Evaluation and Emergy Analysis of the Cobscook Bay Ecosystem

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Abstract - A naturally eutrophic, estuarine ecosystem with many unique features has developed in Cobscook Bay over the past four thousand years under the influence of six meter tides and rich flows of nitrogen from the deep waters of the Gulf of Maine. In this paper, measurements of primary production and water column properties made in the Bay from 1995 to 1996 and information from past studies are used to construct an energy systems model of the Bay's ecosystem and to evaluate the annual flows of energy and matter coursing through this network. The properties of this ecosystem network were analyzed in terms of the solar emjoules (emergy) required to support primary and secondary production. In Cobscook Bay there is an extraordinary convergence of emergy, 7.4E+12 sej m^{-2}, from renewable sources. This level of emergy is one of the highest natural empower densities that we have found. Eighty-four percent of this emergy is from the tides and wave action. Transformities calculated in this analysis show that emergy is being used, most effectively, to support populations of large brown alga, i.e., *Ascophyllum nodosum*, *Fucus vesiculosus*, and *Laminaria longicruris*, and the diverse community of benthic organisms that thrive in the intertidal and shallow subtidal zone along the shore. Phytoplankton production is less efficient apparently due to light limitation, but phytoplankton and resuspended benthic microalgae support highly productive beds of filter feeders. Empower density in Cobscook Bay is similar to that required elsewhere for intensive fish culture; therefore, aquaculture may be a good human use of the rich convergence of natural emergy found there. The nitrogen entering Cobscook Bay from salmon culture is 19% of the net annual flux of new nitrogen entering from the coastal waters. The Bay's great resource wealth supports economic activities such as salmon culture and commercial dragging for scallops and urchins that, in turn, alter the concentrations of nutrients and suspended sediments locally in the Bay and may cause increased sedimentation and changing benthic communities in the Bay as a whole.

Introduction

Scientists and engineers recognize that energy is the source and control of all things (Odum and Odum 1976), but this fact has seldom been taken as the starting point for analyzing the structure and function of marine and estuarine systems. In this study, the energy basis for biological productivity in a macrotidal estuary, Cobscook Bay, ME, was documented and analyzed.

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Every place on earth can be thought of as having its own unique biological characteristics and endowment of energies, but the convergence of nature's energies has been extraordinary in the world's coastal ecosystems because the energies of land and sea meet there. In addition, Cobscook Bay has received an extraordinary inflow of tidal energy for the last 4 to 7 thousand years, for it was during this time that the Gulf of Maine-Bay of Fundy system gradually took on macrotidal characteristics (Campbell 1986, Grant 1970). The biological result has been the development of numerous, and in some cases abundant, sources of plant production that provide the basis for a diverse web of life within the Bay, as well as a large export of organic matter from the Bay to adjacent coastal waters. The primary producers of this region are known to support ecosystems of high commercial, recreational, and aesthetic value to society.

The physical basis for biological production in the Gulf of Maine and its estuaries has been a subject of scientific inquiry since Henry Bigelow first documented the physical circulation and biological productivity of the Gulf through research cruises on vessels of the United States Bureau of Fisheries carried out from 1912 to 1928. In the present study, a multi-disciplinary team of researchers documented the sources of primary production in Cobscook Bay through a series of field studies in 1995 and 1996. The physical basis for biological production in the Cobscook Bay was documented by constructing and evaluating an energy systems model of this estuarine ecosystem and using it to trace the energy supplied by the forcing functions, i.e., solar radiation, fresh water inflow, tide, wind, and nutrients, through the web of ecosystem components to account for the energy flows in primary and secondary production.

The methods of environmental accounting (Odum 1996) can be used to sort out the relative contributions of the various energy sources of different kinds to the support of biological productivity and ecological organization in the Bay. To accomplish this, the various energy inflows to the Bay are expressed in the same units (i.e., solar joules), making them directly comparable. Odum (1987, 1996) defined a new quantity, emergy, and an accounting process for its determination to make possible an evaluation of the energy basis for ecological networks.

Emergy is the available energy of one kind previously used up directly and indirectly to make a product or service. Its unit is the *emjoule*. Emergy can use any kind of energy as the common base, for example coal joules, solar joules, etc. However, in evaluating environmental systems, we commonly use solar energy as the base unit. *Solar emergy* is the available solar energy used up to make a product or service in an ecological or economic system. Its unit is the *solar emjoule* (sej). *Available energy* is energy with the capacity to do work

sometimes called *exergy*. *Empower* is the emergy flow per unit time and *empower density* is the emergy flux per unit area.

In this study, the ecological flows of nutrients and primary production were first documented and then compared in terms of the mass of nitrogen taken up or the quantity of carbon fixed. The fate of this carbon was also examined using data from this study, information from the literature, and convenient but reasonable assumptions about its disposition (e.g., all detritus produced by aquatic macrophytes was assumed to behave in a similar manner even though decomposition rates, palatability, etc. may vary somewhat among species). Next, the mass flows were converted to energy, and the solar energy equivalents or the emergy (Odum 1996) that was used in making a joule of each kind of primary production was determined.

Odum (1987, 1988) first defined emergy and transformity as properties of all energy flow networks. Transformity is significant because it is a universal measure of the position of any ecological component or process within the hierarchical structure of its system and within the larger universe of natural processes. *Solar transformity* is the solar emergy required to make one joule of an item such as an ecological storage or flow. Its units are solar emjoules per joule (sej J^{-1}). Different transformities for the same item are an indicator of the relative efficiency of the production process for that item. The greater the energy flow in the denominator for a given emergy input to the production process (the numerator) the lower the transformity of the item and the higher the efficiency of the production process. For example, the transformity of penaid shrimp produced naturally in the Gulf of Mexico is about 4.0E+6 sej J^{-1} compared to 1.3E+7 sej J^{-1} for shrimp produced by mariculture in Ecuador's coastal ponds (Odum and Arding 1991).

The relationship between emergy and available energy is expressed in the fundamental equation of emergy analysis: emergy = transformity x available energy (exergy). For example, the solar emergy in phytoplankton net primary production is calculated by multiplying the available energy in the organic matter increase by its transformity. Conversely, the solar transformity of an item can be determined, if we know the solar emergy required for that item and the flow of available energy associated with it. In general, ecosystem flows that require more emergy for their support are higher quality (higher transformity) and are expected to have a greater amplifying effect than a lower quality flow (lower transformity), when used in the expected manner within an ecosystem network (Campbell 2001, Odum 1994). For example, a joule of work by a top carnivore, such as an eagle, performs a very different function within the ecosystem (does a different kind of work) than a joule of work done in carbon fixation by kelp. Different material flows can be evaluated in the same units (solar emjoules) through converting

estimates of carbon metabolized to energy (joules) and then multiplying these energy values by their solar transformity. The solar emergy of an energy flow is the sum of the solar emergy from all sources required for a given quantity of energy to flow along its ecological pathway. Average values for the transformity of many items have been calculated and are available in the literature (Odum 1996); however, multiple determinations of the transformity of similar items are not common.

One contribution of this study is that it allowed an independent estimation of transformities for the major sources of primary and secondary production in a macrotidal estuary through an evaluation of a relatively complete ecosystem network. When the magnitude of energy flowing on a pathway in an ecosystem network is expressed as solar emergy, it is directly comparable to other network flows expressed in the same way, so that the relative contributions of each can be determined directly by inspection.

The empower in an ecosystem network is a measure of the complexity of organization and of the expected competitiveness of the ecosystem or an ecosystem component in the evolutionary process (Lotka 1922, Odum 1996). In general, network empower would be expected to increase with increases in species richness, the complexity of interactions among species, and total energy flow through the network. These three factors must be considered together to determine the empower of alternate system designs. Ecological processes are expected to interact and evolve over time toward ecosystem designs that produce higher empower states (Odum 1996), assuming that the suite of forcing functions (emergy signature) supplying the emergy base for the system remains the same. Species and interactions change within ecosystems over time to adjust to the changes in inputs under the imperative to maximize empower under the new conditions.

Information Sources

There is a considerable amount of information available on Cobscook Bay and the Quoddy Region (Fig. 1) as evidenced by the 110 specific Cobscook references and 196 Passamaquoddy references found in Larsen and Webb (1997). Most of this information was obtained during the course of environmental impact studies conducted from the 1930s to 1980 on the possible environmental consequences of developing tidal power in Passamaquoddy Bay (Shenton and Horton 1973, US Army Corps of Engineers 1980). Later, in the 1980s, more data were generated when the consequences of Fundy tidal power development for the Gulf of Maine-Bay of Fundy region were studied (Gordon and Dadswell 1984). Also, a proposal by the Pittston Company to build an oil refinery at Eastport generated scientific studies of the Quoddy area

during the seventies (Trites 1974). The information contained in the literature along with new information gathered in this study was used to construct and evaluate an energy systems model that characterizes the important forcing functions, ecosystem components, processes, and energy flows of the Cobscook Bay ecosystem. The major sources of data used in this analysis range from estimates of zooplankton production determined in the 1950s to the estimates of primary production determined in 1995 and 1996. The underlying assumption is that the older information is still representative of the same ecosystem components in 1995. The ecological network evaluated in this study is not complete because information was not available on all aspects of the Cobscook Bay ecosystem.
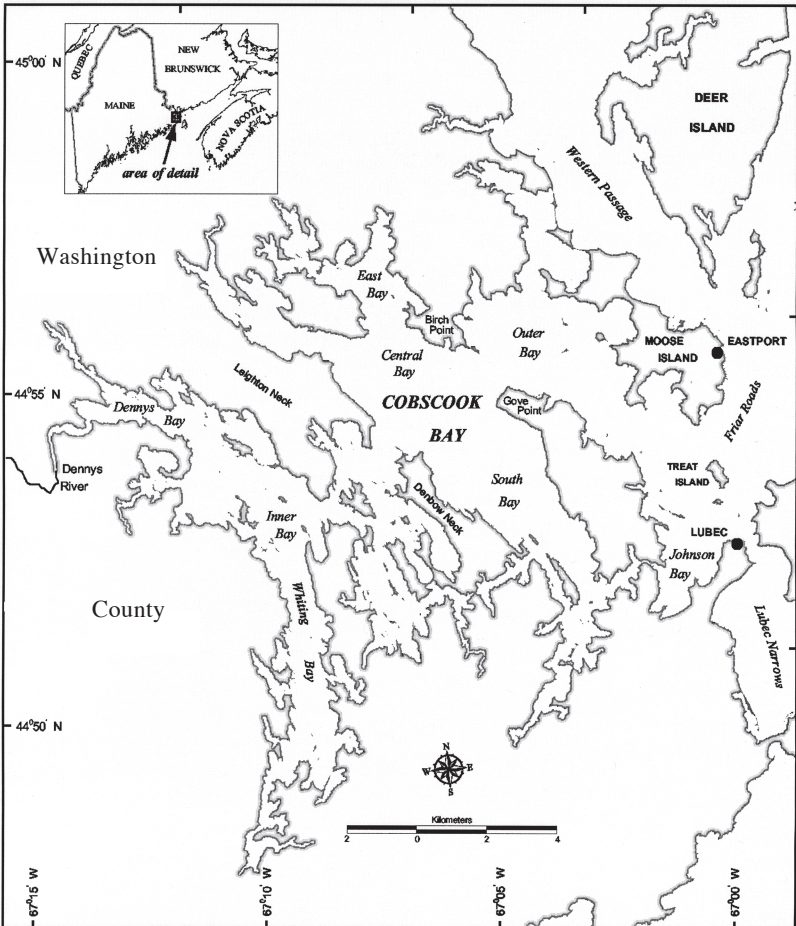

Figure 1. Map of Cobscook Bay, ME, showing some of the place names mentioned in the text.

Methods

Energy systems theory (Odum 1994) is the study of how ecosystem designs are determined by scientific laws and principles including the conservation of energy and mass, the second law of thermodynamics, and the maximum power principle (Lotka 1922, Odum 1995). This scientific approach to systems analysis is a comprehensive, self-consistent methodology for modeling, evaluating, and understanding ecosystems. In this methodology, energy is used as a common denominator to evaluate systems, because the transformation of energy underlies the organization of components and processes in all systems. When taken as a whole, the energy systems approach provides a set of design principles through which ecosystem organization can be understood and interpreted. A potentially powerful explanatory hypothesis underlying this study is that the suite of forcing functions or the emergy signature, of an estuary determines the kind and amount of ecological organization found there (Campbell 2000a, Odum et al. 1977). This principle guided the evaluation of the Cobscook Bay ecological network.

Forcing functions are sources of energy and matter from the next larger system that enter an ecosystem by flowing across its boundaries. Taken together these forcing functions comprise the *energy signature* of the ecosystem. The *emergy signature* is calculated by multiplying each member of the spectrum of available energies by the appropriate transformity (sej J^{-1}). These signatures show the magnitude of the energy or emergy inputs to a system on the ordinate plotted against the categories of energy sources shown in order of increasing transformity on the abscissa. The emergy signature for an ecosystem arises from the dynamic interactions of the next larger system. Once an energy flow crosses the system boundary, its emergy is received by the system. The emergy signature tells us how much of the planet's solar emergy has been concentrated in each of the energy inputs to a particular place. It also shows the relative organizing power of each input when it is used within the system. Quantitative and qualitative differences in the emergy signature of estuaries have been demonstrated to correspond to different ecosystem types (Campbell 2000a, Martin 2000, Odum et al. 1974, Twilly 1995). In this paper, the physical basis for primary and secondary production in the Cobscook Bay ecosystem network was characterized and analyzed by documenting the emergy signature supporting the network. The emergy signature of an estuary is given in tabular and graphic form, and it is documented with a series of notes giving the method of calculation and sources of information.

Energy systems diagrams are used to represent and evaluate ecosystem organization. The first step in diagramming an ecosystem is to construct a conceptual model, which represents the network of forcing

functions, components, and pathways. The conceptual model in this study was constructed using Energy Systems Language (Odum 1994), a set of mathematically defined symbols that can be used to represent common ecological components and processes (e.g., production, consumption, storage, etc.). Definitions of the energy systems language symbols are generally available in the literature (Odum 1971, 1994, 1996). In this step, expert opinion and general knowledge about the system are used to build the initial model. This model is refined as research uncovers additional information that requires it to be modified.

The next step in the modeling process is to numerically evaluate the forcing functions, storages, and flows represented in the model and place these values on the diagram and in an accompanying table. The table gives verbal definitions of each component, process, and forcing function that are keyed to the model diagram through a set of common symbols. This table usually contains a column defining the entry, a column for the value of the storage, flow, or forcing function, a column for the units of the entry, and a column indicating the note where calculations and sources are given in detail. Key unmeasured flows can often be estimated by making reasonable assumptions using the available data. Energy flows associated with undocumented components are aggregated within the appropriate known flow. For example, in this study, the details of the microbial loop were not known or documented, but there is a pathway for the microbial decomposition of organic matter where the microbial loop flows would be included. The process of evaluating a model allows static analyses to be performed and shows the location of data or information gaps and weaknesses that might be filled by further field, laboratory, or literature research. Many properties of the network, e.g., annual production, annual consumption, export, storage, and turnover of energy and materials, can be determined from the completely evaluated model. In addition, an evaluated network model with its emergy signature can be used to calculate values for the transformities of all the flows in the network either by using the emergy algebra rules in Odum (1996) or by constructing sets of equations for each process where the emergy of the outflow is equal to the emergy of the inflows and then solving the set of equations using the eigenvector method given by Collins and Odum (2000).

In this study, the web of carbon and nitrogen flows in the Cobscook Bay ecosystem was evaluated using new field measurements (Beal et al. 2004; Phinney et al. 2004; Vadas et al. 2004a, 2004b, 2004c) combined with past measurements of energy sources and higher trophic level components. The flows of carbon and nitrogen through the system were determined by constructing mass balance budgets for the different ecosystem components. In constructing a mass balance budget, one value can always be calculated by difference. This must be true because matter and energy cannot be created or destroyed; therefore, all of the

carbon fixed annually must be consumed, accumulate as storage or passed on to some component or process within or outside the system. The evaluated network of carbon and nitrogen flows was used to determine the energy flow network. The standard conversion factors, e.g., to go from mass to energy flow or from carbon to nitrogen, are reported in the appendices. The hydrodynamic model of Brooks (2004) and Brooks et al. (1997, 1999) was used to evaluate the physical exchange of materials between Cobscook Bay and the adjacent coastal waters. The energy flow network was analyzed with respect to the emergy signature of the Bay to obtain new estimates for the transformities of energy flows within the ecosystem. Transformities were determined using the emergy algebra rules given in Odum (1996).

Caveat on the numbers

The estimates for primary production are all based on measurements performed during this study, and the standard deviation of the averages reported here can be determined (Beal et al. 2004; Larsen et al. 2004; Phinney et al. 2004; Vadas et al. 2004a,b,c). Estimates used in this paper are based on the same data found in the other papers in this issue, but may be slightly different from the estimates given in them, because different averaging rules were used and/or different assumptions were made about the distribution of values in unsampled areas. Estimates of the fate of primary production rely on literature values of ecosystem components and processes obtained by other investigators in other studies at other times. In addition, the estimates of consumption are predicated on assumptions that often grossly simplify a given problem (Appendix B). Nevertheless, we feel that our numbers provide a first order estimate of the carbon and nitrogen fluxes and the fate of annual primary production in the Cobscook Bay ecosystem. Note that both scientific notation and the computer-based exponential format are used for writing large numbers in this document. The reader should recognize that 10^6 and E+6 both mean one million.

Several different flows have been used by different investigators in this volume as the basis for comparing the magnitude of nitrogen inflows. Nitrogen species in seawater move in and out with the tide. The following flows of all nitrogen species or of nitrate alone might be used as a base for comparison: (1) nitrogen flux in the incoming tide, (2) nitrogen flux in the volume exchanged per tide (Garside and Garside 2004), and (3) net nitrogen flux to the estuary (considers exchange volume and the concentration gradient). In this paper, the net flux of new nitrogen (Dugdale and Goering 1967) to the estuary was considered to be the best quantity to represent the emergy absorbed by the ecosystem. The new nitrogen supplied to the ecosystem is most accurately represented by the net flux of NO_3-N from the sea to the estuary.

Co-products and splits

The designation of an energy flow either as a co-product of a production process or as a split of a single production product makes a difference in the calculation of its transformity (Odum 1996). The entire emergy input to the production process is required to make each co-product, whereas, the emergy input to the production of a product is divided in proportion to the energy on each output pathway of a split. For example, benthic macrofauna feeding on various plant materials assimilate carbon into biomass and produce feces. These two products have different properties and fates in the ecosystem and thus would be classified as co-products. If the benthic biomass produced serves as generic food for several consumers its emergy would be split between those consumers in proportion to the energy in the mass of the food eaten. Sometimes there is not enough biological information to make an accurate determination of whether a particular flow is a split or a co-product. In general, the emergy of a lower trophic level component that is used as food by several higher trophic level components is considered to be split among them in proportion to the energy in the food eaten by each. This convention has been followed here, although in some cases there are reasons to justify both views of a particular pathway. Energy flows through the primary producers are all determined based on a specific area of production, and thus each production area receives its portion of the emergy entering the whole system.

