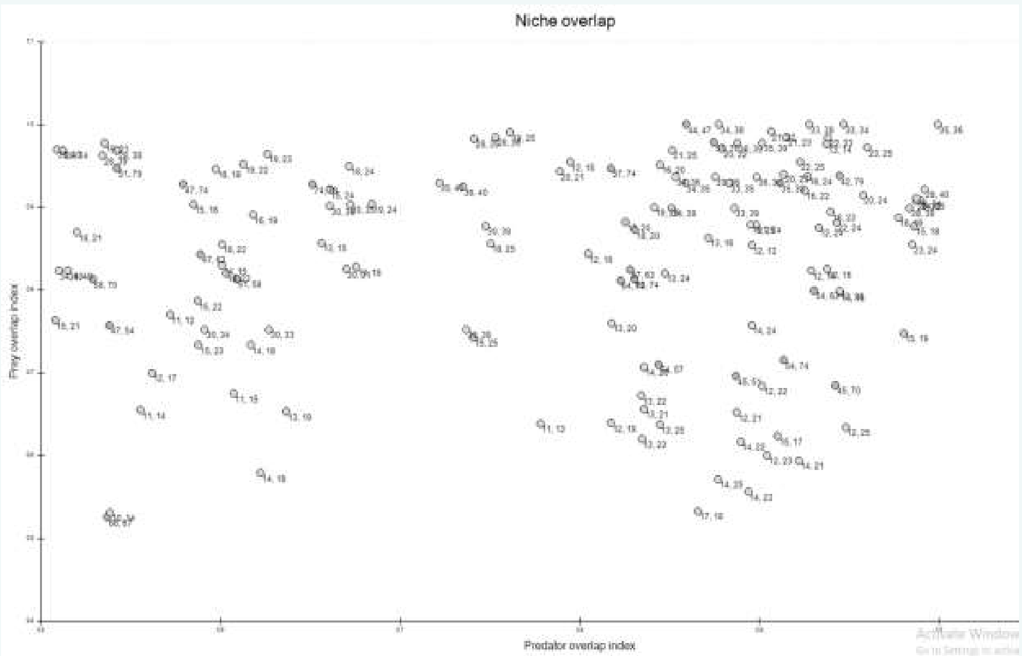

Figure 4: Niche overlap within the food web of Utah Lake. Correlation cutoff = 0.50 was used for this table. Other correlation cutoffs can be easily evaluated using our model. Numbers are taxa groups from Table 2.

Table 4: Respiration related metric results.

Group name	Respiration (t/km²/year)	Assimilation (t/km²/year)	Respiration / assimilation	Production / respiration	Respiration / biomass (/year)
Bacillariophyta	0.00				
Chlorophyta	0.00				
Cryptophyta	0.00				
Cyanophyta	0.00				
Dinophyta	0.00				
Euglenophyta	0.00				
Benthic Algae	0.00				
Macrophytes	0.00				
Epiphytes	0.00				
Protozoa	45.00	270.00	0.17	5.00	20.00
Asplanchnidae	11.06	66.36	0.17	5.00	15.80
Bosminidae	10.92	65.52	0.17	5.00	15.60
Brachionidae	15.60	93.60	0.17	5.00	15.60
Canthocamptidae	3.70	22.18	0.17	5.00	22.00
Ceriodaphnia	10.20	61.20	0.17	5.00	17.00
Chydoridae	3.20	19.20	0.17	5.00	20.00
Cyclopidae	15.10	90.60	0.17	5.00	20.00
Daphnia	8.40	50.37	0.17	5.00	23.00
Diaptomidae	8.80	52.80	0.17	5.00	20.00
Ilyocryptidae	2.64	15.84	0.17	5.00	22.00
Laophontidae	2.64	15.84	0.17	5.00	22.00
Leptodoridae	2.00	12.00	0.17	5.00	20.00
Macrothricidae	2.00	12.00	0.17	5.00	20.00
Moinidae	2.00	12.00	0.17	5.00	20.00
Sididae	2.40	14.40	0.17	5.00	20.00
Acari	1.89	5.04	0.38	1.67	54.00
Amphipoda	18.24	36.48	0.50	1.00	57.00
Chironominae	134.80	269.60	0.50	1.00	40.00
Coleoptera	4.67	10.67	0.44	1.29	31.11
Corbicula sp.	20.00	40.00	0.50	1.00	40.00
Corixidae	6.80	13.60	0.50	1.00	40.00
Decopoda	1.30	2.59	0.50	1.00	37.00
Glossiphoniidae	4.00	8.00	0.50	1.00	40.00
Isopoda	4.40	8.80	0.50	1.00	40.00
Lymnaeidae	1.80	3.60	0.50	1.00	45.00
Physa sp.	1.80	3.60	0.50	1.00	45.00
Odonata	4.57	10.44	0.44	1.29	36.56

