# Food Webs in Long Island Sound: Review, Synthesis and Potential Applications

## Final Report - EPA Grant No. LI-97101401

**Submitted to the**
**United States Environmental Protection Agency**
**Long Island Sound Study**

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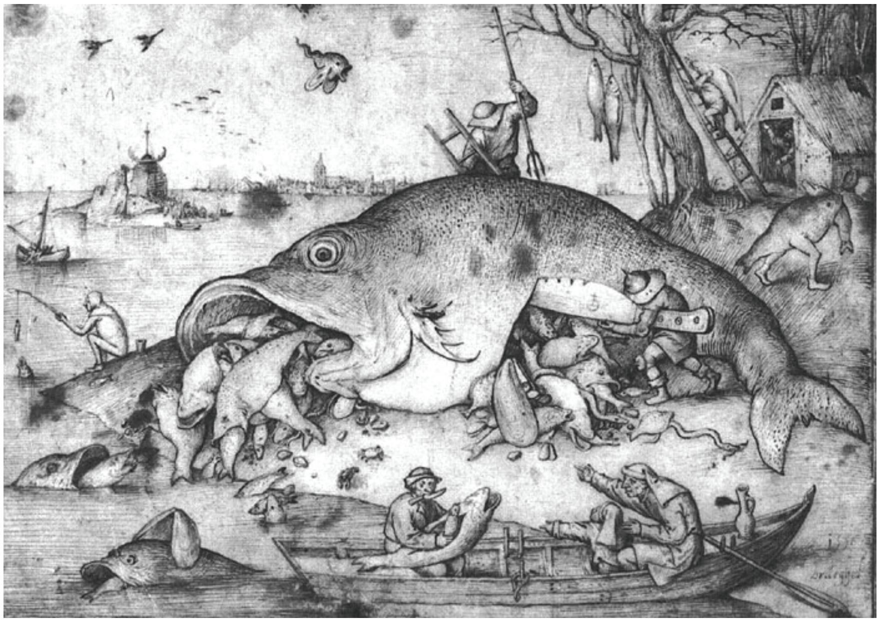

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## Project Summary

Understanding food web structure and dynamics of ecological systems is a key element in the development of more effective environmental assessment and management procedures. Although various components of the Long Island Sound (LIS) ecosystem have been studied in some detail, a framework for food web based research has been lacking. The objectives of this study were to: a) collect and review all pertinent data available in the scientific literature and technical reports on food web components and interactions in different sections of Long Island Sound; b) based on this review, refine initial conceptual food web models and extract pertinent data as available for input into the trophic modeling system Ecopath; c) using the Ecopath models constructed, identify apparent critical food web components and functional groups (particularly those influenced by human activities and management decisions) in LIS, their potential influence on ecosystem dynamics, important linkages along the food web, and the nature of the food web dynamics; and d) make an overall assessment of the gaps in our knowledge and recommendations as to how the work can be built on, and how information from food web analyses such as these and the models themselves, can used to support management efforts focused on the vital resources of Long Island Sound.

We reviewed over 2,200 journal articles and reports to assess and collect data that could be used to develop the food web models for LIS. We also obtained unpublished data from researchers currently working on various components of LIS ecosystem dynamics. Data pertinent to food web construction and analysis were compiled into databases and the literature citations were put into a bibliographic software program (both included in the digital appendix of this report). Based on our assessment of the literature, there is a significant lack of LIS-specific data that can be used for food web model development (i.e. biomass, production, consumption, diet composition), particularly for inshore waters, bays and rivers, and also for many taxonomic groups. In particular these included certain components of the zooplankton, cnidarians (e.g. jelly fish) and ctenophores (comb jellies), polychaete worms, many bivalve species, and arthropods which comprise lower trophic levels (e.g. amphipods). There was also a significant lack of data for ceratin upper trophic levels as well including coastal birds and marine mammals. There is fair amount of data on primary production, and demersal fish and large invertebrate biomass, although not LIS specific diet composition for the latter. Given the paucity of data for certain taxonomic groups and for inshore and nearshore shallow habitats in the Sound, we focused our efforts on developing a food web model for the offshore, deep-water environments of LIS.

The Ecopath model developed was comprised of 32 trophic functional groups / taxa. Of these, there were 5 large aggregated groups: phytoplankton, zooplankton, infaunal deposit feeders, infaunal filter feeders and epifauna- scavengers. Higher trophic levels were comprised of 2 species of crabs, squid, lobsters and 22 fish taxa. Ecopath models require that at least three of four critical variables (biomass, production/biomass ratio consumption/ biomass ratio, and ecotrophic efficiency ) be input into the model. Biomass estimates for all components of the model were obtained from the literature and other available data (except for bay anchovies which was estimated by the modeling software), and a variety of conversion factors were used to convert values into the model units, tons km$^{-2}$ yr$^{-1}$. To the extent possible, we use data that were collected over a 10-year period between 1995 and 2005. However, for some functional groups we had to use older data and / or general data available from other Ecopath models or on internet

sites providing such data (e.g. www.fishbase.org).

The completed model is balanced and used to generate various food web metrics describing the structure of the food web and the flow of biomass among the functional groups in the web. These analyses indicate that there is a high diversity of interactions among the functional groups in the food web, however there are generally two to three links among successive trophic levels within the web which is common to other systems. Efficiencies in trophic transfers from one level to the next were low at low trophic levels but increased with increasing trophic level. Comparison of network flow metrics to other estuarine systems suggests that food web dynamics in Long Island Sound may differ on several accounts from these other systems. However other aspects of network dynamics were similar. Mixed trophic impact analyses indicated that epifauna – scavengers, squid, little skate and to a lesser extent four spotted flounder may have the greatest effects on other groups if their biomass changed, and as such may be keystone functional groups.

The Ecopath model developed in this project is just the first step in the process of developing more details and potentially more accurate food web models for Long Island sound. It provides a framework for continued food web model development and by incorporating the static Ecopath model into dynamic food web modeling routines one can explore various impact and management scenarios.

***Acknowledgments*:** Many individuals made significant contributions to the work presented in this report. Drs. Jim Kremer, Senjie Lin, Hans Dam, George McManus, and Evan Ward of the University of Connecticut provided recently collected data and analytical results from their own work and helpful comments on our efforts. Kurt Gottschall, and Matt Lyman at the Connecticut Department of Environmental Protection Fisheries Division also provided critical data. A number of students at the University of New Haven spent long hours searching the literature for data and developing databases for this research including Cary Chadwick, Donna Cook, Dave Dembosky, Mary Ann Olson-Russello, Shelley Valauskas, and Amanda Wheeler (Neely). To all our most sincere thanks.

# Introduction

Studying the structure and dynamics of food webs is a fundamental aspect of understanding the ecology of any particular environment and its component ecosystems. It is also critical to ecosystem and landscape level management of natural resources (Costanza and Mageau 1999, Pauly et al. 2000, Fulton et al. 2003, and references therein). This final report provides the results of an EPA funded study to assess the availability and quality of data that could be used to conduct research on the structure and dynamics of food webs in Long Island Sound (LIS) and use a portion of this data to develop and analyze a preliminary food web model for LIS and assess these results relative to future research needs and management efforts for LIS.

Food web research includes several avenues of investigation. Detailed reviews on food web research in ecology are given in Cohen (1978) Pimm (1982), Schoener (1989), Polis and Winemiller (1996), Drossel and McKane (2003) and Polis et al. (2004). Much work has focused on determining the species composition of food webs and using this information to assess the structural characteristics of the food web, including, for example, the number of species in the entire food web and within specific trophic levels, the number of linkages among members of the food web, and the degree of connectivity within the entire food web (e.g. Pimm 1982, Hall and Raffaelli 1991, Link 2002, Dunne et al. 2004, Romanuk et al. 2006). The composition of food webs and their structure are determined through direct observations of species predator-prey interactions, herbivory, gut content analyses and radioisotope or immunological studies (e.g. Feller et al. 1979, Fry 1988, Brodeur and Pearcy 1992, Jones and Waldron 2003, Akin and Winemiller 2006). More recently, researchers have focused on whether there are subgroups within the overall food web, the structure of these subgroups, and their effect on web dynamics (Krause et al. 2003). Collectively, these studies seek to determine if there are general trends in food web structure among different environments and address theory that focuses on food web complexity and the ramifications of different levels of complexity. It is generally thought that more complex food webs are more stable, providing redundancy in the flow of materials and energy though the food web and ecosystem. Analyses of food web structure also address questions of top-down verses bottom-up control of web dynamics (e.g. Worm and Duffy 2003, Heck and Valentine 2007).

Another large body of work on food webs address their dynamics primarily via modeling, although some experimental studies of food webs have been conducted (e.g. Breitberg et al. 1999, Morin 1999). Food web modeling generally falls into two areas. One uses mathematical models to explore questions of food web assembly over ecological and evolutionary time scales, and web stability under different conditions (see Drossel and McKane 2004 and references therein). The other area of food web modeling focuses on using information about the structure of the food web to explore the cycling of material through the web based on mathematical formulations of production and consumption. These models are also viewed as ecosystem models to the extent that the movement of both energy and materials through the web is explored, as well as the effects of nutrient levels and cycling and other environmental forcing functions (e.g. Pomeroy and Alberts 1988, Baird and Ulanowicz 1989). Over the past two decades there has been a steady increase in research on marine and estuarine food webs that has focused on the latter types of models, and in particular the use of a modeling framework named Ecopath with Ecosim (EwE) (Polovina 1984, Christensen and Walters 2004). The EwE framework combines software for ecosystem trophic mass balance in which the structure of the food web is developed and mathematical equations are used to quantify food web "dynamics" in a static view, as well as the ability to model food web / ecosystem dynamics over time and space in response to various types of environmental and ecological scenarios (Christensen and Walters 2004).

As management efforts in Long Island Sound (LIS) evolve and begin to include ecosystem level approaches, it will be critical to develop a detailed understanding of food web structure and dynamics in LIS, and how these may vary spatially and temporally. Environmental problems associated with nitrogen additions (and resultant hypoxia/anoxia in some areas), toxic materials and potentially increasing temperatures can have significant effects on communities and populations found in the Sound's varied habitats (e.g. Capriulo et al. 2002, Dove et al. 2004, Howell et al. 2005). In turn, this can affect ecosystem functioning and services (e.g. harvestable resources) and the biogeochemical cycles associated with forcing variables such as nitrogen (e.g. McClelland and Valiela 1998, Breitberg et al. 1999, Raffaelli 1999, Althauser 2003). Our understanding of food web structure and dynamics in LIS is fragmentary at best. Recent work by Capriulo et al. (2002) has provided insights about planktonic food webs in the deeper water portions of LIS. There are different pools of data available for nekton and benthos (see below), however these have not been used in any quantitative way to assess food web structure in Long Island Sound or as input into food web models, nor to identify significant gaps in the data. The main objective of our research was to develop conceptual and quantitative food web models for LIS, and using these models: a) make an initial assessment of what may be the critical food web components in different habitats and their associated functions (e.g., system filtration, nursery function) and b) identify critical data gaps in our present understanding of major food web components and their potential interactions. The quantitative modeling used EcoPath with EcoSim. The modeling results and assessments are meant to provide a focal point for detailed review by the scientific community and environmental mangers which can lead to further refinement and use for developing simulations and analyses to assess the impacts of management decisions on food webs and ecosystem dynamics (e.g. Connolly and Glasser 1998, Okey 2001,Ortiz and Wolf 2002, Zetina-Rejon 2004).

## Conceptual Overview

As a framework for the results of our study that follow we feel that it is worthwhile to provide an overview of food web structure and the general factors that need to be considered when developing food web models. We also present the qualitative conceptual food web models that guided the formulation of this project and our initial efforts. This is not meant to be an exhaustive review of food web theory, as several excellent reviews and books on the topic are available as noted above.

Food webs portray feeding relationships among organisms within an ecosystem. Depending on our knowledge and needs, food web depictions of these relationships can range from simple to extremely complex. For example, Figure 1A shows a very simplified food chain, with phytoplankton at the base of the food chain, or at the first trophic level, and successive levels of consumers leading to the highest trophic level, humans. However, ecosystems are rarely comprised of simple food chains, but rather they are comprised of food webs with a variety of species at different trophic levels and variable connections within and among trophic levels. The ecosystem itself is comprised of the food web, or food webs (see below), and the various abiotic factors that provide energy to the system, in most cases solar energy, and the various nutrients that are used by primary producers and by consumers. A very simple food web depiction for Long Island Sound is shown in Figure 1B, which includes the very important decomposer group and also wastes and dead organic matter (detritus). Indeed, much more detail can be added to the simplified food web in Figure 1, as shown in Figure 2, providing more information on species that comprise each trophic level and general connections among them. However, in order to develop a quantitative food web model for a particular ecosystem, or habitat within an ecosystem, specific components (i.e. the species and/or taxonomic groups) comprising the food web and the interconnections (i.e. feeding / predator/prey relationships) among them need to be identified. This can be also be relatively simple as shown in Figure 3A, a food web depiction of Narragansett Bay, but in this case there are specific nodes and interrelationships. Another example is shown in Figure 3B, which also shows trophic levels which indicate the position of each functional group within the web. Note that primary producers such as phytoplankton, and also detritus are at the base of the food web, or trophic level 1. Consumers form the upper trophic levels, with the top consumers such as marine mammals or tuna, and including humans at trophic level 4 and above.

Constructing food webs, and subsequently analyzing and modeling them, can be very difficult depending on the potential complexity of the food web being studied. The complexity of food webs can vary in relation to several natural factors, but can also depend on how researchers depict species in the web relative to data availability and/or the level of complexity they want to have in the food web model. Food web complexity can increase as the number of species and functional groups that comprise the food web and the interrelationships, or links, among them increase. Generally, the more species that comprise a food web, the more potential links there are among them. Examples of food webs with greater species and linkage complexity relative to those shown in Fig. 3 are shown in Fig. 4. Complexity can also be introduced into food webs by the way specific food web components are depicted. In the food webs shown in Figures 3 and 4, most of the species are represented by a single node, and as such any changes in feeding and diet, and in susceptibility to predation during a species life cycle are not considered, and either only the adult stage characteristics are considered or any of these ontogenetic changes are averaged over the life cycle. However species, particularly those in upper trophic levels, can have significant changes in diet during their life cycle, feeding on phytoplankton and/or zooplankton during larval and early juvenile stages and then higher in the food web as they mature and grow. These situations can be incorporated into a food web by designating separate nodes for distinct stages in a species life cycle, such as larval, juvenile and adult (Figure 5). Adding nodes for different life stages of species in a food web can greatly increase the complexity of the overall food web, and is dependent on having available diet data for each stage.

Many estuarine organisms also exhibit spatial variations in the habitats they occupy during their life cycle. Infaunal and epifaunal organisms such as clams and worms have planktonic larvae and as such are part of the zooplankton during the early stages of their life cycle. Many fish spend their early life stages in salt marshes and/or nearshore areas and embayments. These ontogenetic differences in habitat use link the food webs of inshore, nearshore and off shore deep-water habitats (Figs. 6 and 7). For example, salt marshes have food webs that are distinct but connected to the nearshore, shallow and offshore, deep-water areas of Long Island Sound. Some organisms may spend their entire life cycle in one of these habitats or may be found in two or all three environments depending on their natural history. Those species that migrate among habitats, change habitats during their life cycle, or feed in several different habitats either throughout the year or seasonally, connect the food webs found in each environment. In each of these environments there will also be small to large scale spatial differences in the habitats found. For example, the sea floor of LIS is comprised of a variety of sedimentary patches with different mixes of habitats (Fig. 8). These different habitats support differing benthic infaunal and epifaunal communities (e.g. Zajac et al. 2000). As such, food web structure may vary among these areas over several spatial scales. All of these factors add to the potential complexity of food webs in estuarine environments. We can envision this overall complexity as the whole system being comprised of food web compartments (Fig. 9) that are connected to varying degrees with respect to time (seasons, year to year fluctuations) and space (different habitats and geographic locations (e.g. eastern vs. western ends of Long Island Sound, nearshore vs. offshore). Such compartments can exist also within a particular habitat. For example, in nearshore waters benthic and pelagic portions of the overall food web might behave as compartments with closer interactions within the compartment and relatively weaker interactions among these two compartments. The existence of any such compartments in LIS would add to the overall complexity of the food web.

Although we can hypothesize about the structure and complexity of food webs in LIS, and indeed develop qualitative models of how those food webs are structured, up until this study there have been no quantitative assessments or models developed for food webs in LIS. To initially frame our work, and subsequently guide our food web model development, we developed qualitative food web models for different portions of LIS (Figures 10-12). These simple models depict our initial view of what were thought to be important taxa for food webs in the different areas of LIS, and guided our data collection. It became quickly apparent (as presented in the following sections of this report) that there are serious shortcomings in the types of data that are needed to construct quantitative and dynamic food web models for all of the different kinds of environments, and the habitats they contain, in LIS. Therefore, we focused our modeling efforts on developing a food web model for the environments for which we were able to obtain what we felt to be the best data. These were primarily the offshore, deeper water sections of LIS, and to a lesser extent the shallow water, or nearshore environments of LIS. The model that was developed using an Ecopath approach is primarily a mixed nearshore / offshore model. Appropriate data to model food webs in inshore coves and embayments, and salt marshes are not available to the degree needed, and this remains an important obstacle to developing food web models for these important habitats (see **Discussion**). In the **Materials and Methods** and **Results** sections that follow, we focus on our initial literature search for appropriate food web data for LIS and the Ecopath model that was developed. We return to the question of identifying shortcomings in specific types of data that are needed for food web analyses and modeling in the **Discussion.** We also compare our results to what has been found for other estuarine and coastal systems. Using the Ecopath model constructed, we attempt to identify apparent critical food web components (particularly those influenced by human activities and management decisions) in LIS, their potential influence on ecosystem dynamics, and important linkages along the food web. Finally, we discuss potential future research that can build on the work presented here, and how information from food web analyses such as these and the models themselves, can be used to support management efforts focused on the vital resources of Long Island Sound.

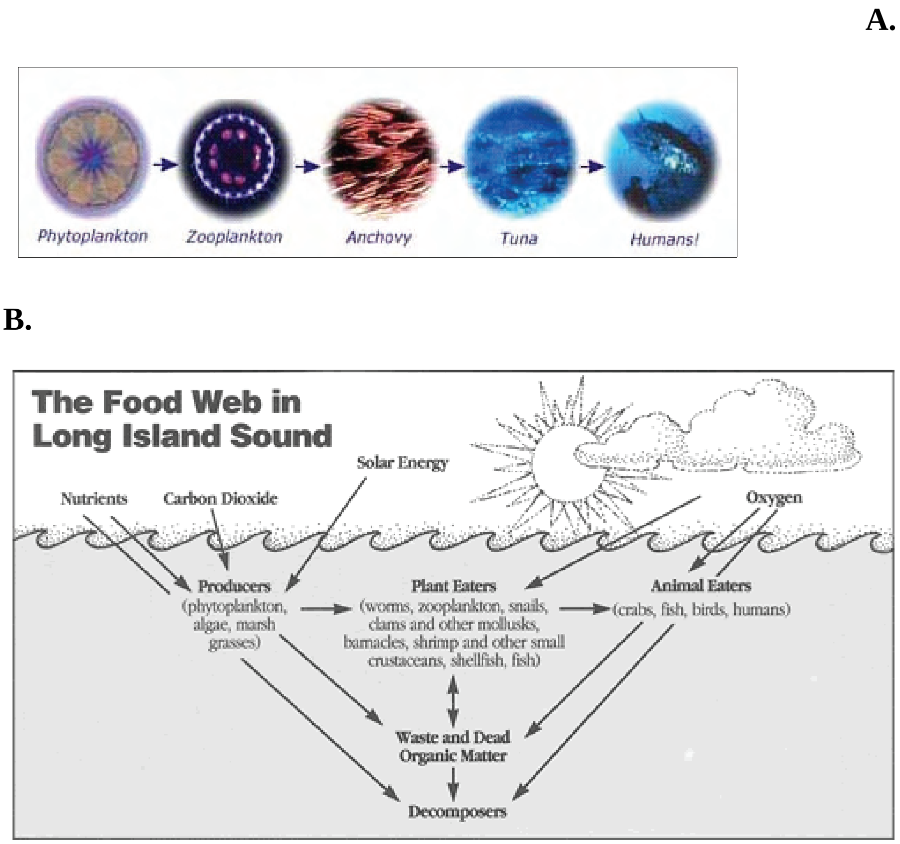


**Figure 1. A)** Example of a simple marine food chain. B) A depiction of the Long Island Sound Ecosystem with basic food web components, energy source and nutrients (from http://soundbook.soundkeeper.org/default.asp**).**

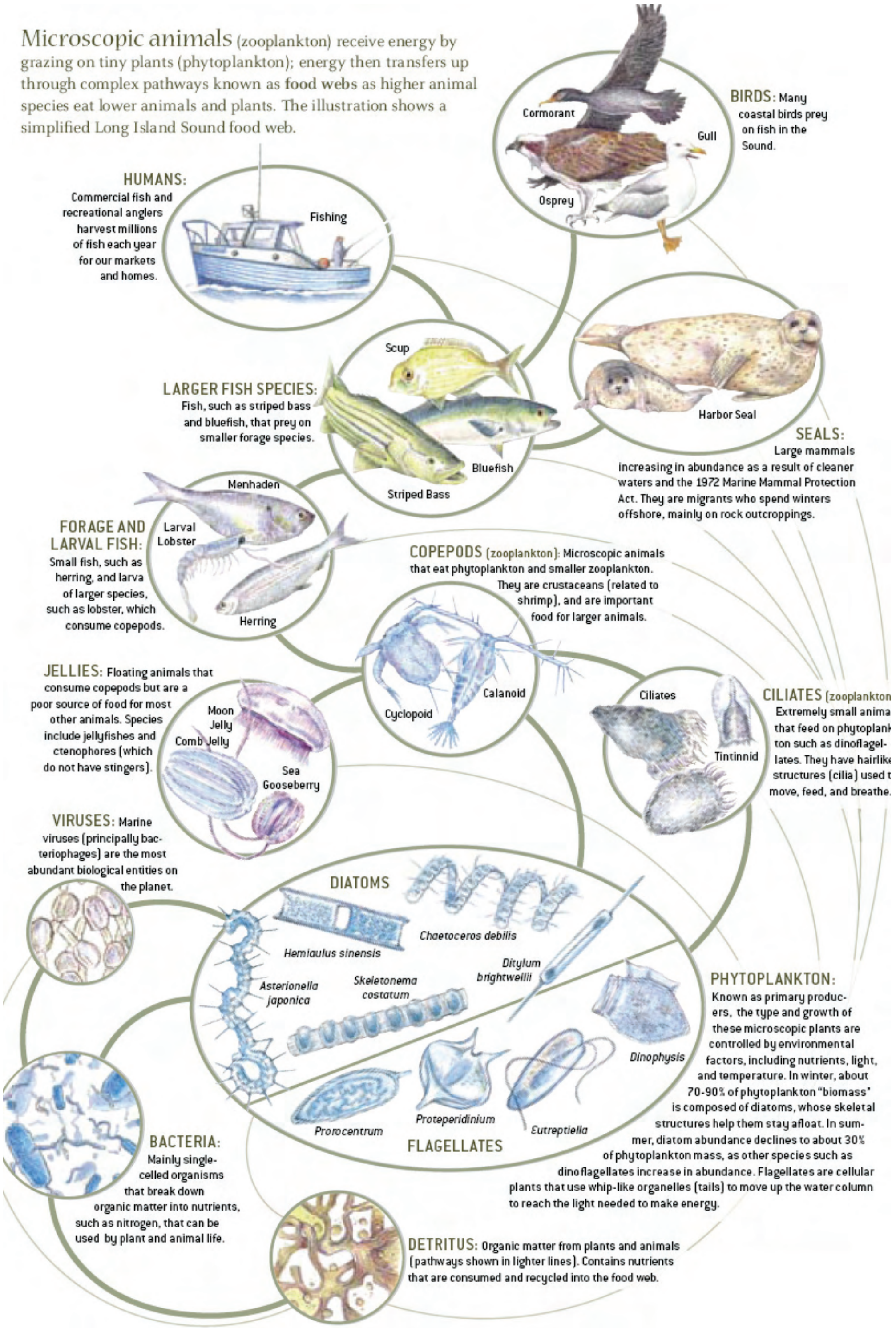


**Figure 2.** Generalized food web for Long Island Sound (from Sound Health 2006 at the Long Island Sound Study website: www.longislandsoundstudy.net).

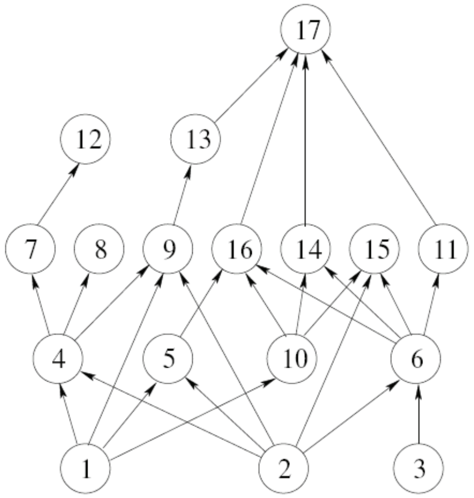


Figure 1: Narragansett Bay food web. 1=flagellates, diatoms; 2=particulate detritus; 3=macroalgae, eelgrass; 4=*Acartia*, other copepods; 5=sponges, clams; 6=benthic macrofauna; 7=ctenophores; 8=meroplankton, fish larvae; 9=pacific menhaden; 10=bivalves; 11=crabs, lobsters; 12=butterfish; 13=striped bass, bluefish, mackerel; 14=demersal species; 15=starfish; 16=flounder; 17=man. (After Kremer and Nixon 1978. *A coastal marine ecosystem*, Springer-Verlag, Berlin.)