Results

Energy and emergy signatures

Campbell (2000a) published energy and emergy signatures for Cobscook Bay. These signatures were modified for this paper to show the relationship of new nitrogen entering from the Gulf of Maine to the sources in the original signatures. The revised energy and emergy signatures for Cobscook Bay are given in Figure 2a and b, respectively. The relevant patterns in the data are shown in Table 1 and the calculations and data sources are documented in the table notes given in Appendix A. The energy signature of Cobscook Bay (Fig. 2a) is dominated by solar energy, but it also shows two distinct peaks in the middle of the spectrum of transformities. One peak in the range of 24,300 to 30,000 sej J^{-1} is created by tidal and wave energy (Table 1); a second peak at 50,000 sej J^{-1} is produced by the chemical potential energy of fresh water in rivers. These two peaks are also present in the emergy signature, but in this case there is a third peak corresponding to the nitrogen received in seawater moving back and forth each day with the tide. The emergy flow received in the new nitrogen contained in seawater is large. However,

only a small fraction (10%) of this emergy is captured by the estuary as a net flux of NO_3-N into the system (Fig. 2b). The total new nitrogen entering the estuary each year (2.58E+6 kg-N y^{-1}) was determined by adding the net new nitrogen supplied by tidal exchange to the nitrogen added by freshwater inflow, salmon culture, and wet and dry deposition from the atmosphere. The emergy base for the Cobscook Bay ecosystem is comprised of the emergy inputs in the tides, waves, and the emergy of the cross boundary flows, i.e., chemical potential energy in fresh water
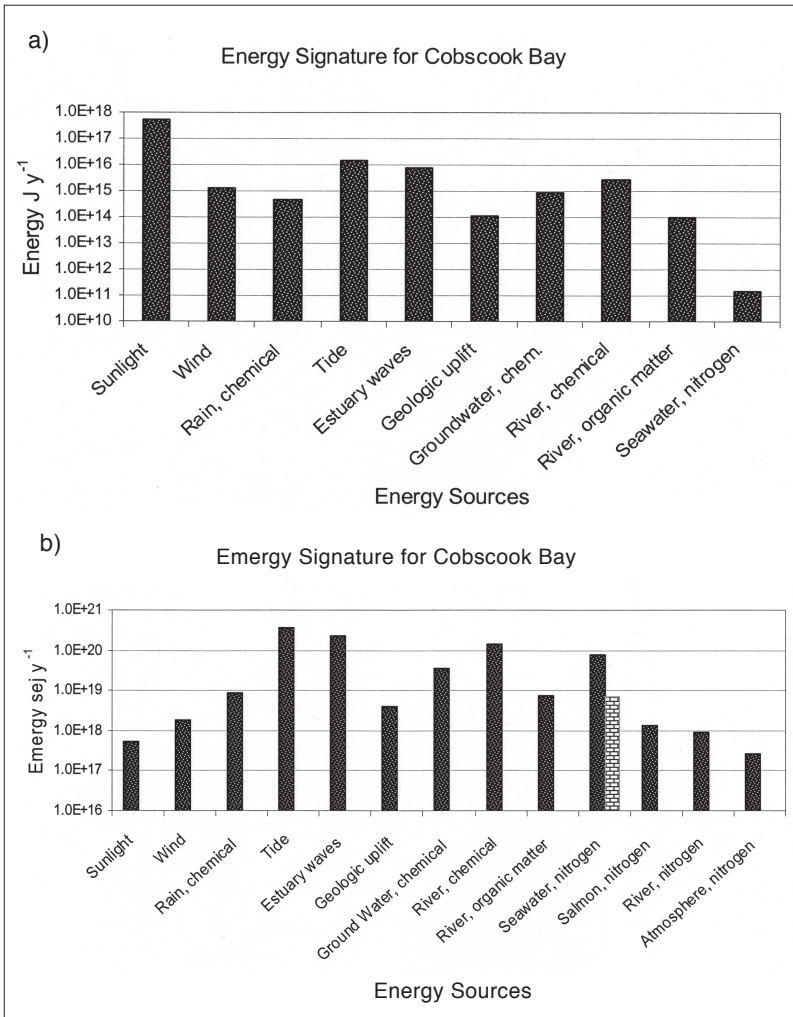

Figure 2. Energy sources supporting the development of the Cobscook Bay ecosystem. (a) The energy signature of the Bay. (b) The emergy signature of the Bay. The patterned bar shows the emergy in the net flux of NO_3-N into the Bay.

and the new nitrogen entering the estuary from the sea, salmon culture, rivers, and the atmosphere (Table 1).

The Cobscook Bay ecosystem model

A preliminary model of the Cobscook Bay ecosystem was constructed in 1993 and used in planning our research. Based on our knowledge of the Cobscook Bay ecosystem, we identified the ecosystem structure including the primary producers that supply two major pathways of consumption in estuaries, the grazing and detritus trophic pathways. Phytoplankton and benthic microalgae are the major sources of suspended material for grazing by either pelagic or sedentary feeders. Brown algae, green algae, red algae, and eelgrass (*Zostera marina* L.) supply carbon to the detritus pathway (Beal et al. 2004; Vadas et al. 2004a,b,c). This division of producers, according to the manner in which they supply carbon to consumers, is not mutually exclusive because a portion of macrophyte carbon is grazed by benthic macrofauna (e.g., periwinkles, sea urchins, etc.) and a percentage of the suspended phytoplankton and benthic microalgae die and become part of the detritus carbon pool where it is metabolized by bacteria. In addition, some detritus of macrophyte origin with its associated microfauna is suspended in the water column where it is eaten by filter-feeding consumers. The final ecosystem network that we evaluated (Fig. 3) included nitrogen sources from salmon culture and the atmosphere as well as seals and the harvest of fish and shellfish by commercial fisheries. Juvenile fish in the preliminary model were combined with adult fish in the final model because there wasn't enough information to

Table 1. Data needed to construct energy and emergy signatures received by Cobscook Bay, ME. Transformities, except for the tide, are from Odum (1996), and they have been rounded to three significant figures and are multiplied by 0.981 to put them on the $9.26E+24$ sej y^{-1} planetary baseline (Campbell 2000b). The transformity for tide is from Campbell (2000b). Appendix A contains the notes explaining each calculation.

Note	Energy source	Energy ($J\ y^{-1}$)	Transformity ($sej\ J^{-1}$)	Emergy received ($sej\ y^{-1}$)
1.	Sunlight	5.15E+17	1	5.15E+17
2.	Wind	1.26E+15	1470	1.85E+18
3.	Rain, chemical	4.80E+14	18,100	8.69E+18
4.	Tide	1.54E+16	24,300	3.74E+20
5.	Estuary waves	7.83E+15	30,000	2.35E+20
6.	Geologic uplift	1.21E+14	33,700	4.07E+18
7.	Ground water, chemical	8.91E+14	40,200	3.58E+19
8.	River, chemical	2.90E+15	50,100	1.45E+20
9.	River, organic matter	9.91E+13	72,500	7.19E+18
10.	Seawater, N received	1.56E+11	4.77E+8	7.47E+19
11.	Seawater, N net influx	1.49E+10	4.77E+8	7.12E+18
12.	Salmon culture, N	2.90E+9	4.77E+8	1.38E+18
13.	Rivers, N inflow	1.95E+9	4.77E+8	9.31E+17
14.	Atmospheric N deposition	5.68E+8	4.77E+8	2.71E+17
15.	Total new nitrogen	2.03E+10	4.77E+8	9.70E+19

evaluate them separately. The results for this part of our project are presented as a numerically evaluated energy systems diagram (Fig. 3) and the table of values and definitions that accompanies it (Table 2). Table 2 gives the definitions, values, and units for the forcing functions, storages, and pathway flows shown on the model diagram. Table 2 references a series of numbered notes, given in Appendix B, which contain the calculations, assumptions, references, and data tables needed to show how the values in Table 2 were obtained.

The units for the entries in Table 2 reflect the material or energy storages and flows that were most convenient given the nature of the

Table 2. The values for forcing functions, storages, and flows in the Cobscook Bay Ecosystem model shown in Figure 3. Average values for all samples over the year or sampling season (191 days from May 2 to Nov. 9) are given per m^2 of the area in production or utilization. Supporting information and additional details about each measurement, e.g., seasonal variation, conversion factors, etc, are given in Appendix B.

Symbol	Definition	Value	Units	Note
Forcing functions				
J_I	Incident solar radiation	3.73E+4	J m^{-2} d^{-1}	1
J_R	Albedo	0.0975	nondim	2
J_W	Runoff from the watershed	0.018	m^{3}m^{-2} d^{-1}	3
J_N	Nitrogen from the watershed	0.007	gN m^{-2} d^{-1}	4
J_{NA}	Nitrogen from aquaculture	0.01	gN m^{-2} d^{-1}	5
J_{NP}	Nitrogen added in rainfall	0.002	gN m^{-2} d^{-1}	6
J_T	Tidal exchange volume	0.067	m^3 m^{-2} d^{-1}	7
N_T	NO$_3$ conc. in seawater	0.052	gN m^{-3}	8
P_T	Phytoplankton conc. in seawater	0.029	gC m^{-3}	9
Z_T	Zooplankton conc. in seawater	4.3E-4	gC m^{-3}	10
N_R	NO$_3$ conc. in river water	0.08	gN m^{-3}	11
JB_i	Shorebird immigration	3.47E-6	gC m^{-2} d^{-1}	12
JB_e	Shorebird emigration	3.51E-6	gC m^{-2} d^{-1}	12
JF_i	Fish immigration	0.065	gC m^{-2}d^{-1}	13
JF_e	Fish emigration	0.061	gC m^{-2}d^{-1}	13
System components or storages				
P	Phytoplankton	0.22	gC m^{-2}	14
BM	Benthic microalgae	2.07	gC m^{-2}	15
N	Nitrogen, NO$_3$, NO$_2$, NH$_4$	0.78	gN m^{-2}	16
MA	Macroalgae (total)	1239	gC m^{-2}	17
MA$_k$	Macroalgae, kelp	92	gC m^{-2}	17
MA$_f$	Macroalgae, fucoids	1096	gC m^{-2}	17
MA$_g$	Macroalgae, greens	21	gC m^{-2}	17
MA$_r$	Macroalgae, reds	30	gC m^{-2}	17
EG	Eelgrass	15.2	gC m^{-2}	17
Z	Zooplankton	0.006	gC m^{-2}	18
D	Detritus	5.2	gC m^{-2}	19
M	Benthic macrofauna	12.0	gC m^{-2}	20
B	Shorebirds	0.002	gC m^{-2}	12
F	Fish	8.3	gC m^{-2}	13
E	Eagles	6.4E-5	gC m^{-2}	21
S	Seals	0.064	gC m^{-2}	22

stored quantity. For example, flows of sunlight are in J m^{-2} d^{-1}, nitrogen uptake by plants is tracked as gN m^{-2} d^{-1}, and the metabolic flows of animals are tracked as gC m^{-2} d^{-1}. Where a material flow must be converted to energy or to the flow of another material, the conversion factor is given in the notes. All storages and flows are shown on the basis of a

Table 2, continued.

Symbol	Definition	Value	Units	Note
Pathway flows				
J1	NPP for phytoplankton	0.27	gC m^{-2} d^{-1}	23
J2k	NPP for macroalgae, kelp	1.25	gC m^{-2} d^{-1}	17
J2f	NPP for macroalgae, fucoid	1.7	gC m^{-2} d^{-1}	17
J2g	NPP for macroalgae, greens	0.33	gC m^{-2} d^{-1}	17
J2r	NPP for macroalgae, reds	1.0	gC m^{-2} d^{-1}	17
J3	NPP for eelgrass	0.35	gC m^{-2} d^{-1}	17
J4	NPP for benthic microalgae	0.95	gC m^{-2} d^{-1}	24
J5	N uptake by phytoplankton	0.045	gN m^{-2} d^{-1}	25
J6k	N uptake by macroalgae, kelp	0.066	gN m^{-2} d^{-1}	26
J6f	N uptake by macroalgae, fucoid	0.145	gN m^{-2} d^{-1}	26
J6g	N uptake by macroalgae, greens	0.029	gN m^{-2} d^{-1}	26
J6r	N uptake by macroalgae, reds	0.079	gN m^{-2} d^{-1}	26
J7	N uptake by eelgrass	0.013	gN m^{-2} d^{-1}	26
J8	N uptake by benthic microalgae	0.16	gN m^{-2} d^{-1}	27
J9	Zooplankton grazing	0.0012	gC m^{-2} d^{-1}	28
J10	Benthic macrofauna grazing	0.16	gC m^{-2} d^{-1}	29
J11	Phytoplankton settling to bottom	0.18	gC m^{-2} d^{-1}	29
J12	Macroalgal detritus production	0.35	gC m^{-2} d^{-1}	30
J13	Eelgrass detritus production	0.32	gC m^{-2} d^{-1}	30
J14	Benthic microalgae detritus	0.36	gC m^{-2} d^{-1}	31
J15	Microalgae eaten by macrofauna	0.47	gC m^{-2} d^{-1}	29
J16	Macrofauna fecal production	0.19	gC m^{-2} d^{-1}	29
J17	Detritus eaten by macrofauna	0.09	gC m^{-2} d^{-1}	32
J18	Detritus processed by bacteria	0.35	gC m^{-2} d^{-1}	33
J19	Detritus buried	0.09	gC m^{-2} d^{-1}	33
J20	Detritus exported	0.33	gC m^{-2} d^{-1}	19
J21	Macrofauna consumed by birds	0.0004	gC m^{-2} d^{-1}	34
J22	Macrofauna eaten by fish	0.17	gC m^{-2} d^{-1}	35
J23	Zooplankton eaten by fish	0.0005	gC m^{-2} d^{-1}	36
J24	Fish eaten by seals	0.0035	gC m^{-2} d^{-1}	42
J25	Fish consumed by eagles	6.4E-7	gC m^{-2} d^{-1}	37
J26	Nitrogen recycled by bacteria	0.017	gN m^{-2} d^{-1}	38
J27	Nitrogen recycled by macrofauna	0.031	gN m^{-2} d^{-1}	38
J28	Nitrogen recycled by zooplankton	1.1E-4	gN m^{-2} d^{-1}	38
J29	Nitrogen recycled by shorebirds	8.0E-5	gN m^{-2} d^{-1}	38
J30	Nitrogen recycled by fish	0.017	gN m^{-2} d^{-1}	38
J32	Nitrogen recycled by seals	7.0E-5	gN m^{-2} d^{-1}	38
J33	Phytoplankton export or import	0.021	gC m^{-2} d^{-1}	40
J34	Nitrogen export or import	0.067	gN m^{-2} d^{-1}	39
J35	Zooplankton export or import	-0.0007	gC m^{-2} d^{-1}	41
J36	Waterfowl consumed by eagles	3.7E-6	gC m^{-2} d^{-1}	37
J37	Benthic macrofauna harvested	0.0068	gC m^{-2} d^{-1}	43
J38	Fish harvested	8.5E-5	gC m^{-2} d^{-1}	43

meter square of the area over which the component is present. For example, there are, on average, 15.2 gC m^{-2} of eelgrass biomass in the areas of the Bay where eelgrass is present. Similarly, the annual average phytoplankton production was 0.27 gC m^{-2} d^{-1} over the average area occupied by open water. Table 3 gives the area estimates associated with each category of primary and secondary production in Cobscook Bay. To simplify the diagram, macroalgae is shown as an aggregate category in Figure 2. However, the biomass and primary production for all measured primary producers are given in the tables and in the notes (Appendix B).

Model description. The flows (J_i's) of nitrogen and carbon through the network of components in the Cobscook Bay ecosystem are shown in Figure 3. Flows of solar radiation (J_1) and nutrients (J_5, J_6, J_7, J_8; nitrogen is assumed to be the limiting nutrient) interact to fix carbon (J_1, J_2, J_3, J_4) and drive flows of energy and matter through the ecosystem. All major primary producers in the system were evaluated including phytoplankton (P) and benthic microalgae (BM, Phinney et al. 2004), macroalgae (MA; Vadas et al. 2000, 2004a,b,c) and eelgrass (EG, Beal et al. 2004). There is a small area of fringing salt marsh (Larsen et al.
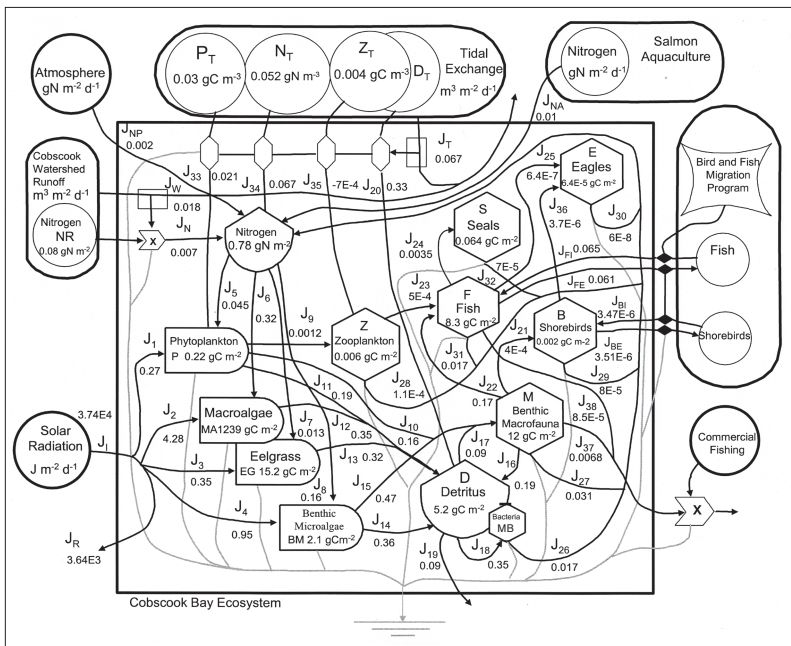

Figure 3. An evaluated energy systems model of the Cobscook Bay ecosystem. Ecosystem components are shown as producers (bullet symbols), consumers (hexagons), storage tank, and energy sources (circles). The label, value, and units are given for each symbol. The pathway flows (lines) are labeled as J_i and have units of mass or energy flux m^{-2} d^{-1} as determined by the storage or source with which they are associated.

2004) that contributes organic matter to the Bay, but it was not evaluated in this study. The net carbon fixed in phytoplankton primary production is grazed (J_9) by herbivorous zooplankton (Z) and (J_{10}) benthic macrofauna (M). Phytoplankton settling to the bottom (J_{11}) contributes to the detritus pool (D) in the estuary. I assumed that a small fraction (10%) of macroalgal biomass (J_2) and eelgrass biomass (J_3) was grazed by benthic macrofauna (Cebrian and Duarte 2002). The remaining carbon fixed by each contributed to the detritus pool (J_{12} and J_{13}). Benthic microalgae (BM) contribute to the detritus pool (J_{14}) and are grazed (J_{15}) by benthic macrofauna. Detritus is fed upon (J_{17}) by benthic macrofauna and utilized (J_{18}) by microbes and bacteria (MB). There is a net export of detritus (J_{20}) from the Bay over the course of the year. Benthic macrofauna are fed upon (J_{21}) by shorebirds (B) and by fish (J_{22}). Fish (F) also eat zooplankton (J_{23}) and are fed upon (J_{24}) by seals (S) and (J_{25}) eagles (E). Nitrogen is recycled by the metabolism of all consumers including bacteria (J_{26}), macrofauna (J_{27}), zooplankton (J_{28}), shorebirds (J_{29}), eagles (J_{30}), fish (J_{31}), and seals (J_{32}). There is a net export of phytoplankton on average (J_{33}) but this relationship is variable over the year (Table B25). On average, a net flux of inorganic nitrogen (J_{34})

Table 3. Areas used to determine net primary production, NPP, and other ecosystem flows based on classification of Larsen et al. (2004), Vadas et al. (2004c), Barker (Maine Department of Marine Resources, unpubl. data), and assumptions about the area of the estuary utilized by higher trophic level components.

Item	Formula	Area, ha
Area of estuary	Classes 1 to 17[1]	10,751
Intertidal area	Classes 8 to 17[1]	3584
NPP for phytoplankton	Classes 1 to 7 + one half intertidal[1]	8959
NPP for benthic microalgae	Classes 1 to 8 and 13 X 0.71	5629
NPP for macroalgae, kelp	Barker's estimate[3]	96
NPP for macroalgae, fucoid	Classes 9,11, 14 to 17[4]	995
NPP for macroalgae, greens	Vadas et. al. (2004c)	916
NPP for macroalgae, reds	Vadas et. al. (2004c)	212
NPP for eelgrass	Barker's estimate[3]	186
Detritus pool & bacteria	Classes 1 to 7 + one half intertidal[1]	8959
Zooplankton	Classes 1 to 7 + one half intertidal[1]	8959
Benthic macrofauna	Half the area for phytoplankton	4480
Fish	Classes 1 to 7 + one half intertidal[1]	8959
Shorebirds	Area of sand and mud flats[5]	1810
Eagles	High tide surface area[6]	10,360
Seals	High tide surface area[6]	10,360
Commercial fish	Classes 1 to 7[1]	7167
Commercial shellfish	Half the area for phytoplankton	4480

[1]Larsen et al. (2004).
[2]See Appendix B, note 15.
[3]See Table B17 for cover in flow type.
[4]See Table B15 for cover in class.
[5]US Army Corps (1980).
[6]Fogeron (1959).

enters the Bay. This is true for all seasons except the fall, when a large net export was observed (Phinney et al. 2004). There is a net flux of zooplankton (J_{35}) from the Bay to the coastal waters. Eagles eat birds, usually waterfowl, for which we were unable to find data. For convenience in evaluating energy flows in the ecosystem network, the consumption of birds by eagles is represented by a flow (J_{36}) from shorebirds to eagles. The harvest of shellfish (J_{37}) and fish (J_{38}) by commercial fisheries operating in the Bay leave the ecosystem as inputs to the Maine economy. Birds and fish immigrate to and emigrate from Cobscook Bay along pathways J_{BI} and J_{BE} and J_{FI} and J_{FE}, respectively, controlled by seasonal migration programs.