Oligochaetes	22.00	44.00	0.50	1.00	40.00
Ostracod	2.82	5.64	0.50	1.00	47.00
Tanypodinae	34.22	78.22	0.44	1.29	31.11
BlackBullhead1	2.77	12.77	0.22	3.62	5.53
BlackBullhead2	12.25	22.05	0.56	0.80	8.75
BlackBullhead3	8.27	9.25	0.89	0.12	1.28
BlackCrappie1	1.97	6.26	0.31	2.18	10.08
BlackCrappie2	2.13	3.83	0.56	0.80	7.50
BlackCrappie3	6.57	7.51	0.88	0.14	1.40
Bluegill1	1.05	3.18	0.33	2.04	12.23
Bluegill2	6.13	11.03	0.56	0.80	8.75
Bluegill 3	8.10	9.11	0.89	0.13	1.60
GreenSunfish1	1.32	3.08	0.43	1.33	16.50
Green Sunfish 2	1.56	2.81	0.56	0.80	6.25
Green Sunfish 3	0.76	0.86	0.88	0.13	1.52
ChannelCatfish1	3.44	10.46	0.33	2.04	12.72
ChannelCatfish2	6.00	12.00	0.50	1.00	2.00
ChannelCatfish3	8.80	9.90	0.89	0.13	1.76
Channel Catfish 4	0.13	0.14	0.93	0.08	1.30
CommonCarp1	3.91	11.91	0.33	2.04	7.83
CommonCarp2	15.00	45.00	0.33	2.00	1.00
CommonCarp3	51.64	58.24	0.89	0.13	0.59
Fathead Minnow1	0.73	2.55	0.29	2.50	10.40
FatheadMinnow2	4.50	10.50	0.43	1.33	9.00
Fathead Minnow 3	0.60	0.68	0.89	0.13	1.20
June Sucker 1	5.08	12.33	0.41	1.43	17.50
June Sucker 2	15.00	27.00	0.56	0.80	15.00
June Sucker 3	0.80	0.86	0.93	0.08	1.30
Northern Pike 1	0.01	0.02	0.53	0.89	15.75
Northern Pike 2	0.01	0.01	0.56	0.80	2.50
Northern Pike 3	0.01	0.01	0.75	0.33	1.26
Northern Pike 4	0.00	0.00	0.95	0.05	1.07
Walleye1	0.70	2.10	0.33	2.00	10.00
Walley2	8.25	14.25	0.58	0.73	13.75
Walleye3	1.75	1.96	0.89	0.12	8.50
Walley 4	0.01	0.01	0.92	0.09	1.09
WhiteBass1	14.00	42.00	0.33	2.00	10.00
WhiteBass2	9.90	26.40	0.38	1.67	6.60
WhiteBass3	23.10	26.40	0.88	0.14	2.10
White Bass 4	1.22	1.31	0.94	0.07	1.11

YellowPerch1	2.25	4.25	0.53	0.89	11.25
YellowPerch2	1.50	2.70	0.56	0.80	3.75
YellowPerch3	0.48	0.55	0.87	0.14	1.05
Bacteria	0.00				
Detrital Snow	0.00				
Detritus	0.00				

There was much overlap in prey items by predators. Prey and predator overlap results are in S3 and S4. Niche overlaps are presented in Figure 4. Most niche overlaps were zooplankton taxa due to resolution of their diets. Other strong overlaps were mostly the detritivores and early life stages of fishes (Figure 4).