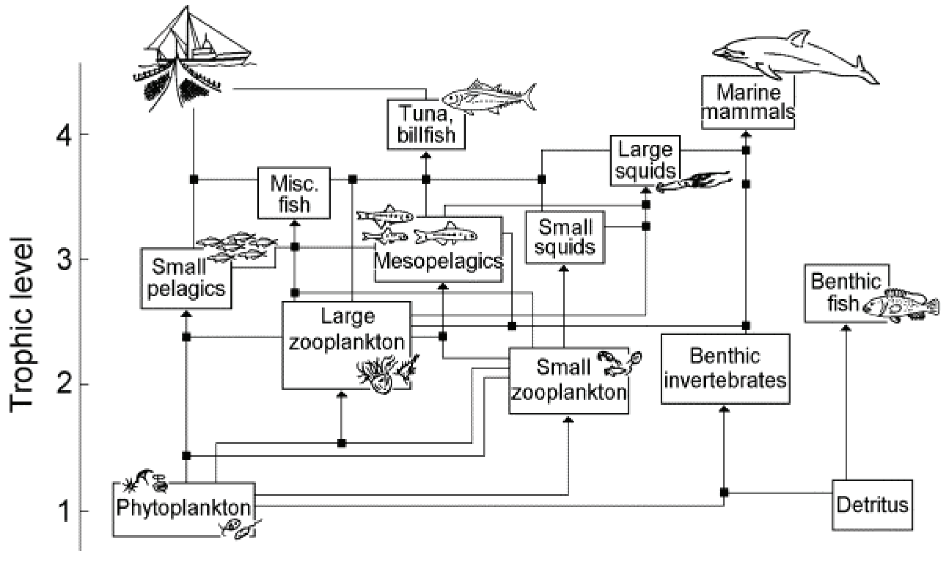
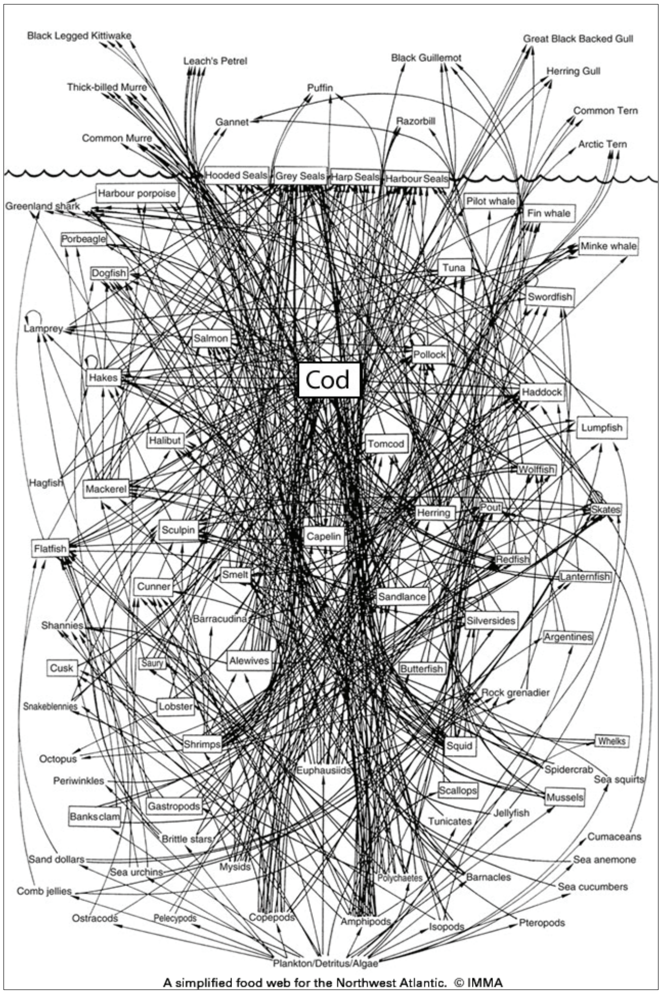


**Figure 3.** A) Top panel shows food web structure for Narragansett Bay, B) bottom panel a generalized oceanic food web. Both are examples of simplified food webs, which define the various elements of such webs (‘functional groups’), the flow between them (the links shown), and so-called ‘trophic levels’, which indicate the position of each functional group within the web. In the bottom figure, trophic levels are calculated as 1.0 plus the mean trophic level of the species that they consume.



A simplified food web for the Northwest Atlantic. © IMMA

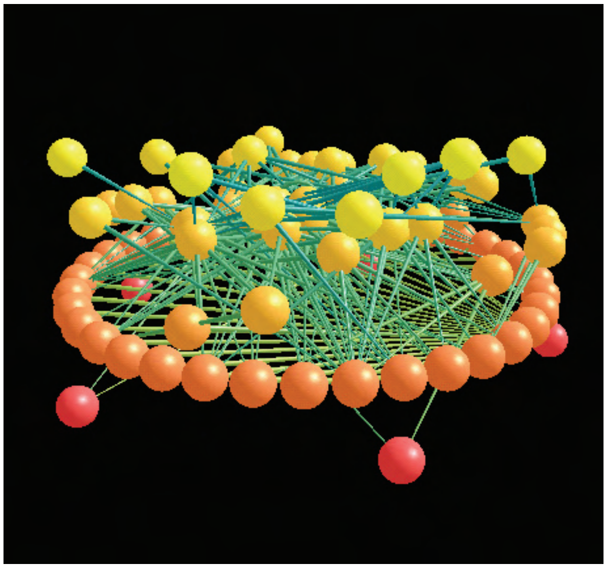


**Figure 4.** Top panel shows food web structure for the northwest Atlantic Ocean. Although the caption in the figure notes that this is a "simplified" food web model, it is considerably more complex than those shown in Fig. 3, with many more species and linkages among them. The bottom panel shows a food web for the Ythan Estuary in Scotland. In this depiction the primary producers at the lowest trophic levels are represented by the red spheres, or nodes, at the bottom of the web. The next trophic level, zooplankton and other taxa (primarily benthic organisms ) that consume the primary producers are shown as a ring of orange nodes. Upper trophic levels are depicted above the ring as light orange and yellow nodes.

"Classical" Food Web of the North Sea

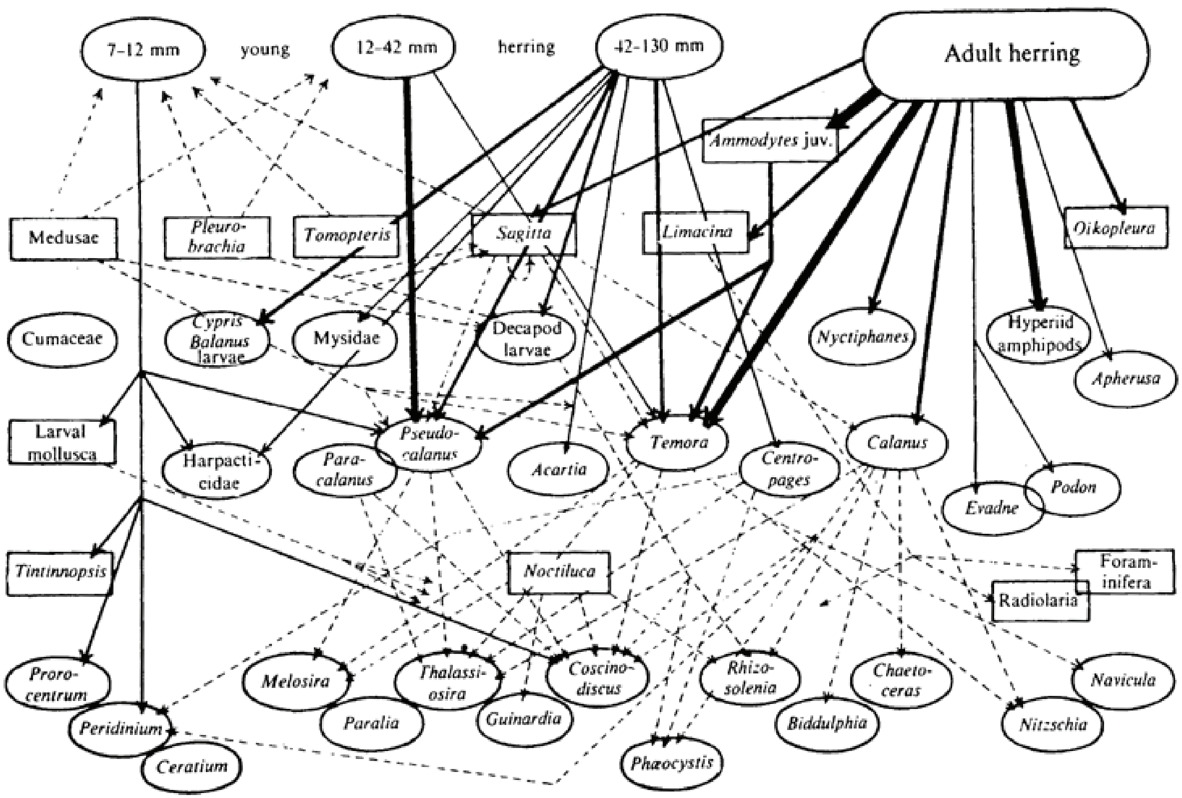


Figure 55. The food web upon which the North Sea herring depends during its life cycle (Hardy, 1924).

**Figure 5.** Example of a food web incorporating ontogenetic changes in feeding in herring *Clupea harengus* Hardy (1924) in the North Sea. The arrows point from the predator to the prey, the thickness of arrows being roughly related to the degree of influence on the prey.

**Figure 6.** Aerial photo of the West Haven / Milford shore of Connecticut. In the foreground is a salt marsh which has a food web that is distinct but connected to the nearshore, shallow and offshore, deep-water areas of Long Island Sound in the background. Some organisms may spend their entire life cycle in one of these habitats or may be found in two or all three environments depending on their natural history. Those species that migrate among habitats, change habitats during their life cycle, or feed in different habitats connect the food webs found in each environment. A depiction of this is shown in Figure 7.
(Photo from: http://www.yale.edu/amst401a/image_index.html)

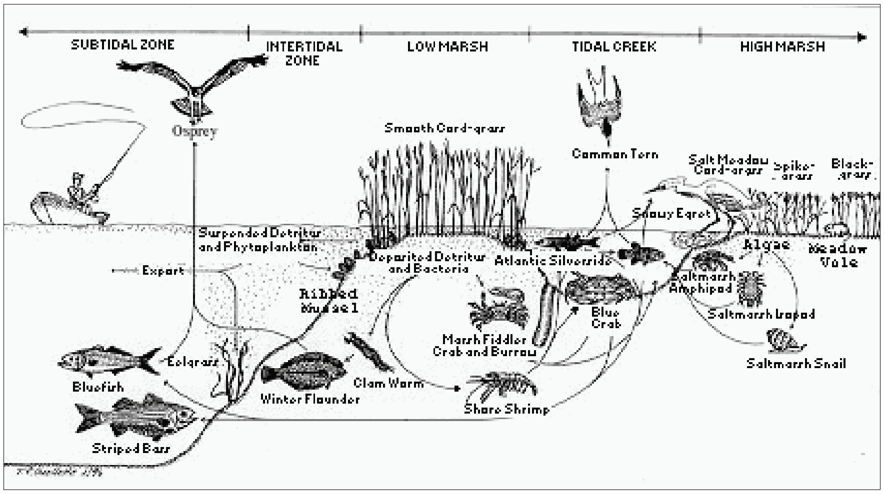


**Figure 7.** Depiction of nearshore and salt marsh food webs showing food web linkages within and among these environments. (Illustration from: http://camel2.conncoll.edu/ccrec/greennet/arbo/publications/34/CHP3A.HTM).

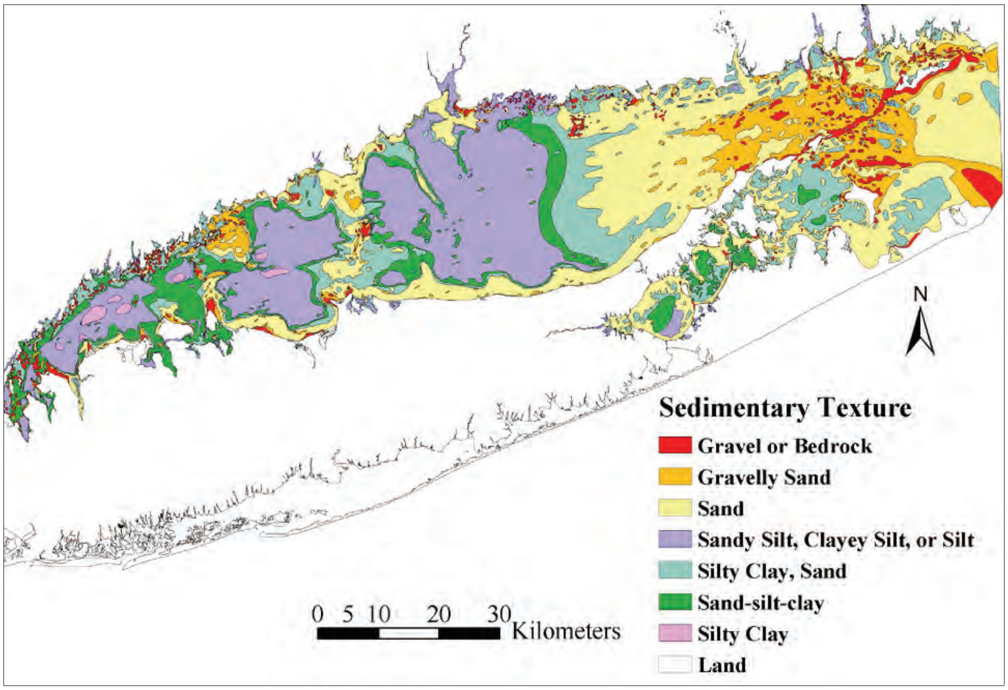
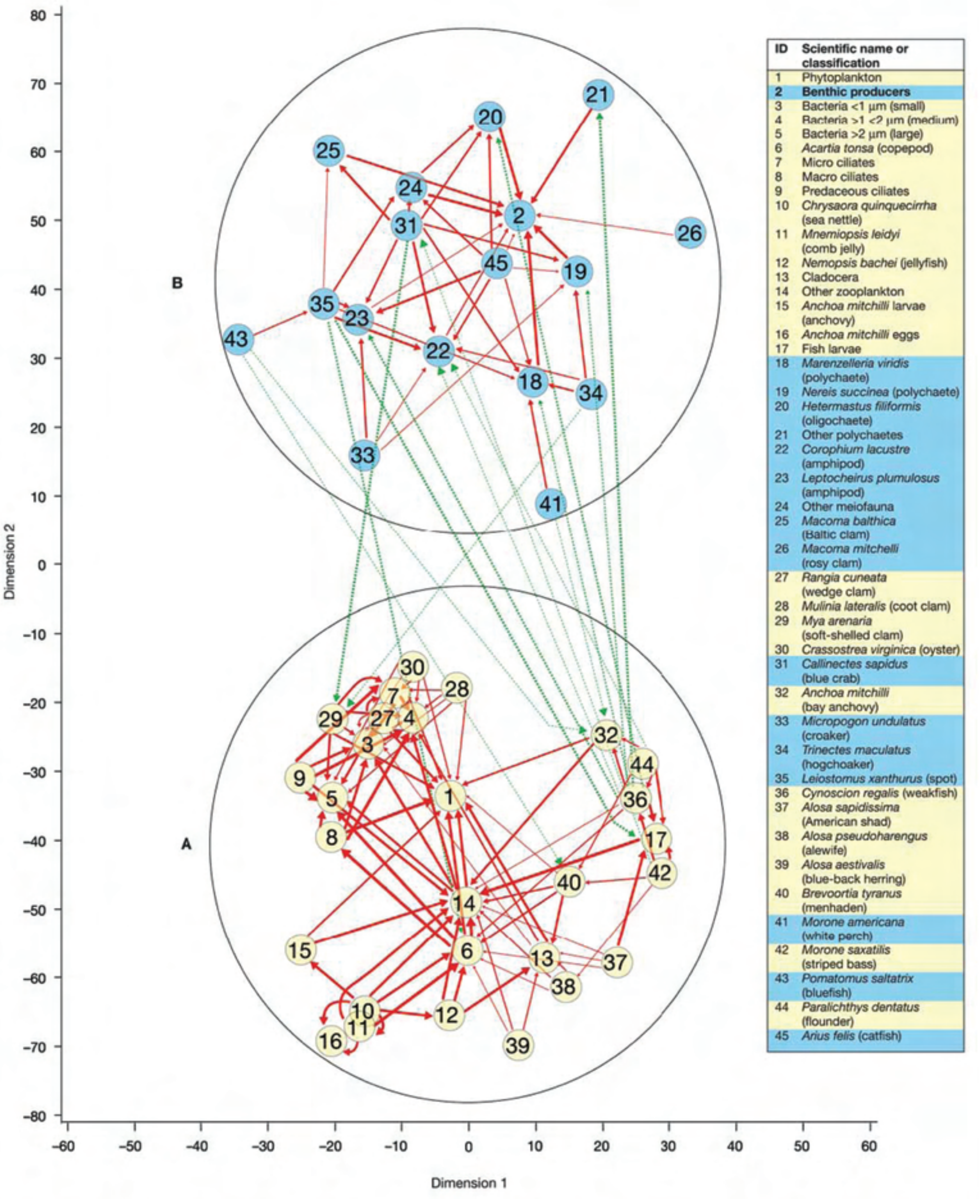


**Figure 8.** Sediment texture of the Long Island Sound Sea floor. These constitute benthic patches making up the sea floor landscapes of LIS. The patches contain varying habitats and support differing benthic infaunal and epifaunal communities. As such, food web structure may vary among these patches and habitats.



| ID | Scientific name or classification |
|---|---|
| 1 | Phytoplankton |
| **2** | **Benthic producers** |
| 3 | Bacteria <1 µm (small) |
| 4 | Bacteria >1 <2 µm (medium) |
| 5 | Bacteria >2 µm (large) |
| 6 | *Acartia tonsa* (copepod) |
| 7 | Micro ciliates |
| 8 | Macro ciliates |
| 9 | Predaceous ciliates |
| 10 | *Chrysaora quinquecirrha* (sea nettle) |
| 11 | *Mnemiopsis leidyi* (comb jelly) |
| 12 | *Nemopsis bachei* (jellyfish) |
| 13 | Cladocera |
| 14 | Other zooplankton |
| 15 | *Anchoa mitchilli* larvae (anchovy) |
| 16 | *Anchoa mitchilli* eggs |
| 17 | Fish larvae |
| 18 | *Marenzelleria viridis* (polychaete) |
| 19 | *Nereis succinea* (polychaete) |
| 20 | *Hetermastus filiformis* (oligochaete) |
| 21 | Other polychaetes |
| 22 | *Corophium lacustre* (amphipod) |
| 23 | *Leptocheirus plumulosus* (amphipod) |
| 24 | Other meiofauna |
| 25 | *Macoma balthica* (Baltic clam) |
| 26 | *Macoma mitchelli* (rosy clam) |
| 27 | *Rangia cuneata* (wedge clam) |
| 28 | *Mulinia lateralis* (coot clam) |
| 29 | *Mya arenaria* (soft-shelled clam) |
| 30 | *Crassostrea virginica* (oyster) |
| 31 | *Callinectes sapidus* (blue crab) |
| 32 | *Anchoa mitchilli* (bay anchovy) |
| 33 | *Micropogon undulatus* (croaker) |
| 34 | *Trinectes maculatus* (hogchoaker) |
| 35 | *Leiostomus xanthurus* (spot) |
| 36 | *Cynoscion regalis* (weakfish) |
| 37 | *Alosa sapidissima* (American shad) |
| 38 | *Alosa pseudoharengus* (alewife) |
| 39 | *Alosa aestivalis* (blue-back herring) |
| 40 | *Brevoortia tyranus* (menhaden) |
| 41 | *Morone americana* (white perch) |
| 42 | *Morone saxatilis* (striped bass) |
| 43 | *Pomatomus saltatrix* (bluefish) |
| 44 | *Paralichthys dentatus* (flounder) |
| 45 | *Arius felis* (catfish) |

**Figure 1** Graphical display of the results for the Chesapeake Bay food web with 45 taxa and weighted by interaction strength. Units are relative distances based on the inverse of the density of interactions. Within-compartment distances were decreased by a factor of 6.2 for aesthetic purposes. Circles indicate compartment boundaries and numbers identify taxa (yellow, within compartment A; blue, within compartment B). Arrows indicate interactions between taxa (solid red, within compartment; dashed green, between compartments; thickness indicates rank of associated interaction strength) and point from predator to prey.

**Figure 9.** Example of food web compartments as depicted for Chesapeake Bay. Figure is from Krause et al.( 2003).

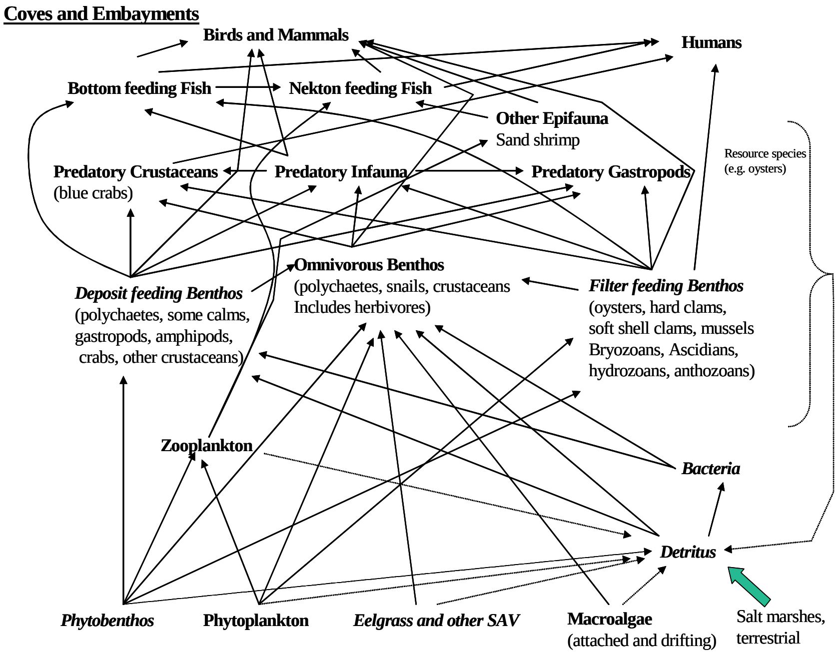


**Figure 10.** Conceptual food web for coves and embayments in Long Island Sound.

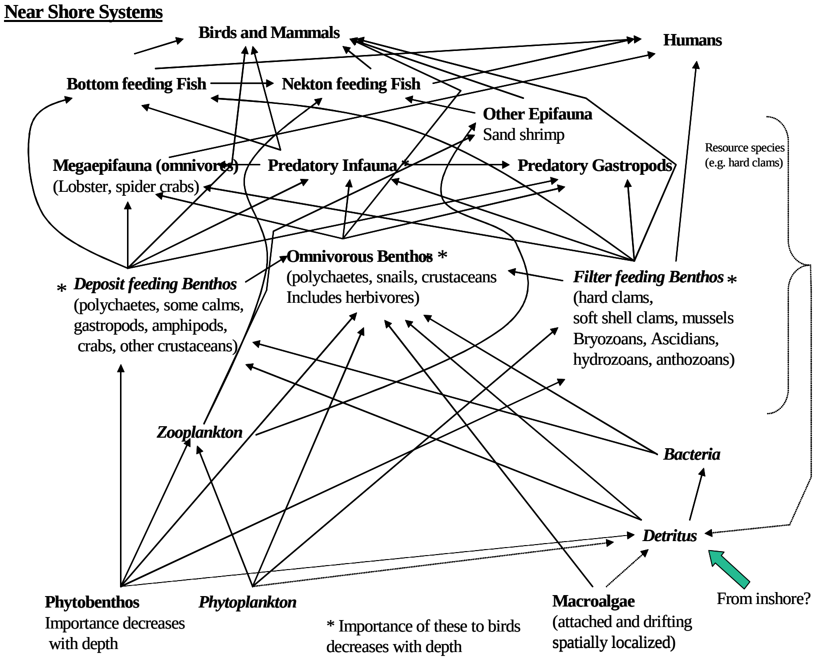


**Figure 11**. Conceptual model of food web in the nearshore waters of Long Island Sound

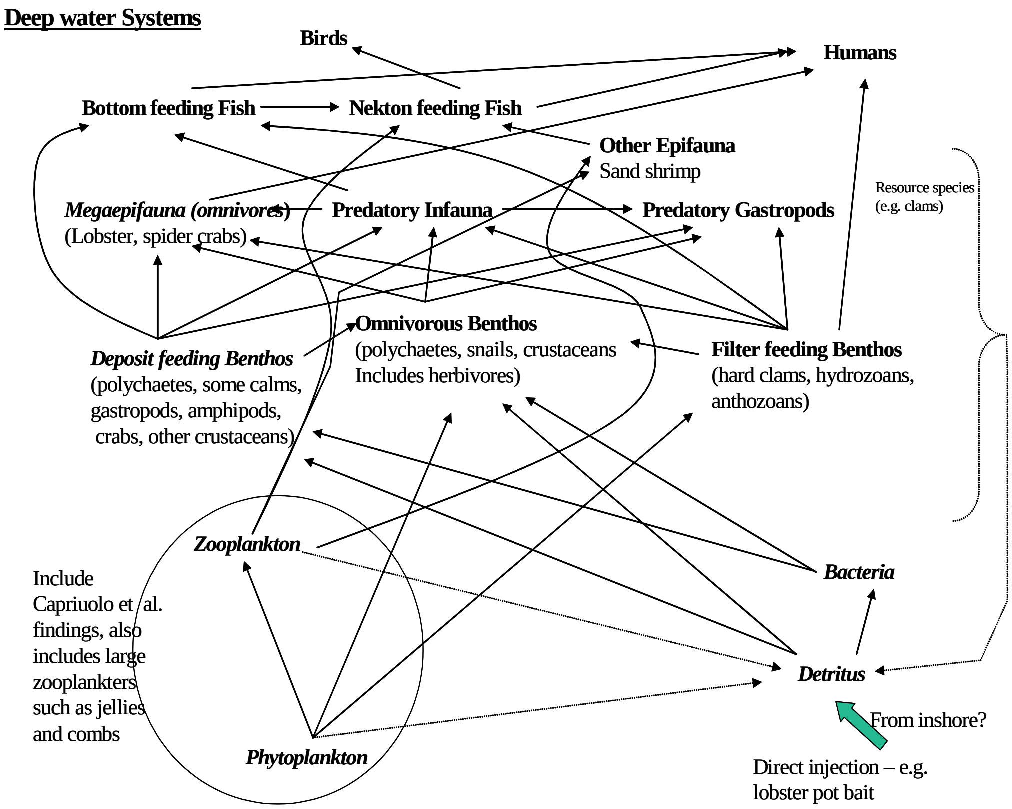


**Figure 12.** Conceptual model of deep water food webs in Long Island Sound.

## Materials and Methods

*General Approach*

Food webs in a particular region can vary both spatially and temporally (Deegan and Garritt 1997, Ortiz and Wolff 2002, Althauser 2003), which can have significant effects on ecosystem dynamics. We initially developed conceptual food web models for three regions of LIS (Figures 10-12), including inshore, shallow water coves and embayments, the nearshore area ($\lesssim$ 30 ft) and offshore, deep water areas ($\gtrsim$ 30 ft). The regions used for these models reflect natural breaks in the distribution of habitat characteristics which shape species composition in LIS (e.g Gottschall et al 2000, Zajac et al. 2000), and likely food web dynamics. These conceptual models were meant to act as a starting point for collecting, assessing and organizing data for each region, and as an initial template for structuring the food webs and identifying critical components in each region.