Model evaluation. Inorganic nitrogen enters the Cobscook Bay in seawater brought into the Bay with each tide, in fresh water runoff, in wet and dry deposition from the atmosphere, and in the feed and fish added to the Bay for salmon culture. The annual flux of all nitrogen species into the estuary in the volume exchanged from the sea is very large (3.3E+7 kgN y^{-1}), but the net flux of all species is much smaller (8.43E+5 kgN y^{-1}). The relative magnitude of new nitrogen sources to the estuary is shown in Figure 3 and Table 4. Seventy-three percent of the new nitrogen entering the Bay over the course of a year comes in with the net influx of nitrate in coastal water driven by tidal exchange. Salmon aquaculture operations add the second largest amount of new nitrogen to Cobscook Bay or about 14% of the total. The latter is 1.5 times what enters the Bay in runoff from the watershed and 5 times the nitrogen supplied from the atmosphere. Sowles and Churchill (2004) estimated the nitrogen input from salmon culture using two different calculation methods. Their estimate is about 10% lower than the number calculated for Table 4. Tables 4 and 5 can be used to compare the sources supplying new nitrogen to Cobscook Bay with the nitrogen requirements of the plants estimated from measurements of primary production in the Bay. New nitrogen supplies 47% of the nitrogen required to support primary production in Cobscook Bay, thus the net influx of nitrogen from the sea supplies 34% of the plant's nitrogen requirements. The remainder is supplied by remineralization.

Table 4. Inputs of new nitrogen to Cobscook Bay, assuming the area of the Bay is 1.036E+8 m^2 (US Army Corps 1980).

Nitrogen source	N inflow (kgN y^{-1} x 10^5)
Runoff from the watershed	2.47
Salmon aquaculture	3.67
Wet and dry deposition from the atmosphere	0.72
Net influx of NO_3-N in tidal exchange	18.90
Total new N inflows	25.76

The annual net primary production per meter square for each category of primary producer and the nitrogen used in making that production is shown in Table 5. Multiplying the nitrogen required $m^{-2} y^{-1}$ by the area (m^2) occupied by a primary producer gives the annual amount of nitrogen needed to support that producer in the Bay. The nitrogen needed to support the total primary production (Table 5) is 2.1 times greater than the new nitrogen (Table 4) entering the Bay. The excess nitrogen requirement (N used - new N) must be made up by nitrogen recycled within the Bay by consumers during the course of a year. Thus, the ratio of recycled nitrogen to new nitrogen is 1.12:1. Primary production of benthic microalgae and phytoplankton accounted for 87% of the nitrogen used by plants in the Bay. Primary production of *Ascophyllum nodosum* (Le Jolis, 1863) and *Fucus vesiculosus* (Linnaeus, 1753), accounts for 72% of the remaining nitrogen uptake.

The annual primary production in Cobscook Bay is shown for each primary producer in Table 6. Benthic microalgae, phytoplankton, and

Table 5. Estimated nitrogen requirements for net primary production, NPP, using the values in Table 2.

Primary producer	NPP ($gC\ m^{-2} y^{-1}$)	N used ($gN\ m^{-2} y^{-1}$)	Area (ha.)	N needed ($kgN\ y^{-1} \times 10^5$)
Phytoplankton	99	16.5	8959	14.78
Benthic diatoms	348	58.0	5628	32.64
Eelgrass	128	4.7	186	0.09
Fucoid algae	628	53.0	995	5.27
Green algae	121	10.8	916	0.99
Kelp	475	24.1	96	0.23
Red algae	368	28.8	212	0.61

Total N required: 54.6 x 10^5 kgN y^{-1}
Recycled to new nitrogen: 1.12:1

Table 6. Annual primary production in Cobscook Bay and its possible fate.

Producer	Primary production ($kgC\ y^{-1} \times 10^6$)	Consumer	Annual consumption ($kgC\ y^{-1} \times 10^6$)
Phytoplankton	8.80	Zooplankton grazing	0.05
Benthic diatoms	19.50	Benthic filter feeders	10.14
Eelgrass	0.24	Grazing on macrophytes	0.89
Fucoid algae	6.25	Detritus filtered	1.49
Green algae	1.11	Detritus, direct deposit[1]	12.05
Kelp	0.46	Detritus, total deposited	15.59
Red algae	0.78	Detritus export[2]	12.53
Total production[2]	37.14	Total consumption[3]	12.56
Detritus production[4]	26.10		

[1]Detritus deposited directly is equal to total production minus detritus exported and total consumption.
[2]An estimate of export (Table B20) using one tide in July was applied to the whole year.
[3]Sum of zooplankton grazing, grazing on macroalgae, benthic filter feeding, and detritus filtered.
[4]Sum of detritus produced by phytoplankton, benthic microalgae, eelgrass, and macroalgae.

the fucoid algae together account for 93% of the carbon fixed in the Bay. Benthic microalgae fix the largest amount of carbon (52%), followed by phytoplankton (24%) and the fucoid algae (17%). The remaining 7% of the carbon is fixed by green algae, red algae, kelp, and eelgrass.

On the right side of Table 6, estimates of the annual consumption of net primary production based on past studies of Cobscook Bay are listed. Legare and MacLellan (1960) measured the zooplankton abundance in Cobscook Bay during 1957 and 1958, and we have no reason to believe that zooplankton is more or less abundant today than it was then. Therefore, a grazing rate of 0.05×10^6 kgC y^{-1} was used for 1995 based on the earlier biomass values. This grazing rate accounts for only a small fraction of the carbon fixed by phytoplankton and benthic diatoms. The remainder must be either consumed by other pelagic grazers or by benthic grazers, or settle into the detritus pool (Appendix B, notes 29, 31, and 32). If feeding is nonselective and grazers consume on average 50% of daily production, the data and other assumptions in Note 30 can be used to estimate that filter-feeding macrofauna consume 10.1 $\times 10^6$ kgC y^{-1} of phytoplankton and benthic microalgae. In note 31, macrofaunal grazing on benthic microalgae was estimated using an alternative method. Based on these data and assumptions, benthic suspension feeders were the largest consumers (27%) of Cobscook Bay primary production in the grazing trophic pathway. The detritus produced by microalgae ranged from 10.1×10^6 to 11.8×10^6 kgC y^{-1}, depending on the estimation method. If benthic macrofauna graze 10% of the annual macrophyte production and the remainder becomes detritus over the course of a year, 8.9×10^5 kgC y^{-1} are grazed (Note 31) and 8.0×10^6 kgC y^{-1} of detritus are produced. Approximately 12.5×10^6 kgC y^{-1} or 33% of the total primary production is exported from Cobscook Bay as detritus, and a large fraction of this material may be of macroalgal origin (Table 6). If benthic macrofauna feed on detritus at 10% of the rate at which algae are eaten, macrofauna consumed 1.5×10^6 kgC y^{-1} of detritus based on the data and additional assumptions given in Note 32. However, if benthic macrofauna feed on detritus without selection, 15.6×10^6 kgC y^{-1} of detritus might have been consumed by filter feeders (Note 32). Benthic grazers consumed between 34 and 69% of the total carbon fixed annually in Cobscook Bay depending on the assumptions used about their feeding behavior and abundance. The remainder of the fixed carbon goes into the detritus pool, which is either exported or settles to the bottom to support benthic infaunal, meiofaunal, and bacterial respiration. The detritus produced by primary producers in the Bay was 26.1×10^6 kgC y^{-1} based on the information given in Table 6. If the estimates for export and consumption given above are approximately correct, then at least 12.1×10^6 kgC y^{-1} of detritus was directly deposited in the Bay. In fact,

this number must be somewhat larger because macrofaunal feces add to the total. If macrofauna assimilated 70% of the food consumed, macrofaunal feces add 3.49 x 10^6 kgC y^{-1} to the detritus deposited. This analysis shows that roughly a third of the annual primary production in the Bay is grazed, a third is deposited directly as detritus, and a third is exported to the coastal waters of the Gulf of Maine.

The dominant forcing function for Cobscook Bay is the tide, and tidal exchange controls ecological processes in the Bay through the transport of materials into and out of the estuary in proportion to the concentration gradient. Table 7 shows the import-export balances of the material fluxes of NO_3, NH_4, PO_4, SiO_3, and phytoplankton C for the five sampling trips on which transect measurements were taken. The October 24–26 sample dates stand out because all five quantities were being exported from the Bay, and the largest quantities of NO_3, PO_4, and SiO_3, were being transported at that time. This pattern is very different from that displayed by nitrate and ammonium during most of the year. Nitrate is imported on all dates except the October sampling, and ammonium is imported on the May and July sample dates but not in October or November. Phosphorus was exported on all dates except those in November, but the amount being exported in October was 2 to 8 times larger than that exported on the other sampling dates. Approximately, 1.0 x 10^7 gSi d^{-1} are imported or exported over the sample dates in May and July; however, twice this amount was exported in November, and the export of silicate increased to 5.5 x 10^7 gSi d^{-1} in October. Phytoplankton carbon was exported in the spring and fall and imported in the summer. The largest phytoplankton carbon flux was the import of carbon from Head Harbor Passage during July on the spring tide sample dates.

The upper trophic levels in Cobscook Bay are represented in Figure 3 as described above. The literature sources, calculations, and assumptions needed to document these flows are given in Appendix B and in ancillary information posted on the worldwide web (US Environmental Protection Agency 2005a). The carbon flowing through these trophic levels and the nitrogen recycled by them are shown in Figure 3. The estimates of secondary production and standing stock in the higher trophic levels are

Table 7. Import (+) and export (-) balance for materials moving across the Eastport to Lubec transect on the sample dates in 1995.

Date	NO_3 (gN d^{-1})	NH_4 (gN d^{-1})	PO_4 (gP d^{-1})	SiO_3 (gSi d^{-1})	Phyto. C (gC d^{-1})
May 2, 3, 4	1.0E+7	1.6E+6	-4.3E+5	1.0E+7	-2.7E+6
July 11, 12, 13	4.2E+6	8.9E+6	-1.5E+6	-1.1E+7	9.8E+6
July 21, 22, 23	4.4E+6	1.2E+7	-3.0E+6	1.3E+7	3.2E+7
October 24, 25, 26	-3.0E+7	-3.9E+5	-8.2E+6	-5.5E+7	-1.1E+7
November 7, 8, 9	5.0E+6	-4.8E+6	1.1E+6	-2.2E+7	-7.8E+6

rough approximations compared to the estimates of primary production and biomass, because the primary producers are documented based on 1995 and 1996 field measurements, while the estimates of secondary production and standing stocks in the higher trophic level animals are calculated based on measurements of animal abundance that were made in Cobscook Bay between 1957 and 1992. In addition, the measurements used to represent the fish community in Cobscook Bay were taken from trawls made in the adjacent Western Passage of Passamaquoddy Bay (Tyler 1971).

The sea scallop, *Placopecten magellanicus* (Gmelin, 1791), the soft-shelled clam, *Mya arenaria* (Linnaeus, 1758), and the green sea urchin, *Strongylocentrotus droehbachiensis* (O.F. Müller, 1776), are benthic macrofauna that feed on the abundant microalgae and support major commercial fisheries in the Bay. An early report on the commercial fisheries of Cobscook Bay by Dow (1959) gave evidence to show that the commercial production of intertidal soft-shelled clams in Cobscook Bay was poor to fair when compared to other areas of Washington County, ME. He also stated that mussels were abundant in the Bay, but for the most part were too small to be commercially valuable. The extent and importance of subtidal mussel beds was not known at that time. The Washington County clam harvest declined drastically from the mid-1980s to the time of this study. A study comparing settling and recruitment on clam flats in Washington and Cumberland County indicated that the supply of clam larvae limits the productivity and recovery on "Down East" clam flats (Ellis and Waterman 1998). The commercial harvest of fish and shellfish from Cobscook Bay in 1996 was estimated to be 2.2 metric tons (MT) and 111 MT, respectively, using data supplied by Keri Lyons and Margaret Hunter of the Maine Department of Marine Resources (see Note 43).

Emergy analysis of the Cobscook Bay ecosystem

Figure 4 and Table 8 present the results of an emergy analysis of the Cobscook Bay ecosystem. The transformities shown in Table 8 are based on an emergy input of 7.64 x 10^{20} sej y^{-1} as presented in Figure 4 and in Table 8. The column of transformities in Table 8 shows the solar emjoules needed to support a joule of energy flow along each pathway of the ecosystem network. The transformity of any pathway can also be derived by dividing the value of the emergy required for the pathway (bold) by the pathway's energy flow (italics) as shown on Figure 4. The energy flux on each pathway is also shown in the first column of numbers in Table 8, and the emergy required to support that pathway is given in the second column. The emergy base for the flows though any component can be traced on the diagram (Fig. 4) by summing the bold values of emergy entering each

producer, consumer, or storage symbol. Brown algae (fucoids and kelp) have the lowest transformities (2.7 x 10^5 sej J^{-1} and 3.7 x 10^5 sej J^{-1}, respectively) of all primary producers in the Bay. Red algae and benthic diatoms have transformities about 50% higher than the brown algae followed by the less efficient groups (eelgrass, green algae, and phytoplankton) that have transformities ranging from 5 to 6.4 times that of the fucoid algae. If we count the total energy flow through any ecosystem component as if it is all of one kind (i.e., any part of the flow is substitutable for any other, thus the flow can be split [Odum 1996]), and then determine the transformity of the throughput, we find that the transformities of Cobscook Bay ecosystem components range over two orders of magnitude from 2.7 x 10^5 sej J^{-1} to 1.7 x 10^6 sej J^{-1} for primary producers up to 1.03 x 10^7 sej J^{-1} for seals. The transformity of detritus was 5.5 x 10^5 sej J^{-1}, which is in the lower part of the range of transformities determined for the primary producers. The mid-range of transformities in the ecosystem is occupied by benthic macrofauna (1.93 x 10^6 sej J^{-1}), zooplankton (3.47 x 10^6 sej J^{-1}),
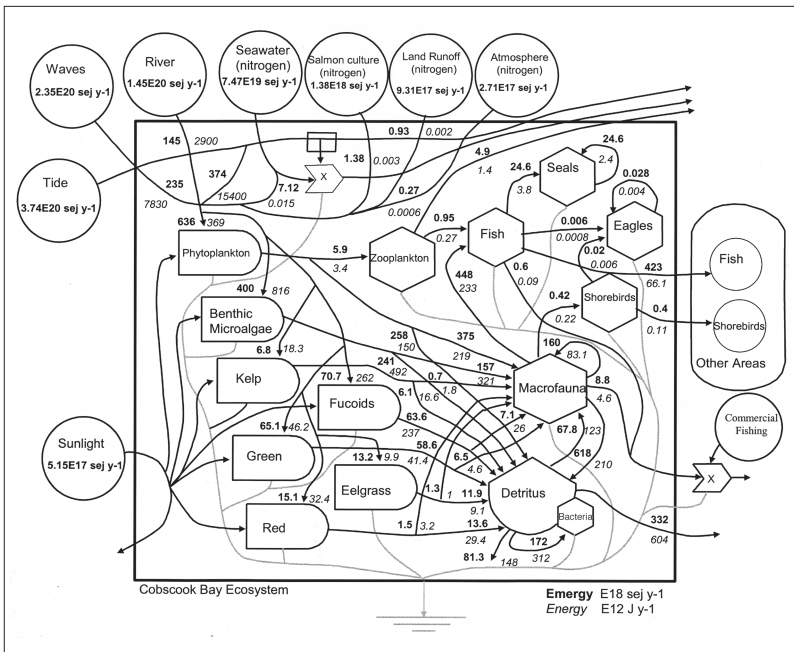

Figure 4. Emergy evaluation of the Cobscook Bay ecosystem network. The emergy received by the ecosystem is shown on the energy sources arrayed around the edge of the box representing the ecosystem in order of increasing transformity. Flows within the system are labeled with two numbers: (1) the emergy in sej y^{-1} required for that pathway (bold), and (2) the energy flow along the pathway in J y^{-1} (italics). Dividing (1) by (2) gives the transformity of the pathway in sej J^{-1}.

Table 8. Transformities of Cobscook Bay ecosystem flows based on estimates of net primary production, NPP, given and the annual emergy inflow to the Bay. All transformities are calculated relative to the 9.26×10^{24} sej y^{-1} planetary baseline proposed by Campbell (2000b). The emergy base for Cobscook Bay (7.64×10^{20} sej y^{-1}) was taken as the sum of the emergy available in waves (2.35×10^{20} sej y^{-1}), the chemical potential energy delivered in fresh water runoff (1.45×10^{20} sej y^{-1}), the chemical potential energy of new nitrogen entering the Bay from all sources (9.7×10^{18} sej y^{-1}), and the tidal energy dissipated in Cobscook Bay (3.74×10^{20} sej y^{-1}). The network structure used to calculate the emergy of the pathways is shown in Figure 4.

Ecosystem flow	Energy flux (J y^{-1} x 10^{12})	Emergy of pathway (sej y^{-1} x 10^{18})	Transformity (sej J^{-1} x 10^5)
Primary production:			
NPP phytoplankton	369	636	17.2
NPP benthic microalgae	816	400	4.90
NPP kelp	18.3	6.82	3.72
NPP fucoid	262	70.7	2.70
NPP greens	46.2	65.1	14.1
NPP reds	32.4	15.1	4.65
NPP eelgrass	9.94	13.2	13.3
Detritus production:			
Phytoplankton detritus	150	258	17.2
Benthic microalgae detritus	492	241	4.90
Kelp detritus	16.6	6.14	3.71
Fucoid detritus	237	63.6	2.68
Green detritus	41.4	58.6	14.1
Red detritus	29.4	13.6	4.62
Eelgrass detritus	9.09	11.9	13.1
Detritus use:			
Detritus is a split	1190	653	5.5
Detritus exported (average)	604	332	5.5
Detritus eaten by macrofauna	123	67.8	5.5
Bacterial decomposition	312	172	5.5
Detritus buried	148	81.3	5.5
Grazing:			
Zooplankton grazing on phyto.	3.41	5.88	17.2
Macrofauna grazing on phyto.	219	375	17.2
Macrofauna grazing on kelp	1.82	0.68	3.74
Macrofauna grazing on fucoid	26.0	7.07	2.71
Macrofauna grazing on greens	4.56	6.51	14.3
Macrofauna grazing on reds	3.23	1.51	4.66
Macrofauna grazing on eelgrass	1.00	1.32	13.2
Macrofauna grazing on b. algae	321	157	4.90
Zooplankton production:			
Zooplankton prod. is a split	1.70	5.88	34.7
Eaten by fish	0.27	0.95	34.7
Growth, export, and mortality	1.42	4.93	34.7
Macrofauna production:			
Macrofauna prod. is a split	320	618	19.3
Feces is a by-product	210	618	29.4
Eaten by birds	0.22	0.42	19.3
Eaten by fish	233	448	19.3
Harvested	4.58	8.83	19.3
Growth and other mortality	83.1	160	19.3

and shorebirds (3.7×10^6 sej J^{-1}). The transformities for both zoo-plankton and shorebirds are 2 times greater than the transformity of their principal food supply. The transformity of benthic macrofauna is 3.9 times that of the benthic microalgae and 35 times that of detritus, their principal food sources. Fish (6.4×10^6 sej J^{-1}), eagles (6.3×10^6 sej J^{-1}), and seals (1.03×10^7 sej J^{-1}) occupy the highest trophic levels. High quality (high transformity) outputs of the Cobscook Bay ecosystem include shorebird out migration (4.0×10^{17} sej y^{-1}) and the harvest of fish (6.0×10^{17} sej y^{-1}) and shellfish (8.8×10^{19} sej y^{-1}).

Discussion

Data and analysis in this volume can be used to demonstrate that Cobscook Bay is a macrotidal estuary that is naturally eutrophic. Garside and Garside (2004) come to this conclusion and they point out that high nutrients are not necessarily a bad thing because they can potentially support tremendous ecological and economic productivity and do not necessarily lead to eutrophication as manifested by an over-growth of primary producers. Many unique characteristics of this macrotidal estuary were identified over the course of two years of field work and many subsequent years of discussions and data analysis (Beal et al. 2004; Brooks 2004; Brooks et al. 1997, 1999; Garside and Garside 2004; Kelley and Kelly 2004; Larsen and Gilfillan 2004; Larsen et al. 2004; Phinney et al. 2004; Trott 2004a,b; Vadas et al. 2000, 2004a,b,c) Energy systems modeling was used in this paper to integrate field studies and data analysis into an overall picture of the Cobscook Bay ecosystem, and emergy analysis was applied to gain insights into its functioning by evaluating the physical basis for biological productivity and ecological organization in the Bay.

Table 8, continued.