Several important ecosystem statistics are presented in Table 5. Estimated System Omnivore Index (SOI) for Utah Lake was 0.15, which is on the low end established by Libralato [46]. This indicates an unstable environment for the few trophic groups considered omnivores, which means that the lake ecosystem had few connections between its trophic groups (omnivores). This suggests that Utah Lake is vulnerable to impacts on omnivorous groups and the plasticity to obtain resources by other means could be affected [47]. The loss of trophic groups can also occur because the impact can spread throughout the system in the form of a trophic cascade [48,49], which we hypothesized to be true. Connectance Index (CI) for Utah Lake was 0.17. This value is lower than values reported elsewhere [50], and supports our SOI result suggesting an unstable environment. Additional ecosystem statistics are in Table 5. Trophic level transfer efficiencies, estimated flows and biomasses from primary producers and detritus, and estimated biomass by trophic level are in Table 6 through 9.

The entire lake system was aggregated in the form of discrete trophic levels. Transfer efficiencies (expressed in %) of two consecutive trophic levels were estimated as the ratio between the sum of exports from a given trophic level (including the flow that was transferred from one trophic level to the next) and throughput at the trophic level [51]. The estimated proportion of total flow originating from detritus in Utah Lake was 0.65. This demonstrated not only a water column primary production-based ecosystem but inefficient transfer within the water column towards a detritus-based driven food web. Estimated transfer efficiencies (calculated as geometric mean for TL II-IV) from primary producers = 31.79%, from detritus = 28.56%, and total =29.70%. Benthic primary producers including macrophytes, benthic algae, and periphyton on macrophytes have a minor role in the Utah Lake ecosystem function. See Matthias et al. [52], for interpretation of TTEs. See Bhavan et al. [41], for more detailed interpretations of other output metrics of our model.

Figure 5 illustrates the Keystoneness (relative total impact) for each taxonomic group modeled by us for the Utah Lake food web (see Libralato et al. [53], Nuttall et al. [54], Christensen and Walters [45], for derivation and description of EwE Keystoneness index). The larger size classed Common Carp (3) was the greatest keystone taxon group followed closely by Chironominae, and White Bass. Other taxa also had large relative total impacts (Figure 5). On the opposite end of keystonness, for example, large Walleye (4) and macrophytes contribution to the food web was negligible (Figure 5 and 6).

Mixed trophic impacts are presented in S6 and S7. Estimated trophic level flows and biomasses from primary producers are in Table 7 and from detritus in Table 8.

The Lindeman spine [55], in Figure 7 shows the general functional structure of the system based on the aggregation of the Utah Lake trophic groups into eighty-one trophic levels and describes the flow transfer between the trophic levels. Total System Throughput (TST%), Trophic Level (TL) Exports (t km^2 y^{-1}) (including export from detritus to TL II), detrital exports, and respiration rates all decreased from detritus to primary producers through the other seven trophic levels (Figure 7). Detrital exports were greatest from primary producers (P) that we ascribe to inefficient grazing from zooplankton (TL II) [1]. The highest transfer efficiency (TE) was estimated at TL III = 0.22, followed by TL II and TL IV at 0.15 and 0.19, respectively. The lowest TE was TL VII at < 0.01 and exports and catches were mostly from TL II to TL III and III to TL IV (Figure 7).

Estimated total system throughput for Utah Lake was 4883 t km^2 year^{-1} indicative of a eutrophic system, similar to but greater than values reported from productive lagoons and coral reef systems in the Yucatan Peninsula, Mexico [56-58].