Food web model development comprised three general phases of work, including a) data collection, b) data extraction and development of a food web model, and c) assessments of food web structure and potential dynamics in LIS. Using the conceptual food web models as a framework, we collected and reviewed pertinent data available in the scientific literature and technical reports on potential food web components and interactions in LIS. We also reviewed information from other geographical areas that share similar sets of species to collect the necessary data for developing a food web model for LIS. Based on our review, we assessed the availability of data to develop food web models and extracted pertinent data as available for input into the Ecopath (Pauly et al. 2000) food web modeling system. This portion of the work revealed that there was not sufficient data to develop complete Ecopath models for each region of LIS and that the only complete model that could be developed was one that was focused mainly on the deeper water sections of the Sound, generally > 10 m depth. We constructed an Ecopath model for the deep water portion of LIS and analyzed the resulting model for various food web characteristics, identified critical food web components and functional groups, their potential influence on ecosystem dynamics, important linkages along the food web, and the nature of the food web dynamics. We then made an overall assessment of the state of our knowledge regarding trophic dynamics in LIS and identified critical gaps that need to be addressed. We also make recommendations as to how the work can be built on to successfully develop dynamic models which can be used to aid in managing Long Island Sound.

*An overview of Long Island Sound*

Long Island Sound (Figure 13) is one of the largest estuaries on the North American Atlantic coast and considered a unique estuarine environment due to the east end opening directly to the ocean, whereas the western end connects through a narrow passage between New York City and Long Island. Additionally, all the major sources of fresh water enter along the northern border of the estuary. It covers approximately 3,400 km$^2$ with 90% of the freshwater input coming from the Thames, Housatonic, and Connecticut Rivers. Circulation patterns in the

Sound are complex and determined by the estuarine characteristics noted above and presence of three shoals/ sills, arranged north to south, that create three basins. The offshore environment ranges from 20 m to 45 m in the deepest areas and contains a variety of sediment ranging from clay to coarse sand (Fig. 8). The Sound is strongly affected by seasonal changes with temperatures dropping to their lowest (~ 0-4˚ C) in the February and reaching their peak (~23˚ C) in September (Vieira, 2000). Salinities range between 23 and 35 ppt, creating a complex circulation of high salinity flowing westward at the bottom and low saline waters flowing eastward at the surface (Welsh, 1993). LIS is also highly impacted, with 20 million people living within 50 miles of the Sound. It has been used for shipping, fishing, and industrial waste disposal since the 16th century (Andersen, 2003). Human activities, from the initial settlement of colonists, have created serious problems, including hypoxia and chemical pollution in the western portions of the Sound. Currently, Connecticut has 82 sewage treatment plants and New York has 23 that discharge into the Sound (LISS, 2003). Only in the last 35 years have serious efforts been made to understand the contamination and habitat loss caused by anthropogenic influences and to restore the Sound back to a healthy state (Schimmel et al., 1999).

### *Data Mining and Review*

In order to develop food web models for LIS, and explore their potential dynamics, it was necessary to compile data on the trophic characteristics and interactions of species in the Sound to the extent possible. Using our conceptual models (Figures 10-12) as a guide, we conducted an extensive literature review to collect these types of data, including trophic level, diet composition, production, abundances, biomass, and consumption rates. Concurrently, we also reviewed the literature for other geographic areas with similar estuarine habitats (e.g. Narragansett Bay, Chesapeake Bay) and supplemented the development of our Ecopath models by reviewing published food web models for other coastal systems (e.g. Baird and Ulanowicz 1989, Hall and Raffaelli 1991, Guénette and Murato 2001, Herman et al. 2001), incorporating structural components and trophic data as appropriate. We performed searches using several large data bases including The Aquatic Sciences & Fisheries Abstracts; BIOSIS Previews, Science Citation Index, Science Direct, The LIS Resource Center data base, Wilson Web, and Ingenta, as well as general web based search engines such as Google and Google Scholar. This phase made use of data sets developed by the CT DEP on fisheries in LIS (e.g. Gottschall et al. 2000), and other sources that contain applicable information on food web components and trophic characteristics (e.g. Steimle et al. 2000, Guénette et al. 2001, and references therein). We collected data stretching back to the mid 1900's in LIS, but tried to use the most recent data available for food web model development. Information collected on each species or taxonomic group (e.g. phytoplankton) was entered into a Excel database and references were entered into a bibliographic data base (Endnote). These are provided as part of the digital appendix to this report. We also made use of several online data bases to extract certain types of information. In particular we used Fishbase (http://www.fishbase.org/) to obtain information (e.g. trophic interactions, diet composition, predators, production, consumption) on fishes included in the food web model.

### *Development of Ecopath food web models*

## Ecopath Overview

Advances in computer based modeling have allowed scientists to assemble more complex food webs and provide quantitative tools that allow for expanded analysis (Drossel & McKane, 2003). One of these approaches, Ecopath with Ecosim (Christensen et al., 2000), is being increasingly used for estuarine and marine systems (Okey, 2001; Stanford & Pitcher, 2004; Christensen et al., 2005). It creates a static, mass balanced model of a system through values of biomass, production, consumption, diet composition and fishing pressure and includes a dynamic simulation module for policy exploration. It was first successfully applied to ecosystems by Christensen and Pauly (1992) in the Alaska Gyre. The basic program was introduced as a steady state model based on Polvina's (1984) regression equations for estimating organism biomass. Since then, numerous ecological theories have been incorporated into the program, such as Ulanowicz's (1986) analysis of flows between elements of an ecosystem, creating a steady-state model that assumes that the mass balance over a given year returns to its original state (Christensen & Walters, 2004; Okey, 2001). Ecopath provides a modeling approach that summarizes knowledge of a particular ecosystem, allowing for environmental policy exploration and scenario modeling. Since Christensen and Pauly's (1992) application in the northeast Pacific, scientists in over 120 countries have applied Ecopath to other ecosystems such as the Baltic sea (Sandberg et al., 2000; Harvey et al., 2003), coral reefs (Arias-González et al., 2004: Grigg et al., 1984), lakes (Kitchell et al., 2000), and numerous other aquatic systems in a variety of locations.

Despite certain difficulties, ecologists are increasingly developing food web models for estuarine environments. For example, Monaco and Ulanowicz (1997) created food webs for Chesapeake Bay, Delaware Bay, and Narragansett Bay with Ecopath and network analysis software in order to determine which of the three was more impacted. Their comparative analyses of food web statistics, such as net production or biomass and respiration ratios, showed that Narragansett Bay was the least impacted while Chesapeake and Delaware Bays had a better ability in adapting to environmental stresses. Ecopath modeling has been applied to the estuaries of northwest France. Rybarcyzk et al. (2003) and Rybarcyzk and Elkaim (2003) have created detailed biomass flow diagrams and characterized the maturity, recycling, and development of the Bay of Somme and Seine estuaries through examination of Ecopath web statistics and network indices, such as ascendancy, development capacity, and omnivory indexes. However, all of these estuarine food web models had less then 20 species groups involved, creating a less complex framework for examination of system dynamics and production. Some food webs, including the Atlantic continental shelf (Okey, 2001) and a newly constructed model of Chesapeake Bay (Christensen et al., 2005), are much larger food webs with 55 and 45 species groups, respectively. Investigation of flow diagrams and other statistics is much more complex in these larger systems since an increase in species interactions creates a more intricate web (Pimm, 2002). Creation of food web models, especially through Ecopath with Ecosim, in larger estuarine systems can constitute a critical first step in understanding these complex systems and in a sense creating a "map" of the biological interactions which drive a system (Christensen et al., 2000).

## Ecopath Model Structure

Ecopath creates a static mass-balanced model of resources and interactions in an ecosystem through linked biomass components. Instead of creating a web from the bottom up method associated with most food webs, Ecopath generates the web in a piecemeal fashion. Components could be a single species or a guild of multiple species that constitute a trophic level (Christensen et al., 2000). The model is comprised of two equations for each trophic or functional group (i): one for production and one for energy balance. The net production equation represents the basic parameters that are needed in the model with:

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

or

$$P_i = Y_i + B_i * M2 + E_i + BA_i + P_i *(1 - EE_i)$$

Where $P_i$ is the total production rate, $Y_i$ is the fisheries catch per unit area/time, $B_i$ is biomass, M2 is total predation rate, $E_i$ is net migration rate (emigration - immigration), $BA_i$ is biomass accumulation rate, and $P_i * (1\text{-}EE_i)$ is other mortality such as disease or old age. Redefining of this equation yields the basic parameters needed to construct the model,

$$B_i * (P/B)_i * EE_i = Y_i + \Sigma B_j * (Q/B)_j * DC_{ji} + BA_i + NM_i$$

Where $P/B_i$ is the production/biomass ratio, $EE_i$ is the ecotrophic efficiency (proportion of production utilized in system), $Q/B_i$ is the food consumption/biomass ratio, $DC_{ij}$ is the contribution of prey to the diet of predators, and $NM_i$ is the net migration of prey (Christensen et al., 2000; Christensen & Walters, 2004). Allen (1971) found that, under normal conditions, the production/biomass ratio corresponds to the total mortality rate, Z.

The Ecopath program sets up the linear equation for each functional group of the proposed model and solves for one of the following, biomass, production/biomass, consumption/biomass ratio, or ecotrophic efficiency. Therefore, at least three of the four previous mentioned parameters must be entered into the model, although it is not necessary for the same parameter to be entered for all the functional groups/taxa. Other parameters including migration rate, catch rate, biomass accumulation rate, assimilation rate, and diet compositions are not estimated by the model and must therefore be entered by the modeler.

Through numerous loop algorithms in the parameterization routine, estimated values are generated for any missing parameters. The loop algorithms are given in the Ecopath with EcoSim Help System (www.ecopath.org). After all missing values are estimated, the linear equation for each functional group is solved through generalized matrix inversions (Mackay, 1981).

The mass balance of each completed production equation is checked through an energy balance equation:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food}$$

or,

$$Q_i = P_i + R_i + U_i$$

If the consumption for the model does not equal the production and loss terms, then the biomass would change overtime disrupting the steady state assumption of the model. It should be noted that nutrient related data could be successfully substituted for energy related terms, with the removal of the respiration term.

After all the missing parameters are estimated, the model must be balanced. Any $EE_i > 1$ represents a thermodynamic problem or an unbalanced group. For these “unbalanced groups,” the energy produced is greater than the predatory or fishing demand on that group. Balance is restored by manipulating input values and running the parameterization routine again until the $EE_i$ of all groups are less then one. Typically, balancing is completed by manual alterations to the data by the user. However, several problems are associated with manual balancing; reliable data is often changed to adjust unreliable data, intense knowledge and discipline of the model system is required for good decision making, and final results are usually non-unique (Christensen et al., 2004; Kavanagh et al., 2004). Therefore, Kavanagh et al. (2004) created an automated balance approach that utilizes autobalancing algorithms. For this approach, the user sets confidence intervals that define the range of perturbations allowed from the original values of the inputted parameters. The selected perturbations can be random and defined by the user through percentage of standard deviation, or a gradient descent with the step sized defined by set pedigrees for each parameter. The parameters with the least reliable data should have the broadest confidence intervals, thus preventing the alteration of more dependable parameter data. The program can be run multiple times, until EE’s of less then one are achieved for all the functional groups/taxa. For a detailed description of the balancing algorithms, refer to Kavanagh et al. (2004).

Balancing of the model should not only be based on the automated mass balance program described above. Manual manipulation may also be required. For example, it is important to examine the P/Q rates and cannibalism of species since these variables may not be directly affected in automatic balancing (Christensen et al., 2000; Okey, 2001). For marine fish species, acceptable P/Q values should range between 0.1 and 0.5, with the lowest values occurring in top predators (Stanford & Pitcher, 2004). Cannibalism within unbalanced functional groups/taxa should also be reduced in order to redirect energy flow to trophic connections.

Once the model is balanced, Ecopath produces summary statistics, ecosystem indices, and biomass flow graphs. These indices and diagrams are used to identify the key food web species on overall food web structure and balance, and also help to identify areas of missing data.

Summary statistics of the overall balanced model describe the production, consumption, and respiration of the entire system. They are provided to assess ecosystem status, such as system maturity, and will be discussed in the Discussion. The indices, defined by Odum (1969) and Ulanowicz (1986), can measure the organization and upper limit to the size of the food web.

Total System Throughput (T) reflects the size and power of the food web in terms of the sum of flows through all the functional groups/taxa. Ascendancy (A) reflects the size and organizations between the functional groups/taxa and lies between 0 and the development capacity (C), the upper limit to the ascendancy. Overhead (Φ) accounts for the imperfections of the system, or in other words the cost to the system. The system's growth, organization, and development can be measured through the A/C (ascendancy/development capacity) ratio, with lower values representing stressed and less mature or organized systems. Additionally, higher development capacity values indicate systems that contain more energy reserves to counteract any outside disruptions (Monaco & Ulanowicz, 1997; Christensen & Pauly, 1992).

## Ecosim

Ecosim is a simulation program that is incorporated into the Ecopath modeling software. It has yet to be applied to the LIS model, however we provide an example of how it can be used in the **Discussion** portion of this report. Ecosim consists of time dynamic simulations in Ecopath that fits predicted biomasses to time series data or allows for the manipulation of the biomass of functional groups in the food web model. In both cases, simulations are used to assess how changes in the biomass of one or a set of functional groups will affect the others over time in response to altered fishing pressures or environmental conditions. The program can also split and model the separate dynamics of the lower plankton levels and upper fish levels where production and consumption differ greatly. Derived from Ecopath, Ecosim sums consumption rates and expresses predation by all predators through coupled differential equations,

$$dB_i/dt = g_i \sum Q_{ji} - \sum Q_{ij} + I_i - (MO_i + F_i + e_i) * B_i$$

where $dB_i/dt$ is the growth rate during a time interval dt in terms of (i), $g_i$ is the net growth efficiency, $MO_i$ the estimated non predation natural mortality, $F_i$ is the fishing mortality rate, $e_i$ the emigration rate, and $I_i$ the immigration rate. The program is not as well developed as Ecopath, but it addresses temporal variations in food web dynamics and structure that Ecopath does not (Walters et al., 1997; Walters et al., 2000).

## Data Sources

The information and data needed to develop the Ecopath model for offshore Long Island Sound, including species composition, biomass, production, consumption, and diet composition were collected from an extensive query of several large data bases (ASFA: Aquatic Sciences & Fisheries Abstracts; BIOSIS Previews, Science Citation Index, Science Direct, CT DEP Long Island Sound Resource Center, Wilson Web, Ingenta) and comments from persons with LIS expertise in government and private agencies. Other Ecopath models, or those currently being developed, for systems similar to LIS, such as Chesapeake Bay, were also used to provide supplement information in the development of the LIS model. There was no restriction on the time period of when and where the data was collected, however data from a 10 year period, 1995 to 2005, were used to the extent possible.

## Functional Group Descriptions and Basic Input Parameters

Thirty two functional groups/taxa were incorporated into the LIS offshore Ecopath model (Table 1). These were selected based on natural history and diet data acquired in the literature from discussions with other researchers, and from the conceptual models shown in Figs. 10-12. All parameters for the functional groups/taxa were entered as tons per km$^2$ in wet weight. All data sources are listed in Table 2.

### *Detritus*

Detritus biomass was based on reported findings in Mann (2000). A value of 300 t/km$^2$ represents the minimum amount of detritus that has been found in estuaries such as Long Island Sound.

### *Phytoplankton and Zooplankton*

Phytoplankton biomass was calculated from chlorophyll *a* data collected by the CTDEP Water Quality Program during 2000-2005. Surface and bottom samples were averaged from 17 offshore stations in central LIS. Each station's average was multiplied by half of the station depth to convert the value from cubic kilometers to square kilometers. All chlorophyll *a* values were converted to carbon with a 40:1 ratio and then to wet weight by a multiplier of 20 (Crisp, 1975; De Jonge, 1980 ).

Phytoplankton production was taken from Goebel and Kremer’s (2007) report of 400 g C/m$^2$/year. Production was converted to wet weight by a multiplier of 20 given by Crisp (1975) and divided by the phytoplankton biomass to yield a final P/B value of 117.57 t/km$^2$ wet weight.

Zooplankton biomass was determined from data in Dam and McManus (2006). Biomass was averaged from 5 offshore sites in Long Island Sound and converted from cubic meters to square meters by dividing by half of the station depth. The final values were converted from dry weight to wet weight biomass by a conversion factor of 5:1 given in Cushing et al. (1958).

P/B and Q/B values for zooplankton in LIS were not found in the literature and efforts to calculate these values from the available biomass data were unsuccessful. Therefore values were substituted from the Chesapeake Bay constructed by Christensen et al. (2005).

### *Epifauna and Infauna*

Data for benthic organisms were broken down into two categories: epifaunal scavengers and infauna. Additionally, infaunal organisms were categorized as either deposit or filter feeders. Biomass and P/B values for all benthic groups were taken from Mann (2000) and

Sanders (1956). Epifaunal scavengers were converted from DW t/km$^2$ to wet weight with a 5:1 factor (Lampitt et al., 1986). The biomass of infaunal filter feeders, 28.85 DW t/km$^2$, was converted to wet weight by a 15:1 conversion factor described by Lampitt et al. (1986). An ash free dry weight to wet weight conversion of 15:1 was used for infaunal deposit feeders using a reported biomass value of 6.6 AFDW t/km$^2$ (Okey, 2001).

The Q/B values for all three functional groups were taken from the Chesapeake Bay Ecopath model (Christensen et al., 2005) due to lack of Long Island Sound data.

### *Other Invertebrates*

Four large invertebrates are represented in the offshore model: long finned squid (*Loligo pealeii*), blue crabs (*Callinectes sapidus*), spider crabs (*Libinia emarginata*), and American lobster (*Homarus americanus*). Biomass estimates for all four groups were based on averages computed from CT DEP trawl survey data collected from 1995 to 2005 (CTDEP, 2006). The CT trawl survey utilized a stratified random sampling design, employing a 14 m otter trawl with a 51mm codend. The nearshore and offshores areas of LIS are divided into 1 x 2 nautical mile blocks with sampling sites selected randomly in each block. Sampling occurs in spring and fall periods with 40 sites sampled monthly for a total of 200 sites annually.

Squid, blue crab, and spider crab P/B values were taken from an Atlantic Bight model created by Okey (2001). American lobster P/B was determined from natural moralities described by Briggs and Mushacke (1984) and fishing mortalities reported by the National Marine Fisheries Service. Blue crab, spider crab, and American lobster Q/B values were also taken from Okey (2001) while the squid Q/B ratio was taken from Christensen et al. (2005).

### *Finfish*

Finfish that represented more the 0.1% of the CTDEP trawl survey catch and had sufficient life history data were considered for the model.

Finfish biomass values were calculated by averaging biomass data collected from each trawl performed by the CT DEP trawl survey previously described. Bay anchovy (*Anchoa mitchilli*) was present in the trawl survey, however the CTDEP did not measure biomass due to low net retention. Therefore, an EE of 0.95 was entered into the model, as described by Christensen et al. (2000), in order to allow Ecopath to estimate bay anchovy biomass.

Limited published data was found concerning P/B ratios for Long Island Sound finfish. Therefore total mortality (Z), or the combination of natural mortality (M) and fishing mortality (F), was used as a proxy for P/B values in finfish species. Natural mortality was calculated for finfish species with the empirical equation given by Pauly (1980):

$$M = K^{0.65} * L_{inf}^{-0.279} * T^{0.463}$$

Where K is the von Bertalanffy growth constant, $L_{inf}$ is the asymptotic length in cm, and T is the LIS average water temperature of 12.5 ºC. K values were taken from studies of similar habitats listed in www.fishbase.org while $L_{inf}$ was calculated from length frequencies presented in the CT DEP trawl survey (Table 4). Fishing mortality was calculated as F = fish catch/biomass from the reported Connecticut commercial and recreational fish landings for bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), scup (*Stenotomus chrysops*), winter flounder (*Pseudopleuronectes americanus*), summer flounder (*Paralichthys dentatus*), and tautog (*Tautoga* onitis) only. These finfish represent the dominant fishing industries in the Sound while any fishing associated with the other finfish was considered to small to be significant in the fishing mortality calculation.

Similarly, Q/B values for finfish were calculated with Palomares and Pauly's (1998) refined empirical equation:

$$\text{Log } Q/B = 7.964 - 0.204\log W_{inf} - 1.965T' + 0.083A + 0.532h + 0.398d$$

Where T' is 1000/average temperature in Kelvin, $W_{inf}$ is the asymptotic weight in grams, A is aspect fin ratio, d is equal to 1 for carnivores and 0 for herbivores and detritivores, and h is equal to 0 for carnivores and 1 for herbivores and detritivores. $W_{inf}$ was determined from lengths report in CT DEP (2006) and length to weight frequencies presented in fishbase.org (Froese and Pauly, 2000). Estimations based on the above variables were calculated by a "Q/B calculator" presented in www.fishbase.org (2006).

Length to weight frequencies were not available for scup, red hake (*Urophycis regia*), striped sea robin (*Prionotus evolans*), windowpane flounder (*Scophthalmus aquosus*), winter flounder, and blueback herring (*Alosa aestivalis*). Therefore, the Q/B values for these finfish were taken from Christensen et al. (2005).

### *Diet Composition*

Diet compositions represent the trophic links between the functional groups and are entered as percent weight. The data sources are listed in Table 2 and percentages in Table 5. Unfortunately, diet description for Long Island Sound species is very limited. The majority of finfish diet compositions came from feeding areas surrounding Long Island Sound examined by Bowman et al. (2000) with supplemental information obtained from the Chesapeake Bay model (Christensen et al., 2005).

### *Fishery Data*

As mentioned previously, annual recreational fish landings (lbs) for bluefish, striped bass, scup, tautog, winter flounder, and summer flounder in Connecticut were taken from the CTDEP Recreational Fishing Survey from 1995-2005. Landings for party/charter boat mode and private/rental boat mode were included only. Commercial landings data (lbs) were collected from the NMFS database (http://www.st.nmfs.gov/st1/ commerical/index.html) for the five recreational finfish species as well as American Lobster. All landings were converted to catch/km$^2$ and mortalities were determined through F=biomass/catch. The fishing mortalities calculated from these are presented in Table 4. Landings from New York and Rhode Island were not included in order to reduce the influence on offshore Atlantic fishing on the Long Island Sound data and calculations.

## 3-D Food Web Modeling

Another software program, FoodWeb3D (Yoon et al., 2003), was also employed to enhance visualization and understanding of the structure of the LIS food web. FoodWeb3D creates webs from .web or .tro data files and displays the results as a 3-dimensional web display file (.wdf). Species are classified by a number and each interaction from the finalized Ecopath model was entered into a column. For example, species 1 eats species 3, 5 and 7. Three separate entries are made representing each of these interactions until every pathway has been accounted for. Once the model is completed, the user is allowed to change its size, move it left/right and up/down, and alter its arrangement. Webs can be viewed from a rectangular or cylindrical aspect and nodes representing functional groups can be rearranged by linkedness, generality, or vulnerability. The software was only recently created and is still in the process of being development. One problem developers are currently working on is the ability to add labeling to the nodes for easier identification of food web components. Examples of visualizations of the LIS food web are given in the results and the Foodweb3D software and associated file for the LIS food web are provided in the Digital Appendix of this report.

**Table 1:** Common and scientific names of the 32 functional groups/taxa selected for the LIS offshore model.

| **Common Name** | **Scientific Name** |
|---|---|
| Striped Bass | *Morone saxatilis* |
| Bluefish | *Pomatomus saltatrix* |
| Tautog | *Tautoga onitis* |
| Weakfish | *Cynoscion regalis* |
| Black Sea Bass | *Centropristis striata* |
| Scup | *Stenotomus chrysops* |
| Red Hake | *Urophycis regia* |
| Silver Hake | *Merluccius bilinearis* |
| Striped Sea Robin | *Prionotus evolans* |
| Smooth Dogfish | *Mustelus canis* |
| Little Skate | *Leucoraja erinacea* |
| Winter Flounder | *Pseudopleuronectes americanus* |
| Windowpane Flounder | *Scophthalmus aquosus* |
| Summer Flounder | *Paralichthys dentatus* |
| Fourspot Flounder | *Paralichthys oblongus* |
| Butterfish | *Peprilus triacanthus* |
| American Shad | *Alosa sapidissima* |
| Atlantic Herring | *Clupea harengus* |
| Bay Anchovy | *Anchoa mitchilli* |
| Alewife/Blueback Herring | *Alosa psuedoharengus /Alosa aestivalis* |
| Spot | *Leiostomus xanthurus* |
| Atlantic Menhaden | *Brevoortia tyrannus* |
| Long finned squid | *Loligo pealeii* |
| American Lobster | *Homarus americanus* |
| Blue crabs | *Callinectes sapidus* |
| Spider crabs | *Libinia emarginata* |
| Epifauna - scavengers | - |
| Infauna - filter feeders | - |
| Infauna - deposit feeders | - |
| Mesozooplankton | - |
| Phytoplankton | - |
| Detritus | - |

Table 2: Ecopath with Ecosim input parameter data sources for each functional groups/taxa. See Table 1 for species scientific names. Estimated values were used for the mesozooplankton and smaller invertebrates based on general ecological behavior. For example, mesozooplankton's diet was assumed to be 100% phytoplankton.

| Group | Biomass (t km $^{-2}$) | P/B (year$^{-1}$) | Q/B (year$^{-1}$) | Diet Composition |
|---|---|---|---|---|
| Detritus | Mann, 2000 | - | - | - |
| Phytoplankton | CT DEP LIS Water Quality Monitoring Program, 2005 | Goebel & Kremer, 2007 | - | - |
| Mesozooplankton | Dam & McManus, 2006 | Christensen et al., 2005 | Christensen et al., 2005 | Estimate |
| Infauna - deposit feeders | Mann, 2000; Sanders, 1956 | Mann, 2000 | Christensen et al., 2005 | Estimate |
| Infauna - filter feeders | Mann, 2000; Sanders, 1956 | Mann, 2000; Sanders, 1956 | Christensen et al., 2005 | Estimate |
| Epifauna - scavengers | Mann, 2000; Sanders, 1956 | Mann, 2000; Sanders, 1956 | Christensen et al., 2005 | Christensen et al., 2005 |
| Spider crabs | CT DEP, 2006 | Christensen et al., 2005 | Christensen et al., 2005 | Okey, 2004 |
| Blue crabs | CT DEP, 2006 | Christensen et al., 2005 | Christensen et al., 2005 | Christensen et al., 2005 |
| American Lobster | CT DEP, 2006 | Briggs & Mushacke, 1984 | Okey, 2001 | Okey, 2004 |
| Long finned squid | CT DEP, 2006 | Okey, 2001 | Okey, 2001 | Macy, 1982; Bowman et al, 2000 |
| Atlantic Menhaden | Christensen et al. , 2005 | Okey, 2001; Christensen et al. , 2005 | Okey, 2001 | Bowman et al, 2000 |
| Spot | CT DEP, 2006 | Christensenet al. , 2005 | Palomares & Pauly, 1998; CT DEP, 2006 | Christensen et al., 2005 |
| Alewife/Blueback Herring | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Pauly, D. 1989 | Bowman et al, 2000 |
| Bay Anchovy | - | Christensen et al., 2005 | Christensen et al., 2005 | Christensen et al., 2005 |
| Atlantic Herring | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998; CT DEP, 2006 | Christensen et al., 2005 |
| American Shad | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998; CT DEP, 2006 | Bowman et al, 2000 |
| Butterfish | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998; CT DEP, 2006 | Bowman et al, 2000 |
| Four Spotted Flounder | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998; CT DEP, 2006 | Bowman et al, 2000 |
| Summer Flounder | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998; CT DEP, 2006 | Christensen et al., 2005 |