Ecosystem flow	Energy flux (J y^{-1} x 10^{12})	Emergy of pathway (sej y^{-1} x 10^{18})	Transformity (sej J^{-1} x 10^5)
Fish production:			
Fish production is a split	70.0	448	64.1
Consumed by eagles	0.0008	0.006	64.1
Eaten by seals	3.83	24.6	64.1
Harvested	0.093	0.6	64.1
Growth, mortality, and export	66.1	423	64.1
Shorebird production:			
Shorebirds prod. as a split	0.115	0.425	37.0
Consumed by eagles (fowl)	0.006	0.022	37.0
Growth and out-migration	0.109	0.402	37.0
Seals: (growth and mortality)	2.37	24.6	103
Eagles: (growth and mortality)	0.004	0.028	62.8

The Cobscook Bay ecosystem is the product of an extremely rich (Brown and Bardi 2001, Campbell 2000a) convergence of natural energies in tides, waves, fresh water, and nitrogen from the deep waters of the Gulf of Maine (Fig. 2). These natural energies support a productive, diverse system of life, especially in the shallow subtidal and intertidal areas of the Bay. Phytoplankton production is less than expected based on the available nutrients (Phinney et al. 2004), but benthic diatoms are highly productive leading to large populations of benthic filter feeders that apparently control phytoplankton growth and prevent eutrophication despite high levels of nutrients. This productive benthos has supported historical and present fisheries for scallops and clams, as well as more recent fisheries for urchins, periwinkles, rockweed, and sea cucumbers. At present, salmon culture is the most important economic use of Cobscook Bay's marine resources. Salmon culture was second in value only to lobsters in recent Maine landings, and the majority of salmon culture operations are located in Washington County (Sowles and Churchill 2004). In the discussion below, we will explore some of Cobscook Bay's characteristics as a naturally eutrophic ecosystem and then consider insights into the structure and function of the Bay gained from an emergy analysis of its ecosystem network.

Cobscook Bay: a naturally eutrophic ecosystem

Cobscook Bay receives high nitrogen concentrations via a natural process, tidal exchange, rather than from sewage or non-point runoff like many other estuaries on the Atlantic coast (Garside and Garside 2004, Nixon and Pilson 1984). The concentrations of NO_3 and NH_4 (≈ 2 micromoles per liter) found in Cobscook Bay in the summer months (Tables B25 and B26) are within the middle of the range of summer concentrations of these same nitrogen species found by Nixon (1986) in culturally eutrophic estuaries such as the Narragansett Bay. East coast estuaries, other than those in the macrotidal Gulf of Maine (Garside et al. 1978), have been exposed to high nutrient concentrations for a relatively short period of time due to the inflow of sewage and other wastes (Nixon 1997). Cobscook Bay has been a high nutrient macrotidal system for about 4000 years (Campbell 1986), giving it time to build an ecosystem capable of organically exploiting high nutrient levels. Some estuaries affected by sewage appear to have adapted by developing large populations of suspension feeding bivalves that control excess phytoplankton production (Cloern 1982). Officer et al. (1982) proposed benthic filter feeding as a natural mechanism capable of controlling the effects of eutrophication. The results given elsewhere in this volume (Garside and Garside 2004, Larsen and Gilfillan 2004) and results of the analysis presented in this paper indicate that Cobscook Bay is an example of a naturally eutrophic ecosystem regulated by benthic filter feeding, supporting the thesis of Officer et al. (1982).

New nitrogen supply and utilization

Perhaps the most extraordinary feature of Cobscook Bay is the tremendous flux of nitrogen that enters the Bay on each flood tide with a volume comparable to the average flow of the Mississippi River (Brooks et al. 1999). Much of this nitrogen is removed again as the tide ebbs, but over most of the year there is a smaller net flux to the estuary that results in constant replenishment of this usually limiting nutrient. Emergy in the nitrogen received by the estuary is high, but a relatively small fraction is actually used by primary producers. Nitrogen is abundant in the coastal waters adjacent to Cobscook Bay because nitrogen rich deep water from the Gulf of Maine enters the glacially carved channel at the mouth of Passamaquoddy Bay and is mixed upward by strong tidal flows as the channel shoals. This flux of nitrogen from outside the ecosystem leads to a low ratio of recycled to new nitrogen (1.12:1) within the system compared to eight estuaries examined by Kemp et al. (1982), who found that this ratio ranged between 2:1 and 8:1. Campbell (1986) showed that this ratio is about 2:1 for the Gulf of Maine as a whole. Thus, Cobscook Bay is even richer in new nitrogen than the Gulf of Maine. Even though Cobscook Bay is rich in new nitrogen, the nitrogen required by primary producers exceeds the net flux of new nitrogen into the Bay, thus plant production must also depend on recycle and remineralization. At times and in certain areas of the Bay when other conditions are most favorable for primary production, the supply of new and recycled nitrogen may be insufficient to meet the local demands of dense primary producers as evidenced by the failure of nori to flourish at South Bay farms in some years. (S. Crawford, Eastport, ME, pers. comm).

Benthic microalgae are probably the largest users of nitrogen in the Bay, accounting for 60% of the nitrogen required to support net primary production. In the past, marshes, phytoplankton, eelgrass, and macroalgae have been viewed as the major sources of primary production in estuaries. Production by benthic diatoms was often considered to be small, and therefore, it was seldom measured in the past. The standing stock and productivity of benthic diatoms in Cobscook Bay is similar to that measured for intertidal benthic diatoms in the salt marshes of the North Inlet, SC (Pinckney and Zingmark 1993). The daily rates of benthic microalgal production in July (Table B22) were 1.5 to 5.5 times greater than the maximum gross benthic algal production (0.8 gC m^{-2}d^{-1}) measured on intertidal mudflats in the Minas and Cumberland Basins of the Bay of Fundy (Hargrave et al. 1983). The upper bound of biomass and productivity measured in Cobscook Bay in July exceeds the highest values measured in the North Inlet.

At certain times, green algae bloom on tidal mud flats in the Bay and eventually form fantastic roped structures under the influence of tides

and wind (Vadas and Beal 1987). This study showed that high concentrations of nitrogen are often present in the estuary. These nitrogen concentrations represent a storage of energy that is waiting to be exploited. Odum et al. (1995) presented a pulsing paradigm that explains many ecological phenomena based on the observation that the accumulation of a stored resource and its subsequent rapid consumption appears to maximize power in ecological networks. Cobscook Bay is a system where an accumulator (stored nitrogen resource) is nearly always charged waiting for a consumer capable of rapid growth (green algae), to exploit it. Observations of pulsed nutrient consumption in Cobscook Bay, like the intertidal green algae blooms observed by Vadas and Beal (1987), may be an example of such maximum power pulsing.

Fate of production

In this study, I estimated that intertidal and subtidal benthic suspension feeders consume about one third of the total carbon fixed annually in the Bay. The fact that benthic suspension feeders play a large role in the natural economy of the Bay is not surprising given the results of Garside and Garside (2004), Garside et al. (1978), and Larsen and Gilfillan (2004); however, it does not necessarily mean that their productivity will be realized in large commercially exploitable populations of shellfish. Many small animals can consume more food than the same biomass of large ones. In the case of the sea scallop, high primary production appears to be translated into the production of a commercially valuable population because the Bay has supported a scallop fishery at least since the 1940s (Dow and Baird 1960), albeit with large variations in the abundance of year classes. On the other hand, soft-shelled clams appear to grow slowly in the large intertidal area (Dow 1959). Clam populations in Washington County declined drastically from the mid-1980s to 1996 (Ellis and Waterman 1998). In light of the apparent importance of benthic suspension feeders in the natural as well as the human economy of the Bay, it would be prudent to investigate the role of this component within the Cobscook Bay ecosystem in future studies.

Import-export patterns

There has been a long standing debate on the role of estuaries as sinks for or sources of organic matter (Haines 1979, Hopkinson 1985, Odum 1980). Our analysis of Cobscook Bay estimated that over the course of a year 12,500 MT of 31,000 MT of carbon fixed in the Bay were exported to the surrounding coastal waters. Visual observations indicated that much of this material was in the form of macroalgal detritus, although definitive analyses were not performed. Assuming that detritus is exported in proportion to its production, around 45% of macroalgal primary production is exported while the remainder is

transferred to the benthic community and grazers. If the exported detritus is mainly of macroalgal origin, the nitrogen exported in this form is about 30% of the net flux of new NO_3 nitrogen received from the sea (see Table B23). The typical pattern for the import and export of nutrient materials is for NO_3, NH_4, and SiO_3 to be imported into the Bay and for PO_4 to be exported in spring and summer. The import and export of phytoplankton carbon to and from the Bay appears to be driven by the annual cycles of production offshore and within the Bay. Phytoplankton carbon was imported during July when there is usually an offshore bloom and exported in the spring and fall when chlorophyll concentrations in the Bay exceed those in the offshore waters.

The effects of dragging on the marine environment (Watling and Norse 1998) and the changes it can induce in nutrient and sediment distributions (Pilskaln et al. 1998) have been considered for the Gulf of Maine. The import-export balance of chemical constituents during the fall and ancillary observations can be used to gain some insight into probable effects of urchin and scallop dragging on the Bay in 1995. In October, the distribution of NO_3 concentrations shows that the Outer Bay is serving as a source of nitrate for both the Inner Bay and Friar Roads. Furthermore, the stations with high nitrate values are grouped along the northern shore of the Outer Bay. Boats were observed dragging this area for urchins during the October sample dates and at least one sample was taken in the plume from a dragger (D. Phinney, Bigelow Laboratory fo Ocean Sciences, West Boothbay Harbor, ME, pers. comm.). The largest differences between low and high tide concentrations of NO_3, NO_2, PO_4, and SiO_3 across the Eastport to Lubec line exist at this time reflecting a net export of these materials. This lends circumstantial support to the view that the roiling of the bottom by draggers has increased the ebb tide concentrations of these chemicals. There is also a small net seaward flux of the ammonium ion at this time, but the export of ammonium is an order of magnitude greater in November.

On October 24, 25, and 26, average daily wind speed at the Portland airport was less than 10 mph (16.7 kph). There were only 3 days in October prior to the sampling period with average wind speed over 10 mph (16.7 kph), but one of these was a 24-hour period with winds averaging around 20 mph (33.4 kph). Nutrient samples for NO_3, NO_2, PO_4, and SiO_3 taken at the surface and bottom of the water column in Friar Roads during the October sampling show that fall winds had not yet been sufficient to overturn the water column offshore. Thus, the nutrient concentrations in the water entering the Bay from Friar Roads are near their annual low in late October. In the absence of dragging, concentrations of these materials inside the Bay would be expected to stand at similar low levels. By the November sample dates, the offshore waters were apparently well mixed, because high concentrations of NO_3

and PO_4 were present in the water entering as well as within the Bay, resulting in a net import of NO_3 and PO_4. Between October 27th and November 9th, there were 5 days with average wind speed greater than 10 mph (16.7 kph), one of which was a 24-h period with sustained high winds. During the period between sampling times, ammonium concentrations outside the Bay declined more rapidly than inside, resulting in a large export of NH_4 during the November sampling. The actual ammonia flux out of the Bay may be somewhat lower, because data from the Gove–Birch Point line was substituted in the calculation for missing data on the Eastport–Lubec line.

Scallop dragging began in November and the disturbance of the bottom that accompanies this activity might have been sufficient to account for the continued export of SiO_3 from the Bay despite a doubling of the offshore (Friar Roads) concentrations of this substance ("offshore" stations probably reflect natural conditions in the Bay at this time). High concentrations of silicates were found in the Outer Bay during October when it was being dragged for urchins, and in November, the silicate concentrations are high in the Central and South Bays where the scallop draggers fish. Excess sediment present in the water at this time may account for the September to October depression in eelgrass production at Mahar Point observed by Beal et al. (2004). Trott (2004b) presents evidence that the species composition of benthic communities in the Inner Bay has altered from the seventies and early eighties to 2002, perhaps from the chronic effects of increased sedimentation. Urchin landings in Washington County rapidly increased from 325 MT in 1987 to a peak of 5131 MT in 1994 then rapidly fell to 1065 MT in 2002 (M. Hunter, Maine Department of Marine Resources, pers. comm.); 4749 metric tons were landed in 1995. Also, sedimentation in the Bay could be connected to other observed biological effects such as slow clam growth and low clam recruitment.

What are the limits on the human use of the ecosystem?

The tremendous daily volume of tidal exchange has the capacity to cleanse the estuary of wastes as it supplies it with new nitrogen to support primary production, which in turn supports a diverse network of consumers. While ecosystems are resilient, humans have the capacity to push systems under exploitation beyond even the most liberal limits afforded by nature such as macrotidal exchange. Strain et al. (1995) used a modeling study to show that the Letang estuary, a macrotidal system in New Brunswick, Canada, exposed to multiple waste streams including wastes from fish processing, a pulp mill, and salmon aquaculture was close to the threshold of biochemical oxygen demand (BOD) loading that would produce harmful low dissolved oxygen levels at times during the year. Salmon aquaculture is now the

second largest source of new nitrogen to Cobscook Bay, supplying
19% of the net influx brought in annually by the tide. Sowles and
Churchill (2004) convincingly argue that nitrogen additions from
salmon aquaculture are not presently a problem in Cobscook Bay.
Nevertheless, local effects of nutrient addition are seen in sediment
carbon concentration and in benthic community structure below the
salmon pens (Table 9, Heinig and Bohlin 1995). In addition, 60% of
the nitrogen from salmon culture enters the Bay from July to October.
If other human uses of the estuary, such as fish processing plants
(prominent in the past), are developed in the future, it may be prudent
to establish a baseline for ammonia in the late summer and fall and
then monitor the ammonia level in the Bay during this time as an early
warning to determine when salmon aquaculture or other uses begin to
have major effects on the fall ammonium distribution in the Bay. The
fall nutrient signal will be masked by dragging, and thus the base
monitoring period must end before the urchin season opens.

Even though Cobscook Bay appears to be to be in good overall
condition based on energy flows through the ecosystem, evidence pre-
sented here also shows that human activities in the Bay alter water column

Table 9. Selected benthic stations taken along transects below salmon pens in the
Outer Bay (Heinig and Bohlin 1995) showing low to moderate impacts on the benthic
community from salmon aquaculture waste. Percent *Capitella* is an indictor of the
degree of impact.

Location	Individuals (# 0.1 m^{-2})	Species (#)	Silt-clay (%)	TOC[1] (%)	*Capitella* (%)
Broad Cove					
1	28,678	53	8.1	1.44	56.0
4	11,390	31	7.9	0.90	47.0
6	9564	29	7.7	1.83	63.0
Deep Cove					
2	19,300	48	42.2	1.73	9.1
3	12,315	62	42.3	2.11	1.3
7	32,491	70	24.1	2.62	4.9
8	32,615	69	10.2	1.42	8.3
Johnson Bay					
1	234	26	84.1	1.56	0.4
5	57	22	82.2	1.92	1.8
9	279	25	58.9	1.53	0.4
10	191	27	85.5	1.61	0.0
Dudley Island					
1	529	27	16.0	0.97	6.4
Shakford Head					
6	310	34	6.0	1.35	11.9
1	415	41	9.0	1.24	19.8
Birch Point					
1	181	35	20.0	1.44	10.5

[1]Total organic carbon.

properties during the urchin and scallop seasons (Phinney et al. 2004), degrade benthic communities below and adjacent to salmon pens (Heinig and Bohlin 1995), regularly overfish commercial populations of fish and shellfish (Dow and Baird 1960; Ellis and Waterman 1998; M. Hunter, Maine Department of Marine Resources, pers. comm.; urchin landings data), and may be responsible for long term loss of benthic biodiversity in the Inner Bay (Trott 2004b). The negative effects of these human activities were not quantified in emergy terms; therefore, the environmental liabilities (Campbell 2005) incurred through the loss of empower in the natural ecosystem cannot be compared to the concomitant empower gains in the economy. This comparison should be made in the future as an aid to planning and decision making for the Bay.

Comparison of Cobscook Bay emergy indicators to other ecosystems

The emergy signature of Cobscook Bay has an empower density of renewable resources (renewable empower density) that is higher than any of the 19 terrestrial and lake ecosystems compiled by Brown and Bardi (2001). In general, aquatic ecosystems have higher renewable empower densities than terrestrial ecosystems, but Cobscook Bay's empower density is also high compared to other estuaries (Table 10). The empower density in the Bay ($7.4E+12$ sej m^{-2}) is comparable to that found for Tilapia fish culture in Nayarit, Mexico ($8.0E+12$ sej m^{-2}; Brown and Bardi 2001). Odum (2000) evaluated salmon pen culture in British Columbia using data from Bjorndal (1990). He estimated that the minimum empower density required for salmon culture was $2.3E+12$ sej m^{-2}. Cobscook Bay supplies over three times the minimum environmental emergy needed for salmon culture. These facts imply that salmon culture may be a good human use of the Bay's rich emergy signature.

The emergy signature of the Bay is dominated by tide and waves. The emergy inflows of tide, waves, chemical potential energy of runoff, and new nitrogen were found in the ratio of 3.8:2.4:1.5:1. A balanced ratio of the dominant energies in the emergy signature is hypothesized to support the development of more diverse biological systems (Odum

Table 10. Comparison of Cobscook Bay's empower density (emergy per unit area in sej m^{-2}) from renewable sources to the renewable empower density of four other estuaries and two lakes.

Estuary	Empower density (sej m^{-2} x 10^9)	Source
Cobscook Bay, ME	7375	This study
Newnans Lake, FL	3488	Brown and Bardi (2001)
Estuary for salmon culture	2300	Odum (2000)
York River, VA	1600	Campbell (2000a)
Lake Okeechobee, FL	1114	Brown and Bardi (2001)
Mosquito Lagoon, FL	144	Campbell (2000a)
Prince William Sound, AK	100	Brown et al. (1993)

et al. 1974). The high diversity of intertidal and subtidal fauna in Cobscook Bay is well known (Trott 2004a, Verrill 1872, Webster and Benedict 1887) and may be explained based on the large and relatively balanced (1.58:1) emergy of the tides and waves supporting ecological organization of the intertidal and shallow subtidal areas of the Bay. The transformities for the principal primary producers show that emergy is being most effectively used to fix carbon by the brown algae (fucoids and kelp), red algae, and benthic diatoms in the subtidal and intertidal areas of the Bay. Thus, available energy is captured most efficiently by the intertidal and subtidal algal ecosystems of the Bay.

We can see if Cobscook Bay transformity values are plausible and learn more about the ecosystem by comparing transformities to those from an a similar ecosystem in another estuary, Prince William Sound, AK (Brown et al. 1993). The model that we used to calculate the transformities of higher trophic level components assumes that all emergy enters the network through the primary producers (Fig. 3). A parallel structure was used in the Prince William Sound evaluations, and thus the results of our transformity calculations should be comparable.

Brown et al. (1993) evaluated an aggregated model of Alaska fjords from Parsons (1987) and a detailed trophic web for Prince William Sound based on the observations of McRoy and Wyllie-Echeverria (1991). Since the flows through the ecosystem were not known in this more complex model, they used a method similar to Kercher and Shugart (1975) to evaluate the effective trophic position of the components. The transformities determined by this method will vary according to the network structure and the efficiency assumed for the trophic transfers The transformities that were determined by estimating the biomass and energy flows through the various ecosystem components of Cobscook Bay were compared to the transformities of similar components in the Prince William Sound ecosystem using the estimates based on a 10% trophic transfer efficiency between levels reported by Brown et al. (1993).

Lower trophic levels were compared to the transformities calculated using the aggregated model based on an evaluation of flows between trophic levels in Alaskan fjords (Parsons 1987). The transformity of phytoplankton is two orders of magnitude higher than expected based on the Prince William Sound analysis and the value for estuarine net production given in Odum (1996). Benthic diatoms, the macroalgae, and eelgrass in the Bay all have transformities an order of magnitude greater than expected. Phinney et al. (2004) documented low levels of phytoplankton production in the Bay compared to that expected based on nutrient concentrations. In addition, the emergy received per unit area in the Bay is very high, principally due to the tides. The large quantity of emergy received by the Bay is not being effectively transferred into

phytoplankton primary production, most probably due to intense mixing and turbidity resulting in light limitation (Phinney et al. 2004). In addition, circumstantial evidence indicates that phytoplankton biomass is heavily grazed by suspension feeding bivalves (Garside and Garside 2004). In contrast, the lower transformities of benthic diatoms and macroalgae indicate that they are more effectively using the emergy available to support primary production than phytoplankton, but they are also less efficient in using the available emergy to fix carbon than expected in a typical estuary. The order of magnitude difference in expected transformity is transmitted through the grazing chain to zooplankton (3.47×10^6 sej J^{-1} compared to 1.0×10^5 sej J^{-1}). This difference is also seen in benthic macrofauna feces, which was 70 times higher than the transformity of herbivore feces determined by Brown et al. (1993), although detritus was only 15 times greater. However, benthic macrofauna in the Bay are only 2.4 times greater than the transformity found for macrofauna in Prince William Sound (1.9×10^6 sej J^{-1} versus 8.1×10^5 sej J^{-1}) and fish in Cobscook Bay have a transformity of 6.4×10^6 sej J^{-1} which is six times higher than the transformity for apex predators calculated from the aggregated Alaskan fjord model (Parsons 1987). If we compare the transformity of fish in Cobscook Bay to individual fish determined from the complex trophic web model (Brown et al. 1993), we find that demersal fish such as cod (*Gadus macrocephalus* Tilesius), walleyed pollock (*Theragra chalcogramma* Pallas), rockfish (*Sebastes* spp.), and sole (Pleuronectidae), which are similar to species found in Cobscook Bay, have a transformity of 1.1×10^7 sej J^{-1}, which is 70% greater than the estimate in this study. The transformity for harbor seals, *Phoca vitulina* (Linnaeus, 1758), is within the range of transformities estimated for the harbor seal, *Phoca vitulina richardsi* (L.) in Alaska (2.6×10^6 sej J^{-1} to 4.6×10^8 sej J^{-1}). Our estimate of the transformity for shorebirds is about half of the estimate made for Arctic Terns (*Sterna paradisaea* Pontoppidan) and the Black Legged Kittiwake (*Rissa tridactyla* L.) and one third of the transformity for Glacous-winged Gulls (*Larus glaucescens* Naumann), Tufted Puffins (*Lunda cirrhata* Pallas), and Pigeon Guillemots (*Cepphus columba* Pallas) found in Alaskan fjords. The transformity for Cobscook Bay Bald Eagles (*Haliaeetus leucocephalus* L.) is one fourth of the transformity found for Bald Eagles in Prince William Sound.