Utah Lake ascendency and % ascendency, overhead, % overhead, capacity and % capacity results are in Table 10. Ascendency by each taxon are in S7. Interpretation of these Utah Lake values was not straightforward ([6-62] Ulanowicz and Christensen for descriptions and importance of these metrics). Estimated Utah Lake Overhead and % Overhead was 32,535 and 83%, respectively. Finn's cycling index [63], for Utah Lake was modeled at 15.66% and Finn's mean path length = 7.06 suggesting the lake is susceptible to disturbances and the lake likely poorly utilized organic matter within the system [50]. Ecological network indices such as ascendency, overhead and capacity are links for the system organization and collectively measure the system robustness. System robustness, R stands for the sustainability of the system based on the survival of the most robust unit (taxon) [64]. Utah Lake total ecosystem relative Ascendancy, α = 1.37 and R = 0.18 (Table 11 and 12) indicating an immature (chronic early succession) system, with low resilience, and below optimal trophic functioning [41-65].

Carp Removal Program

Carp removal was estimated at 3 t km-2 yr-1 which was about 3.33% removal per year. Consequently, fishing mortality rate was estimated to be 9% y-1 for medium sized carp, and 3% y-1 for large carp. Carp removal subsequently was a minor component of the food web based on overall carp production and biomass, however mixed trophic level impacts suggested that the carp removal program had substantial negative and positive effects on the food web (Table 13). The Carp removal program had negative mixed trophic level impacts on several taxa, the removal program itself, detrital snow, and detritus. These groups, and others, decreased in biomass when carp were removed (Table 13). Due to their aggressive benthic feeding, removal of carp had positive impacts (i.e., increased biomass) on other groups including macrophytes, lymnaeid snails, oligochaetes, chironomids, and several fish ontogenetic groups, including June Sucker (Table 13).

Table 5: Ecosystem Statistics.

Parameter	Value	Units
Sum of all consumption	2696	T km-^{2} year^{-1}
Sum of all exports	51	T km-^{2} year^{-1}
Sum of all respiratory flows	640	T km-^{2} year^{-1}
Sum of all flows into detritus	1494	T km-^{2} year^{-1}
Total system throughput	4882	T km-^{2} year^{-1}
Sum of all production	3292	T km-^{2} year^{-1}
Calculated total net primary production	884	T km-^{2} year^{-1}
Total primary production/total respiration	1.38	
Net system production	243	T km-^{2} year^{-1}
Total primary production/total biomass	5.09	
Total biomass/total throughput	0.04	T km-^{2} year^{-1}
Total biomass (excluding detritus)	173	T km-^{2}
Connectance Index	0.17	
System Omnivory Index	0.15	
EcoPath pedigree	0.16	
Measure of fit, t*	1.44	
Shannon diversity index	2.30	

Table 6: Trophic Level Transfer Efficiencies (%).

Source \ Trophic level	II	III	IV	V	VI	VII
Producer	35.33	34.55	26.32	19.14	12.45	6.75
Detritus	35.19	25.85	25.61	20.83	15.78	10.20
All flows	35.24	28.71	25.90	20.14	14.49	9.07

Table 7: Estimated flows and biomasses (tons km-2) from primary producers.

Trophic level \ Flow	Import	Consumption by predators	Export	Flow to detritus	Respiration	Throughput
VIII		0.00	0.00	0.00	0.00	0.00
VII		< 0.01	0.00	< 0.01	< 0.01	< 0.01
VI		< 0.01	0.00	0.188	0.43	0.62
V		0.62	0.00	1.692	3.22	5.54
IV		5.54	< 0.01	7.00	6.85	19.40
III		19.40	0.07	17.08	15.86	52.41
II		52.41	0.02	67.59	51.92	171.90
I	0.00	171.90	0.00	1278.00	0.00	1450.00
Sum	0.00	249.90	0.09	1371.00	78.30	1700.00

Table 8: Estimated flows and biomasses (tons km-2) from detritus

Trophic level \ Flow	Import	Consumption by predators	Export	Flow to detritus	Respiration	Throughput
VII		< 0.01	0.00	< 0.01	< 0.01	< 0.01
VI		< 0.01	0.00	0.03	0.07	0.10
V		0.10	< 0.01	0.54	1.15	1.80
IV		1.80	< 0.01	6.01	11.02	18.84
III		18.84	2.001	43.25	69.11	133.20
II		133.20	3.10	634.00	345.30	1116.00
I	5.00	1116.00	944.50	0.00	0.00	2065.00
Sum	5.00	1270.00	949.60	683.80	426.60	3335.00

Table 9: Estimated biomass by trophic level.