Table 2. Continued

| | | | | |
|---|---|---|---|---|
| Windowpane Flounder | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Christensen et al., 2005 | Bowman et al, 2000 |
| Winter Flounder | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Christensen et al., 2005 | Bowman et al, 2000 |
| Little Skate | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998; CT DEP, 2006 | Bowman et al, 2000 |
| Smooth Dogfish | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998; CT DEP, 2006 | Bowman et al, 2000 |
| Striped Sea robin | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998;CT DEP, 2006 | Richards, et al. 1979 |
| Silver Hake | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Pauly, D. 1989 | Bowman et al, 2000 |
| Red Hake | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Christensen et al., 2005 | Bowman et al, 2000 |
| Scup | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Christensen et al., 2005 | Bowman et al, 2000 |
| Black Sea Bass | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998; CT DEP, 2006 | Bowman et al, 2000 |
| Weakfish | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998; CT DEP, 2006 | Hartman & Brandt, 1995 |
| Tautog | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998; CT DEP, 2006 | Christensen et al., 2005 |
| Bluefish | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998; CT DEP, 2006 | Bucket et al, 1998;<br>Richards, 1976 |
| Striped Bass | CT DEP, 2006 | Pauly, 1980; CT DEP, 2006 | Palomares & Pauly, 1998; CT DEP, 2006 | Hurst & Conover, 2001 |

Table 3. Natural mortality (M) calculation variables for given finfish species for the LIS Ecopath model.  K is the von Bertalanffy growth constant taken for fishbase.org , T is the average annual temperature of LIS,  $L_{max}$ is the maximum length, $L_{inf}$ is the asymptotic length, and SE is the standard error.

| Common Name | K (/year) | T (c ) | $L_{max}$ (cm) | $L_{inf}$ (cm) | M based on K | SE |
|---|---|---|---|---|---|---|
| Bluefish | 0.26 | 12.5 | 101.6 | 104.5 | 0.34 | 0.22 - 0.51 |
| Tautog | 0.1 | 12.5 | 67 | 69.3 | 0.18 | 0.12 - 0.28 |
| Weakfish | 0.2 | 12.5 | 91 | 93.7 | 0.28 | 0.19 - 0.43 |
| Black Sea Bass | 0.19 | 12.5 | 57 | 59.2 |  | 0.20 – 0.46 |
| Scup | 0.18 | 12.5 | 45.7 | 47.6 | 0.31 | 0.2 - 0.47 |
| Silver Hake | 0.65 | 12.5 | 39 | 40.7 | 0.84 | 0.55 - 1.27 |
| Red Hake | 0.24 | 12.5 | 52 | 54 | 0.37 | 0.25 - 0.56 |
| Striped Sea Robin | 0.17 | 12.5 | 44 | 45.8 | 0.3 | 0.2 - 0.45 |
| American Shad | 0.38 | 12.5 | 51 | 53 | 0.53 | 0.35 - 0.8 |
| Smooth Dogfish | 0.26 | 12.5 | 129 | 132 | 0.32 | 0.21 - 0.48 |
| Little Skate | 0.36 | 12.5 | 50 | 52 | 0.51 | 0.36 - 0.82 |
| Summer Flounder | 0.25 | 12.5 | 77 | 79.5 | 0.35 | 0.23 - 0.53 |
| Fourspot Flounder | 0.28 | 12.5 | 40 | 41.7 | 0.44 | 0.29 - 0.67 |
| Windowpane Flounder | 0.29 | 12.5 | 36 | 37.6 | 0.47 | 0.31 - 0.71 |
| Winter Flounder | 0.18 | 12.5 | 53.3 | 55.4 | 0.35 | 0.25 - 0.89 |
| Alewife | 0.19 | 12.5 | 32 | 33.5 | 0.35 | 0.23 - 0.53 |
| Butterfish | 0.52 | 12.5 | 25 | 26.3 | 0.79 | 0.52 - 1.2 |
| Atlantic Herring | 0.26 | 12.5 | 34 | 35.6 | 0.44 | 0.29 - 0.66 |
| Blueback Herring | 0.19 | 12.5 | 30 | 31.5 | 0.36 | 0.24 - 0.54 |

Table 4: Fishing mortality of dominant recreational and commercial fisheries in LIS. F values were determined by biomass/catch after conversion of landing data to catch/km$^2$.

| Fish | F (catch/km$^2$) |
|---|---|
| Striped Bass | 1.21 x 10-6 |
| Bluefish | 1.04 x 10-6 |
| Tautog | 1.07 x 10 -7 |
| Winter Flounder | 2.97 x 10-7 |
| Scup | 1.67 x 10-7 |
| Summer Flounder | 1.44 x 10-6 |
| American Lobster | 1.4 x 10-6 |

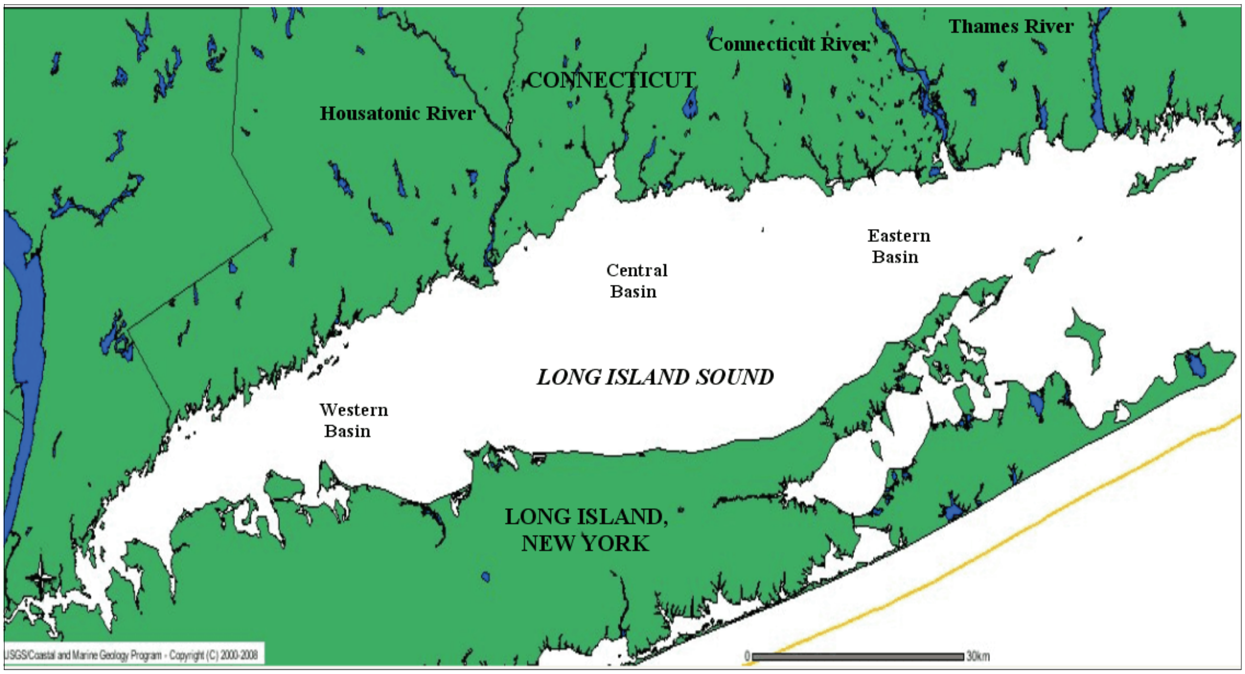


Figure 13: Map of Long Island Sound. Image provided by United States Geological Survey (USGS) Marine Geology Program (http://woodshole.er.usgs.gov/project-pages/longislandsound/index.htm)

## RESULTS

### *Literature Review and Data Assessment*

We reviewed over 2,200 papers and reports published or made available prior to 2005 and screened them to identify which ones might provide information that would be pertinent to elucidating the stucture and dynamics of food webs in LIS. We primally reviewed publications and reports that were specifically focused on Long Island Sound, but also considered some studies that were done in nearby geographic areas. Approximately 407 of these publications and reports were selected as potentially usable, and entered into trophic-level specific Endnote Libraries (see Digital Appendix) and reviewed in terms of the suitability of the data they contained as needed for the Ecopath model. Separate libraries were developed for plants/plankton, crustaceans/gastropods, other benthic organisms, fish, birds/mammals, studies that contained multiple levels, and other studies that could not be categorized in the previous groups.

Our assessment of the literature shows that most studies that potentially contained food web related data have focused on primary producers and benthos (Fig. 14), but that does not necessarily mean they contained data suitable for food web modeling. Furthermore, many of these studies were conducted in the 1970's and 1980's (Fig. 14), indicating that most food web applicable data for LIS are generally approximately 20 - 30 yrs old and few publications and data sets are available reflecting current (early 2000's) conditions in LIS. The candidate studies that we felt might provide the best information were grouped into the general depth-based groupings including studies conducted in coves and embayments, nearshore waters (< 10 m) or deeper water areas (> 10 m). Studies which spanned several depth ranges were included in each group. Data on various food web variables such as abundance , biomass, production and P/B ratios were then extracted for each study and compiled in Excel data bases (see Digital Appendix). Review of these data bases indicates that most studies report abundance values, but very few provided food-web critical data such as for production, biomass, and P/B. For example, there 12, 6, and 3 papers that provided data on phytoplankton / plant production in coves and embayments, nearshore and deep water areas, respectively, but only 4 papers that provided this data for any upper, i.e. consumer, trophic levels. A similar situation was found for biomass data. Particularly lacking was biomass and production data for infauna and epifauna, although secondary production has been studied in a few species. Diet information was also not available for many species specifically from LIS and more general diet composition studies (e.g. Bowman et al. 2000) needed to be used to assign diets for the Ecopath model development. Given this lack of information for many areas of LIS and the taxa that inhabit them, we focused our efforts on constructing a nearshore/ offshore mixed model as these were the portions of LIS where the most data was available either in data bases such as the CT DEP Trawl Survey or recent data and assessments by other researchers. Some however were from recent work conducted in other estuarine and coastal systems (see Table 2). A more detailed assessment of data needs based on our review is provided in the **Discussion** section of this report.

### *Ecopath food web model of Long Island Sound*

The LIS food web model we developed consists of 32 functional groups / taxa, including 22 fish groups, four large invertebrates groups, three general benthic faunal groups, mesozooplankton, phytoplankton, and detritus. The unbalanced input parameters are given in Tables 5 and 6. This information and the initial diet compositions were used to estimate the other food web parameters need in the model and to balance the model. The finalized, balanced parameters are given in Tables 7 and 8.

After the initial basic parameterization, 11 functional groups / taxa had an EE > 1 (Table 9), i.e. they were unbalanced as EE by definition is $\leq 1$. Additionally, six fish taxa had P/Q values either < 0.1 or > 0.5. Before the automatic mass balance program was utilized, the P/B or Q/B values of these taxa (Table 10) were altered to achieve the recommended P/Q values. The P/B values for striped bass, tautog, and black sea bass were increased while the Q/B values for striped searobin, Atlantic herring, and alewife/blueback herring were decreased.

For this model, we felt that the least reliable data set was the diet compositions (DC). Therefore, for automatic balancing, the diet composition for each group was set with the broadest confidence intervals while the biomass data had the lowest confidence intervals. Additionally, a gradient descent approach was selected (see EWE User's Guide) since the perturbations for the steps could be set for the least robust data. Confidence intervals of ± 80% for DC, ±10% for biomass, and ±30% for P/B and Q/B plus perturbations of 25% for DC, 5% for biomass, and 20% for P/B and Q/B resulted in all EE's <1. These settings showed the least number of required runs to achieve EE's <1 and the smallest adjustments to the original parameter data. The changes in the values of the model variables as a result of automatic balancing can be seen by comparing the finalized, balanced values (Tables 7 and 8) with the unbalanced values (Tables 5 and 6). In this fashion the food web model was balanced which then allowed for the calculation of various food web metrics which characterize the LIS food web and its dynamics.

## Food web structure and trophic flows

Based on the balanced model, the functional groups / taxa (herein just functional groups) comprising the LIS offshore food web span trophic levels 1- 4.12 (Figure 15, Table 7). [Note: "In Ecopath, the trophic levels [in some of the analyses] are not necessarily integers (1, 2, 3...)..., but can be fractional (e.g., 1.3, 2.7, etc.)... A routine assigns definitional trophic levels (TL) of 1 to producers and detritus and a trophic level of 1 + [the weighted average of the preys' trophic level] to consumers. Following this approach, a consumer eating 40% plants (with TL = 1) and 60% herbivores (with TL = 2) will have a trophic level of $1 + [0.4 \cdot 1 + 0.6 \cdot 2] = 2.6$." (EWE User's Guide 2004)] Bluefish, weakfish, silver hake, and four spotted flounder comprised trophic levels over 4, representing the top consumers (predators) of the web as constructed. The remaining fish taxa (including both open water and demersal species), crustacean taxa, and long finned squid dominate trophic level 3. Four species of fish, including butterfish, Atlantic herring, scup and Atlantic menhaden were in the mid to upper trophic level 2, whereas mesozooplankton and the infaunal and epifaunal functional groups represent the lower trophic 2 levels. Phytoplankton and detritus are assigned to trophic level 1. The bulk of the web is between trophic levels 2 and ~3.5.

The connectance web (Figure 16) shows that the LIS food web as constructed has a complex set of predator / prey and consumption interactions among the functional groups in the web. The three dimensional representation of the LIS food web model (Figures 17 and 18) shows this complexity in greater detail. In this depiction, the color of each node represents its trophic level. Trophic level 1, detritus and phytoplankton, are the red nodes at the bottom of the web. Trophic levels 2 and 3 are shown as orange nodes and the functional groups found in trophic level 4 are the yellow nodes. The predator/prey links follow an opposite color scheme, with interactions at lower levels being yellow and interactions at higher trophic levels being more purple. In the arrangements shown in Figure 17 and 18, the nodes that have the most links to predators and prey point the farthest to the rear. For example, the 3D web images show that the epifauna-scavengers functional group has the most predator-prey linkages. The loops that go from a node to itself represent cannibalism, generally larger fish of a species consuming younger/smaller fish of the same species. A full description and demonstration of the 3D web model of the LIS food web is given in the Digital Appendix, along with the software and the file needed to run the visualization.

The EcoPath software provides modules for creating connectance plots for individual functional groups in the food web. An example for the zooplankton functional group shows that in the model as constructed they feed exclusively on phytoplankton and that they are fed upon by various fish taxa, and interestingly, quite heavily by the epifauna-scavengers functional group (Figure 19).

The connectance web, along with the balanced model and diet composition matrix allows for the calculation of various metrics quantifying the paths, structure and linkages in the web and the flows along those paths within the web. Overall there are 1,162 cycles (linked pathways) in the food web, an average mean length of 6.7 (which is calculated by dividing the total number of links in all the cycles by the total number of cycles). There are 1,298 pathways leading from phytoplankton to upper trophic levels, with a mean path length of 6.79. There are 739 pathways from detritus to upper level consumers with a mean path length of 6.13. Other measures of connectance and path length are given in Table 11. Different measures of path length, roughly the number of functional groups biomass passes through in the system, ranged from ~2.3 - 3.1, indicating relatively short food chains among the functional groups in the food web. The top predators feed primarily from trophic level 2 and 3, with bluefish and silver hake only consuming from level 3. The species in trophic level 3 fed more heavily on infauna, epifauna and mesozooplankton, as well as on other species in trophic level 3. All fish species lower then trophic level 3 showed a small percentage of detritus in their diets. The fish species of trophic level 2 feed on infauna and epifauna and zooplankton also located in trophic level 2, as well as organisms in trophic level 1.

The complexity of the LIS food web, as revealed by the connectance plots and the high number of pathways that occur within the system, reflects the fact that there is high niche overlap in terms of diets and predation within the food web. Many of the species show extensive diet overlap (Figure 20) and measures of niche overlap indicate that 15 functional groups have high prey overlap and that 8 functional groups have high overlap of both prey and predators (Figure 21). Functional groups that have high very overlap were mostly those between trophic levels 2 and 3. These included striped sea robin, smooth dogfish, little skate, winter flounder windowpane flounder and summer flounder and also long finned squid, American lobster and blue crabs.

The EcoPath software generates numerous measures of how biomass flows and cycles through the food web and related food web network metrics, providing insights into the overall dynamics of the system. Before presenting these results for the LIS food web model we present a brief overview of some of these measures taken from http://www.glerl.noaa.gov/EcoNetwrk/EcoNetwrkterms.htm :

> Ulanowicz (1986) has developed a suite of ecosystem level indices based on information theory. These indices characterize the state of a food web. They include total system throughput, ascendency, developmental capacity, overhead, and redundancy. Total system throughput is simply the sum of all the flows that occur in that food web; it characterizes the overall activity of the ecosystem. Ascendency is a measure of the size and organization of flows and can be interpreted as the tightness of the constraints that channel trophic linkages. Higher values for ascendency represent a food web with more trophic specialists, increased cycling, and higher efficiency, while lower values for ascendency represent a more generalist-based food web, decreased cycling, and lower transfer efficiencies. The limit, or upper bound, to ascendency is the developmental capacity. Developmental capacity is proportional to the variety of flows in a network, and is a surrogate for the complexity of an ecosystem. Developmental capacity minus ascendency equals overhead. Overhead represents the amount of developmental capacity that does not appear as organized structure or constraints. That is, overhead represents all the ambiguities of connection and incoherencies of flow (i.e., disordered activity) that are available to be reorganized as an ecosystem develops. Redundancy is that component of the overhead that reflects parallelisms in the internal pathways of trophic transfers so that any two compartments cannot be severed by elimination of a single intervening link.

Biomass flow diagrams indicate basic food web parameters (biomass, production, flow to detritus for each functional group (Figure 22) as well biomass flow among the functional groups (Figure 23). Trophic level 2 had the highest biomass per level of 277.709 t/km$^2$. Trophic level 1 was second with 68.045 t/km$^2$ while trophic levels 3 and 4 were lower at 10.323 t/km$^2$ and 0.627 t/km$^2$.

The calculation of trophic flows from one trophic level to the next in Ecopath is based on discrete trophic levels, and not the fractional trophic levels shown in the connectance plots of the food web. In this case Ecopath aggregates the entire system into discrete trophic levels, using a routine, based on an approach suggested by Ulanowicz (1995), that reverses the routine for calculation of fractional trophic levels. “Thus, for the example when a group obtains 40% of its food as a herbivore and 60% as a first-order carnivore, the corresponding fractions of the flow through the group are attributed to the herbivore level and the first consumer level” (EWE Users Guide 2004). The flows among trophic levels deceased sharply at each successive trophic level, typical of food web dynamics. The largest flows up the web were at trophic levels I - III. These levels also made the largest contributions to the flow to detritus and also system throughput. EcoPath also calculates the contribution to trophic flows of each functional group. For example, Table 13 provides the contribution of each functional group to the flow to detritus. Phytoplankton (trophic level I) biomass contributes the most to the flow of detritus at 3237.865 t/km$^2$/year. Trophic level II functional groups including zooplankton, infauna and epifauna also have significant contributions to the flow of detritus. The fish and larger invertebrate species of the higher trophic levels had much lower contributions.

A critical food web statistic is the efficiency with which the transfer of biomass occurs from one trophic level to the next. “The transfer efficiencies between successive discrete trophic levels [are] calculated as the ratio between the sum of the exports from a given trophic level, plus the flow that is transferred from trophic level to the next, and the throughput on the trophic level’ (EWE Users Guide 2004). In general, transfer efficiencies range from 5 - 20% in ecological systems, and average at ~ 10%. Based on the LIS food web model, trophic efficiencies ranged from 1 to 14.5%, and interestingly increased with trophic level (Table 14). This pattern is assessed in more detail in the Discussion.

Based on their food web characteristics (biomass, production, consumption, diet composition) the functional groups in an EcoPath model can be analyzed to assess their relative impacts on each other. These interactions are referred to as mixed trophic impacts and measure the effect that changes in the biomass of a functional group will have on the biomass of other groups in a system. Mixed trophic impact assessment for the LIS food web model indicates that several functional groups could have significant effects on other portions of the food web if their biomass changes (Figure 23). Increases in the biomass of phytoplankton would have positive effects on most groups as might be predicted in this type of analysis. However several other functional groups appear to potentially have both larger positive and negative impacts. These include epifauna-scavengers, the long finned squid, four spotted flounder, little skate and weakfish.

## Network Analyses and Summary Statistics

Summary statistics for the LIS food web model are provided in Table 15. Some of these values will be examined individually, however their full interpretation is achieved through comparison with similar systems. The LIS statistics will be compared to other estuarine and coastal systems in the **Discussion**.

The large system throughput of 19,553 t km$^{-2}$ yr$^{-1}$ for LIS represents the sum of all the flows in the system and is a measurement of total activity. LIS’s throughput indicates that the system is large and has high overall activity (Ulanowicz, 1986; Rybarczyk & Elkaim, 2003). According to Odum (1969), the high net production value (5,696.466 t km$^{-2}$ yr$^{-1}$) suggests that LIS is a less impacted then similar systems with smaller net production values.

The ascendancy (A) for the LIS model was 24,614.4 t km$^{-2}$ yr$^{-1}$ , with development capacity (C) and overhead (Φ) being 55,110.8 t km$^{-2}$ yr$^{-1}$ and 30495.1 t km$^{-2}$ yr$^{-1}$ (Table 16). This ascendancy, which represents system development, suggests that LIS is relatively mature and stable against outside perturbations. The ascendancy is also only half of the development capacity, which indicates the maximum potential for development in the system (Rybarczyk et al., 2003). Although the ascendancy value suggests that LIS is a mature system, it has yet to reach its full developmental potential. The higher value of overhead, calculated by A - C, represents this difference and quantifies conditions in the LIS food web that inhibit overall ecosystem development (Ulanowicz, 1986, Monaco & Ulanowicz, 1997). These are addressed in the **Discussion** and in reference to similar systems. The relative ascendancy (A/C) of 44.7 % also represents the possible organization and maturity that is actually realized in LIS. In other words, LIS has the potential to almost double its current development and organization (Ulanowicz, 1986; Rybarczyk & Elkaim, 2003).

Table 5: Input parameters, for the LIS offshore model, extracted from data sources and entered into Ecopath with Ecosim before balancing. B is biomass, P/B is the production/biomass ratio, Q/B is the food consumption/biomass ratio, and EE is ecotrophic efficiency.

| Group Name | B (t/km²/year) | P/B (t/km²/year) | Q/B (t/km²/year) | EE |
|---|---|---|---|---|
| Striped Bass | 0.0512 | 0.15 | 2.3 | |
| Bluefish | 0.184 | 0.34 | 3 | |
| Tautog | 0.0386 | 0.18 | 2.5 | |
| Weakfish | 0.0484 | 0.28 | 2.6 | |
| Black Sea Bass | 0.00355 | 0.31 | 3.5 | |
| Scup | 0.422 | 0.31 | 5.5 | |
| Red Hake | 0.0131 | 0.37 | 5 | |
| Silver Hake | 0.0056 | 0.84 | 3.85 | |
| Striped searobin | 0.0567 | 0.3 | 5 | |
| Smooth Dogfish | 0.147 | 0.32 | 2.7 | |
| Little Skate | 0.198 | 0.51 | 4 | |
| Winter Flounder | 0.175 | 0.35 | 4.9 | |
| Windowpane Flounder | 0.0524 | 0.47 | 4.9 | |
| Summer Flounder | 0.0507 | 0.35 | 2.8 | |
| Four Spotted Flounder | 0.0325 | 0.44 | 4 | |
| Butterfish | 0.251 | 0.79 | 5.7 | |
| American Shad | 0.00712 | 0.53 | 3.2 | |
| Atlantic Herring | 0.0399 | 0.44 | 4.59 | |
| Bay Anchovy | | 3 | 10.9 | 0.95 |
| Alewife/Blueback Herring | 0.00354 | 0.355 | 8.62 | |
| Spot | 0.00057 | 1 | 4.5 | |
| Atlantic Menhaden | 0.00743 | 0.3 | 7.8 | |
| Long Finned Squid | 0.09 | 1.7 | 7 | |
| American Lobster | 0.21 | 1.545 | 8.2 | |
| Blue crabs | 0.00142 | 1.38 | 4 | |
| Spider crabs | 0.0283 | 1.38 | 4 | |
| Epifauna - scavengers | 23.5 | 3 | 5 | |
| Infauna - filter feeders | 114.25 | 2.45 | 5 | |
| Infauna - deposit feeders | 99 | 3.74 | 5 | |
| Mesozooplankton | 49.729 | 25 | 83.33 | |
| Phytoplankton | 68.045 | 117.57 | | |
| Detritus | 300 | | | |

Table 6: Diet matrix, for the LIS offshore model, extracted from data sources and entered into Ecopath with Ecosim before balancing.  All values reported as a percentage of total diet.

| | Striped Bass | Bluefish | Tautog | Weakfish | Black Sea Bass | Scup | Red Hake | Silver Hake | Striped searobin | Smooth Dogfish |
|---|---|---|---|---|---|---|---|---|---|---|
| Striped Bass | | | | | | | | | | |
| Bluefish | | | | | | | | | | |
| Tautog | | | | | | | | | | |
| Weakfish | | | | | | | | | | |
| Black Sea Bass | | | | | | | | | | |
| Scup | | | | | 0.15 | | | 0.216 | 0.002 | 0.078 |
| Red Hake | | | | | | | | 0.09 | | |
| Silver Hake | | 0.006 | | | | | 0.315 | 0.15 | | |
| Striped Searobin | | | | | | | | | | |
| Smooth Dogfish | | | | | | | | | | |
| Little Skate | | | | | | | | | | |
| Winter Flounder | | | | | | | | | | |
| Windowpane Flounder | | | | | 0.019 | | | | 0.001 | |
| Summer Flounder | | | | 0.14 | | | | | 0.001 | |
| Four Spotted Flounder | | | | | | | | | | |
| Butterfish | 0.01 | 0.069 | | | | 0.008 | | 0.217 | | |
| American Shad | | | | 0.019 | | | | | | |
| Atlantic Herring | | | | | 0.065 | | | | | |
| Bay Anchovy | 0.019 | 0.581 | 0.101 | 0.078 | 0.073 | | | 0.216 | 0.004 | |
| Alewife/Blueback Herring | 0.009 | | 0.12 | | | | | | | |
| Spot | 0.01 | | | 0.005 | | | | | | |
| Atlantic Menhaden | | 0.166 | | 0.221 | | | | | | |
| Long Finned Squid | | 0.116 | | | 0.016 | | | 0.032 | | 0.007 |
| American Lobster | | | | | | | | | | |
| Blue Crabs | 0.006 | 0.006 | 0.2 | 0.018 | 0.201 | | | | | |
| Spider Crabs | 0.006 | | | | 0.225 | | | | | |
| Epifauna – scavengers | 0.718 | 0.056 | 0.377 | 0.092 | 0.076 | 0.182 | 0.625 | 0.079 | 0.912 | 0.896 |
| Infauna – filter feeders | 0.114 | | 0.101 | | 0.016 | 0.051 | | | 0.04 | 0.019 |
| Infauna – deposit feeders | | | 0.101 | | 0.011 | 0.397 | 0.06 | | 0.04 | |
| Mesozooplankton | 0.009 | | | | 0.148 | 0.005 | | | | |
| Phytoplankton | | | | | | | | | | |
| Detritus | | | | | | 0.357 | | | | |