The transformities for all the higher trophic level components calculated for Cobscook Bay are well within the bounds of uncertainty established by applying trophic transfer efficiencies of 5, 10, and 30% to similar components of the Prince William Sound food web. Lower trophic level components have higher transformities than those determined from an aggregated food web model for Alaskan fjords and in Odum (1996). This comparison revealed that the emergy converging in

Cobscook Bay is not transferred as efficiently into primary productivity as in other estuaries. This inefficiency is reflected in higher transformities for zooplankton in the pelagic grazing pathway and for detritus and macrofaunal feces in the detritus pathway. However, as the energy of primary production moves through the benthic grazing and detritus pathways into the higher trophic levels (macrobenthos, fish, and seals), transformities gradually approach the expected values. The emergy base for the higher trophic levels in Cobscook Bay and the productivity of these components result in efficiencies close to those found in other estuaries. Shorebirds and eagles have transformities somewhat lower than expected based on Brown et al. (1993), perhaps implying that the Bay is particularly good habitat for them. In other words, primary producers in the Bay are working with excess emergy resources over what they can optimally use, whereas, the higher trophic levels, i.e., eagles, seals, and shorebirds appear to be effectively using their resource-rich habitats.

Even the most efficient primary production process in Cobscook Bay (the brown macroalgae) has a transformity an order of magnitude higher than that expected for aquatic primary producers from other estuarine systems (10^5 versus 10^4). This may indicate that our estimates of the energy base for the Bay are too high, or it may be that Cobscook Bay has so much emergy converging in one place that primary producers are unable to use all of it efficiently. If the latter is true, we expect the available energy in the signature to be used to create rare biological, chemical, physical, or geological structures in the environment. Many of the unique features of the Bay are derived from processes using the available energy in its large tides. For example tidal mixing cools the surface waters in summer resulting in an extremely foggy environment that protects intertidal creatures from dessication and may support the development of a diverse and sometimes giant intertidal fauna; swift tidal currents account for rare hydrologic features such as reversing falls and whirlpools, and scour has produced a large expanse of hard bottom (Kelly and Kelly 2004); a large tidal exchange volume and strong vertical mixing result in extremely high nitrate concentrations in the estuary for most of the year.

The most uncertain value in the emergy signature is that of the emergy contributed by waves, but even if the average wave height in the Bay was reduced by 50% from 0.2 to 0.1 m, the calculated transformities for primary producers would only fall by 25% and the order of magnitude difference in the transformity of Cobscook net primary production versus the values found by Brown et al. (1993) and Odum (1996) would be maintained. Only a few estuarine ecosystems have been evaluated using emergy analysis; therefore, we may find that estuaries, in general, have higher transformities for primary producers than fresh water or terrestrial ecosystems.

Future research needs

Campbell (1998) performed an emergy analysis of the State of Maine in which he examined sustainable development and the quality of life in Maine relative to other states and the nation. One conclusion of that study was that emergy analyses of regions within the State are needed to obtain a better understanding of how to improve the quality of life for all Maine's people. At that time, Washington County was economically depressed, but rich in natural resources and it was singled out as a place that could benefit from a regional emergy analysis. In this study, the emergy basis for biological productivity in Cobscook Bay was evaluated including its nutrient budgets and how they are affected by salmon culture in the Bay. However, we did not evaluate the environmental–economic interface that might be developed to take full advantage of the renewable emergy input to the Bay, nor did we trace existing links between the local economy and its environmental support systems. Development alternatives utilizing Cobscook Bay's rich emergy sources have been proposed in the past and rejected on the basis of environmental and safety concerns (Trites 1974, US Army Corps of Engineers 1980).

Odum (2000) found that 4.2 sej of purchased economic emergy were invested in salmon culture operations for every solar emjoule provided by the environment. The buyer of farm-raised salmon receives twice as much real wealth (emergy) as he or she would receive by spending the same amount of money on an average product in the economy. Odum's work shows how evaluating the ecological–economic interface is a logical next step to translate our improved understanding of the Cobscook Bay ecosystem into an assessment of the costs incurred and the benefits gained from its sustainable use. This analysis indicated that future field and laboratory studies in Cobscook Bay should focus on improving our knowledge of the factors controlling biological diversity, sediment resuspension and deposition, and benthic secondary production, as well as the ecological effects of commercial fishing and aquaculture operations.

Conclusions

Analysis of the Cobscook Bay ecosystem network has given us a clearer, though not unexpected, picture (Garside et al. 1978) of the physical basis for the Bay's ecological structure and function. Cobscook Bay can be characterized as a naturally eutrophic estuarine ecosystem driven by tidal forcing and dominated by new nitrogen inflows from the sea that provide excess nutrients to support primary production during most of the year. The large quantity of energy provided by the tides is primarily responsible for the transport of new nitrogen into the Bay, thereby removing most nutrient limitations on primary production. The

excess tidal energy also produces vigorous mixing regimes that reduce the exposure of suspended algae to light, thereby establishing new limits on phytoplankton primary production. Also, mixing supplies abundant food resources to bottom dwelling suspension feeders that consume excess plant production and keep the nutrient rich system form experiencing an overgrowth of unicellular algae.

Emergy represents the organizing power of the available energy inflows to a place, and the convergence of emergy inflows from land and sea in Cobscook Bay has produced many unique hydrographic, climatic, geological, biological, and chemical features as discussed in this volume and above. Emergy analysis of the Cobscook Bay ecosystem network revealed that primary production in the Bay has higher transformities than expected when compared to primary production in two other estuaries. Thus, primary producers in this macrotidal estuary transfer the available emergy inflow into net production less efficiently than in many other terrestrial and aquatic ecosystems. As energy is transformed through the ecosystem network and into the higher trophic levels, the difference in transformities compared to those found at similar trophic levels in other estuaries becomes less, so that transformities are comparable at the highest trophic levels. A comparison of the transformities among primary producers showed that the emergy resources of the Bay are best suited to the production of fucoid algae and benthic diatoms. The high empower density of renewable resources indicated that salmon aquaculture may be a good use of the Bay's abundant supply of tidal emergy. Emergy analysis indicated that the ecological network in Cobscook Bay is a diverse and productive ecosystem in good condition overall; nonetheless, emergy evaluation of the observed and potential impacts of human activities on the ecosystem, identified in this study and elsewhere in this volume, should be performed to document the magnitude of environmental liabilities and economic gains that are being incurred as a result of the present economic use of the Bay.

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Appendix A. Calculation of the energy and emergy signatures for Cobscook Bay including a new transformity for NO_x in the world ocean.

Cobscook Bay quick facts: area = 103600000 m^{-2} (US Army Corps of Engineers 1980); depth = 8.5 m (Trites 1974); length of shoreline = 375,000 m (D. Campbell, estimate); intertidal volume = 5.4E+8 m^3 (Brooks et al. 1999); tidal exchange volume = 3.61E+8 m^3 (Brooks et al. 1999).

1. *Solar Energy Absorbed*: Insolation = 4.97E+9 J $m^{-2}y^{-1}$; interpolation between Portland and Caribou (US Department of Energy 1999).
Albedo = 0.0975 (von Arx 1962). Use a decimal fraction at latitude 44.9 N
Formula for the energy in solar radiation = (area)(insolation)(1-albedo).
Annual energy absorbed = 5.14892E+17 joules y^{-1}.
Transformity = 1 sej J^{-1}.
Annual emergy absorbed = 5.14892E+17 sej y^{-1}.

2. *Wind Absorbed:* height = 1000 m (Odum et al. 1983); density = 1.23 kg m^{-3} (Odum et al. 1983); diffusion coefficient 14.9 $m^3m^{-2}s^{-1}$, average Nov–Apr and May–Oct for Albany (Odum et al. 1983); wind gradient = 0.00458 m $s^{-1}m^{-1}$, tabulated by National Oceanic and Atmospheric Administration (NOAA) for Portland (US Department of Commerce 1975); conversion factor = 3.15E+7 s y^{-1}.
Formula for wind energy absorbed =
    (height)(density)(diffusion coef.)(wind gradient)(area).
Note that another formula may also be used: Energy absorbed in the boundary layer = D = ρ C v^3, where ρ is the density of air (1.3 kg m^{-3}), v is velocity in the geostrophic boundary layer (m s^{-1}), and C is the drag coefficient (1.0E-3) for winds 10 m s^{-1} or less. Winds over land are about 0.6 of what the pressure system would generate in the absence of friction (H.T. Odum, unpubl. manuscript).
Annual energy absorbed = 1.26E+15 joules y^{-1}.
Transformity = 1470 sej J^{-1}.
Annual emergy absorbed = 1.85E+18 sej y^{-1}.

3. *Chemical potential in rainfall* = 1.104 m y^{-1}, 36 yr. avg. Eastport, ME.; Gibbs free energy, G, = 4.1933 J g^{-1}; Solute concentration in rain = 13 ppm (National Atmospheric Deposition Program 1999); solutes in ppm = 0.65(conductivity μs cm^{-1}); salinity at mouth = 31,800 ppm (US Army Corps of Engineers 1980), solute ppm, average for 1957 and 1958, Table 10, conversion 1.0E+6 g m^{-3} water.
Formula for chemical potential energy in rain =
    (area)(rainfall)(Gibbs free energy).
Annual energy absorbed = 4.80E+14 joules y^{-1}.
Transformity = 18100 sej J^{-1}.
Annual emergy absorbed = 8.69E+18 sej y^{-1}.

4. Tidal energy absorbed: height $= 6.46$ m, NOAA Tide Tables (US Department of Commerce 1993); density $= 1.03E+3$ kg m^{-3} seawater 35 ‰; gravity $= 9.8$ m s^{-2}; tides per year $= 706$.
Tidal energy absorbed $=$
    (area elevated)(0.5, center of gravity)(tides y^{-1})(height^2)(density)(gravity).
Annual energy absorbed $= 1.54E+16$ joules y^{-1}.
Transformity $= 24,300$ sej J^{-1}.
Annual emergy absorbed $= 3.74E+20$ sej y^{-1}.

5. Wave energy absorbed: average wind speed $= 7.85$ knots, seasonal average using monthly data for 1975 (US Department of Commerce 1975); fetch $= 8.32$ nmi., average of nw-se and ne-sw axes; wave period $= 6$ s (Pierson et al. 1958); wave velocity $= 8.854$ m s^{-1}, (gravity x depth)$^{.5}$ for shallow water waves; wave height $= 0.244$ m, (Pierson et al. 1958, nomogram Figure 2.4b).
Wave energy absorbed $=$
    (shore length)(1/8)(density)(gravity)(velocity)(seconds per year)(height^2).
Annual energy absorbed $= 7.83E+15$ joules y^{-1}.
Transformity $= 30,000$ sej J^{-1}.
Annual emergy absorbed $= 2.35E+20$ sej y^{-1}.

6. Geologic basement heat flux $= 37$ m W m^{-2} (Decker 1987); heat flux from the earth per year $= 1.17E+6$ J m^{-2} y^{-1}.
Earth cycle energy $=$ (heat flux)(area).
Annual energy flux $= 1.21E+14$ joules y^{-1}.
Transformity $= 33,700$ sej J^{-1}.
Annual emergy used $= 4.07E+18$ sej y^{-1}.

7. Groundwater chemical potential: dissolved solids in water $= 225$ ppm, at Meddybemps and Lubec, 0.65(avg. conductivity; Weddle et al. 1988); Gibbs free energy (G) $= 4.166$ J g^{-1}; ground water flow $= 2.13E+08$ m^3 y^{-1}, assume 20% of precipitation enters ground water and that (in the long run) infiltration is balanced by inflow to the ocean.
Annual energy received $=$ (volume of flow)(density of water)(G).
Annual energy received $= 8.91E+14$ joules y^{-1}.
Transformity $= 40,200$ sej J^{-1}.
Annual emergy used $= 3.58E+19$ sej y^{-1}.

8. River, chemical potential: density $= 1.0E6$ g m^{-3}; dissolved solids in water $= 23$ ppm, avg. of 63 measurements 1978–86, for Narraguagus River (US Environmental Protection Agency 2005b); Gibbs free energy (G) $= 4.192$ J g^{-1}; average discharge $= 21.9$ m^{3}s^{-1}, Dennys River average discharge of 75 cfs from a 240.6 km^2 area (the value for the Denny's was prorated over the ungauged watershed area); volume of flow $= 6.91E+8$ m^{3}y^{-1}.
Annual energy received $=$ (Volume of Flow)(density)(G).
Annual energy received $= 2.90E+15$ joules y^{-1}.
Transformity $= 50,100$ sej J^{-1}.
Annual emergy used $= 1.45E+20$ sej y^{-1}.

9. *Organic matter in river*: organic matter concentration = 8.57 g m^{-3}, Narraguagus River, n = 20 (US Environmental Protection Agency 2005b); volume of flow = 6.91E+8 m^3 y^{-1}.

Annual energy received = (volume of flow)(organic matter conc)(4 kcal g^{-1})(4186 J kcal^{-1}).

Annual energy received = 9.91E+13 joules y^{-1}.

Transformity = 72,500 sej J^{-1}; top soil organic matter from Table C4 in Odum (1996) is used here.

Annual emergy used = 7.19E+18 sej y^{-1}.

10. *Nitrogen in Seawater*: Concentration difference, 0.0074 g NO$_3$-N m^{-3}, average annual concentration difference between Cobscook Bay and the Eastport–Lubec transect; tidal exchange coefficient, 0.67, fraction of tidal inflow that is new water based on a well-mixed Cobscook Bay and a tidal excursion volume that greatly exceeds the tidal volume (Brooks et al. 1999); Gibbs free energy of formation, G$_f$, per mole of N as aqueous HNO$_3$ relative to N$_2$, -110.5 joules mole^{-1}.

Nitrogen influx in grams = (intertidal volume)(tides/y)(tidal exchange coefficient)(conc. sea - conc. estuary)

Annual nitrate nitrogen received= 1.98E+10 gNO$_3$-N y^{-1}

Annual influx of NO$_3$-N in moles = 1.98E+10 gNO$_3$-N y^{-1} / 14 g mole^{-1} = 1.4 E+9 moles y^{-1}

Annual Chemical potential energy received by Cobscook Bay = (moles)/(G$_f$ per mole) = 1.563 E+11 joules y^{-1}

Transformity of NO$_x$-N based on global fluxes (this study) = 4.77E+8 sej J^{-1}

Annual emergy received = 7.47 E+19 sej y^{-1}

For comparison: Specific emergy for N from Odum (1996) = 4.19E+9 sej g^{-1}

Annual emergy received = 8.3 E+19 sej y^{-1}

Transformity of chemical potential energy in NO$_x$-N: The Gibbs free energy of formation for HNO$_3$ in aqueous solution is -26.41 thermo-chemical calories per mole (Weast 1981). There are 4.184 joules in a thermo-chemical calorie or -110.5 joules mole^{-1} relative to diatomic nitrogen in the atmosphere; Annual global flux of NO$_x$ through all compartments including one half of land plant uptake was 2458 Tg y^{-1} (Campbell 2003).

Annual chemical potential energy in global NO$_x$ flux = (Flux of NO$_x$ g y^{-1})/(14g mole^{-1})(-110.5 j mole^{-1}) = 1.94E+16 joules y^{-1}

Annual global emergy Campbell (2000b) = 9.26E+24 sej y^{-1}

Transformity of NO$_x$ flux through global system (ocean, land, and atmosphere) = 4.77E+8 sej J^{-1}

11. *Seawater, net influx of Nitrogen*: From Table 4 and Note 40 in Appendix B, the net annual influx of NO$_3$-N is 1.890E+09 g. (Flux of NO$_3$-N)/(14g mole^{-1}) (-110.5 j mole^{-1}) = 1.492E+10 J y^{-1}.

12. *Salmon culture, N input*: From Table 4 and Note 5 in Appendix B, the net annual influx of N is 3.67E+08 g. (Flux of N)/(14g mole^{-1})(-110.5 j mole^{-1}) = 2.90 E+09 J y^{-1}.

13. *Rivers, N inflow*: From Table 4 and Note 4 in Appendix B, the net annual influx of N is 2.47 E+08 g. (Flux of N)/(14g mole^{-1})(-110.5 j mole^{-1}) = 1.95 E+09 J y^{-1}.

14. *Atmospheric N deposition*: From Table 4 and Note 6 in Appendix B, the net annual influx of N is 7.2E+07 g. (Flux of N)/(14g mole^{-1})(-110.5 j mole^{-1}) = 5.68E+08 J y^{-1}.

15. *Total New Nitrogen*: From Table 4, the net annual influx of N is 2.576E+09 g. (Flux of new N)/(14g mole^{-1})(-110.5 j mole^{-1}) = 2.03E+10 J y^{-1}.

Appendix B: Evaluation of the energy systems model of Cobscook Bay.

The notes and tables given in this appendix are intended to supply all the necessary information needed to allow the reader to reproduce the results. In some cases the information used is too detailed to report in this appendix; therefore, we have posted it on the worldwide web (US Environmental Protection Agency 2005a). The reader should refer to this web site as referenced in the notes. Unless stated otherwise, the same factors are used to convert from wet weight to dry weight (x 0.2), from dry weight to carbon (x 0.5), and from dry weight to energy (x 5 kcal/g dry weight and x 4183 J/kcal).

1. The solar radiation received at Eastport was estimated using two data sources.
A. NOAA measured incident solar radiation at Portland and Caribou, ME, from 1961 to 1990 using a flat plate 0 degree tilt solar collector(US Department f Energy 1999). We estimated the solar radiation received at Eastport (44.9 °N) by linearly interpolating the data from Caribou (46.9 °N) and Portland (43.7 °N).
B. The percent possible solar radiation was measured daily at Eastport from 1893 to 1951 (Shenton and Horton 1973). Three sets of estimates for the solar radiation received at Eastport were obtained by substituting monthly average values of the percent possible sunlight into Angstrom's equation (List 1951) using the clear day light, Q_0, received for atmospheric transmission coefficients, a, of 0.7, 0.8, and 0.9 (Table B1).
Divide the annual average insolation by 365 to get the daily average on the diagram.

Table B1. Day of the year and annual average values for solar radiation received at Eastport in joules $m^{-2} d^{-1}$ for different atmospheric transmission coefficients.

Day of the year	Flat plate	a = 0.7	a= 0.8	a= 0.9
15	6.42E+06			
30	9.80E+06			
35		6.33E+06	7.07E+06	8.06E+06
60	1.37E+07			
80		1.25E+07	1.37E+07	1.51E+07
90	1.68E+07			
120	1.96E+07			
126		1.83E+07	1.99E+07	2.16E+07
151	2.14E+07			
173		2.08E+07	2.25E+07	2.44E+07
182	2.10E+07			
212	1.86E+07			
220		1.89E+07	2.06E+07	2.24E+07
243	1.43E+07			
266		1.25E+07	1.37E+07	1.52E+07
274	9.60E+06			
304	5.92E+06			
312		5.76E+06	6.45E+06	7.35E+06
335	4.98E+06			
356		3.77E+06	4.27E+06	4.96E+06
Annual average	1.36E+07	1.24E+07	1.35E+07	1.49E+07

2. Estimated as a decimal fraction of the solar radiation incident on the sea at latitude 44.9 °N from (von Arx 1962).

3. Daily discharge data for the Denny's River gauging station is available from October 1955 to the present. The average water discharge from a 240.6 km^2 gauged area of the Denny's River from 1956 to 1994 was 5.44 m^3 s^{-1} (United States Geological Survey [USGS] 1993). If this discharge is prorated over the entire watershed area (962.6 km^{-2}), 6.864 x 10^8 m^3 y^{-1} enter the estuary from the watershed. Divide this number by 365 and again by 1.04 x 10^8 m^2, the high tide area of the Bay (US Army Corps of Engineers 1980), to get the m^3 fresh water inflow per m^{-2} d^{-1} shown in Figure 3.