Trophic level	Living (t/km^2)	Detritus (t/km^2)	Total (t/km^2)	Non-hidden
VII	< 0.01		< 0.01	< 0.01
VI	0.72		0.72	0.81
V	4.53		4.53	5.64
IV	20.34		20.34	29.74
III	79.83		79.83	137.7
II	34.21		34.21	65.14
I	7.24	6.00	13.25	13.25

Table 10: Estimated Total Ascendency, % Ascendency, Overhead, % Overhead, Capacity, and % Capacity.

Source	Ascendency (flowbits)	Ascendency (%)	Overhead (flowbits)	Overhead (%)	Capacity (flowbits)	Capacity (%)
Import	0.00	0.00	0.00	0.00	0.00	0.00
Internal flow	5,979.00	15.05	27,922.00	70.93	33,900.00	86.11
Export	64.13	0.16	400.50	1.01	478.20	1.21
Respiration	775.40	1.97	4,213.00	10.70	4,989.00	12.67
Total	6,818.00	17.32	32,535.00	82.65	39,367.00	100.00

Table 11: Cycles and Pathways Lengths.

Parameter	Value	Unit
Throughput cycled (excluding detritus)	9.55	t/km^2/year
Predatory cycling index	0.45	% Throughput without detritus
Throughput cycled (including detritus)	764.50	t/km^2/year
Finn's cycling index	15.66	% Total throughput
Finn's mean path length	7.06	none
Finn's straight-through path length	3.15	without detritus
Finn's straight-through path length	5.95	with detritus

Table 12: Relative ascendency (α) and robustness, R for Utah Lake food web

Source	Ascendency (flowbits)	Capacity (flowbits)	Relative Ascendency α	Robustness, *R*
Import	6.44	49.88	0.13	-0.11
Internal flow	29114.00	18767.00	1.55	0.30
Export	4194.00	2733.00	1.53	0.29
Respiration	905.30	3505.00	0.26	-0.15
Total	34220.00	25054.00	1.37	0.18

Table 13: Mixed trophic level impacts of Carp removal program (fleet).

Negative impacts

Common Carp 3	-0.51
Carp Reduction	-0.43
Glossiphoniidae	-0.13
Amphipoda	-0.11
Isopoda	-0.11
Detrital Snow	-0.10
Epiphytes	-0.10
Ostracod	-0.09
Decopoda	-0.08
Corbicula sp.	-0.08
Benthic Algae	-0.07
Detritus	-0.07

Positive Impacts

Macrophytes	0.51
Lymnaeidae	0.33
Oligochaetes	0.24
Tanypodinae	0.15
GreenSunfish1	0.12
Walleye1	0.11
June Sucker 3	0.11
Green Sunfish 3	0.10
Chironominae	0.10
Physa sp.	0.10
NorthernPike1	0.09
BlackBullhead2	0.08
Green Sunfish 2	0.07
JuneSucker2	0.07
YellowPerch2	0.06
Bluegill 3	0.05