Table 6 cont'd:

| | Little Skate | Winter Flounder | Windowpane Flounder | Summer Flounder | Four Spotted Flounder | Butterfish | American Shad | Atlantic Herring | Bay Anchovy | Alewife/Blueback Herring |
|---|---|---|---|---|---|---|---|---|---|---|
| Striped Bass | | | | | | | | | | |
| Bluefish | | | | | | | | | | |
| Tautog | | | | | | | | | | |
| Weakfish | | | | | | | | | | |
| Black Sea Bass | | | | | | | | | | |
| Scup | | | | | | | | | | |
| Red Hake | | | | 0.107 | | | | | | |
| Silver Hake | | | 0.079 | | 0.026 | | 0.163 | | | |
| Striped Searobin | 0.009 | | | 0.107 | | | | | | |
| Smooth Dogfish | | | | | | | | | | |
| Little Skate | | | | | | | | | | |
| Winter Flounder | 0.005 | | | | | | | | | |
| Windowpane Flounder | | | | | | | | | | |
| Summer Flounder | 0.002 | | | | | | | | | |
| Four Spotted Flounder | 0.002 | | | | | | | | | |
| Butterfish | | | | 0.067 | 0.169 | | | | | |
| American Shad | | | | | | | | | | |
| Atlantic Herring | | | | | | | | | | |
| Bay Anchovy | | | 0.157 | 0.158 | | | | | | |
| Alewife/Blueback Herring | | | | | | | | | | |
| Spot | | | | | | | | | | |
| Atlantic Menhaden | | | | | | | | | | |
| Long Finned Squid | | | | | 0.453 | | 0.011 | | | |
| American Lobster | | | | | | | | | | |
| Blue Crabs | | | | | | | | | | |
| Spider Crabs | | | | | | | | | | |
| Epifauna – scavengers | 0.65 | 0.448 | 0.737 | 0.487 | 0.247 | 0.465 | 0.004 | | 0.073 | 0.28 |
| Infauna – filter feeders | | 0.137 | | | 0.055 | 0.037 | | | | |
| Infauna – deposit feeders | 0.217 | 0.31 | 0.027 | | 0.05 | | | | | |
| Mesozooplankton | | | | | | 0.056 | 0.822 | 0.5 | 0.927 | 0.65 |
| Phytoplankton | | | | | | | | 0.1 | | |
| Detritus | 0.115 | 0.105 | | | | 0.442 | | 0.4 | | 0.07 |

**Table 6. continued**

| | Spot | Atlantic Menhaden | Long Finned Squid | American Lobster | Blue crabs | Spider crabs | Epifauna - scavengers | Infauna - filter feeders | Infauna - deposit feeders | Mesozooplankton |
|---|---|---|---|---|---|---|---|---|---|---|
| Striped Bass | | | | | | | | | | |
| Bluefish | | | | | | | | | | |
| Tautog | | | | | | | | | | |
| Weakfish | | | 0.040 | | | | | | | |
| Black Sea Bass | | | | | | | | | | |
| Scup | | | | | | | | | | |
| Red Hake | | | | | | | | | | |
| Silver Hake | | | 0.075 | | | | | | | |
| Striped Searobin | | | | | | | | | | |
| Smooth Dogfish | | | | | | | | | | |
| Little Skate | | | | | | | | | | |
| Winter Flounder | | | | | | | | | | |
| Windowpane Flounder | | | | | | | | | | |
| Summer Flounder | | | | | | | | | | |
| Four Spotted Flounder | | | | | | | | | | |
| Butterfish | | | | | | | | | | |
| American Shad | | | | | | | | | | |
| Atlantic Herring | | | 0.058 | | | | | | | |
| Bay Anchovy | | | 0.160 | | | | | | | |
| Alewife/Blueback Herring | | | 0.030 | 0.005 | | | | | | |
| Spot | | | | | | | | | | |
| Atlantic Menhaden | | | 0.046 | 0.015 | | | | | | |
| Long Finned Squid | | | 0.011 | | | | | | | |
| American Lobster | | | | | | | | | | |
| Blue Crabs | | | | 0.080 | | | | | | |
| Spider Crabs | | | | 0.090 | | | | | | |
| Epifauna – scavengers | 0.778 | | 0.580 | 0.760 | 0.655 | 0.700 | 0.020 | | | |
| Infauna – filter feeders | | | | | 0.235 | 0.040 | | | | |
| Infauna – deposit feeders | | | | | | 0.040 | | | | |
| Mesozooplankton | | 0.859 | | | | 0.010 | 0.380 | | | |
| Phytoplankton | | | | | | | 0.400 | 1.000 | | 1.000 |
| Detritus | 0.222 | 0.141 | | 0.050 | 0.110 | 0.210 | 0.200 | | 1.000 | |

Table 7: Finalized parameters after balancing completed for the LIS offshore model. Bold numbers represent values estimated by Ecopath with Ecosim. B is biomass, P/B is the production/biomass ratio, Q/B is the food consumption/biomass ratio, EE is ecotrophic efficiency, and P/Q is production/food consumption ratio.

| Group Name | Trophic Level | B (t/km$^2$/year) | P/B (t/km$^2$/year) | Q/B (t/km$^2$/year) | EE | P/Q |
|---|---|---|---|---|---|---|
| Striped Bass | **3.39** | 0.0461 | 0.23 | 0.575 | **0** | **0.100** |
| Bluefish | **4.04** | 0.166 | 0.34 | 0.75 | **0** | **0.113** |
| Tautog | **3.61** | 0.0347 | 0.25 | 0.625 | **0** | **0.100** |
| Weakfish | **4.08** | 0.0436 | 0.28 | 0.65 | **0.548** | **0.108** |
| Black Sea Bass | **3.78** | 0.00319 | 0.35 | 0.875 | **0** | **0.1** |
| Scup | **2.72** | 0.422 | 0.31 | 3.0 | **0.270** | **0.103** |
| Red Hake | **3.92** | 0.0144 | 0.491 | 0.839 | **0.905** | **0.116** |
| Silver Hake | **4.12** | 0.00616 | 1.47 | 2.464 | **0.971** | **0.218** |
| Striped searobin | **3.38** | 0.0567 | 0.3 | 3.0 | **0.965** | **0.100** |
| Smooth Dogfish | **3.43** | 0.147 | 0.32 | 2.7 | **0** | **0.119** |
| Little Skate | **3.18** | 0.198 | 0.51 | 4 | **0** | **0.128** |
| Winter Flounder | **3.08** | 0.175 | 0.35 | 3.5 | **0.065** | **0.1** |
| Windowpane Flounder | **3.63** | 0.0472 | 0.47 | 1.114 | **0.011** | **0.138** |
| Summer Flounder | **3.80** | 0.0458 | 0.35 | 1.792 | **0.547** | **0.125** |
| Four Spotted Flounder | **4.08** | 0.0309 | 0.44 | 3.20 | **0.117** | **0.110** |
| Butterfish | **2.75** | 0.251 | 0.79 | 5.7 | **0.237** | **0.139** |
| American Shad | **3.37** | 0.00641 | 0.53 | 1.311 | **0.202** | **0.166** |
| Atlantic Herring | **2.50** | 0.0399 | 0.44 | 4.40 | **0.565** | **0.10** |
| Bay Anchovy | **3.03** | **0.191** | 3 | 10.9 | **0.276** | **0.275** |
| Alewife/Blueback Herring | **3.04** | 0.00390 | 0.621 | 3.5 | **1.0** | **0.101** |
| Spot | **3.10** | 0.00057 | 1 | 4.5 | **0.787** | **0.222** |
| Atlantic Menhaden | **2.86** | 0.00817 | 0.525 | 1.55 | **1.0** | **0.194** |
| Long Finned Squid | **3.76** | 0.0810 | 1.7 | 1.75 | **4.95** | **0.243** |
| American Lobster | **3.47** | 0.189 | 1.545 | 2.050 | **0** | **0.188** |
| Blue crabs | **3.16** | 0.00156 | 2.415 | 4 | **1** | **0.345** |
| Spider crabs | **3.08** | 0.0298 | 1.452 | 4 | **1** | **0.345** |
| Epifauna - scavengers | **2.41** | 23.5 | 3 | 5 | **0.076** | **0.600** |
| Infauna - filter feeders | **2.00** | 114.25 | 2.45 | 5 | **0.001** | **0.490** |
| Infauna - deposit feeders | **2.00** | 99 | 3.74 | 5 | **0.002** | **0.748** |
| Mesozooplankton | **2.00** | 49.729 | 25 | 83.33 | **0.038** | **0.30** |
| Phytoplankton | **1.00** | 68.045 | 117.57 |  | **0.595** | **-** |
| Detritus | **1.00** | 300 |  |  | **0.084** | **-** |

**Table 8:** Finalized diet matrix for LIS offshore model after balancing completed. Bold numbers represent values altered by Ecopath with Ecosim in the balancing process. All values reported as a percentage of total diet.

| | Striped Bass | Bluefish | Tautog | Weakfish | Black Sea Bass | Scup | Red Hake | Silver Hake | Striped searobin | Smooth Dogfish |
|---|---|---|---|---|---|---|---|---|---|---|
| Striped Bass | | | | | | | | | | |
| Bluefish | | | | | | | | | | |
| Tautog | | | | | | | | | | |
| Weakfish | | | | | | | | | | |
| Black Sea Bass | | | | | | | | | | |
| Scup | | | | | **0.177** | | | 0.216 | 0.002 | 0.078 |
| Red Hake | | | | | | | | 0.09 | | |
| Silver Hake | | **0.007** | | | | | 0.315 | 0.15 | | |
| Striped Searobin | | | | | | | | | | |
| Smooth Dogfish | | | | | | | | | | |
| Little Skate | | | | | | | | | | |
| Winter Flounder | | | | | | | | | | |
| Windowpane Flounder | | | | | **0.022** | | | | 0.001 | |
| Summer Flounder | | | | **0.245** | | | | | 0.001 | |
| Four Spotted Flounder | | | | | | | | | | |
| Butterfish | 0.01 | **0.084** | | | | 0.008 | | 0.217 | | |
| American Shad | | | | **0.024** | | | | | | |
| Atlantic Herring | | | | | **0.077** | | | | | |
| Bay Anchovy | 0.019 | **0.682** | **0.140** | **0.545** | **0.086** | | | 0.216 | 0.004 | |
| Alewife/Blueback Herring | 0.009 | | **0.038** | | | | | | | |
| Spot | 0.01 | | | **0.006** | | | | | | |
| Atlantic Menhaden | | **0.017** | | **0.035** | | | | | | |
| Long Finned Squid | | **0.141** | | | **0.019** | | | 0.032 | | 0.007 |
| American Lobster | | | | | | | | | | |
| Blue Crabs | 0.006 | **0.001** | **0.02** | **0.006** | **0.057** | | | | | |
| Spider Crabs | **0.004** | | | | **0.266** | | | | | |
| Epifauna – scavengers | **0.819** | **0.068** | **0.522** | **0.140** | **0.090** | 0.182 | **0.784** | 0.079 | 0.912 | 0.896 |
| Infauna – filter feeders | 0.114 | | **0.140** | | **0.019** | 0.051 | | | 0.04 | 0.019 |
| Infauna – deposit feeders | | | **0.140** | | **0.013** | 0.397 | **0.083** | | 0.04 | |
| Mesozooplankton | 0.009 | | | | **0.175** | 0.005 | | | | |
| Phytoplankton | | | | | | | | | | |
| Detritus | | | | | | 0.357 | | | | |

**Table 8** continued

| | Little Skate | Winter Flounder | Windowpane Flounder | Summer Flounder | Four Spotted Flounder | Butterfish | American Shad | Atlantic Herring | Bay Anchovy | Alewife/Blueback Herring |
|---|---|---|---|---|---|---|---|---|---|---|
| Striped Bass | | | | | | | | | | |
| Bluefish | | | | | | | | | | |
| Tautog | | | | | | | | | | |
| Weakfish | | | | | | | | | | |
| Black Sea Bass | | | | | | | | | | |
| Scup | | | | | | | | | | |
| Red Hake | | | | **0.060** | | | | | | |
| Silver Hake | | | **0.033** | | **0.011** | | **0.101** | | | |
| Striped Searobin | 0.009 | | | **0.1113** | | | | | | |
| Smooth Dogfish | | | | | | | | | | |
| Little Skate | | | | | | | | | | |
| Winter Flounder | 0.005 | | | | | | | | | |
| Windowpane Flounder | | | | | | | | | | |
| Summer Flounder | 0.002 | | | | | | | | | |
| Four Spotted Flounder | 0.002 | | | | | | | | | |
| Butterfish | | | | **0.071** | **0.172** | | | | | |
| American Shad | | | | | | | | | | |
| Atlantic Herring | | | | | | | | | | |
| Bay Anchovy | | | **0.172** | **0.167** | | | | | | |
| Alewife/Blueback Herring | | | | | | | | | | |
| Spot | | | | | | | | | | |
| Atlantic Menhaden | | | | | | | | | | |
| Long Finned Squid | | | | | **0.460** | | **0.014** | | | |
| American Lobster | | | | | | | | | | |
| Blue Crabs | | | | | | | | | | |
| Spider Crabs | | | | | | | | | | |
| Epifauna – scavengers | 0.65 | 0.448 | **0.765** | **0.589** | **0.251** | 0.465 | **0.005** | | 0.073 | 0.28 |
| Infauna – filter feeders | | 0.137 | | | **0.056** | 0.037 | | | | |
| Infauna – deposit feeders | 0.217 | 0.31 | **0.030** | | **0.051** | | | | | |
| Mesozooplankton | | | | | | 0.056 | **0.879** | 0.5 | 0.927 | 0.65 |
| Phytoplankton | | | | | | | | 0.1 | | |
| Detritus | 0.115 | 0.105 | | | | 0.442 | | 0.4 | | 0.07 |

**Table 8.** continued

| | Spot | Atlantic Menhaden | Long Finned Squid | American Lobster | Blue crabs | Spider crabs | Epifauna - scavengers | Infauna - filter feeders | Infauna - deposit feeders | Mesozooplankton |
|---|---|---|---|---|---|---|---|---|---|---|
| Striped Bass | | | | | | | | | | |
| Bluefish | | | | | | | | | | |
| Tautog | | | | | | | | | | |
| Weakfish | | | **0.047** | | | | | | | |
| Black Sea Bass | | | | | | | | | | |
| Scup | | | | | | | | | | |
| Red Hake | | | | | | | | | | |
| Silver Hake | | | **0.011** | | | | | | | |
| Striped Searobin | | | | | | | | | | |
| Smooth Dogfish | | | | | | | | | | |
| Little Skate | | | | | | | | | | |
| Winter Flounder | | | | | | | | | | |
| Windowpane Flounder | | | | | | | | | | |
| Summer Flounder | | | | | | | | | | |
| Four Spotted Flounder | | | | | | | | | | |
| Butterfish | | | | | | | | | | |
| American Shad | | | | | | | | | | |
| Atlantic Herring | | | **0.068** | | | | | | | |
| Bay Anchovy | | | **0.188** | | | | | | | |
| Alewife/Blueback Herring | | | **0.006** | **0.002** | | | | | | |
| Spot | | | | | | | | | | |
| Atlantic Menhaden | | | **0.006** | **0.002** | | | | | | |
| Long Finned Squid | | | **0.013** | | | | | | | |
| American Lobster | | | | | | | | | | |
| Blue Crabs | | | | **0.008** | | | | | | |
| Spider Crabs | | | | **0.109** | | | | | | |
| Epifauna – scavengers | 0.778 | | **0.661** | **0.818** | 0.655 | 0.700 | 0.020 | | | |
| Infauna – filter feeders | | | | | 0.235 | 0.040 | | | | |
| Infauna – deposit feeders | | | | | | 0.040 | | | | |
| Mesozooplankton | | 0.859 | | | | 0.010 | 0.380 | | | |
| Phytoplankton | | | | | | | 0.400 | 1.000 | | 1.000 |
| Detritus | 0.222 | 0.141 | | **0.061** | 0.110 | 0.210 | 0.200 | | 1.000 | |

**Table 9:** Functional groups with ecotrophic efficiency's (EE) greater then 1 after Ecopath with Ecosim's basic parameterization of the LIS offshore food web model.

| Group | EE |
|---|---|
| Weakfish | 1.86 |
| Red Hake | 3.53 |
| Silver Hake | 18.74 |
| Striped Searobin | 1.31 |
| Summer Flounder | 1.48 |
| Atlantic Herring | 2.13 |
| Alewife/Blueback | 31.93 |
| Spot | 3.17 |
| Atlantic Menhaden | 78.18 |
| Blue Crabs | 84.60 |
| Spider Crabs | 4.06 |

**Table 10:** Balancing alterations made to the production/biomass (P/B) and food consumption/biomass (Q/B) values of the LIS offshore Ecopath model after basic parameterization. All units reported as t/km²/year.

| Group | Alteration |
|---|---|
| Striped Bass | P/B up 0.15 to 0.23 |
| Tautog | P/B up 0.18 to 0.25 |
| Black Sea Bass | P/B up 0.3 to 0.35 |
| Striped Searobin | Q/B down 5.0 to 3.0 |
| Atlantic Herring | Q/B down 6.0 to 4.4 |
| Alewife/Blueback Herring | Q/B down 5.0 to 3.5 |

**Table 11.** Cycling and path length statistics from the LIS Ecopath model

| *Parameter* | *Value* | *Notes* |
|---|---|---|
| Throughput cycled (excluding detritus) | 2.35 | t/km²/year |
| Predatory cycling index | 0.03 | % of throughput without detritus |
| Throughput cycled (including detritus) | 527.54 | t/km²/year |
| Finn's cycling index | 2.7 | % of total throughput |
| Finn's mean path length* | 2.444 | no units |
| Finn's straight-through path length | 3.0894 | without detritus |
| Finn's straight-through path length | 2.378 | with detritus |

* The path length is defined as the average number of groups that an inflow or outflow passes through (Finn 1980). It is calculated as
Path length = Total System Throughput / (∑ Export + ∑ Respiration).
As diversity of flows and recycling is expected to increase with maturity, so is the path length. (EWE Users Guide 2004). Also as note by Finn (1980), the cycling index measures the proportion of flow that cycles through all the components of the system. Path Length is the average number of components that a unit of flow passes through from inflow to outflow. Straight through path length is that portion of PL attributable to flow passing straight through the system without cycling.

**Table 12**. Flows ($t•km^{-2}•year^{-1}$) by trophic levels. Trophic level I is the level of primary producers and detritus. Upper trophic levels are not pre-defined and calculated based on diet compositions (see Results text).

| Trophic level / Flow | Consumption by | Export | Flow to Detritus† | Respiration* | Throughput** |
|---|---|---|---|---|---|
| VIII | 0 | 0 | 0.0001 | 0.0001 | 0.0002 |
| VII | 0.0002 | 0 | 0.0005 | 0.0006 | 0.0013 |
| VI | 0.0013 | 0 | 0.0041 | 0.0043 | 0.0096 |
| V | 0.0096 | 0 | 0.0625 | 0.0569 | 0.1291 |
| IV | 0.1291 | 0 | 1.2518 | 1.0049 | 2.3858 |
| III | 2.3858 | 0 | 35.7818 | 13.0087 | 51.1763 |
| II | 51.1763 | 0 | 2941.12 | 2289.751 | 5282.048 |
| I | 5282.048 | 5696.224 | 3237.865 | 0 | 14216.14 |
| Sum | 5335.75 | 5696.224 | 6216.086 | 2303.827 | 19551.89 |
| Total throughput | | | | | 19551.89 |

As noted in the EWE Users Guide: 2004

† The flow to the detritus consists of what is egested (the non-assimilated food) and those elements of the group, which die of old age, diseases, etc, (i.e., of sources of ‘other mortality’, expressed by 1 - Ecotrophic Efficiency).

* Respiration is the part of the consumption that is not used for production or recycled Respiration cannot be used by the other groups in the system.

**The total system throughput is the sum of all flows in a system, expressed, in $t \cdot km^{-2} \cdot year^{-1}$. It is estimated as the sum of four flow components, i.e., Total system throughput =
Total consumption + Total export + Total respiration + Total flows to detritus.
It characterizes the overall activity of the ecosystem.

**Table 13:** Flow to detritus in the LIS offshore model, determined by Ecopath with Ecosim, for each functional group

| Group Name | Flow to Detritus (t/km²/year) |
|---|---|
| Striped Bass | 0.016 |
| Bluefish | 0.081 |
| Tautog | 0.013 |
| Weakfish | 0.011 |
| Black Sea Bass | 0.002 |
| Scup | 0.349 |
| Red Hake | 0.003 |
| Silver Hake | 0.003 |
| Striped searobin | 0 |
| Smooth Dogfish | 0.126 |
| Little Skate | 0.259 |
| Winter Flounder | 0.18 |
| Windowpane Flounder | 0.032 |
| Summer Flounder | 0 |
| Four Spotted Flounder | 0.032 |
| Butterfish | 0.437 |
| American Shad | 0.004 |
| Atlantic Herring | 0.043 |
| Bay Anchovy | 0 |
| Alewife/Blueback Herring | 0.003 |
| Spot | 0 |
| Atlantic Menhaden | 0.003 |
| Long Finned Squid | 0.074 |
| American Lobster | 0.369 |
| Blue crabs | 0.001 |
| Spider crabs | 0.024 |
| Epifauna - scavengers | 88.628 |
| Infauna - filter feeders | 393.929 |
| Infauna - deposit feeders | 468.373 |
| Mesozooplankton | 2025.225 |
| Phytoplankton | 3237.865 |
| Detritus | 0 |

**Table 14** Trophic transfer efficiencies (%) expressing how efficiently transfers are from one trophic level to the next. Transfer efficiencies between successive discrete trophic levels are calculated as the ratio between the sum of the exports from a given trophic level, plus the flow that is transferred from trophic level to the next, and the throughput on the trophic level.

| Source / Trophic Level | ii | iii | iv | v | vi | vii | viii | ix | x |
|---|---|---|---|---|---|---|---|---|---|
| Producer | | 1 | 4.7 | 5.4 | 7.1 | 12.8 | 14.5 | | |
| Detritus | | 0.4 | 3.7 | 5.7 | 16.8 | | | | |
| All flows | 1 | 4.7 | 5.4 | 7.5 | 13.2 | 14.5 | 13 | 16.8 | 15.9 |

Proportion of total flow originating from detritus: 0.34
Transfer efficiencies (calculated as geometric mean for TL II-IV)
  From primary producers: 3.0%
  From detritus: 2.0%
  Total: 2.9%

**Table 15:** Ecopath with Ecosim summary statistics for the LIS offshore food web model.

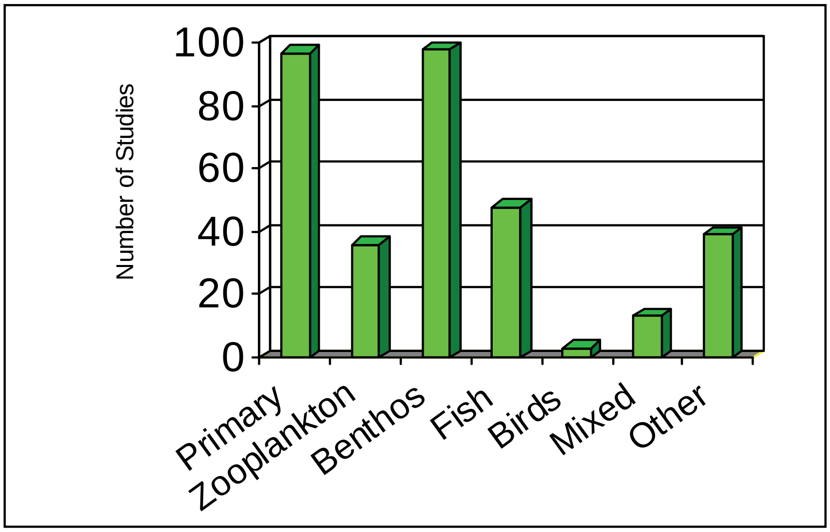
| Parameter | Value | Units |
|---|---|---|
| Sum of all consumption | 5338.532 | t/km²/year |
| Sum of all exports | 5694.467 | t/km²/year |
| Sum of all respiratory flows | 2305.584 | t/km²/year |
| Sum of all flows into detritus | 6214.39 | t/km²/year |
| Total system throughput | 19553 | t/km²/year |
| Sum of all production | 9965 | t/km²/year |
| Calculated total net primary production | 8000.05 | t/km²/year |
| Total primary production/total respiration* | 3.47 | |
| Net system production | 5694.466 | t/km²/year |
| Total primary production/total biomass | 22.426 | |
| Total biomass/total throughput | 0.018 | |
| Total biomass (excluding detritus) | 356.73 | t/km² |
| Connectance Index | 0.148 | |
| System Omnivory Index** | 0.165 | |

*****According to the EWE User's manual (2004), this dimensionless ratio is "considered to.. be an important ratio for description of the maturity of an ecosystem. In the early developmental stages of a system, production is expected to exceed respiration, leading to a ratio greater than 1. In systems suffering from organic pollution, this ratio is expected to be less than 1. Finally, in mature systems, the ratio should approach 1; the energy that is fixed is approximately balanced by the cost of maintenance."

** According to the EWE User's manual (2004), "the system omnivory index is defined as the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake (the latter is estimated as biomass times the consumption / biomass ratio). The logarithms is used as weighting factors because it can be expected that the intake rates are approximately log normally distributed within the system." This is a better way to characterize the extent to which a system displays web-like features," than the connectance index because the latter his sensitive to the number of functional groups are taxa that are used in developing the food web model.