4. Because water quality data have been seldom measured in the Cobscook watershed, USGS data from the nearby Narraguagus River watershed were used under the assumption that total N discharged from the two watersheds per unit area was similar. The total N discharged from the Narraguagus River was 0.48 gN m^{-3} over 5 years from 1982–1986 and 0.36 gN m^{-3} for the 38 year record from the Storet data base (US Environmental Protection Agency 2005b). The estimated total N input to the Cobscook Bay estuary is: (6.864 x 10^8 m^3 y^{-1}) (0.36 gN m^{-3}) = 2.47 x 10^8 g N y^{-1}. Divide by 365 d y^{-1} and 1.04 x 10^8 m^2 to get 0.0065 gN m^{-2} d^{-1}.

5. An estimate of the nitrogen, N, input to the estuary as a result of salmon aquaculture can be obtained by subtracting the nitrogen removed in the fish harvested from the nitrogen added in feed plus smolts. The following information is calculated from data on salmon aquaculture in Cobscook Bay, which was supplied by L. Churchill of the Maine Department of Marine Resources. From July 1994 through June 1995 the total feed given was 7,522,590 kg (16,549,897 lbs); 1,081,522 fish were harvested weighing 5,499,934 kg (12,100,000 lbs) (Sowles and Churchill 2004); and 498,729 mortalities were counted. Assuming that salmon aquaculture operations in Cobscook Bay are in steady state, the smolt added in this calendar year will equal the fish harvested plus any mortality. We estimate that a minimum of 1,580,251 smolt were added. The smolt added weighed about 143 g each (L. Churchill, Maine Department of Marine Resources, pers. comm.), thus 2.26 x 10^5 kg live weight of fish were added. Assuming that *Salmo salar* smolt have the same chemical composition as the adults 3.25 % of the live weight of these fish was nitrogen (Vinogradov 1953). Thus, 7345 kgN y^{-1} were added in the smolt. Salmon feed contains from 46% to 50% crude protein, depending on the age of the fish. Assuming an average crude protein content of 48% (D. Mcphee, Sure Gain Feed Co., pers. comm.) and that Kjeldahl N is 0.16 of crude protein (Moreau et al. 1995),

(1.6550 x 10^7 lbs y^{-1}) (0.45454 kgs lb^{-1})(.48) (0.16) = 5.7774 x 10^5 kgN y^{-1}

enters in feed. The N removed in fish harvested and mortalities, respectivley, is:

(12.1 x 10^6 lbs y^{-1}) (0.45454 kgs lb^{-1}) (0.0325) = 1.78 x 10^5 kgN y^{-1}

(498,729 fish) (5.5 lbs per fish) (0.45454 kgs lb^{-1}) (0.0325) = 0.40 x 10^5 kg N y^{-1}

Thus, (5.7774 x 10^5 kgN y^{-1}) - (1.78 x 10^5 kgN y^{-1}) - (0.40 x 10^5 kg N y^{-1})+ (7345 kgN y^{-1}) = 3.67 x 10^5 kgN y^{-1} are added to Cobscook Bay as a consequence of salmon aquaculture. This converts to 0.01 gN m^{-2} d^{-1}. This number is close to the 3.3 to 3.4 x 10^5 kgN y^{-1} estimate made by Sowles and Churchill (2004) using two different methods.

6. The nitrogen added directly to Cobscook Bay as a result of wet and dry deposition from the atmosphere was estimated using data from National Atmospheric Deposition Program (1999). The area of the Bay at high water is approximately 103.6×10^6 km^{-2}. The average wet deposition of NH_4 and NO_3 from 1982 to 1995 at the NADP station in Acadia National Park, Bar Harbor, ME, was 3.46 kgN ha^{-1}y^{-1}. If dry deposition is approximately equal to the measured rate of wet deposition, approximately 6.92 kg N ha^{-1}y^{-1} would have been deposited directly on Cobscook Bay from the atmosphere. The atmospheric deposition of N on the Bay surface is estimated to be (6.92 kgN ha^{-1} y^{-1}) (10,360 ha) = 0.717×10^5 kgN y^{-1} or 0.002 gN m^{-2}d^{-1}.

7. The tidal exchange coefficient is defined as the fraction of water from Head Harbor Passage that remains in the Bay after each tidal cycle. From Brooks et al. (1999), we know that the tidal prism is approximately 1/3 of the mean estuary volume. We assumed that each incoming tide brings in only new water from Head Harbor Passage. This is a reasonable assumption if the volume of Head Harbor Passage, as defined by the depth of the passage and the area of the tidal excursion, is large compared to the tidal prism of Cobscook Bay (Fogeron 1959) and if the waters in the Passage are completely mixed. If the tidal prism is 1/3 of the Bay's volume and if Cobscook Bay waters are well-mixed, then 2/3 of the Head Harbor Passage water that enters the Bay on an incoming tide must remain in the Bay and the tidal exchange coefficient is approximately 0.67. The tidal prism volume was estimated as 0.54×10^9 m^3 (Brooks et al. 1999). The tidal exchange volume is then $0.67 (0.54 \times 10^9$ m$^3) = 3.61 \times 10^8$ m^3. Multiply by 1.934 tides d^{-1} and divide by the area of the Bay to get the daily exchange per m^2, which is 0.067 m^3 m^{-2} d^{-1}.

8. The nitrate concentration at high tide along the Eastport-to-Lubec line sampled in this study was used to estimate NO_3 in the offshore water entering Cobscook Bay (Table B2). An average of the surface and bottom values on May 2, 3, and 4 taken at 6 stations along the line was 5.75 μmoles NO_3 [(5.75 μM)(62 μgNO_3 μM^{-1}) = (356 μgNO_3 l^{-1}) (14/62) = 80.4 μgN l^{-1} = 0.08 gN m^{-3}]. The average concentration of N in water entering the Bay over the 5 sample periods was 0.052 g N m^{-3}.

9. Phytoplankton carbon in the waters entering Cobscook Bay is estimated from the average concentration of chlorophyll *a* at high tide along the Eastport–Lubec line (Table B3). The average of surface and bottom chlorophyll for the five sampling periods was 0.96 g chl*a* m^{-3}, which is multiplied by 30 gC per g chl*a* (Strickland 1960) to give 0.029 gC m^{-3}.

Table B2. Average NO_3 concentrations at high tide along the Eastport–Lubec line on the dates given.

Date (1995)	μmoles NO_3
May 2, 3, 4	5.75
July 11, 12, 13	1.85
July 21, 22, 23	1.85
October 24, 25, 26	1.40
November 7, 8, 9	7.63

10. The zooplankton entering Cobscook Bay from the sea (Table B4) was estimated from the average displacement volume at the 3 passage stations sampled monthly in 1957 and 1958 by Legare and MacLellan (1960). Zooplankton displacement volume was expressed per volume of water by assuming that the towing speed used was about 3 knots, giving approximately 1000 m^3 of water filtered in a 15 min tow. Displacement volume in cc m^{-3} was converted to mgC m^{-3} using the regression relationship established by Wiebe et al. (1975). The annual average zooplankton concentration in the passage outside Cobscook Bay was 0.43 mgC m^{-3}.

11. Water quality data from the Cobscook watershed are minimal; therefore, USGS data from the neighboring Narraguagus River watershed were used under the assumption that the N discharged from the two watersheds per unit area was similar. Nitrate measurements of 0.01 g m^{-3} in Denny's River water and 0.13 g m^{-3} in water from the Hobart stream (Shenton and Horton 1973) compared to nitrite plus nitrate concentrations ranging from < 0.1 g m^{-3} to 0.26 g m^{-3} (average 0.077 ± 0.47 gN m^{-3}, assuming that < 0.1 g m^{-3} = 0.05 g m^{-3}) measured in the Narraguagus River from 1981–1986 (USGS 1982, 1983, 1984, 1985, 1986, 1987) indicate that the N input from the Narraguagus watershed may be similar to the N input from the Cobscook Bay watershed.

Table B3. Average phytoplankton chlorophyll measured at high tide along the Eastport–Lubec line on the dates given.

Date (1995)	μg chla l^{-1}
May 2, 3, 4	0.12
July 11, 12, 13	1.84
July 21, 22, 32	2.37
October 24, 25, 26	0.24
November 7, 8, 9	0.22

Table B4. Average monthly zooplankton displacement volumes in cubic centimeters (cc) for 1957 and 1958 at the Passage stations of Legare and MacLellan (1960) were conversed to cc m^{-3} using assumptions given in Appendix B note 10.

Month	1957 (cc)	1958 (cc)	Avg. cc m^{-3}	mgC m^{-3}*
January	18	40	0.029	0.734
February	9	15	0.012	0.246
March	6	9	0.0075	0.138
April	5	12	0.0085	0.161
May	5	7	0.006	0.104
June	6	30	0.018	0.407
July	5	85	0.045	1.26
August	3	16	0.0095	0.184
September	17	10	0.0135	0.285
October	36	8	0.022	0.52
November	8	26	0.017	0.380
December	10	52	0.031	0.797

*Log (DV cc m^{-3}) = -1.429 + 0.808 (Log mg C m^{-3}) Wiebe (1975)

12. McCollough and May (1980) observed the numbers of the six most abundant species of shorebirds on mudflats inside and outside Cobscook Bay during 1979 (Table B5). They also determined the number of birds found on the mudflats inside and outside (Table B6) during the southward fall migration. At the peak use from August 10th to 20th, 14,348 birds were feeding in the Bay or 14,348 birds /1.81E+3 ha mud flat (US Army Corps of Engineers1980) = 8 birds ha^{-1} of mudflat. The numbers in Table B6 indicate that about 60% of the feeding birds were found on mudflats inside the Bay when all areas were examined. If this proportion is applied to the observations in Table B5 we can estimate the average biomass found in the Bay during each ten day period. To calculate biomass, each species of bird was assigned an average weight from the literature and the weight of an average bird present in the Bay was determined for each ten day period (US Environmental Protection Agency 2005a). Multiplying the weight of an average bird by the number of birds present in each 10 day period and multiplying by 0.6 gives the average biomass of shorebirds inside the Bay in each 10 day period. Dividing this number by the area of mudflat inside the Bay gives the wet weight of shorebirds inside the Bay per unit area. Converting wet weight to carbon using the standard factors in note 19 and averaging over the spring and fall migration periods gives 3.35 E-5 gC m^{-2} of shorebird biomass per meter square of mudflat present in the Bay during the spring migration and 0.002 gC m^{-2} present during the fall migration. Table B7 combines the information in Tables B5 and B6 to estimate the number of birds ha^{-1} mudflat moving in or out of Cobscook Bay each day. Total annual immigration for both spring and fall was 3.47E-6 gC m^{-2}d^{-1} and emigration was 3.51E-6 gC m^{-2}d^{-1}.

Table B5. Maximum counts of feeding and roosting shorebirds within Cobscook Bay in each ten day period during the spring migration 1980 and fall migration 1979. Both inner and outer shorelines are included in these estimates (McCullough 1981, McCullough and May 1980). SpS = Semipalmated Sandpipers, *Calidris pusilla* L.; Sa = Sanderlings, *Calidris alba* Pallas; YL = Greater, *Tringa melanoleuca* Gmelin; and Lesser, *Tringa flavipes* Gmelin, Yellow Legs; RT = Ruddy Turnstone, *Arenaria interpres* L.; SpP = Semipalmated Plover, *Charadrius semipalmatus* Bonaparte; BbP = Black-bellied Plover, *Pluvialis squatarola* L.

Date	SpS	Sa	YL	RT	SpP	BbP	Total
Spring 1980 (spring migration)							
April 14–27	0	0	1	0	0	0	1
April 28–May 4	0	0	14	0	0	0	14
May 5–11	0	0	11	0	0	5	16
May 12–21	34	0	2	1	2	87	126
May 22–25	54	0	3	2	5	38	102
May 26–June 1	144	0	0	0	0	69	213
June 2–8	42	0	0	0	0	5	47
Summer 1979 (fall migration)							
July 1–10	11	0	31	0	0	0	42
July 10–20	748	0	36	0	3	0	787
July 20–30	24,093	123	71	10	1012	4	25,313
Aug. 1–10	23,600	70	20	11	1206	11	24,918
Aug. 10–20	75,782	51	10	134	928	2066	78,971
Aug. 20–30	25,900	395	40	15	2816	369	29,535
Sep. 1–10	2505	0	0	0	7	55	2567
Sep. 10–20	5448	6	10	4	222	132	5822
Sep. 20–30	76	0	0	0	16	0	92

13. The fish community on a 3.3 by 1.7 km area of mud bottom near Western Passage just inside Passamaquoddy Bay was characterized by Tyler (1971). This fish community is assumed to be similar to the fish community found in Cobscook Bay. Tyler's mean numbers per 0.5 mi. tow were converted to number m^{-2} assuming his 3/4-35 Yankee trawl with a 12.3 m (40 ft) ground line had a net opening of about 6.15 m (20 ft) between the wings and that the trawl's fishing efficiency was 25% (Table B8). The weight of an average fish present in each month was determined by finding the relative proportions of the dominant species in the catch for that month (Tyler 1971), then multiplying these fractions by estimates of average fish wet weight determined from Bigelow and Schroeder (1953) based on Tyler's average size distributions for each species, and then adding up the products to obtain the average biomass for a fish caught in each month. This value was multiplied by the number of fish in the stock or moving in and out of the Bay as determined by month to month differences in

Table B6. Maximum number of the six dominant shorebird species on the major and minor mudflats inside and outside Cobscook Bay during the 1979 southward migration (McCullough 1981, McCullough and May 1980).

| | Maximum number | |
Location	Feeding	Roosting
Outside		
Lubec Flats	2900	
Lubec Center	864	13,691
Town of Lubec	1100	5084
Lubec gravel bar	6775	
Lubec salt marsh	1525	
International Bridge	400	
Johnson Cove	6800	
Carlow Island	3480	300
Gleason Cove	2000	
Subtotal	10,744	34,175
Inside		
Broad Cove	1758	
Carrying Place Cove	6000	65,000
Half Moon Cove	4160	
Birch Point	400	250
Goose Island	200	
East Bay	500	
Sipp Bay	469	
Pennamaquan River	46	
Hersey Cove	300	
Hardscrabble River	18	
Denny's River	8	
Hobart Stream	20	
Edmunds	187	
Whiting Bay	482	
Nutter Cove	0	
Federal Harbor	a few	
Hallowell Island	150	
Subtotal	14,348	65,600
Total	25,092	99,775

the number of a species caught to obtain the following estimates. The average annual standing stock of fish in the Bay was 8.3 gC m^{-2} with 0.065 gC m^{-2}d^{-1} entering the Bay and 0.061 gC m^{-2}d^{-1} leaving the Bay on average over the year. Tyler did not catch a large number of juvenile fish possibly because juvenile fish could escape through the liner mesh size of 1 in. Most fish caught were larger than 10 cm. Species that appeared to have young of the year (fish < 10 cm length) present in the size distributions presented by Tyler were alewives (*Alosa pseudoharengus* Wilson), redfish *(Sebastes marinus* Cuvier), longhorn sculpin *(Myoxocephalus octodecemspinosus* Mitchill), and silver hake *(Merluccius bilinearis* Mitchill). Size distributions from seine samples taken

Table B7. Estimates of shorebirds entering and leaving feeding grounds in Cobscook Bay by combining the information in Tables B5 and B6.

Date	Relative use (Number)	Feeding inside (Number ha^{-1})	Gain or loss (Number ha^{-1}da^{-1})
Spring 1980			
April 14–27	1	0.0001	+0.00001
April 28–May 4	14	0.001	+0.00013
May 5–11	16	0.002	+0.00014
May 12–21	126	0.013	+0.00081
May 22–25	102	0.010	-0.00043
May 26–June 1	213	0.022	+0.0022
June 2–8	47	0.005	-0.0024
Summer 1979			
July 1–10	42	0.004	+0.0004
July 10–20	787	0.08	+0.0076
July 20–30	2531	32.56	+0.248
Aug. 1–10	24,918	2.56	+0
Aug. 10–20	78,971	8.00	+0.544
Aug. 20–30	29,535	2.99	-0.500
Sep. 1–10	2567	0.26	-0.273
Sep. 10–20	5822	0.590	+0.033
Sep. 20–30	92	0.009	-0.0581

Table B8. Fish abundance of all species by month from a mud bottom in Passamaquoddy Bay assuming that the net swept approximately 5000 m^{-2} (Tyler 1971). In and out migration are calculated based on these abundance measurements.

Month	# m^{-2}	# m^{-2} entering (+) or leaving (-)
April	0.26508	-0.10272
May	0.16236	-0.05488
June	0.1074	0.07208
July	0.1795	0.13436
August	0.31392	-0.05404
September	0.25988	-0.11428
October	0.1456	0.05632
November	0.20192	0.00748
December	0.2094	-0.11452
January	0.09488	-0.02252
February	0.07236	0.00888
March	0.08124	0.18384

along the inner Passamaquoddy shore (MacDonald et al. 1984) show that juvenile winter flounder *(Pseudopleuronectes americanus* Walbaum) and cod *(Gadus morhua* L.) use Passamaquoddy Bay in the spring.

14. Average chlorophyll *a* from surface and bottom measurements taken throughout the Bay (Table B9) was converted to carbon using 30 mgC per mg chl*a* (Strickland 1960). The average annual phytoplankton stock from Table B9 is 0.224 gC m^{-2}, which was obtained by averaging the spring neap sample dates and applying each average estimate to a time determined from the center of each pair of sample dates (US Environmental Protection Agency 2005a). The October–November value, which was equal to 0.6 of the May to November average, was assumed to represent the winter–spring period when no samples were taken. This may be a reasonable assumption because Weatherbee and Thomas (2002) found that winter chlorophyll concentrations in the eastern Gulf of Maine coastal area were 0.67 of the average chlorophyll during the summer and fall.

15. The benthic microalgae carbon m^{-2} was estimated based on benthic chlorophyll *a* measured in this study and a carbon to chlorophyll ratio calculated in the phytoplankton section of this report (Table B10). Only 71% of the bottom samples attempted had suitable benthic diatom habitat; therefore, 71% of Larsen et al.'s (2004) Class 1, 2, 3, and 7 areas were used to calculate benthic microalgal stock and production in the Bay. The average annual benthic microalgae carbon m^{-2} was 2.07 gC m^{-2} when determined by the method given for phytoplankton in Note 14.

Table B9. Average of surface and bottom chlorophyll measured in Cobscook Bay was converted to carbon using a ratio of 30 mgC / mg chl*a* l^{-1} (Strickland 1960). The average sonic depth, 8.5 m, was used to calculate biomass m^{-2}.

Dates (1995)	Avg. μg chl*a* l^{-1}	mgC m^{-3}	gC m^{-2}
May 2, 3, 4	0.39 ± 0.22	11.8	0.10
May 16, 17, 18	0.69 ± 0.51	20.8	0.18
July 11, 12, 13	2.08 ± 0.81	62.3	0.53
July 21, 22, 23	1.70 ± 0.83	50.9	0.43
October 24, 25, 26	0.68 ± 0.43	20.5	0.17
November 7, 8, 9	0.54 ± 0.32	16.2	0.14

Table B10. Average benthic carbon was estimated from benthic chlorophyll *a* measured in Cobscook Bay.

Dates (1995)	gC m^{-2}
May 2, 3, 4	1.15
May 16, 17, 18	2.26
July 11, 12, 13	1.13
July 21, 22, 23	3.11
October 24, 25, 26	1.90
November 7, 8, 9	2.35

16. Surface and bottom concentrations of nitrate, nitrite, ammonia, phosphate, and silicate were measured at 32–36 stations throughout Cobscook Bay at six times during 1995 (see Tables B11 and B12 for inorganic nitrogen). On May 2, 3, and 4, there were 0.6 gN m^{-2} in the Bay. The annual average concentration of nitrogen in the Bay was 0.78 gN m^{-2} using the averaging method given in Note 14.

17. Macrophyte biomass and productivity in Cobscook Bay was measured in this study by Bob Vadas of the University of Maine (Vadas et al. 2000, 2004a,b,c). This note uses data on the annual average biomass and productivity provided by Vadas et al. (2000) to evaluate the model (Table B13 and B14). Data on the areas covered by the various plants were determined by Larsen et al. (2004) from a recent satellite photo (Table B15) and by S. Barker (Maine Department of Marine Resources, unpubl. data) based on modifications to Timson (1976)'s CMGE classification. I distributed the productivity and bio-mass which Vadas found at high and low flow across the areas measured by Larsen et al. (2004) according to the proportion of area in a flow type deter-mined by S. Barker (Maine Department of Marine Resources, unpubl. data), who applied the velocity predictions of Brook's (2004) hydrodynamic model to Timson's (1976) data on bottom communities (Table B16). I used Barker's estimates for sub-tidal eelgrass and kelp (Table B17). Larsen et al. (2004) found that the two area estimates agreed within 10% of the total. The annual estimates of macrophyte biomass and production by species group in Cobscook Bay are given in Table B18. I used Vadas et al. (2000) for the area covered by green and red algae. Also, the conversion factors given by Vadas et al. (2000) were used to change the wet weight biomass and productivity values in Table B18 to the carbon storages or flows shown in Figure 3 and Table 1.