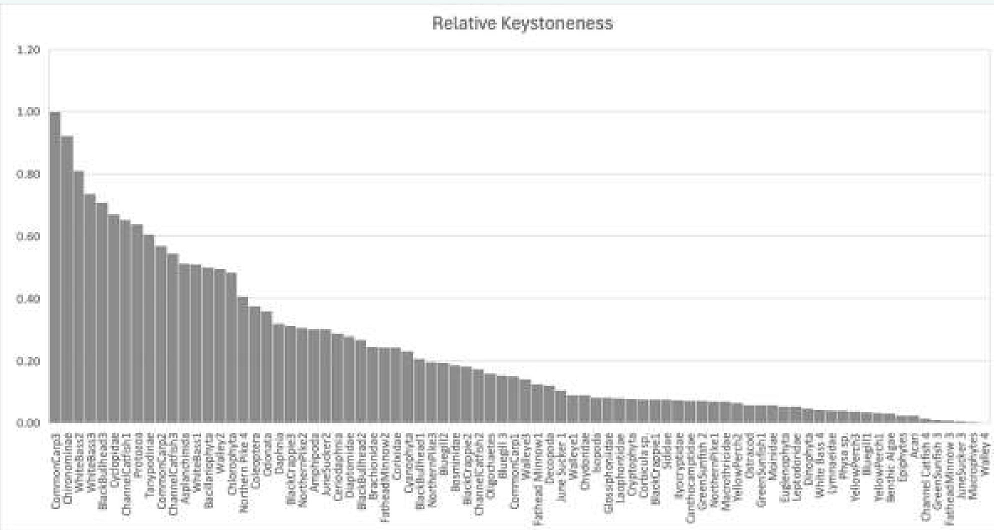

Figure 5: Relative total impact (Keystoneness) of individual taxa..

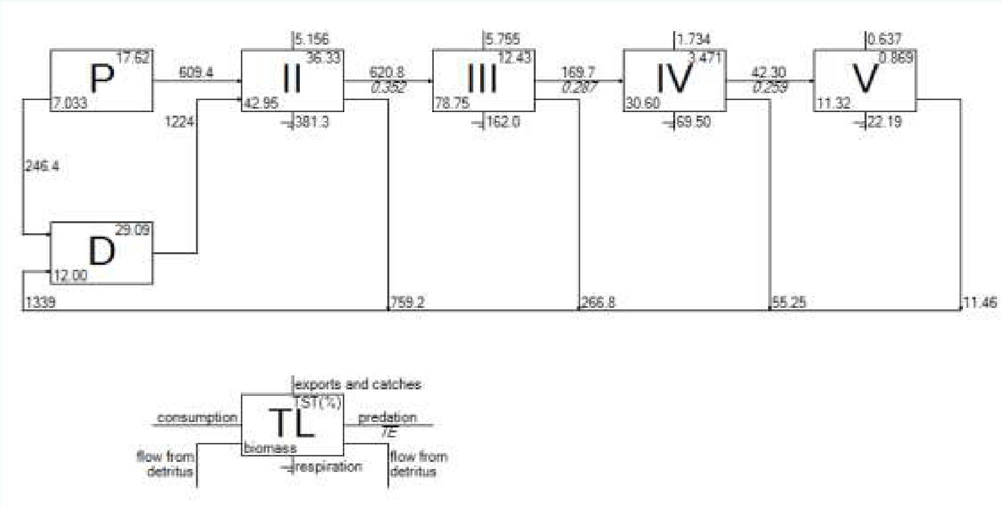

Figure 6: Lindeman spine representation of Utah Lake. Trophic flows are transferred from primary producers (P) and detritus (D) to the trophic levels I to V, where TST (%): Total System Throughput and TE: transfer efficiency. Flows are represented in tons km^{-2} year^{-1} and biomass in tons km^{-2}.

DISCUSSION

Results from this food web, ecosystem function model support our understanding of the Utah Lake ecosystem: a longtime-chronically-abused lake. Its food web is dominated by invasive fishes predominantly larger sized Common Carp, White Bass, and catfish (i.e., Black Bullhead, Channel Catfish), and by water column protozoans and benthic Chironominae larvae. Biomass of carp far exceeded all other taxa. Estimated total biomass of carp in the lake was more than 125% of the total biomass of all other organisms combined including plankton. Chironominae larvae biomass was equal to all other benthic invertebrate biomasses combined. Chironomidae are well established indicators of degraded ecosystems including Utah Lake however, their larvae are well known and often beneficial ecosystem engineers [66-68]. Chironomids are the only remaining benthic invertebrates in the lake that appear to be contributing substantially to positive ecosystem function [25].

Primary production was co-dominated by water column phytoplankton and benthic detritus with large amounts of underutilized plankton that fell as detrital snow further supporting the detritivore community. Benthic photosynthetic primary production in the form of macrophytes, periphyton, and benthic algae was almost absent in Utah Lake, another strong signal that such a shallow lake is out of balance. Many of the generated results and indices/metrics in the EcoPath model also pointed towards a dysfunctional ecosystem including system robustness, omnivory index, etc.