**Table 16.** Measure of ascendancy, overhead and capacity in the LIS ecopath food web model. See results text for further explanation of these parameters. The flowbits unit for these measures is the product of flow (t·km$^{-2}$ year$^{-1}$) and bits. Here the 'bits' is an information unit derived from network theory, corresponding to the amount of uncertainty associated with a single binary decision.

| Source | Ascendency (flowbits) | Ascendency % | Overhead (flowbits) | Overhead % | Capacity (flowbits) | Capacity % |
|---|---|---|---|---|---|---|
| Import | 0 | 0 | 0 | 0 | 0 | 0 |
| Internal flow | 10626.1 | 19.3 | 25861.1 | 46.9 | 36487.2 | 66.2 |
| Export | 9417.2 | 17.1 | 717.7 | 1.3 | 10134.9 | 18.4 |
| Respiration | 4569.9 | 8.3 | 3897.7 | 7.1 | 8467.5 | 15.4 |
| Total | 24613.1 | 44.7 | 30476.5 | 55.3 | 55089.6 | 100 |



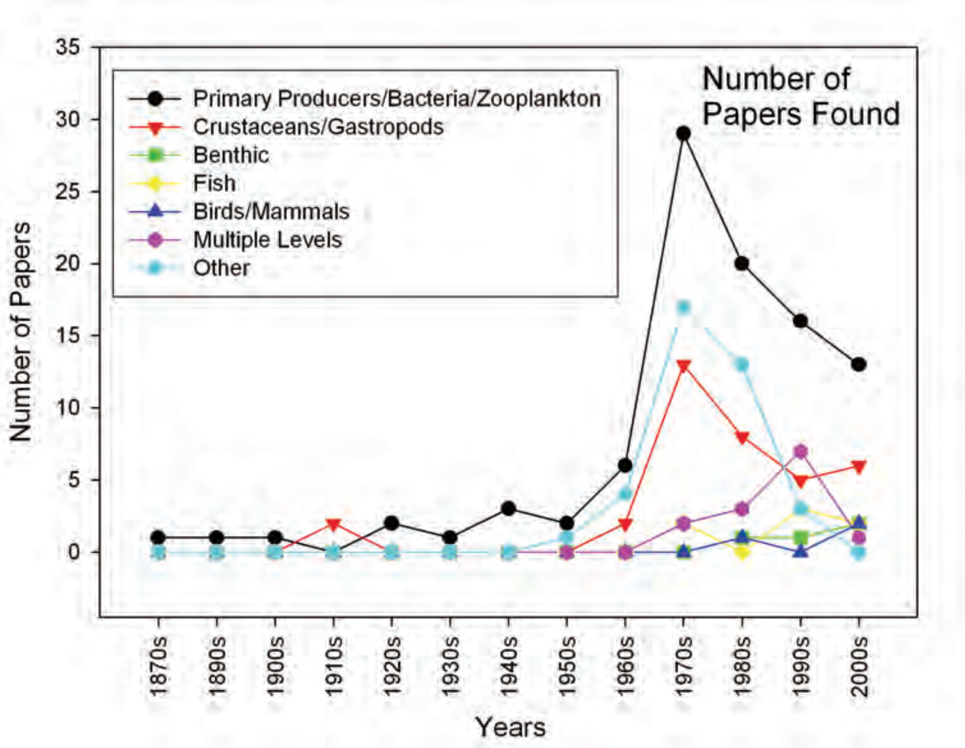


**Figure 14.** Top: Number of studies found that may provide food web model data for LIS categorized by trophic level. Bottom: Number of papers found by year of publication for different trophic levels that contain potential food web data for LIS.

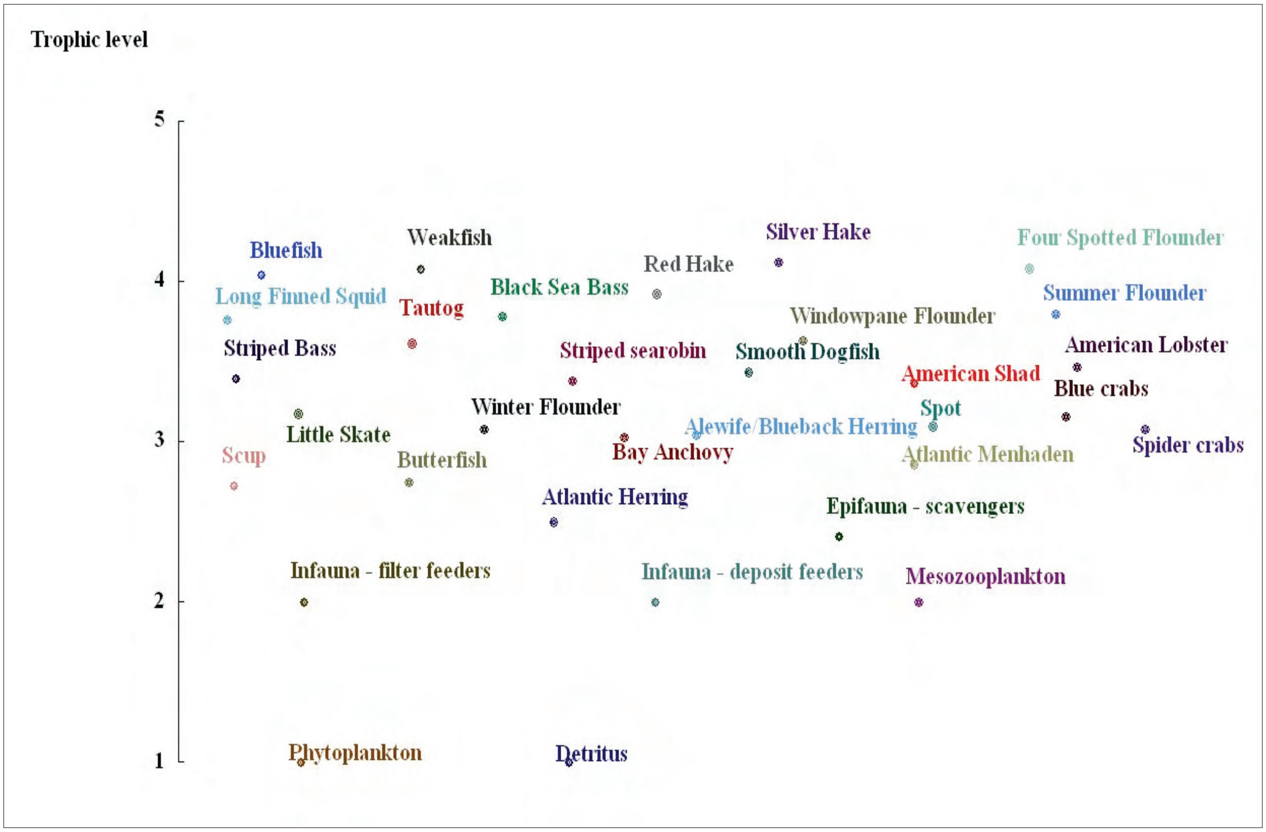


**Figure 15:** Connectance web created by Ecopath with Ecosim for the LIS offshore food web. Trophic pathways are not shown in order to clearly show the trophic level for each functional group/taxa.

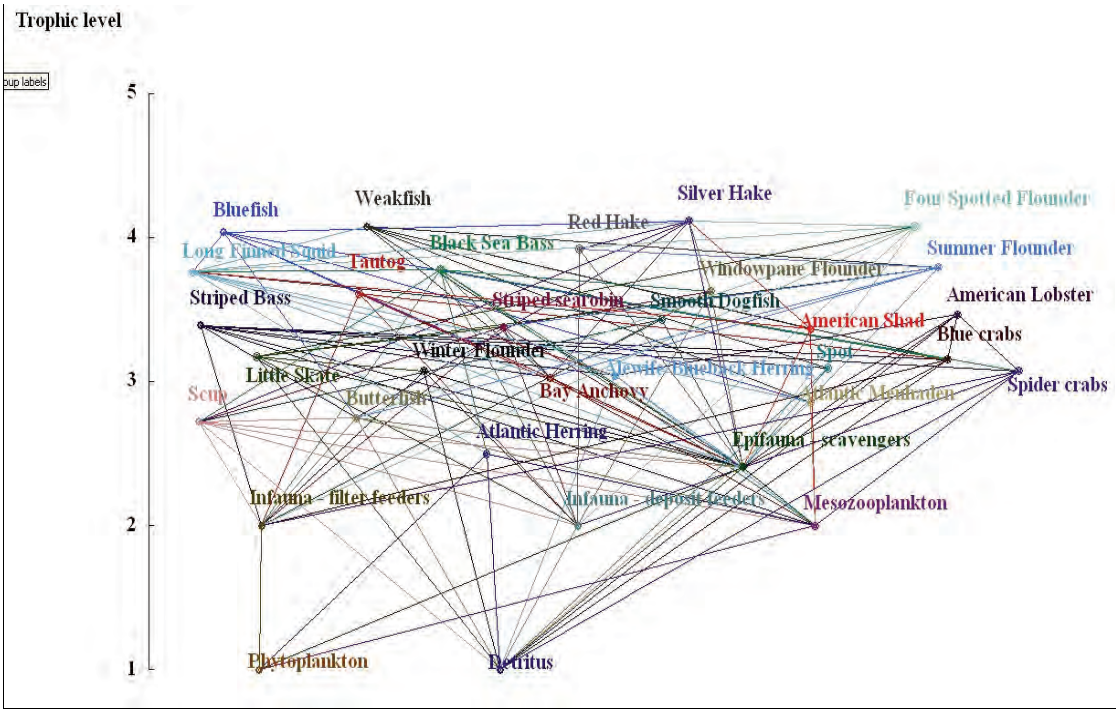


**Figure 16:** Connectance web created by Ecopath with Ecosim for the LIS offshore food web. Trophic pathways shown for each functional group.

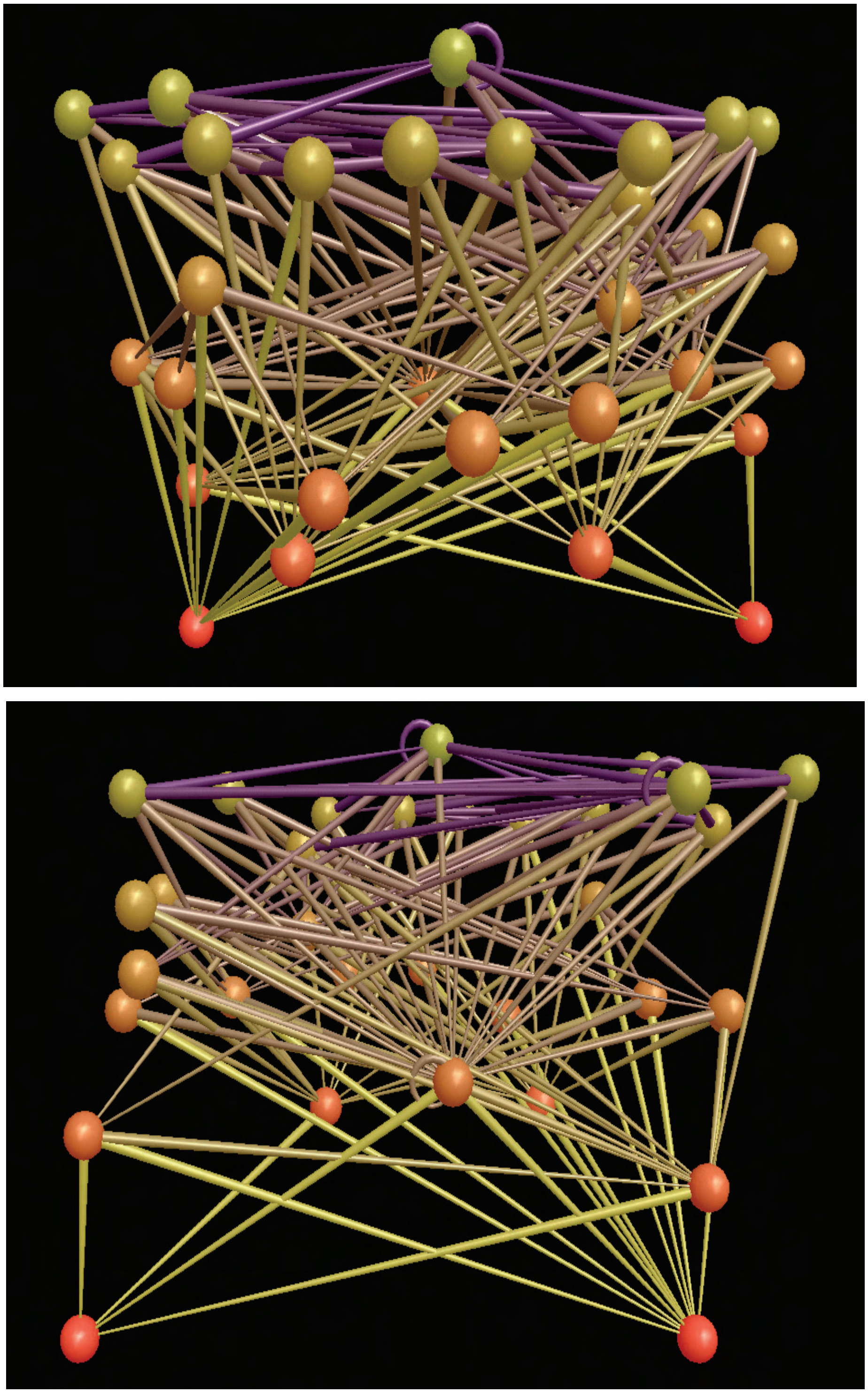


**Figure 17:** 3-D food web for the LIS offshore model created by FoodWeb3D (Image produced with FoodWeb3D, written by R.J. Williams and provided by the Pacific Ecoinformatics and Computational Ecology Lab (www.foodwebs.org, Yoon et al. 2004)). Top figure represents a front view while the bottom figure is a back view of the model. Dark color nodes represent the functional groups with the lowest trophic levels. Light color nodes represent functional groups at the highest trophic levels. Trophic pathways lighten in color as they reach the lowest trophic nodes.

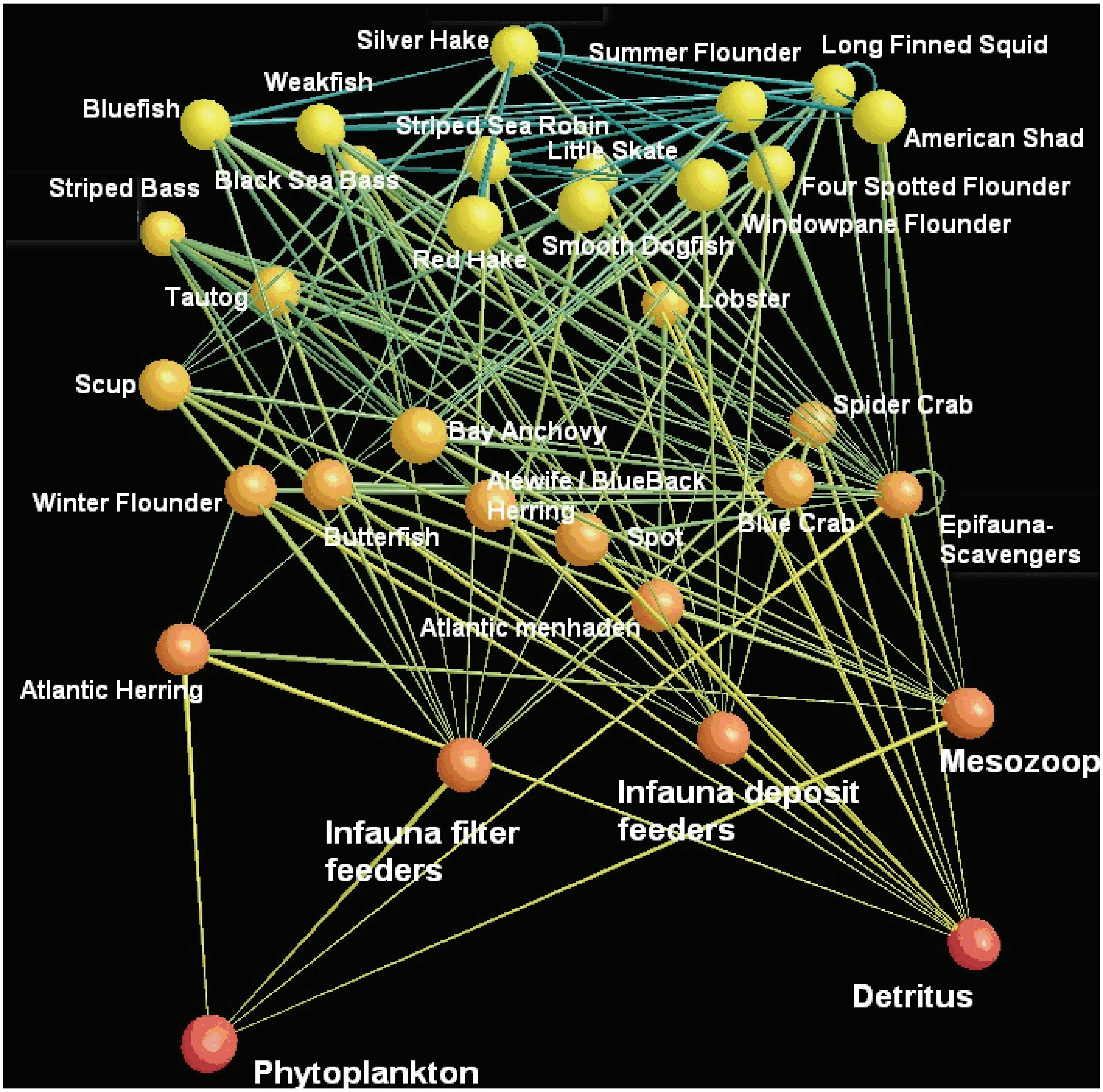


**Figure 18.** Three dimensional representation of the Long Island Sound offshore food web model with nodes (representing the functional groups / taxa ) labeled.

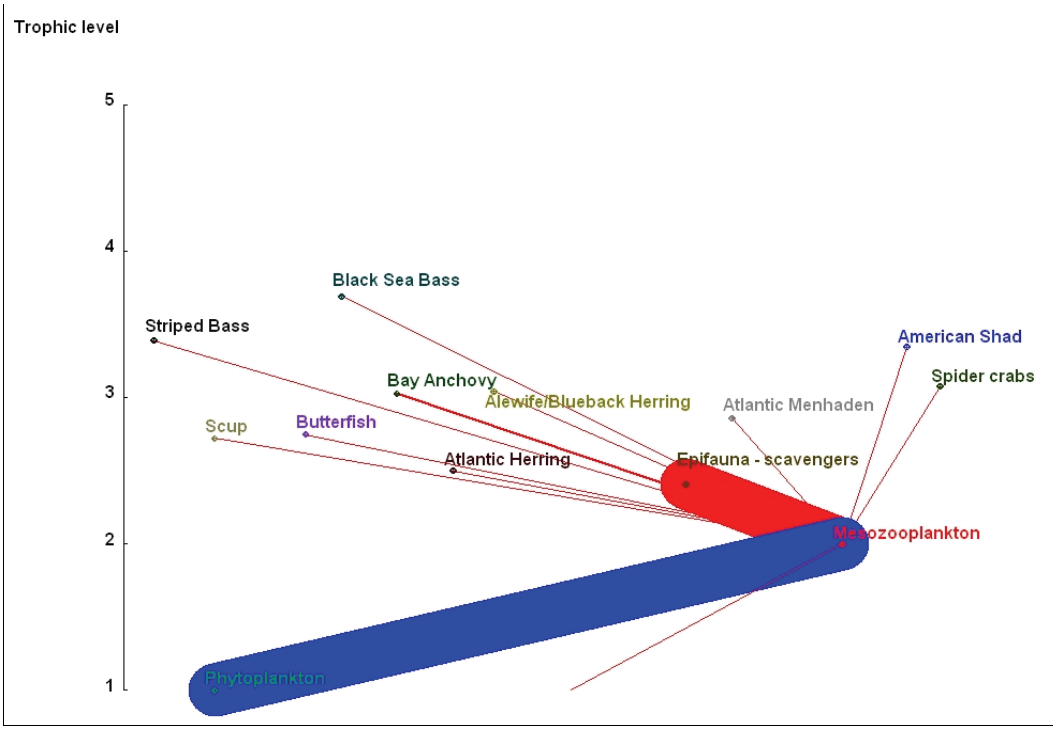
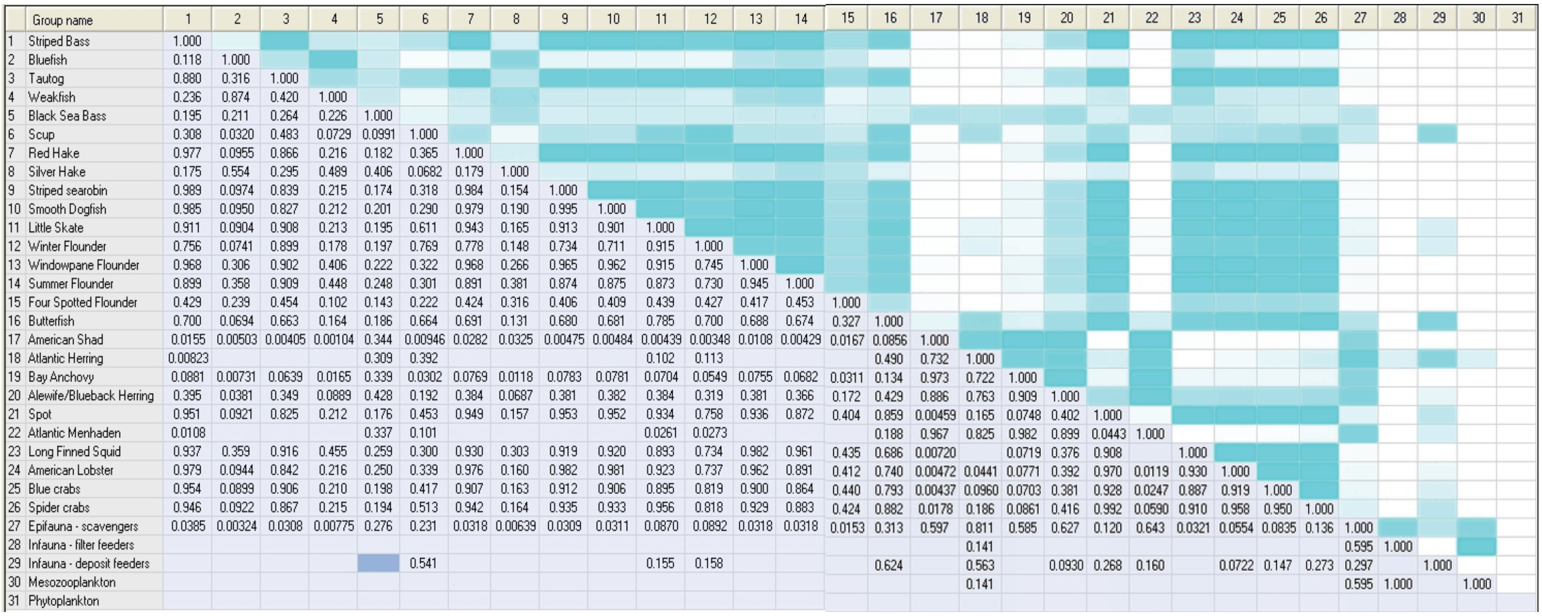


**Figure 19.** Connectance graph for mesozooplankton as constructed by the EcoPath software. Line thicknesses have been scaled two show predation strength. The heavy blue line indicates that zooplankton feed exclusively on the phytoplankton functional group; the lines emanating to the upper trophic levels indicate functional groups that feed on the zooplankton.



|  | Group name | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Striped Bass | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 2 | Bluefish | 0.118 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 3 | Tautog | 0.880 | 0.316 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 4 | Weakfish | 0.236 | 0.874 | 0.420 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 5 | Black Sea Bass | 0.195 | 0.211 | 0.264 | 0.226 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 6 | Scup | 0.308 | 0.0320 | 0.483 | 0.0729 | 0.0991 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 7 | Red Hake | 0.977 | 0.0955 | 0.866 | 0.216 | 0.182 | 0.365 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 8 | Silver Hake | 0.175 | 0.554 | 0.295 | 0.489 | 0.406 | 0.0682 | 0.179 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 9 | Striped searobin | 0.989 | 0.0974 | 0.839 | 0.215 | 0.174 | 0.318 | 0.984 | 0.154 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 10 | Smooth Dogfish | 0.985 | 0.0950 | 0.827 | 0.212 | 0.201 | 0.290 | 0.979 | 0.190 | 0.995 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 11 | Little Skate | 0.911 | 0.0904 | 0.908 | 0.213 | 0.195 | 0.611 | 0.943 | 0.165 | 0.913 | 0.901 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 12 | Winter Flounder | 0.756 | 0.0741 | 0.899 | 0.178 | 0.197 | 0.769 | 0.778 | 0.148 | 0.734 | 0.711 | 0.915 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 13 | Windowpane Flounder | 0.968 | 0.306 | 0.902 | 0.406 | 0.222 | 0.322 | 0.968 | 0.266 | 0.965 | 0.962 | 0.915 | 0.745 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 14 | Summer Flounder | 0.899 | 0.358 | 0.909 | 0.448 | 0.248 | 0.301 | 0.891 | 0.381 | 0.874 | 0.875 | 0.873 | 0.730 | 0.945 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 15 | Four Spotted Flounder | 0.429 | 0.239 | 0.454 | 0.102 | 0.143 | 0.222 | 0.424 | 0.316 | 0.406 | 0.409 | 0.439 | 0.427 | 0.417 | 0.453 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 16 | Butterfish | 0.700 | 0.0694 | 0.663 | 0.164 | 0.186 | 0.664 | 0.691 | 0.131 | 0.680 | 0.681 | 0.785 | 0.700 | 0.688 | 0.674 | 0.327 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 17 | American Shad | 0.0155 | 0.00503 | 0.00405 | 0.00104 | 0.344 | 0.00946 | 0.0282 | 0.0325 | 0.00475 | 0.00484 | 0.00439 | 0.00348 | 0.0108 | 0.00429 | 0.0167 | 0.0856 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 18 | Atlantic Herring | 0.00823 |  |  |  | 0.309 | 0.392 |  |  |  |  | 0.102 | 0.113 |  |  |  | 0.490 | 0.732 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 19 | Bay Anchovy | 0.0881 | 0.00731 | 0.0639 | 0.0165 | 0.339 | 0.0302 | 0.0769 | 0.0118 | 0.0783 | 0.0781 | 0.0704 | 0.0549 | 0.0755 | 0.0682 | 0.0311 | 0.134 | 0.973 | 0.722 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |  |
| 20 | Alewife/Blueback Herring | 0.395 | 0.0381 | 0.349 | 0.0889 | 0.428 | 0.192 | 0.384 | 0.0687 | 0.381 | 0.382 | 0.384 | 0.319 | 0.381 | 0.366 | 0.172 | 0.429 | 0.886 | 0.763 | 0.909 | 1.000 |  |  |  |  |  |  |  |  |  |  |  |
| 21 | Spot | 0.951 | 0.0921 | 0.825 | 0.212 | 0.176 | 0.453 | 0.949 | 0.157 | 0.953 | 0.952 | 0.934 | 0.758 | 0.936 | 0.872 | 0.404 | 0.859 | 0.00459 | 0.165 | 0.0748 | 0.402 | 1.000 |  |  |  |  |  |  |  |  |  |  |
| 22 | Atlantic Menhaden | 0.0108 |  |  |  | 0.337 | 0.101 |  |  |  |  | 0.0261 | 0.0273 |  |  |  | 0.188 | 0.967 | 0.825 | 0.982 | 0.899 | 0.0443 | 1.000 |  |  |  |  |  |  |  |  |  |
| 23 | Long Finned Squid | 0.937 | 0.359 | 0.916 | 0.455 | 0.259 | 0.300 | 0.930 | 0.303 | 0.919 | 0.920 | 0.893 | 0.734 | 0.982 | 0.961 | 0.435 | 0.686 | 0.00720 |  | 0.0719 | 0.376 | 0.908 |  | 1.000 |  |  |  |  |  |  |  |  |
| 24 | American Lobster | 0.979 | 0.0944 | 0.842 | 0.216 | 0.250 | 0.339 | 0.976 | 0.160 | 0.982 | 0.981 | 0.923 | 0.737 | 0.962 | 0.891 | 0.412 | 0.740 | 0.00472 | 0.0441 | 0.0771 | 0.392 | 0.970 | 0.0119 | 0.930 | 1.000 |  |  |  |  |  |  |  |
| 25 | Blue crabs | 0.954 | 0.0899 | 0.906 | 0.210 | 0.198 | 0.417 | 0.907 | 0.163 | 0.912 | 0.906 | 0.895 | 0.819 | 0.900 | 0.864 | 0.440 | 0.793 | 0.00437 | 0.0960 | 0.0703 | 0.381 | 0.928 | 0.0247 | 0.887 | 0.919 | 1.000 |  |  |  |  |  |  |
| 26 | Spider crabs | 0.946 | 0.0922 | 0.867 | 0.215 | 0.194 | 0.513 | 0.942 | 0.164 | 0.935 | 0.933 | 0.956 | 0.818 | 0.929 | 0.883 | 0.424 | 0.882 | 0.0178 | 0.186 | 0.0861 | 0.416 | 0.992 | 0.0590 | 0.910 | 0.958 | 0.950 | 1.000 |  |  |  |  |  |
| 27 | Epifauna - scavengers | 0.0385 | 0.00324 | 0.0308 | 0.00775 | 0.276 | 0.231 | 0.0318 | 0.00639 | 0.0309 | 0.0311 | 0.0870 | 0.0892 | 0.0318 | 0.0318 | 0.0153 | 0.313 | 0.597 | 0.811 | 0.585 | 0.627 | 0.120 | 0.643 | 0.0321 | 0.0554 | 0.0835 | 0.136 | 1.000 |  |  |  |  |
| 28 | Infauna - filter feeders |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.141 |  |  |  |  |  |  |  |  | 0.595 | 1.000 |  |  |  |
| 29 | Infauna - deposit feeders |  |  |  |  |  | 0.541 |  |  |  |  | 0.155 | 0.158 |  |  |  | 0.624 |  | 0.563 |  | 0.0930 | 0.268 | 0.160 |  | 0.0722 | 0.147 | 0.273 | 0.297 |  | 1.000 |  |  |
| 30 | Mesozooplankton |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.141 |  |  |  |  |  |  |  |  | 0.595 | 1.000 |  | 1.000 |  |
| 31 | Phytoplankton |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

**Figure 20.** Prey overlap as calculated by EcoPath. Niche overlap values are given in the lowers sub diagonal were as a color representation of the intensity of overlap is given in the upper sub diagonal. Darker blue colors represent higher levels of prey overlap.