Table B11. Average of surface and bottom concentrations of nitrate, nitrite, and ammo-nium in μmoles measured in Cobscook Bay.

Date (1995)	NO$_3$ (μmoles)	NO$_2$ (μmoles)	NH$_4$ (μmoles)
May 2, 3, 4	3.81 ± 0.87	0.11 ± 0.1	1.13 ± 0.32
May 16, 17, 18	3.66 ± 1.07	0.11 ± 0.1	3.11 ± 1.07
July 11, 12, 13	0.86 ± 0.86	0.12 ± 0.11	1.89 ± 1.14
July 21, 22, 23	0.87 ± 0.60	0.23 ± 0.13	2.32 ± 0.98
October 24, 25, 26	2.60 ± 2.67	0.33 ± 0.23	1.98 ± 0.86
November 7, 8, 9	6.91 ± 0.70	0.48 ± 0.15	3.16 ± 1.79

Table B12. Average nitrate, nitrite, and ammonium nitrogen m^{-2} if the average depth is 8.5 m.

Dates (1995)	NO$_3$ (gNm^{-2})	NH$_4$ (gN m^{-2})	NO$_2$ (gN m^{-2})	Total (gN m^{-2})
May 2, 3, 4	0.45	0.13	0.01	0.60
May 16, 17, 18	0.44	0.37	0.01	0.82
July 11, 12, 13	0.14	0.23	0.01	0.38
July 21, 22, 23	0.10	0.28	0.03	0.41
October 24, 25, 26	0.31	0.24	0.04	0.58
November 7, 8, 9	0.82	0.38	0.06	1.26

Table B13. Average biomass and productivity of the major types of aquatic macrophytes in Cobscook Bay from Vadas et al. (2000). High flow values for greens are given first for low and next for high nutrient supply.

Macrophyte biomass and productivity[1]	Low flow	High flow
Kelp (*Laminaria longicruris* Bach. Pyl.)		
Biomass[2]	2.13	1.16
Productivity	8.65	6.97
Productivity range	1.8–26.6	2.2–15.5
Fucoids (*Ascophyllum nodosum*)		
Biomass[2]	17.8	20.7
Productivity	6.8	8.9
Productivity (adjusted)[3]	10	13
Biomass range[4]	11.4–28.9	8.5–26.7
Productivity range	3.8–8.9	4.4–14.9
Eelgrass (*Zostera marina*)		
Biomass (above ground)[5]	0.23	0.13
Productivity	1.81	1.22
Productivity range	0.32–2.72	0.17–2.22
Greens (*Enteromorpha* and *Ulva*)		
Productivity[6]	1.12	1.39

[1]Units of biomass are kg wwt. m^{-2} and units for productivity are kg wwt. m^{-2} y^{-1}.
[2]Multiply wet weight by 0.2 to get Vadas et al.'s (2000) dry weight estimates, and by 0.06 to get carbon.
[3]Using fall and spring measurements, Vadas et al. (2000) was able to adjust his two low flow sites to account for winter mortality of shoots. I applied the average increase in adjusted low flow productivity to adjust high flow productivity, which was not measured.
[4]Vadas et al. (2000) found no significant difference between the standing stocks of *Ascophyllum nodosum* at high and low flow sites.
[5]Multiply wet weight by 0.2 to get Vadas et al.'s (2000) dry weight estimates, and by 0.076 to get carbon.
[6]Productivity of high flow high intertidal was assumed to be equal to low flow regime high intertidal production.

Table B14. Average biomass and productivity for green and red algae in Cobscook Bay. Production and biomass were measured relative to position in the intertidal area (see Vadas et al. 2004c).

Biomass and Productivity[1]	Low	Mid	High
Greens (*Enteromorpha* and *Ulva*)			
Biomass[2]	0.4	0.2	0.018
Productivity[3]	1.29	0.7	0.17
Productivity range	0.025–4.84	0.003–6.07	0.001–0.29
Reds (*Palmaria palmata* (L.) O. Kuntze))			
Biomass[2]	0.5		
Productivity[3]	6.1		
Productivity range	0.26–9.94		

[1]Units of biomass are kg wwt. m^{-2} and units for productivity are kg wwt. m^{-2} y^{-1}.
[2]Multiply wet weight by 0.2 to get Vadas et. al.'s (2004c) dry weight estimates, and by 0.06 to get carbon.
[3]Productivity from Table 4-4 in Vadas et al. (2000).

18. The zooplankton in Cobscook Bay was estimated from the average displacement volume at the two Cobscook stations sampled monthly in 1957 and 1958 by Legare and MacLellan (1960). Using data in Table B19 and assuming an average depth of 8.5 m, the 1957–1958 annual average concentration of zooplankton in Cobscook Bay was 0.73 mgC m^{-3} or 6.2 mgC m^{-2}. The annual average standing stock of zooplankton in the Bay is 0.733 mgC m^{-3} x 8.0E+8 m^3 average volume of the Bay = 5.86E+5 gC.

19. Some information on the concentration of suspended matter in Cobscook Bay was available from a summer project by Schroeder (1977). Table B20 summarizes his data as reported in US Army Corps (1980). Detritus export from Cobscook Bay in July was estimated as 0.1 mg l^{-1} tide^{-1} by subtracting the average concentration on ebb tide from the average concentration on flood. The average stock of detritus suspended in the water column for July 1975 was 1.85 mg l^{-1} or (15.7 g m^{-2}) x (0.33 C/dwt.) = 5.2 gC m^{-2}, assuming 8.5 m is the average

Table B15. Area weighted average intertidal macrophyte cover for brown and green algae from Larsen et al. (2004). See Table 3 and Larsen et al. (2004) for definition of the cover classes.

Cover class	% cover	Area (ha)	Area weighted cover (ha)
Brown Algae (Fucoids)			
Class 9 and 11	25	589.4	0.072
Class 14	5	270.5	0.007
Class 15	50	247.4	0.061
Class 16	90	595.7	0.263
Class 17	50	340.6	0.084
Total		2043.6	0.487
Green Algae			
Class 10	90	435.5	0.239
Class 9 and 11	25	589.4	0.090
Class 12	50	344.9	0.105
Class 14	5	270.5	0.008
Total		1640.3	0.442

Table B16. Fraction of macrophyte area identified by Seth Barker (Maine Department of Marine Resources, unpubl. data) that was found in each flow type: high, low, or medium velocity. Low flow type includes medium and low flow areas identified using results from Brooks et al. (1999).

Macrophyte flow type	Area (ha)	Flow type fraction	Covered area (ha) in flow type[*]
Brown algae (Fucoids)			
Low flow	1028	0.84	836
High flow	203	0.16	159
Green algae			
Low flow	10.4	0.84	609
High flow	2.0	0.16	116

[*] The covered area in a flow type was calculated by applying Barker's fraction of area in a flow type to Larsen et al. (2004) estimate of area covered.

depth of the Bay. Additional data from Schroeder (1977) presented in US Army Corps of Engineers (1980) show that the Inner Bay exported 1.5 mg l^{-1} of detritus per tide to the Outer Bay during July 1977. Detritus export from the Bay in July can be estimated by multiplying the detritus concentration difference by the tidal exchange volume, (0.15 g m^{-3})(3.61E+8 m^{-3} $tide^{-1}$) = (5.415E+7 g dwt.)(1.9342 tides d^{-1}) = (1.047E+8 g dwt. d^{-1})/(1.04E+8 m^{2}) = (1 g m^{-2} d^{-1})(0.33 gC/g dwt) [see Table B20] = 0.33 gC m^{-2} d^{-1}. The 0.33 C to dwt. ratio assumes that exported detritus is mostly derived from macroalgae. If this gradient is maintained over the year, 120 gC m^{-2} y^{-1} of detritus are exported which is equal to 12.53 x 10^{6} kgC y^{-1}. During the first July 1995 sampling period, I observed numerous fragments of macroalgae of all sizes suspended in the water and present on the millipore filters.

Table B17. The area weighted average for the subtidal macrophyte cover of eelgrass and kelp for two flow types from Seth Barker's (Maine Department of Marine Resources, unpubl. data) analysis. Medium and high flow areas identified by Barker using the model of Brooks et al. (1999) are combined. See Table B15 and B16 for definitions of cover classes and flow types.

Cover class	% cover	Area (ha)	Covered fraction in area	flow type
Kelp				
Low flow				
Cover class 1	5	0.4	0.02	
Cover class 2	15	110.0	16.5	
Cover class 3	55	14.3	7.8	
Cover class 4	85	14.6	12.4	
Subtotal		139.3	36.7	0.38
Med. and high flow				
Cover class 1	5	0.9	0.05	
Cover class 2	15	100.9	15.1	
Cover class 3	55	28.3	15.6	
Cover class 4	85	32.9	28.0	
Subtotal		163.0	58.75	0.62
Eelgrass				
Low flow				
Cover class 1	5	44.9	2.24	
Cover class 2	15	114.5	17.2	
Cover class 3	55	160.1	88.1	
Cover class 4	85	35.2	29.9	
Subtotal		354.7	137.4	0.74
Med. and high flow				
Cover class 1	5	10	0.5	
Cover class 2	15	28.7	4.3	
Cover class 3	55	61	33.6	
Cover class 4	85	11.7	9.9	
Subtotal		111.4	48.3	0.26

Table B18. Average macrophyte biomass and productivity per m^{-2} of covered area weighted by the fraction of area in a flow type. Barker's (Maine Department of Marine Resources, unpubl. data) medium flow areas were grouped with low flow for browns and greens and with high flow for kelp and eelgrass. Use the factors in the notes to Table B13 to convert from wet weight to carbon.

Macrophyte	Avg. biomass (kg wwt. m^{-2})	Avg. productivity (kg wwt. m^{-2} y^{-1})	Area (x 10^6 m^{-2})
Intertidal			
Fucoid algae	18.26	10.5	9.95
Green algae	0.35	2.0	9.16[1]
Red algae	0.50	6.1	2.12[1]
Sub-tidal			
Kelp	1.53	7.6	0.96
Eelgrass	0.20	1.7	1.86

[1]Area given in Vadas et al. (2000) based on his cover estimates.

Table B19. Average monthly zooplankton displacement volumes in cubic centimeters (cc) for 1957 and 1958 at the Cobscook stations from Figure 4 in Legare and MacLellan (1960).

Month	1957 (cc)	1958(cc)	Avg. cc m^{-3}	mgC m^{3} *
January	22	125	0.074	2.34
February	12	20	0.016	0.35
March	2	11	0.0065	0.12
April	11	8	0.0095	0.18
May	10	18	0.014	0.30
June	25	15	0.020	0.46
July	14	100	0.057	1.69
August	3	95	0.049	1.40
September	12	38	0.025	0.61
October	18	20	0.019	0.43
November	10	30	0.020	0.46
December	9	30	0.0195	0.45

*Log (DV cc m^{-3}) = -1.429 + 0.808 (Log mgC m^{-3}) Wiebe (1975)

Table B20. Concentrations of suspended matter and the percent organic matter in Cobscook Bay during July 1977.

	Ebb tide		Flood tide	
Quantity	Surface (mg l^{-1})	Bottom (mg l^{-1})	Surface (mg l^{-1})	Bottom (mg l^{-1})
Mean	3	4	3	3
Range	8	9	5	5
% organic	60	50	70	50
Detritus	1.8	2.0	2.1	1.5
Std. deviation	0.6	0.8	1.2	0.9

20. Invertebrate counts from Cobscook Bay intertidal areas were made by McCollough and May (1980), but they were not reported. Larsen et al. (1979) reported the benthic invertebrates found on a low energy rocky intertidal area near Dennysville. Peter Larsen's unpublished data on the benthic community in Broad and Deep Coves was used to estimate benthic biomass and species diversity in Cobscook Bay. The numbers of dominant species were converted to volume based on average sizes and shapes from the published literature. Volume was then converted to wet weight using 1 g /cc. The average number of infauna m^{-2} was 3730 with a range from 870 to 12,970 animals. An average of 12 gC m^{-2} of benthic biomass was present at these sites distributed over an average of 49.5 species. The analysis of these data and ancillary information can be found on the worldwide web (US Environmental Protection Agency 2005a).

21. Todd (1979) studied the ecology of Bald Eagles in Maine. He found that Cobscook Bay supported a dense population of eagles which included 7 occupied breeding sites in 1977 and 1978. Of these seven pairs, 5 bred successfully in 1977, but only 3 were successful in 1978. Seven young chicks were fledged from these nests in 1977 and six in 1978. Cobscook Bay supported 10 adult and 3 immature eagles in the winter of 1977, and 12 adults and 2 immature birds overwintered there in 1978 . From this information, I estimate that in the late seventies Cobscook Bay supported approximately 14 birds or one bird for every 742 ha of the water surface at high tide. If an average bird weighs 4767 g (US Environmental Protection Agency 2005a), there was 6.42E-5 gC m^{-2} of eagle biomass in the Bay at this time.

22. The breeding population of harbor seals, *Phoca vitulina*, in Cobscook Bay was estimated at several hundred individuals (US Army Corps of Engineers 1980). We take 600 as a rough estimate of the resident seal population in 1980. If an average seal weighs 1.1E+5 g, there are 0.064 gC of seal biomass m^{-2} of high tide area in the Bay (US Environmental Protection Agency 2005a).

23. Phytoplankton production was estimated by Phinney et al. (2004) based on water column chlorophyll *a* and light (Table B21). The annual average phytoplankton production was 0.269 gC m^{-2} d^{-1}, calculated using the time averaging method given in Note 14.

Table B21. Average phytoplankton primary production in the waters of Cobscook Bay during six sample times in 1995. Phytoplankton production was calculated by Phinney et al. (2004).

Date (1995)	Phytoplankton production (gC m^{-2} d^{-1})	n
May 2, 3, 4	0.11 ± 0.12	16
May 16, 17, 18	0.17 ± 0.17	18
July 11, 12, 13	1.08 ± 0.44	17
July 21, 22, 23	0.83 ± 0.50	17
October 24, 25, 26	0.09 ± 0.08	18
November 7, 8, 9	0.06 ± 0.06	17

24. The primary production of benthic microalgae (Table B22) was estimated based on benthic chlorophyll *a* measurements made throughout Cobscook Bay and irradiance at the sediment surface (Phinney et al. 2004). The annual average production of benthic microalgae was 0.954 gC m^{-2}d^{-1}, again using the time averaging method given in Note 14.

25. Strickland (1960) suggested a C/N ratio of 6 ± 2 for phytoplankton. Applying this ratio to our net primary production estimates for phytoplankton in Cobscook Bay divided by 0.85 to include phytoplankton respiration at 15% of gross primary production gives 0.053 gN m^{-2} d^{-1} annual average nitrogen uptake by phytoplankton. Divide the numbers in Table B21 by 6 to estimate N uptake by phytoplankton at other times.

26. Vinogradov (1953) gave factors for converting wet weight of algae to dry weight, carbon, or nitrogen (Table B23). These factors are applied to production values in Table 17 as follows:
(1) Browns, (10.48 kg wwt. m^{-2} y^{-1})(0.266 dwt/wwt.)(0.019 fraction N) =
    0.053 kg N m^{-2} y^{-1}.

Table B22. Average primary production of benthic microalgae on the bottom of Cobscook Bay measured at n stations during six sample times in 1995. Benthic algal primary production was determined by Phinney et al. (2004).

Date (1995)	Benthic microalgae production (gC m^{-2}d^{-1})	n
May 2, 3, 4	0.49 ± 0.60	12
May 16, 17, 18	1.55 ± 1.98	12
July 11, 12, 13	1.17 ± 1.17	11
July 21, 22, 23	4.46 ± 3.97	12
October 24, 25,26	0.74 ± 2.28	15
November 7, 8, 9	0.16 ± 0.17	14

Table B23. Conversion factors from Vinogradov (1953).

Plant	% H$_2$O	C as % dwt.	N as % dwt.
Fucoids			
Ascophyllum nodosum	74.4	38.0	2.12 (n = 3)
Fucus vesiculosus	72.3	35.3	1.64 (n = 14)
Average	73.4	36.7	1.88
Greens			
Enteromorpha	70.8	31.5	1.57 (n = 5)
Ulva	78.0	36.1	2.66 (n = 8)
Average	74.4	33.8	2.12
Kelp			
Laminaria digita (Hudson)	81.2	31.9	2.23 (n = 20)
Laminaria saccharina (Lamouroux)	87.1	26.8	1.80 (n = 13)
Average	84.2	29.4	2.02
Reds			
Rhodymenia palmata (L.)	83.6	28.3	2.91 (n = 5)
Eelgrass			
Zostera marina	85	33.9 (n = 12)	1.91 (n = 22)

(2) Greens, (2.0 kg wwt. m^{-2} y^{-1})(0.256 dwt/wwt.)(0.021 fraction N) = 0.011 kg N m^{-2} y^{-1}.

(3) Kelp, (7.61 kg wwt.m^{-2} y^{-1})(0.158 dwt/wwt.)(0.02 fraction N) = 0.024 kg N m^{-2} y^{-1}.

(4) Reds, (6.1 kg wwt. m^{-2} y^{-1})(0.164 dwt/wwt.)(0.029 fraction N) = 0.029 kg N m^{-2} y^{-1}.

(5) Eelgrass, (1.66 kg wwt. m^{-2} y^{-1})(0.15 dwt/wwt.)(0.019 fraction N) = 0.005 kg N m^{-2} y^{-1}.

Multiplying by 1000 g/kg and dividing by 365 d/y gives the numbers for N uptake on Figure 3 and in Table 2.

27. Strickland (1960) suggested a C/N ratio of 6 ± 2 for phytoplankton. We assume that this ratio also applies to benthic diatoms. Dividing the average primary production estimate for benthic microalgae (Table B22), temporally averaged as in Note 15, by 6 gives 0.16 gN m^{-2} d^{-1} for the nitrogen uptake by benthic microalgae.

28. Large zooplankton was assumed to eat approximately 20% of their body weight per day (Parsons and Tagahashi 1973). We estimate that the annual average zooplankton concentration is 6.2 mgC m^{-2} x 0.2 = 1.24 mgC m^{-2}d^{-1} phytoplankton carbon grazed by zooplankton. Zooplankton production of 2.5 mgC m^{-2} d^{-1} is needed to balance the measured demands of feeding and export. This discrepancy could be explained by retention in the Bay if zooplankton do not behave like passive particles.

29. Table B24 shows that during July there was a net influx of chlorophyll *a* into Cobscook Bay from Head Harbor Passage. A minimum estimate for the carbon consumed in the estuary can be made for this time, but not on the other sample dates. The excess chlorophyll that comes into the Bay along with internal production in this month must have been consumed by grazers or settled to the bottom. Using a chlorophyll *a*:carbon ratio of 30 gives 14.1 and 46.2 mgC m^{-3}of phytoplankton imported to the Bay on the first and second sample periods in July, respectively. This is an average of 256 mgC m^{-2} tide^{-1} (z = 8.5 m) or 496 mgC m^{-2} d^{-1} (for 1.9342 tides d^{-1}) of imported phytoplankton during July, which is either grazed or settles to the bottom. Internal net production (Tables B21 and B22) during this time (assuming respiration is 15% of gross production) averaged 955 mgC m^{-2} d^{-1} and 2815 mgC m^{-2} d^{-1} for phytoplankton and benthic

Table B24. The difference between average phytoplankton chlorophyll *a* measured at high tide and low tide along the Eastport–Lubec line.

Date (1995)	High tide (μg chla l^{-1})	Low tide (μg chla l^{-1})	Difference (μg chla l^{-1})
May 2, 3, 4	0.12	0.25	-0.13
July 11, 12, 13	1.84	1.37	0.47
July 21, 22, 23	2.37	0.83	1.54
October 24, 25, 26	0.24	0.76	-0.52
November 7, 8, 9	0.22	0.59*	-0.37

*Data from low tide on the Birch Point to Gove Point line.

microalgae, respectively, or an average of 1885 mgC $m^{-2} d^{-1}$ during July. If grazers consume approximately 50% of the available food, approximately 1190 mgC $m^{-2} d^{-1}$ were consumed by grazing in Cobscook Bay during July in the period between samples. Zooplankton grazing is small (1–2 mgC $m^{-2} d^{-1}$), thus 1188 mgC $m^{-2} d^{-1}$ are grazed by the benthic community in July. If this grazing on suspended algae is nonselective (in proportion to the abundance of suspended food items), 75% or 0.90 gC $m^{-2} d^{-1}$ of the food consumed is from benthic microalgae and 25% or 0.30 gC $m^{-2} d^{-1}$ is from phytoplankton. A time weighted average for the year, interpolating data between the sample times, gives 0.62 gC $m^{-2} d^{-1}$ for the annual average consumption of phytoplankton (0.16 gC $m^{-2} d^{-1}$) and benthic microalgae (0.47 gC $m^{-2} d^{-1}$) by benthic macrofauna if benthic grazing occurs in 4480 ha (Note 32). This amount of macrofaunal grazing on phytoplankton leaves 0.18gC $m^{-2} d^{-1}$ to enter the detritus pool in the estuary (8959 ha). Benthic macrofauna graze 10.1 x 10^6 kgC y^{-1} of microalgae. The detritus formed from benthic microalgae and phytoplankton was also estimated to be 0.62 gC $m^{-2} d^{-1}$ or 10.1 x 10^6 kgC y^{-1} by difference. If macrofauna assimilate 70% of the food consumed, 30% or 0.19 gC $m^{-2} d^{-1}$ of feces are produced and added to detritus.