Our Ecopath model was based on limited empirical data. We know of no other large lake ecosystem in the U.S.A. that has been studied so little. An increase in research and monitoring is needed, as is frequent updating model inputs. Diet analyses need to be conducted and updated regularly. Stable isotope analyses are an important addition for long-term general diet assessment and are recommended. Also, an important component of the food web that was not fully modeled was the microbial loop and associated nanoplankton, due to lack of data. Although we did not specifically model the microbial loop, future iterations using relevant literature findings like Munawar et al. [69], or preferably using empirical data collected from the lake should be conducted.

Results from mixed trophic level impacts in this EcoPath food web model showed that for the most part the only taxa groups that negatively affected cyanophytes, were other phytoplankton and zooplankton taxa (S5). Both had only slight negative effects on cyanophytes indicating that ecosystem function improvements need to be made. See S5 for all mixed trophic level impacts. In addition, much of the water column phytoplankton based primary production fell as detrital snow increasing the importance of detritus in the food web, which also happens to be a major food resource for carp. This further illustrates a poorly functioning ecosystem where the zooplankton assemblage has been compromised and cannot further control phytoplankton.

Ecosystem robustness and exergy are important indices for determining the health and sustainability issues of ecosystems [50], and this EcoPath model was able to some extent describe Utah Lake's ecosystem functioning, system hierarchy, and system maturity [70]. For example, several of the succession (maturity) metrics including production, respiration, biomass, and their ratio metrics presented in Table 4 indicated that the lake was in an unnaturally 'younger' or 'bloom' state [71-74]. This is consistent with the classical limnological concept that lakes mature from less productive (oligotrophic) to more productive (eutrophic) state as nutrients accumulate from either natural or human induced watershed sources [71]. Lake eutrophication prevents (reverses) system maturity. The lake also remains in a chronically 'immature' early succession stage because of persistent wave action that consistently disturb unconsolidated sediments and resets the food web thus preventing maturation of the system.

In addition, the internal indices e.g., ecotrophic efficiency (EE), trophic level (TL) and transfer efficiency (TE) can be useful for comparative analyses of temporal changes in functional groups within the lake and for understanding the future functioning of its ecosystem, or lack thereof [75]. As an example, the EcoPath model suggested that Utah Lake's ecosystem did not follow Lindeman's [55-89], 10% law where an increase in TL should result in a decrease in TE. There was an increase in TE from TL II to TL III from 0.15 to 0.22 using the EcoPath model for Utah Lake suggesting trophic level transfer problems within the lake ecosystem.

Results from our model helped identify data gaps that are needed to guide future monitoring and research. Future derivations of our EcoPath model can be compared using different scenarios. EcoSim models can then be used as a time dynamic simulation module for management exploration. EcoSpace can then be used as a spatial and temporal dynamic module once input data are refined. The EwE suite can also be integrated with other ecosystem models including water quality models that are under development by water quality agencies.

This model, along with our long-term research on Utah Lake firmly supports the need for ecosystem restoration necessary for improved ecosystem function. This should include increased consistent carp removal, sediment stabilization, reestablishment of native aquatic plants and mollusks, and most importantly a balanced fishery. We suggest that these actions will increase light penetration to the benthic community, expand the littoral zone, and help alleviate any algal bloom problems.

CONCLUSION

Our EcoPath model of Utah Lake's food web was a critical first step for a more complete understanding of how best to manage the lake including algal blooms and the lake's fisheries. Without this component, Utah Lake cannot be adequately managed. Further refinement of input data is crucial and reflects the poor state of knowledge of Utah Lake's fisheries and other components of its food web. The model performed very well describing, quantifying, and verifying aspects of the lake's ecosystem that until now have not been examined. Our goal is the restoration of Utah Lake including a well-balanced food web and fully functioning ecosystem consisting of native flora and fauna. This model along with additional EwE models in development are important first steps and the foundation for successfully attaining this goal.

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