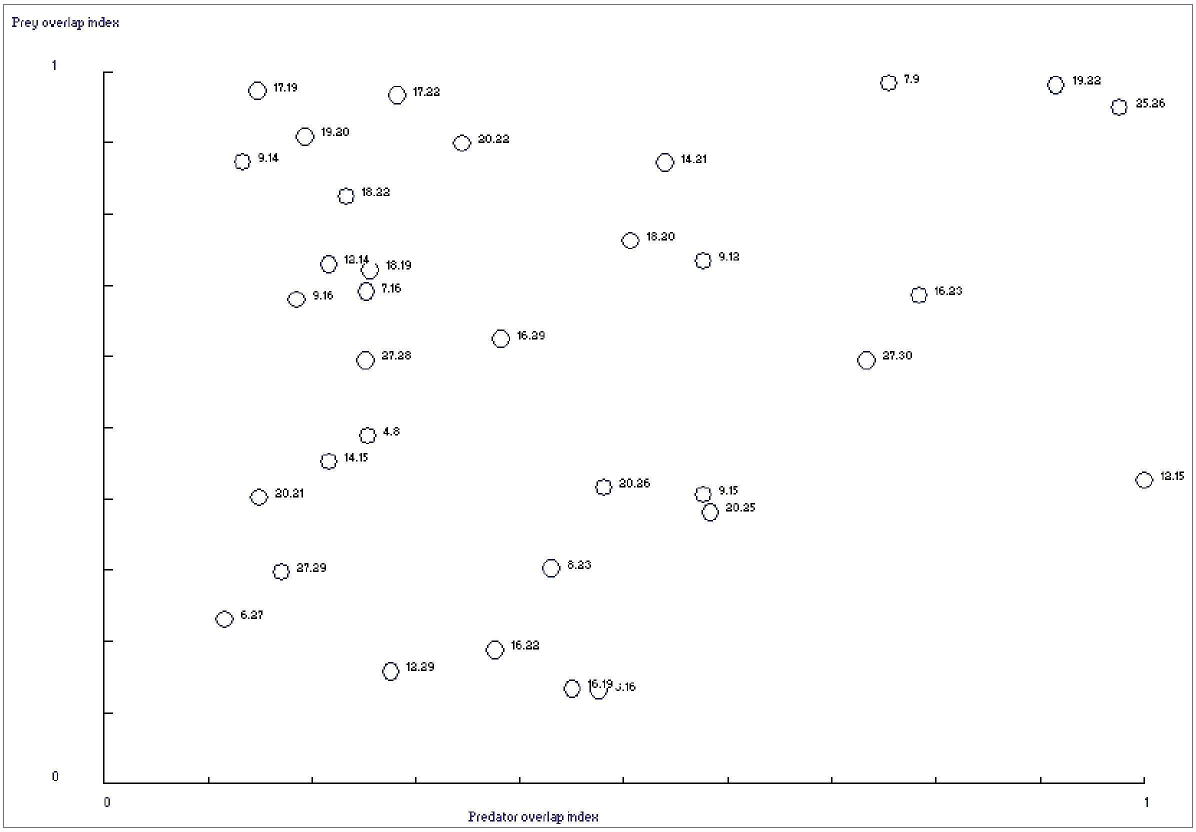


**Figure 21.** Prey versus predator niche overlap index plot as generated by Ecopath. Groups in the in the upper left corner have a very high overlap of prey; groups in the upper right corner have a high overlap of both predators and prey. Group numbers correspond to those given in Figure 20.

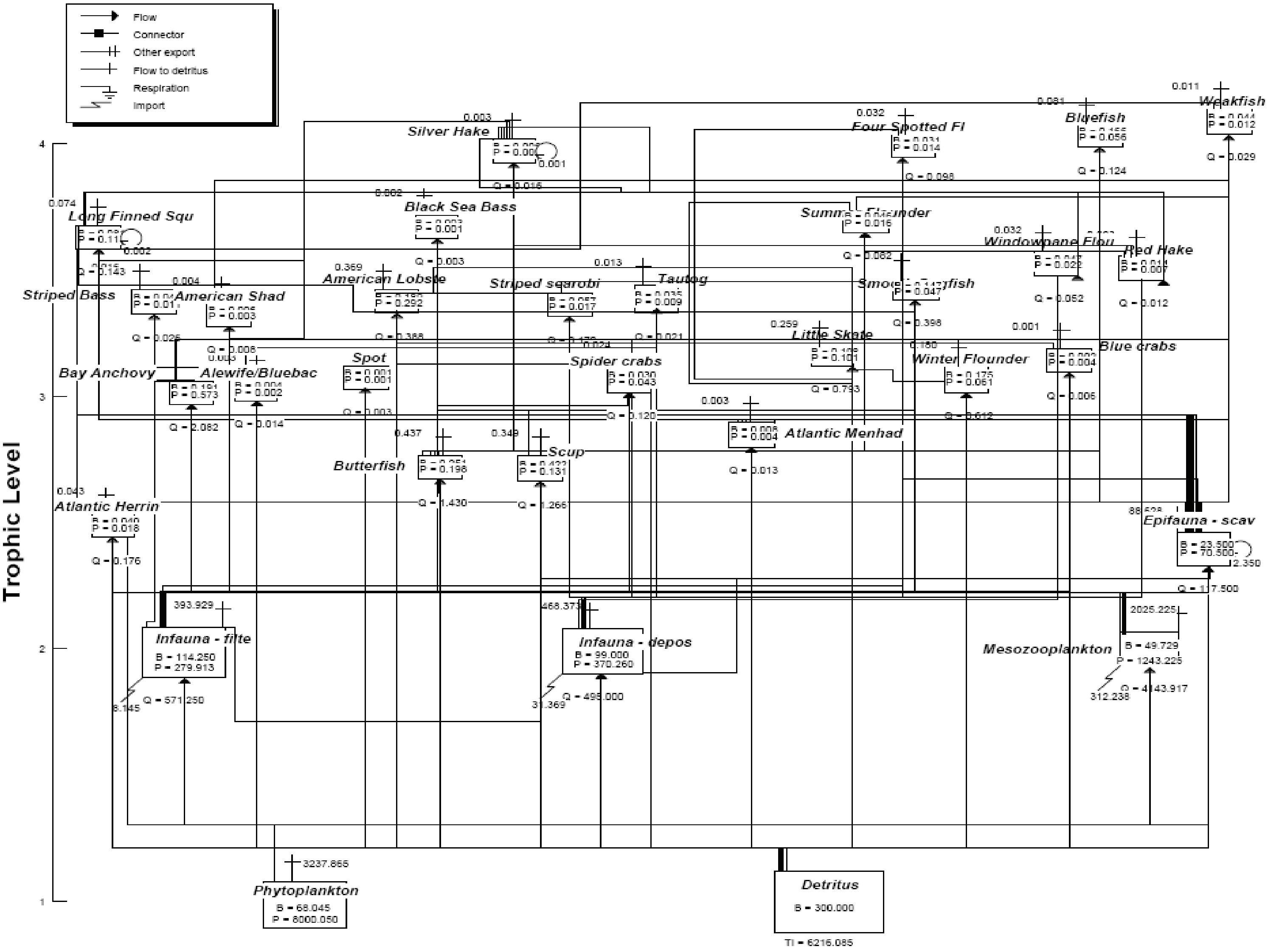


**Figure 22:** Biomass, production, and other flow associated with each functional group (t/km²/year) in the LIS offshore food web model.

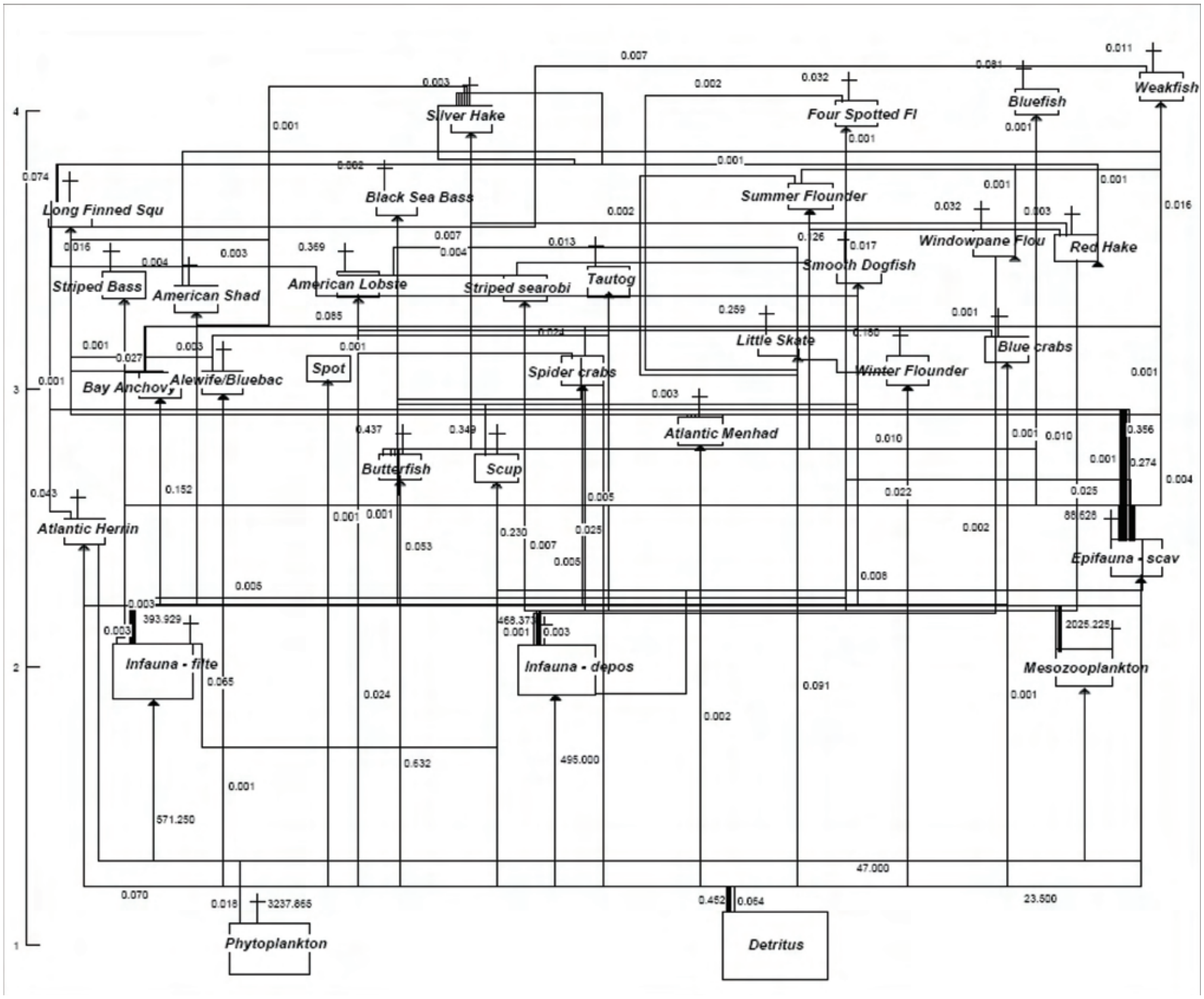


**Figure 23:** Biomass flows among functional group (t/km²/year) in the  LIS offshore food web model.

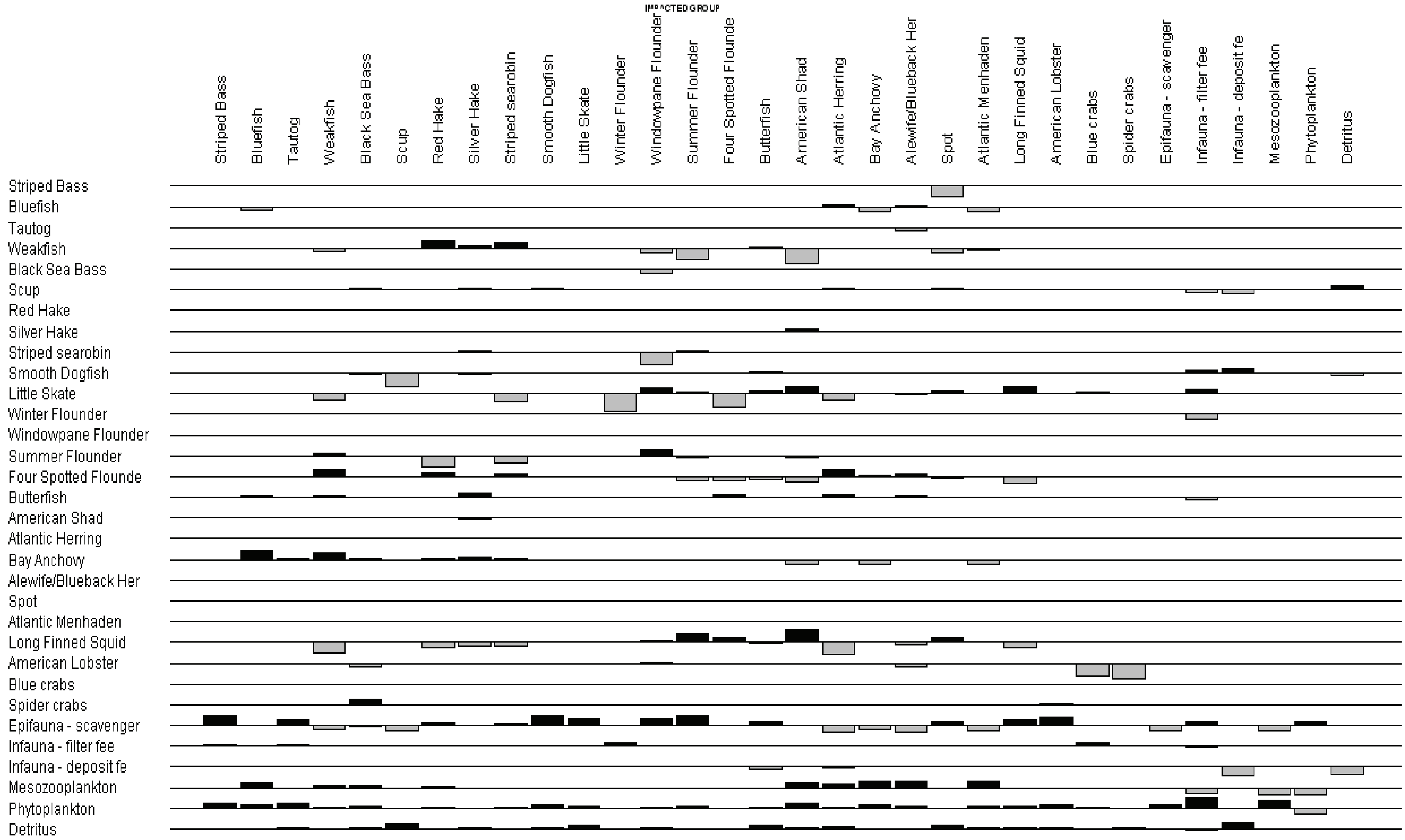


**Figure 24.** Mixed trophic impacts showing the combined direct and indirect trophic impacts that an increase of any of the groups on the left is predicted to have on the groups in the columns. Black colored bars above the line indicate positive effects; gray colored bars below the line indicate negative impacts.

## DISCUSSION

The LIS food web model developed using the Ecopath with Ecosim modeling environment presented here is to our knowledge the first attempt to quantify food web structure and dynamics for this important estuary in the US. We recognize that the model is in no way complete, as discussed below, but we do feel that it provides an important first step in developing more robust models that are more detailed in terms of the organisms included and the trophic interactions among them. In this sense, the model will hopefully act as a " strawman," *sensu* Okey (2001), providing a focus and a framework for future research on food webs and their dynamics in Long Island Sound. The model as constructed does allow for some initial comparisons to be made with other estuarine and coastal systems to assess how similar or different the food web metrics calculated by Ecopath for LIS are relative to these other systems. In this section of the report we first compare our model to those constructed for other estuarine and coastal systems, and then provide an assessment of the literature review relative to the model that we constructed, providing recommendations as to future model development, and finally discuss potential applications of the model and future development of food web model for LIS.

### LIS Food Web Dynamics and Comparison to Other Systems

Comparisons of the LIS model to Ecopath / food web network models constructed for other systems provides insights into the dynamics of LIS relative to these other systems (Table 17), and may also help in assessing future modeling needs. The Seine estuary, Bay of Somme and Chesapeake, Delaware, and Narragansett Bays Ecopath models were constructed using carbon units as opposed to the wet weight units used in the LIS model. Therefore, direct comparisons between these could not be made. However, a conversion factor of 10 for converting mg C to mg wet weight, based on general literature suggestions (e.g. Pauly and Christensen 1995) was used to be able to make general comparisons.

Summary statistics describing food web characteristics and flows in LIS varied in several ways relative to other estuaries and coastal systems (Table 17). Total consumption, detrital flows and total system throughput were 2 - 3 time less than in the northeastern US estuaries and the Seine estuary, but similar to the Bay of Somme and Atlantic Bight, but not in the case of total system throughput for the latter. In contrast, total respiratory flows and production were similar for all the systems, but LIS had somewhat higher total net primary production than the northeast US estuaries. Net system production was also much higher, but similar to the Bay of Somme. As such, it appears that the amount of biomass that cycles through the LIS system and the nature of the system activity has a signature that differs from the other northeast US estuaries but that certain system dynamics are similar. For example, connectance and system omnivory indices and the mean path length provide measures of the web structure within a food web and showed different patterns among the systems compared in Table 17. The connectance index was similar among the LIS, Atlantic Bight, the Bay of Somme and Seine estuary but these were lower than the northeast US estuaries. This index is sensitive to the number of taxa or functional groups in a model and the connections among them. Interestingly, the number of functional groups in the LIS model and the Atlantic Bight was higher than for the other systems, 33 and 55 in comparison to approximately 13 to 14 groups in the other models. Thus there was no apparent trend that was related to the number of functional groups. The small number of functional groups that were used in some of the models had more paths among them than in the more complex LIS and Atlantic Bight models. The mean path length was similar across all the systems, although Narragansett Bay and Chesapeake Bay had somewhat higher values, suggesting slightly longer steps in the various food chains that comprise the food web. The system omnivory index, which measures how weblike the paths are in the food web, was similar among the northeast US estuaries including Long Island Sound, but were lower in the French systems.

The food web network statistics calculated by Ecopath provide measures of the maturity and development of the system (see explanations of these measures in the **Results** section). For these measures, their interpretation for Long Island Sound relative to the other systems being compared leads to somewhat contradictory conclusions. The ratio of total primary production to total respiration (PP/R) is expected to be high in immature systems as productivity is higher than respiration. As such, net system production is expected to be large in immature systems and indeed this metric was larger in LIS relative to the other northeast US estuaries, but similar to that found in the Bay of Somme and the Seine estuary. When systems mature, PP/R is expected to approach 1, whereas in systems that are affected by organic pollution the ratio may be < 1, due to the accumulation of detritus and high levels of respiration. Long Island Sound had a PP/R ratio that was higher than the other northeast US estuaries and the Seine estuary, suggesting that the system is somewhat less mature. In contrast, the ratio of total primary production to total biomass is expected to be higher in more mature systems, yet this ratio was very similar among the US estuaries and only slightly higher for the Seine estuary and the Atlantic Bight. The ratio of total biomass to total throughput is also expected to be higher in more mature systems and again all of the estuaries compared had similar values. Lastly, the relative ascendancy quantifies the organization and efficiency of a system (Monaco & Ulanowicz, 1997). It measures the level of development and organization the system has achieved in terms of development capacity. Of all the estuaries compared in Table 17, LIS had a somewhat higher relative ascendancy, suggesting it has attained the highest maturity in regard to its developmental potential. Therefore, LIS may be more organized and efficient than the other estuaries compared. The trophic efficiencies that were calculated by Ecopath for the LIS food web model were relatively low for the lower trophic levels, ≲ 8% , but for upper trophic levels there were relatively high, > 13%.

The differences among the systems compared relative to LIS may be attributed to several factors. The high PP/R and net system production may reflect high nutrient inputs, in particular nitrogen, to LIS, especially in the western basin and narrows. Whether this represents a less mature system is debatable. LIS is a relatively young system geologically, on the order of approximately 10,000 years, and some of the other northeast US estuaries may have a longer geologic history, not having been covered in ice during the last Pleistocene glaciation (although certainly having their own relevant geologic histories over this period due to change sin sea level). However the interpretation of ecosystem maturity needs to be considered in light of the fact that there are significant nutrient inputs into the Sound and drive high productivity. The relative ascendancy measure suggests that LIS is more organized and efficient which might be expected of a more mature system. Although there is high productivity, Long Island Sound is also the deepest of the systems considered, excluding the Atlantic Bight. As such, a high respiratory load, as may explain the low PP/R for Chesapeake Bay, and the lower total system throughput and lower respiratory flows and consumption may reflect these differences in geomorphology and hydrology. Although these were not directly incorporated into the model, the variability in for example fish biomass across the Sound is eventually reflected in the model parameters as these are averaged and manipulated in model development. Thus, higher ecosystem activity in one portion of the Sound may be masked by lower activity in others due to averaging across areas using data from a variety of studies done in different locations. The resulting network statistics are thus measures io average conditions in these cases.

## Data Availability, Limitations and Needs

The LIS food web model developed provides a framework for starting to explore ecosystem dynamics, and focusing our efforts to better understand the structure of food webs in LIS and the trophic interactions among organisms in this estuary. However, there are data limitations that typically accompany Ecopath models that often force simplifications of trophic interactions and can also lead to inaccuracies in calculated system dynamics and interactions. By identifying and discussing these limitations, hopefully solutions can be formulated and achieved quickly, allowing for development and utilization of improved LIS food web models.

A concern in quantitative food web modeling is the availability of data and how it was collected and processed. The majority of Ecopath models are usually constructed from data that were collected and analyzed for a variety and often different research topics and needs, usually by scientists with different approaches and philosophies (Cohen et al., 1993). For example, in Harvey et al.'s (2003) Ecopath model of the Baltic Sea, biomass values were pieced together from numerous other studies, which were conducted over a period of twenty years. Some of these studies provided biomass data that were collected to study toxicological effects and mitigation methods. In many cases, when trophic data simply do not exist, input values from similar ecosystems are substituted until system specific, and thus potentially more accurate, data are made available. For the LIS model, all the data were taken from previous studies that had other objectives and were not collected for food web modeling. However, some of these studies, such as the CT DEP trawl survey (2006) and Dam and McManus' (2006) zooplankton monitoring provided LIS-specific data. The data from these studies were very applicable to food web modeling and allowed for critical component identification. The biomass data collected from these studies aided in selecting the most abundant and potentially influential species in the LIS environment. Specifically, the CT DEP trawl survey provided a comprehensive list of important fish and large invertebrate species in LIS.

Unfortunately, once the critical components were determined, finding enough Ecopath parameter data specific to LIS was difficult. In order to include a functional group in the model, three of the following must be entered: biomass, P/B, Q/B, or EE. A complete diet matrix must also be developed. Some fish species, such as cunner (*Tautoqolabrus adsersus*), had to be removed from the model due to lack of P/B and diet data. The majority of life history data that was found for the large invertebrates, including long finned squid, crabs, and American lobster, was from the CT DEP trawl survey. Upper trophic level invertebrate and finfish species that were not included in the survey were not included in the model.

For detritus and the infaunal and epifaunal species, the majority of the Ecopath parameter values were from other coastal environments with only limited information on trophic complexity. The use of "general" values from a collection of other environments can result in over and/or underestimation of trophic conditions and interactions in LIS. For the LIS model, the infaunal and epifaunal biomass and consumption data are potentially problematic in particular as these were only generally estimated due to lack of LIS-specific data. Since these functional groups represent lower trophic levels, their effect on the upper levels and the entire web is often significant (Pimm, 2002).