30. The contribution of macroalgae to the detritus pool in Cobscook Bay can be estimated assuming that direct grazing on macroalgae is small. Allowing 10% of net production for direct grazing by benthic invertebrates on macroalgae, 90% of macroalgal net production would go to the detritus pool.
Net production per m^2 of surface covered by algae of a given type is given below:

(1) Browns, (10.48 kg wwt. $m^{-2} y^{-1}$)(0.2 dwt/wwt.)(0.3 C/dwt) =
      0.63 kgC $m^{-2} y^{-1.}$
(2) Greens, (2.0 kg wwt. $m^{-2}y^{-1}$)(0.2 dwt/wwt.)(0.3 C/dwt) =
      0.12 kgC $m^{-2}y^{-1}$.
(3) Kelp, (7.61 kg wwt. $m^{-2} y^{-1}$)(0.2 dwt/wwt.)(0.3 C/dwt) =
       0.46 kgC $m^{-2} y^{-1}$.
(4) Reds, (6.1 kg wwt. $m^{-2} y^{-1}$)(0.2 dwt/wwt. * (0.3 C/dwt) =
      0.37 kgC $m^{-2} y^{-1}$.
(5) Eelgrass, (1.66 kg wwt. $m^{-2} y^{-1}$)(0.2 dwt/wwt.)(0.38 C/dwt) =
      0.13 kgC $m^{-2} y^{-1}$.

Multiplying by the area in algae of a given type gives an estimate of net production in kgC y^{-1} for Cobscook Bay:

(1) Browns, (0.63 kgC $m^{-2}y^{-1}$)(9.95 x$10^6 m^2$) = 6.3 x 10^6 kgC y^{-1}.
(2) Greens, (0.12 kgC $m^{-2}y^{-1}$)(9.16 x $10^6 m^2$) = 1.1 x 10^6 kgC y^{-1} .
(3) Kelp, (0.46 kgC $m^{-2}y^{-1}$)(0.96 x $10^6 m^2$) = 0.44 x 10^6 kgC y^{-1}.
(4) Reds, (0.37 kgC $m^{-2} y^{-1}$)(2.12 x $10^6 m^2$) = 0.78x 10^6kgC y^{-1}.
(5) Eelgrass, (0.13 kgC $m^{-2} y^{-1}$)(1.86 x $10^6 m^2$) = 0.24x 10^6 kgC y^{-1}.

We estimate that macroalgae and eelgrass can supply 0.9 times 8.86 x 10^6 kgC y^{-1} or a total of 7.97 x 10^6 kgC y^{-1}or 0.32 gC $m^{-2}d^{-1}$from eel grass and 0.35 gC $m^{-2}d^{-1}$ from the total area covered by macroalgae. Total grazing on eelgrass is estimated as 2.4 x 10^4 kgC $y^{-1}$and on macroalgae 8.62 x 10^5 kgC y^{-1}.

31. Primary production of benthic microalgae averaged 348 gC m^{-2}y^{-1} (Table 4) or 0.954 gC m^{-2}d^{-1} in areas with suitable habitat. If 56.3 x 10^6 m^2 of the intertidal and subtidal area is suitable for benthic microalgae, 19.6 x 10^6 kgC y^{-1} is consumed by suspension feeders or goes into the detritus pool of Cobscook Bay. We assume that 90% of benthic algae are regularly suspended in the water column (Campbell and Newell 1998), and therefore they are subject to the same processes that govern phytoplankton. We assume that 90% of resuspended benthic microalgal production could be grazed by dense shellfish beds (Newell et al. 1998). If shellfish beds cover one half of the intertidal plus subtidal area (Note 32), 7.9 x 10^6 kgC y^{-1} or 0.48 gC m^{-2} d^{-1} can be grazed by macrobenthos and the remainder or 11.8 x 10^6 kgC y^{-1} or 0.36 gC m^{-2}d^{-1} enters the detritus pool, assuming the detritus pool covers the intertidal and subtidal areas (8959 ha). Export of benthic algae is assumed to be small because their settling rates are high relative to phytoplankton.

32. During July, detrital carbon is about 1.65 times greater than the carbon in suspended phytoplankton. There are (1.85 g dwt. m^{-3} [see Table B20]) (0.33 C/dwt.) = 0.62 gC m^{-3} of organic matter in the water column which included 0.057 gC m^{-3} of phytoplankton (Table B9) and 0.22 gC m^{-3} of benthic microalgae (Table B10) if 90% are resuspended. Subtracting our July 1995 measurements from Schroeder's (1977) earlier estimates of July organic matter gives 0.34 gC m^{-3} of detritus in the water column. We don't know how much detritus is consumed by benthic macrofauna based on the information available, but a maximum estimate for July based on nonselective feeding and a benthos that consumes 50% of the available food gives 0.17 gC m^{-3} d^{-1} If the benthos feed selectively so that detritus is consumed at 10% of the rate algae is eaten, then only 0.017 gC m^{-3}d^{-1} of detritus is eaten. Detritus consumption by the benthos for selective and nonselective feeding ranges from 33 to 330 gC m^{-2} y^{-1}, assuming that the winter consumption rate is 25% of the July consumption rate. If the area of potential shellfish beds is taken as one half of the subtidal (4480 ha) plus one fourth (half the area times half the time inundated) the intertidal (8959 ha), then between 1.5 and 15 x 10^6 kgC y^{-1} are consumed. Using the conservative estimate, 0.09 gC m^{-2} d^{-1} of detritus is consumed by suspension feeders. The annual macrofaunal food consumption was also estimated by applying a consumption to biomass ratio of 11:1 for macrofauna (Warwick et al. 1979) to our biomass estimate which predicted consumption of 132 gC m^{-2} y^{-1} compared to 262 gC m^{-2} y^{-1} estimated by summing average daily consumption in Notes 29 and 32.

33. The consumption of detrital carbon by bacteria was estimated from the detritus deposited (11.2 x 10^6 kgC y^{-1}) plus fecal production by zooplankton and macrofauna (3.1 x 10^6 kgC y^{-1}) assuming 70% assimilation, which gives a total flux to the bottom of 14.3 x 10^6 kgC y^{-1} assuming that 80% of the carbon deposited is consumed (Hargrave 1980). This calculation gave 0.347 gC m^{-2} d^{-1} consumed by bacteria over the high tide area of the Bay. The remainder of the carbon production (0.088 gC m^{-2}d^{-1}) was assumed to accumulate in the sediment and buried over time.

34. An estimate for the macrofauna eaten by shorebirds was made using the bird populations given in McCullough (1981) and the biomass estimated above, assuming that an average 45-g shore bird consumes 8 g of invertebrates per day (Loesch et al. 2002). Given an average shorebird biomass of 0.002 gC m^{-2} d^{-1}, the birds in Cobscook Bay consume an average of 0.0004 gC m^{-2} d^{-1}.

35. Benthic macrofauna accounted for most of the prey items eaten by the fish caught by Tyler (1972). An average daily ration for a fish of 600 g wet weight feeding largely on invertebrates was estimated to average 2% of body weight per day from information given in Langler et al. (1977). Using the biomass of fish given above, 0.166 gC m^{-2} d^{-1} of macrofauna is consumed by fish each day.

36. If herring (*Clupea harengus* L.) consume all excess zooplankton production in April and May when they are abundant, and April–May zooplankton production would otherwise be at the average for the year, herring consume 0.003 gC m^{-2} d^{-1} for those two months. If large numbers of herring are only present in April and May as indicated by the data in Tyler (1971), 0.0005 gC m^{-2} d^{-1} are consumed on average over the year.

37. Eagle diet in the estuaries of coastal Maine was described in Todd (1979) as 81% waterfowl, 14% fish, and 5% mammals. Using a literature estimate of 0.75 lbs of food as a daily ration, Cobscook Bay eagles eat on average 6.4E-7 gC m^{-2} d^{-1} fish and 3.7E-6 gC m^{-2}d^{-1} fowl.

38. Nitrogen recycled by the various consumer groups important in Cobscook Bay follows directly from the calculation of the metabolic requirements for each group using an appropriate C:N ratio. Assume that bacteria recycle nitrogen in proportion to the nitrogen in the detritus that they process. A weighted average based on the nitrogen in the plant sources of detritus gives a C:N ratio of approximately 20 to 1. Under these assumptions bacteria recycle about 0.017 gN m^{-2} d^{-1}. If zooplankton assimilate 80% of the food consumed, spend half of that assimilated on metabolism, and have a C:N ratio of 4.6 to 1 (Vinogradov 1953), they recycle about 1.1E-4 gN m^{-2}d^{-1}. Macrofauna recycle about 0.031 gN m^{-2}d^{-1}, assuming the average organism size from Larsen's (1979) data, the equation developed for polychaete respiration in Cammen (1987), and a C:N ration of 4:1 from data in Vinogradov (1953). Shorebirds in migration metabolize about 75% of their total consumption (Loesch et al. 2002). If their C:N ratio is about 4:1, they recycle 0.00008 gN m^{-2}d^{-1}. If Cobscook Bald Eagles respire at the rate of 17 kcal per bird per day (US Environmental Protection Agency 2005a) and their C:N ratio is about 4:1, approximately 6E-8 gN m^{-2} d^{-1} are recycled. An average rate of metabolism for temperate zone fish is 90 mgO$_2$ kg^{-1}hr^{-1} (Brett and Groves 1979). Applying this factor to the average fish biomass measured by Tyler (1971) and using a C:N ratio of 4:1, 0.017 gN m^{-2} d^{-1} are recycled by fish. The metabolic rate of *Phoca vitulina* was calculated by applying the correction factor in Kooyman (1981) to the rate determined from the standard equation for mammals for a seal of average weight. Given a metabolic rate of 4.4 gC kg^{-1} d^{-1} and a C:N ratio of approximately 4:1, 7E-5 gN m^{-2} d^{-1} are recycled by the seals of Cobscook Bay.

39. The concentration differences inside and outside Cobscook Bay on the sample dates in 1995 were determined for NO_3 (Table B25), NH_4 (Table B26), NO_2 (Table B27), PO_4 (Table B28), and SiO_3 (Table B29). Import-export fluxes

Table B25. The difference between the average concentration of NO_3 at high tide and low tide along the Eastport–Lubec line.

Date (1995)	High tide (μmoles l^{-1} NO_3)	Low tide (μmoles l^{-1} NO_3)	Difference (μmoles l^{-1} NO_3)
May 2, 3, 4	5.75	4.72	1.03
July 11, 12, 13	1.85	1.42	0.43
July 21, 22, 23	1.85	1.40	0.45
October 24, 25, 26	1.40	4.49	-3.09
November 7, 8, 9	7.63	7.12[*]	0.51

[*]Data from low tide on the Birch Point to Gove Point line.

Table B26. The difference between the average NH_4 concentrations at high tide and low tide along the Eastport–Lubec line.

Date (1995)	High tide (μmoles l^{-1} NH_4)	Low tide (μmoles l^{-1} NH_4)	Difference (μmoles l^{-1} NH_4)
May 2, 3, 4	1.55	1.39	0.16
July 11, 12, 13	2.72	1.80	0.91
July 21, 22, 23	3.41	2.18	1.23
October 24, 25, 26	2.19	2.23	- 0.04
November 7, 8, 9	1.36	1.85[*]	- 0.49

[*]Data from low tide on the Birch Point to Gove Point line.

Table B27. The difference between the average NO_2 concentrations at high tide and low tide along the Eastport–Lubec.

Date (1995)	High tide (μmoles l^{-1} NO_2)	Low tide (μmoles l^{-1} NO_2)	Difference (μmoles l^{-1} NO_2)
May 2, 3, 4	0.17	0.18	-0.01
July 11, 12, 13	0.10	0.05	0.05
July 21, 22, 23	0.22	0.16	0.06
October 24, 25, 26	0.16	0.48	-0.32
November 7, 8, 9	0.38	0.48[*]	-0.10

[*]Data from low tide on the Birch Point to Gove Point line.

Table B28. The difference between the average PO_4 concentrations at high tide and low tide along the Eastport–Lubec line.

Date (1995)	High tide (μmoles l^{-1} PO_4)	Low tide (μmoles l^{-1} PO_4)	Difference (μmoles l^{-1} PO_4)
May 2, 3, 4	0.52	0.50	0.02
July 11, 12, 13	0.27	0.34	-0.00
July 21, 22, 23	0.33	0.47	-0.14
October 24, 25, 26	0.14	0.52	-0.38
November 7, 8, 9	0.76	0.71[*]	0.05

[*]Data from low tide on the Birch Point to Gove Point line.

were calculated from these concentration differences (Table 7) by multiplying the concentration differences by the tidal exchange volume ($3.61 \times 10^8 \, m^3 \, tide^{-1}$ (Brooks et al. 1999). For example, the May concentration difference for nitrate was 103 μmoles NO_3, which equals 14.4 mgN $m^{-3} \times 3.61 \times 10^8 \, m^3 \, tide^{-1} = 5.2 \times 10^6$ gN per tide and multiplying by 1.934 tides d^{-1} gives 1.0×10^7 gN d^{-1} or, dividing by area, 0.097 gN $m^{-2} d^{-1}$ imported as NO_3 in May. Table B30 combines data on NO_3, NO_2, and NH_4 to determine the net flux of inorganic nitrogen. A

Table B29. The difference between the average SiO_3 concentrations at high tide and low tide along the Eastport–Lubec line.

Date (1995)	High tide (μmoles l^{-1} SiO_3)	Low tide (μmoles l^{-1} SiO_3)	Difference (μmoles l^{-1} SiO_3)
May 2, 3, 4	8.20	7.68	0.52
July 11, 12, 13	3.32	3.86	-0.54
July 21, 22, 23	4.42	3.75	-2.81
October 24, 25, 26	3.65	6.46	-2.81
November 7, 8, 9	9.63	11.49[*]	-1.15

[*]Data from low tide on the Birch Point to Gove Point line.

Table B30. The net difference in concentrations of inorganic nitrogen at high tide and low tide along the Eastport–Lubec line. Positive values have higher concentrations on the flood.

Date (1995)	NO_3 (mgN m^{-3})	NH_4 (mgN m^{-3})	NO_2 (mgN m^{-3})	net change (mgN m^{-3})
May 2, 3, 4	14.4	2.24	-0.14	16.50
July 11, 12, 13	6.0	12.7	0.70	19.40
July 21, 22, 23	6.3	17.2	0.84	24.34
October 24, 25, 26[*]	-43.3	-0.56	-4.48	-48.34
November 7, 8, 9	7.1	-6.86	-1.14	-0.90

[*]Point altered by dragging. Assume 0 for averaging over the time from July sampling to Oct. 20.

Table B31. The weighted average inorganic nitrogen concentration difference between flood and ebb tide along the Eastport to Lubec line over a year.

Fraction of days	X avg. N concentration = (mgN m^{-3})	Weighted fraction mg (mgN m^{-3})
175/365	(-1.12 + 16.5)/2	3.69
70/365	(16.5 + 19.4)/2	3.44
10/365	(19.4 + 24.3)/2	0.60
95/365	(24.3 + 0)/2	3.16
15/365	(-48.3 - 1.12)/2	-1.02
Sum of weighted fractions for all forms		9.87
175/365	(7.1 + 14.4)/2	5.22
70/365	(14.4 + 6.0)/2	1.96
10/365	(6.0 + 6.3)/2	0.17
95/365	(6.3 - 0)/2	0.82
15/365	(-43.3 + 7.1)/2	-0.74
Sum of weighted fractions for NO_3-N		7.43

weighted average of the concentration differences over the course of the year for all species (Table B31) was 9.87 mgN m^{-3}; that amounts to an import of 0.067 gN m^{-2}d^{-1}. A weighted average of the NO$_3$-N concentration differences over the course of the year, which we assume, indicates the net N influx offshore (Table B32) was 7.43 mgN m^{-3}; that amounts to an import of 0.05 gN m^{-2}d^{-1}.

40. Table B25 shows the chlorophyll *a* concentration difference along the Eastport to Lubec line on the sample dates in 1995. Converting g chl*a* l^{-1} to gC $^{-3}$ and multiplying by the tidal exchange volume gives the phytoplankton carbon imported or exported per tide. Annual average chlorophyll difference of (0.198 μg chl*a* l^{-1})(30 C:chl*a*) gives a concentration difference of 5.94 mgC m^{-3} between inside and outside the Bay or an export of phytoplankton carbon equal to 2.14 x 10^6 gC d^{-1} or 0.021 gC m^{-2}d^{-1}.

41. Zooplankton import or export may be calculated from the information in Table B32 in a manner similar to that used for NO$_3$ and phytoplankton. The average monthly difference between passage and bay stations was -0.283 mgC m^{-3}. This gives an average daily loss of 0.0023 gC m^{-2} d^{-1}. This estimate assumes that zooplankton behave like passive particles, which is not true, and leads to an export estimate which is greater than our estimate of zooplankton production. Assuming that our estimates of zooplankton production and consumption are approximately correct, the net production and export of zooplankton can be estimated by difference as 0.0007 gC m^{-2}d^{-1}. Thus, about 70% of those animals that would leave the Bay daily, if zooplankton behave like passive particles, are retained in the Bay.

42. The food consumption of seals is estimated at 5–6% of their body weight per day (University of Michigan Museum of Zoology 2005). Using the estimate of 600 seals in the Bay given above, 0.0035 gC m^{-2} d^{-1} of fish are consumed by seals in the Bay.

Table B32. The difference between average monthly zooplankton concentrations in mgC m^{-3} at the Passage and Cobscook Bay stations of Legare and MacLellan (1960).

Month	Passages (mgC m^{-3})*	Bay (mgC m^{-3})	Difference (mgC m^{-3})
January	0.734	2.34	- 1.60
February	0.246	0.35	- 0.10
March	0.138	0.12	0.02
April	0.161	0.18	- 0.02
May	0.104	0.30	- 0.02
June	0.407	0.46	- 0.05
July	1.260	1.69	- 0.43
August	0.184	1.40	- 1.22
September	0.285	0.61	- 0.33
October	0.520	0.43	0.09
November	0.380	0.46	- 0.08
December	0.797	0.45	0.35

*Log (DV cc m^{-3}) = -1.429 + 0.808 (Log mgC m^{-3}) Wiebe (1975)

43. Landings data for Washington County in 1996 were supplied by Keri Lyons of the Maine Department of Marine Resources. The major fin fish species taken in that year were white hake *(Melanogrammus aeglefinus* L. [49,962 lbs.]), cod *(Gadus morhua* L., [34,992 lbs.]), pollock *(Pollachius virens* L. [38,756 lbs.], and herring *(Clupea harengus* L. [291,550 lbs.]). Commercial fisheries for soft clams *(Mya arenaria* L.), sea scallops *(Placopecten magellanicus* Gmelin), periwinkles *(Littorina littorea* L.), sea cucumbers *(Cucumaria frondosa* Gunnerus), and urchins *(Strongylocentrotus droebachiensis* Müller) presently exist in Cobscook Bay. The live weights of these species landed in Washington County in 1996 were 938,344 kg (2,064,360 lbs) soft clams, 1,004,629 kg (2,210,212 lbs) sea scallops, 2,886,704 kg (6,350,826 lbs) urchins, 1,164,253 kg (2,561,388 lbs) sea cucumbers, and 144,247 kg (317,347 lbs) periwinkles. Landings reported for Washington County are not reported by the location in the county where they were caught; therefore, Cobscook Bay landings can be only roughly estimated. US Army Corps of Engineers (1980) reported that Cobscook Bay did not appear to have significant commercially valuable fish stocks. Dow (1959) reported that the Cobscook Bay clam harvest averaged 9.5% of Washington County landings from 1948 to 1957. Quoddy scallop landings, which are mostly taken from Cobscook Bay, averaged 43.3% of the County landings over a similar time span. Using the 1996 landings and assuming that 10% of fish landed in Washington County are produced by the Cobscook Bay ecosystem, 8.5E-5 gC $m^{-2} d^{-1}$ of fish are harvested from the Bay. Applying Dow's fractions of sea scallops and soft clams to the 1996 Washington County landings of shellfish and assuming that 34% of the urchins and 10% of sea cucumbers and periwinkles are landed from the Bay (Maggie Hunter, pers. comm.), 0.0068 gC $m^{-2} d^{-1}$ of shellfish are harvested. Additional information can be found on the worldwide web (US Environmental Protection Agency 2005a).