Data from other Ecopath models was also utilized in the construction of the LIS model. For example, length data was available for the calculation of fish P/B and Q/B, but other required parameters such as growth and mortality values were taken from general studies found at fishbase.org (Froese & Pauly, 2000). Additionally, diet matrix data specific to LIS fish species were only found for bluefish (Bucket et al., 1998; Richards, 1976) and striped sea robin (Richards et al., 1979). For all the other fish species, data from coastal areas near LIS were used as given in Bowman et al. (2000). For many of the large invertebrates, data was obtained from Chesapeake Bay (Christensen et. al., 2005) and Atlantic Bight (Okey, 2001) Ecopath models. While these systems are similar to LIS, these data were used to fill in the data requirements of the Ecopath model, and as such are potential weak points in the model. Substantial amounts of data exist for LIS, unfortunately very little is acceptable for food web construction and modeling. However, functional groups and taxa which required data from non-LIS sources have been identified (Table 2, see also Digital Appendix) and therefore future research can be directed to collecting the life history and trophic data required to develop LIS Ecopath models so that they are based more on LIS-specific data and therefore potentially more accurate.

Other limitations of the LIS model involve restrictions of the Ecopath with Ecosim software. The core routine of Ecopath, based on linear equations, only provides an instantaneous snapshot of trophic flows typically on a yearly reference. It does not account for changes in rates of the basic parameters due to numerous possible independent factors (Christensen & Walters, 2004; Christensen et al., 2000). In his model of the North Sea, Christensen (1995) discovered that biomasses changed over the time period the model was applied, causing an over-estimate of mortality rates of various trophic levels. For the LIS model, the majority of the entered Ecopath parameter data were averaged together from the period between 1995 to 2005. Therefore, the results of this model are a 10 year averaged snapshot and do not account for seasonal and/or year to year changes. However, this LIS model can provide a foundation for analyses of seasonal trophic interactions and/or for interactions over yearly time periods. No matter what types of LIS food webs are constructed in the future, modelers should remember that experimental research and numerous other Ecopath scenarios should be combined when attempting to provide a detailed description of the dynamics of the LIS ecosystem and its environmental status.

The success of Ecopath modeling is strongly dependent on the correct separation of species into functional groups for the model (Christensen & Walters, 2004). In the LIS model, the lower trophic levels were aggregated while functional groups for the large invertebrates and finfish were separated by individual species. Attempts were made to aggregate some species, however large differences in life histories and feeding behaviors led to their individual classification. Only alewife and blue herring were combined since these two species are often categorized together by state and federal agencies (CT DEP, 2006). Aggregation is most appropriate in models that have a large number of functional groups, such as the LIS model, since aggregation can simplify a complex web for easier analysis. Species could be treated individually or grouped with other ecologically related species. Taxonomic grouping is possible, but if differences occur in their life history, such as reproductive cycles or migration patterns, similar taxonomic groups should be separated to provide a more balanced approach. However, the aggregation of similar species should still be limited since placing multiple species into one functional group could eliminate quantitative data between species that have the same predator and prey and reduce interactions associated with species diversity (Polis 1991, Cohen et al. 1993). Hammond & O'Brien (2001), Bundy (2001), and Pinnegar et al. (2005) all demonstrated that changes in a model's functional grouping results in different and usually conflicting model dynamics. Pinnegar et al. (2005) showed that models created from functional groups based on taxonomic similarities differed significantly from each other, even though the same number of groups existed for each model. Using individual species in a model leads to more accurate estimates of mortality and consumption since no averaging occurs among species. However, the averaging associated with multiple species groups results in unbiased estimates since more data are used for each functional group (Christensen et al. 2000, Christensen and Walters 2004). Additionally, some consideration should be given to the separation of adults and juveniles of particular taxa into individual functional groups if they display significant differences in their diet compositions and other food web characteristics.

This model was constructed using data, on the most part, from over a 10 year time period, and does not account for any yearly or seasonal variation that occurs in LIS. In construction of the food web, Ecopath uses an average rate for the input data assuming that the effects of time or seasonal effects are not significant enough to affect the parameter (Christensen et al., 2000; Link 2002; Christensen & Walters, 2004). Many species in LIS are migratory species which strongly influences their biomass and diets seasonally and over their life history. For example, bluefish move in and out of LIS annually and also feed both inshore and offshore. The diet matrix created in this model only provides a general overview of their feeding habitats in LIS. However, the LIS Ecopath model provides a foundation for developing models that incorporate these types of differences.

Our initial data mining for information and data that could be used to assess food web structure and use in Ecopath modeling of the LIS system revealed that there is a critical paucity of such data. While there are usable data for specific trophic levels in several environments, the lack of data for other trophic levels precluded the development of quantitative food web models for such environments. For example, in nearshore areas and in coves, embayments tidal rivers and bays, a potentially significant contribution to primary production is made by the phytobenthos, attached and drifting macroalgae and in some areas (mainly east of the Connecticut River along the Connecticut shore and along eastern Long Island on the LIS south shore) also by eel grass and in shallow, brackish areas by other submerged vascular plants such as widgeon grass (*Ruppia maritima).* There are several available studies (e.g. Udell et. al, 1969, Baillie and Welsh, 1980, Welsh et al. 1982, see also Digital Appendix) that provide biomass and production estimates for of various sets of these primary producers in LIS. However, there are very few studies that have estimated and biomass production for upper trophic levels in these environments. Typically, studies have focused on community composition and population structure and only report abundances on the most part. Furthermore, studies that may provide food web applicable data have only been done in a few specific locations in LIS. As such, it is not possible to model trophic dynamics in different regions of the Sound and assess spatial differences in these dynamics.

However we do know that there are significant trends in, for example, benthic species diversity from the eastern to western portion, of the Sound (e.g. Zajac et al. 2000), and likely similar trends in taxa comprising other trophic levels. There are also problems that arise related to data conversion, such as the appropriateness of specific conversion factors for certain taxa.

Based on our literature search and data mining, and the structure of the Ecopath model developed, relative to generally known food web structure and interactions, we recognize the following data needs:

1) *Data on biomass and productivity* - To the extent possible, future studies of all taxonomic groups in LIS should include measurements of biomass, including if possible wet wt, dry wt and carbon content. Studies should be conducted over several years so that productivity can be estimated. This stands as the most critical data need to further our understanding of food web and ecosystem dynamics in LIS. Additionally, for key taxa, ontogenetic differences (e.g. Figure 5) in these variables should be studied, especially how they may change also with respect to the use of different habitats during the life cycle.

2) *Diet composition* - The diet compositions used for this study largely came from data available on www.fishbase.org. These data are valid but are developed from potentially multiple sources and reflect general diets of specific taxa. As such, they are not necessarily representative of the diets of functional groups / taxa in Long Island Sound. A particular species may not be feeding on a preferred food item because it is in short supply in LIS. Such a situation would not be recognized without LIS specific diet composition studies. Therfore it will be critical to perform diet composition studies using gut analyses, isotope or other approaches.

3) *Fish morphometrics to aid in the calculation of consumption* - The consumption to biomass ratio, Q/B, is a critical variable in Ecopath modeling. Estimating consumption can be through direct observational / experimental studies or by utilizing known physiologic relationships. For example, “one such equation is:

$$\log Q/B = 7.964 - 0.204 \log W_{\infty} - 1.965T' + 0.083A + 0.532h + 0.398d$$

where Q/B is the food consumption, $W_{\infty}$ is the asymptotic weight in grams, T’= 1000/(˚C+273), A is the aspect ratio of the caudal fin = h2/s, h=1 and d=0 for herbivores, h=0 and d=1 for detritivores, and h=0 and d=0 for carnivores. Here, one key input is the aspect ratio of the caudal fin... Fish with tails with high aspect ratio consume more food than fish with low aspect ratio tails, other things being equal...[this] equation cannot be used for fish (e.g. eels) which do not use their caudal fin as their main propulsive organ. Other approaches can be used in such cases.” (taken from www.fishbase.org). Morphometric studies of fish in LIS would add to the accuracy of estimating Q/B for these taxa in LIS. For other taxa (e.g. epifauna-scavengers) laboratory and/or field observational studies are be needed.

4) *Taxon / trophic level focused studies* - The structure of the Ecopath model presented here reflects the data available. Clearly, potentially important groups were not represented including bacteria, macro-zooplankton such as jelly fish and ctenophores and micro-zooplankton such as protozoans which together with bacteria participate in the microbial loop which may be critical in

open water food web dynamics. Other groups that were not included in the model were mammals and birds. The importance of these latter two functional groups may not be great for the offshore, deep-water model that was developed, but we know that birds can be significant consumers in shallow water and intertidal habitats. It will be critical to include these groups in models developed for these environments. Human effects were incorporated into the model by calculating mortality as a combination of natural and fishing mortality. Trophic related data for all these groups are especially needed. Also, the fish data used came ftom the CT DEP trawl survey, probably the best ecological data set available for LIS. However, not all open water fish and other taxa are sampled accurately by a bottom trawl. Studies directed toward elucidating larger taxa that occupy the full water column are needed.

5) *Habitat, geographic-based and web compartment studies* - LIS exhibits significant spatial variation in environmental characteristics and dynamics (geomorpholy, hydrology, susceptibility to anoxia / hypoxia etc.). Thus, over the scale of the entire LIS, it is expected that communities comprising different trophic levels (e.g. the benthic community) will exhibit different trophic structure and dynamics. For example, the structure and dynamics of the offshore food web presented here may differ between the western portion of LIS, where annual hypoxia / anoxia occur to varying degrees from year to year, and the central and eastern portions of the Sound where bottom waters are generally not affected by low dissolved oxygen. Obtaining region specific sets of data will be necessary if we are to identify and understand any regional differences in ecosystem dynamics, and potential implications for managing the estuary. There are a variety of different habitats that are found in LIS particularly along the coast and in shallow waters (e.g. intertidal flats, shallow subtidal, rocky outcrops / boulder fields, salt marshes) with distinct sets of taxa / functional groups. Specific food web studies focused on these habitats (e.g. Hall and Raffaelli 1991) would greatly increase our understanding of trophic dynamics is LIS and lay the ground work for exploring food web connections among these habitats, including the deeper offshore waters of LIS. Within habitats, food webs may be comprised of compartments (Figure 9), and exploring portions of food webs would help in revealing if such compartments exists in LIS. For example, we might imagine that an important compartment of the overall food web is comprised of open water phytoplankton and zooplankton. Both groups are potentially diverse, and in particular the zooplankton that is comprised of both the holoplankton (ranging in size from protozoa to large jellyfish) and meroplanton (e.g. larvae of benthic organisms and also fish larvae). Studies should be conducted to elucidate the details of this food web in terms of connections, temporal changes and flows along different pathways (e.g. grazing pathways versus the microbial loop). Similarly, studies should be directed at quantifying benthic food web compartments. The model that was developed has relatively high taxonomic resolution in the upper trophic levels, greater than for many other estuarine food models, but is relatively general for the lower trophic levels by recognizing only four general functional groups (mesozoolankton, infaunal deposit feeders, infaunal suspension feeders and epifauna - scavengers).

Although the collection of the different types of data noted above can be encouraged on an ad hoc basis for researchers working in LIS, it may be more timely and optimal in terms of moving our knowledge of trophic dynamics forward, to call for specific food-web related studies to collect these types of data for specific habitats, taxa and regions in LIS.

## Potential applications and model development

Understanding food web structure and dynamics of ecological systems is a key element in understanding the overall ecology of those systems. In turn, this knowledge can contribute to the development of more effective environmental assessment and management procedures. The construction and analysis of food webs implicitly considers multiple components of an ecosystems, and leads to collation of information from a variety of sources. The model developed here was formulated based on a consideration of available data and brought together information form avariety of sources. We feel that it provides a framework for future work on synthesizing information on LIS at different levels of complexity and addressing the variations in system habitat composition and geography. The model can also help to unravel the complex dynamics of LIS, identify key species or species groups driving the system, and identify how impacts to particular tropic level or functional groups / taxa by various forcing functions (both natural human) may change the system. The LIS Ecopath food web model presented in this report and the data assessment will hopefully enhance these components of food web research in LIS and the management insights gained from this area of research.

The Ecopath model developed indicates that the dynamics of the overall LIS ecosystem in off shore waters may differ from other systems given the mixed similarity among systems in network metrics. These differences may stem from differences in the characteristics among each of the estuaries (e.g. depth, food web composition). As the food web modeling progresses, comparisons among systems and among different habitats and regions within LIS will help researchers and managers accrue a better understanding of the dynamics and their significance. The model also starts to identify key ecosystem components (e.g. keystone species) in LIS. The mixed trophic impacts analysis points to the potential importance of several functional groups / taxa including epifauna - scavengers, long finned squid, and little skate (Figure 24). The biomass and production data used for epifauna - scavengers was based on general information in Mann (2000) and from a study conducted in the 1950's by Sanders (1956). We really do not know very much about the taxa making up this component in terms of ecosystem functioning. Clearly, additional information is needed to increase our understanding of this group to increase our scientific understanding of overall food web dynamics in LIS.

The LIS offshore Ecopath model can be used as a framework for developing more refined food web models and analyses to assess what we know about food web dynamics in the Sound. It also is the basis for developing and applying dynamic models using Ecosim. Ecosim provides the ability of exploring the dynamics of food webs constructed by Ecopath, and testing (simulating) the direct and indirect effects of human activities and other changing environmental conditions on ecosystem dynamics. Ecosim allows for biomass time-dynamic simulations and can analyze temporal variations in the dynamics of the constructed model (Christensen et al. 2000, Pauly et al., 2000). Applications of Ecosim have included assessment of potential inter-annual river flow changes on a small Alabama estuary (Althauser 1999), changes to biomass of major commercial species in the Baltic Sea (Harvey et al. 2003), and changes in predation mortality for a given prey (Christensen et al. 2005). These studies successfully used food web models to obtain more information about resource management concerns. For example, Althauser (1999) found that phytoplankton biomass fluctuates significantly between low and high river flows which in turn impacted biomass of other trophic levels for as long as 10 years. Harvey et al. (2003) and

Christensen et al. (2005) documented similar results regarding the impacts of a loss of species on a food web and changes in prey distribution.

To illustrate the Ecosim time dynamic modeling capability and how it can be applied to LIS, we used the LIS offshore Ecopath model in Ecosim to simulate what the effect would be of continual declines in the lobster population in LIS on other functional groups / taxa (Figure 25). In this simulation lobster mortality was increase steadily over a 10 yr period. In response to this loss of lobster populations the model predicts concomitant increases in the biomass of spider crabs, blue crabs and also sea bass, herring and menhaden. Interestingly, after the catastrophic lobster die off in 1999 and 2000 in the western portions of LIS, and to a lesser extent in other portion of LIS, the biomass of spider crabs increased significantly in the Sound based on data collected by the CT DEP (Figure 25). This indicates that the accuracy of the Ecopath model developed here may be fairly good and captures the nature and scale of trophic interactions in the offshore waters of LIS.

Other such scenarios can be explored. These include, for example, the effects of reductions in the biomass or loss of other major functional groups / taxa such as striped bass or winter flounder and seasonal changes in trophic structure. Seasonal changes maybe particularly important because hypoxia and/or anoxia occur in the western end of the Sound during the middle to late summer months, but not in the eastern end. The many possible applications of Ecosim to the LIS model have the potential to yield important information about how the Sound reacts to natural and anthropogenic impacts and changes. The Ecopath modeling environment also has another dynamic modeling component, Ecospace. Ecospace allow for spatial variation in food web dynamics and fisheries / impacts to be explored. Given the significant spatial variation among different regions and habitats of LIS in many of its abiotic and biotic characteristics, this would be a potentially useful tool. However, the spatially explicit data noted above would need to be collected and developed into Ecopath models for each region / habitat before this modleing module could be utilized.

The information we have collected and contained in the Ecopath data base associated with the model might also be used to help in further development / refinement of other models such as the SWEM water quality model for LIS. The data we collected from various sources are consolidated into the database that are in the Digital Appendix and are also available form the Principal Investigator. We will also make them available via the internet either through a link on the EPA's LISS site (http://www.longislandsoundstudy.net/) or at the PI's website (http://newton.newhaven.edu/rzajac/).

The model presented here is clearly only the first step in creation of food web models for Long Island Sound. Others who have done extensive Ecopath / Ecosim modeling, such as Okey (2001), Pimm (2002), and Christensen & Walters (2004), have emphasized the need for continued examination and revision of food web models for any specific system. The completeness, accuracy, and usefulness of a model are dependent on the acquisition of system specific data and continual review by the scientific and management communities. We hope that the LISS office will disseminate this report to interested researchers, mangers and public groups to get feed-back on the model structure, assess its current usefulness and to identify what steps should be taken next. By including a broad range of scientists and natural resource managers with expertise in different specific taxonomic groups, each trophic level can be assessed and revisions suggested. Revisions could include, for example, different aggregations of taxa into functional groups or disaggregations of groups into individual species, changes in input parameters, diet matrices, and the balancing techniques used (Okey, 2001). Food webs contain complex interactions, creating difficulties for modeling. Constant updating of the Ecopath / Ecosim parameters described here from newly acquired knowledge and comments will likely yield a more accurate description of LIS offshore trophic interactions and also aid in the development of models for different environments in LIS. Collectively, this will move our understanding of the system forward, and hopefully make positive contributions to the management of Long Island Sound.

**Table 17.** Comparison of parameters/indices between LIS and other Ecopath models of similar ecosystems: Atlantic Bight, Bay of Somme, Seine Estuary, Narragansett Bay, Delaware Bay, and Chesapeake Bay. Units provided for necessary parameters. Values for the all systems except LIS and the Atlantic Bight were originally in carbon units (e.g. mg C $m^{-2}$ $yr^{-1}$) which were converted to wet weight tons km $^{-2}$ $yr^{-1}$ using a conversion factor of 10 for mg C to mg wet wt based on general literature values.

| Parameter | Long Island Sound | Atlantic Bight | Bay of Somme | Seine Estuary | Narragansett Bay | Delaware Bay | Chesapeake Bay |
|---|---|---|---|---|---|---|---|
| Sum of consumption (t/$km^2$/year) | 5,339 | 5,912 | 3,227 | 11,102 | 17,900 | 13,831 | 14,937 |
| Sum of respiratory flows (t/ $km^2$/year) | 2,306 | 2,555 | 386 | 6,231 | 3,161 | 3,029 | 6,251 |
| Sum of all detritus flows (t/ $km^2$/year) | 6,214 | 11,353 | 11,132 | 13,213 | 16,875 | 12,759 | 12,312 |
| Total System Throughput (t/ $km^2$/year) | 19,553 | 30,581 | 23,121 | 36,032 | 51,476 | 43,016 | 45,915 |
| Sum of all production (t/ $km^2$/year) | 9,965 | 14,847 | 6,169 | 8,867 | 12,735 | 9,360 | 9,078 |
| Calculated total net primary production (t/ $km^2$/year) | 8,000 | 13,259 | 5,986 | 8,534 | 4,030 | 3,806 | 3,331 |
| Total PP/Total respiration | 3.5 | 5.2 | 15.5 | 1.4 | 1.3 | 1.3 | 0.5 |
| Net system production (t/ $km^2$/year) | 5,694 | 10,703 | 5,600 | 2,302 | 870 | 777 | -2,920 |
| Total PP/total biomass | 22.4 | 35.7 | 21.82 | 38.3 | 24.2 | 28.2 | 30.3 |
| Total biomass/total throughput | 0.018 | 0.012 | 0.01 | 0.01 | 0.04 | 0.04 | 0.03 |
| Connectance Index | 0.148 | 0.205 | 0.25 | 0.24 | 2.6 | 2.6 | 2.5 |
| System Omnivory Index | 0.165 | 0.254 | 0.001 | 0.11 | 0.3 | 0.3 | 0.2 |
| Mean Path Length | 2.44 | - |  | 2.57 | 4.2 | 2.8 | 3.3 |
| Relative Ascendancy (A/C %) | 44.7 | - | 35 | 34.8 | 33.5 | 33.4 | 31.3 |

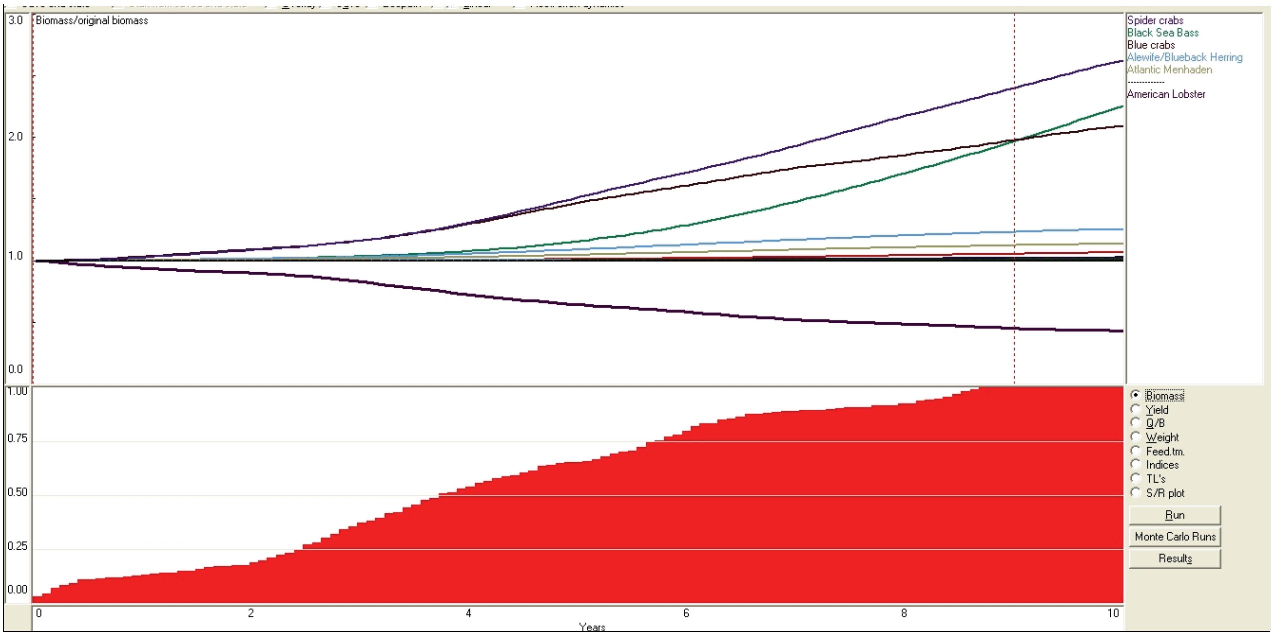


**Figure 24.** Ecosim simulation of increasing lobster mortality in the offshore waters of LIS and its effects on other trophic functional groups / taxa in the Ecopath LIS model. The bottom portion of the figure shows the increase in lobster mortality (in red); the upper position shows the change in biomass of lobsters (declining ) and other groups affected by the decline in lobster relative to their starting biomass.

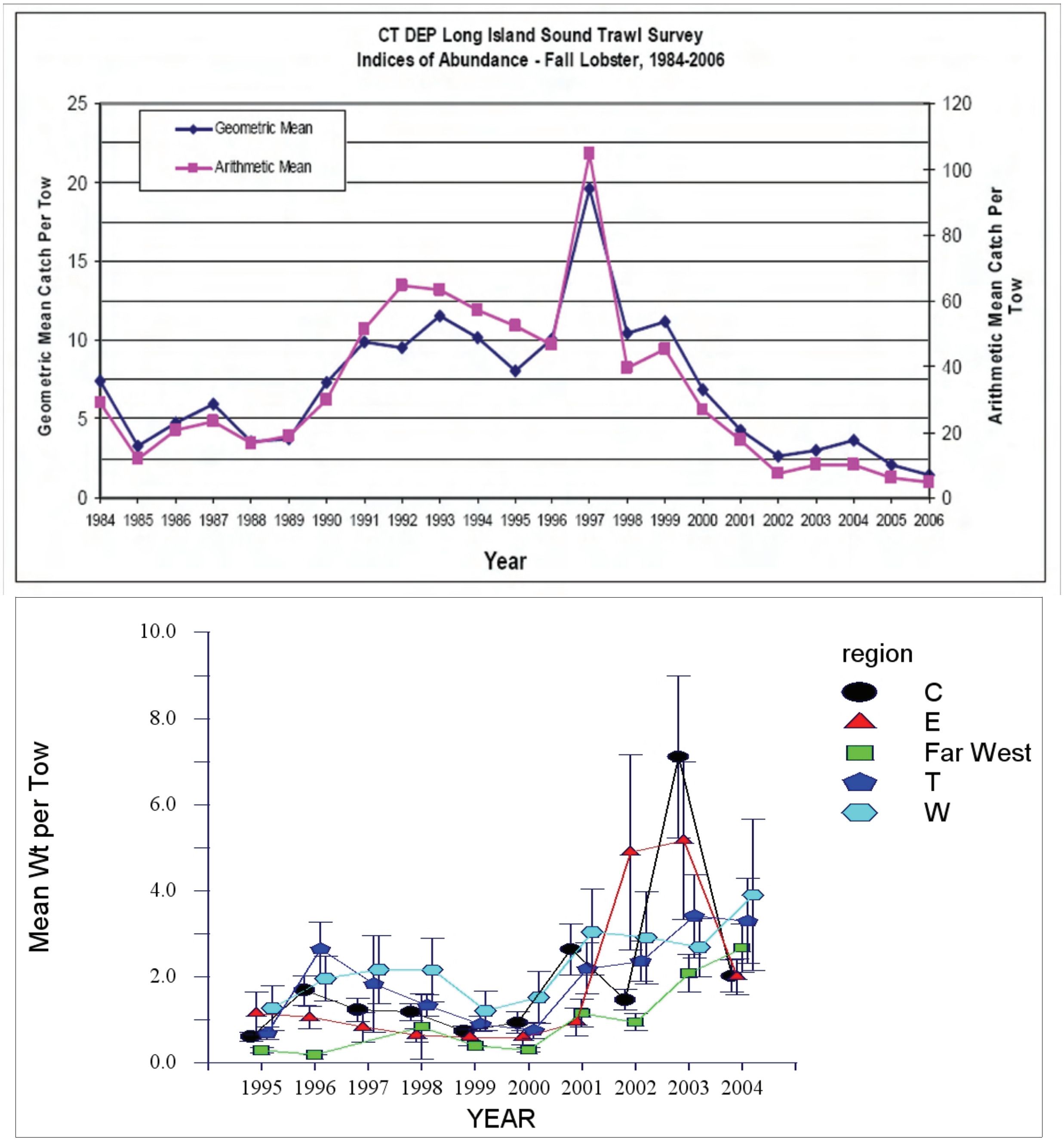


**Figure 25.** TOP: Long Island Sound Trawl Survey fall abundance indices for American lobster, 1984-2006. BOTTOM: Changes in the mean wt per trawl (± 1 SE) of spider crabs in different portion of LIS. Note significant increases of crab biomass after lobster declines in 1999 / 2000.

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