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An Evaluated Model of Larval Herring Recruitment

in Coastal Maine

by

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Abstract

An ecological model for recruitment of herring larvae in coastal Maine was developed based on the following assumptions. Estuaries and the Maine coastal zone shoaler than 100 m together comprise a retention area for larval herring spawned along the Maine coast. The net movement of these larvae is southwestward along the coast carried by longshore currents and winds. Herring larvae are transported into the estuaries by coastal winds and tidal dispersion. Net longshore drift, colonization, and death from predation or starvation remove herring larvae from the coastal waters. Herring larvae present in the nearshore coastal zone are supplied by drift from the northeast or from eggs hatched locally. The size of the spawning stock determines the number of yolk sac larvae hatched. The model includes small (7-15 mm) and large (>15 mm) herring larvae within the estuarine and coastal plankton ecosystems. Sunlight, temperature, winds, tides, and the estimated spawning biomass of herring determine reproductive success and larval survival in the model. Data from the period 1971 to 1972 was used to evaluate the model. The possible recruitment of Georges Bank larvae to the Maine herring fishery from 1965 to 1973 is examined within the context of the model.

Introduction

Long term research on the early life history stages of herring from the Maine coast has established sufficient information on recruitment processes to permit the development of models. Graham (1982) proposed a conceptual model of herring larval recruitment in coastal Maine waters which separates inshore larval mortality into two phases. The first phase is a period of density dependent mortality in the autumn (possibly food limited). The second phase is a density independent or environmentally related mortality associated with the overwintering period from winter to early spring. Larval survival is enhanced by late spawning which shortens the overwintering period and by greater dispersal along the coast and within the estuaries and embayments which opens a larger support area to the larvae. In this view the estuarine and nearshore areas of coastal Maine are a larval retention area (Iles and Sinclair 1982) which establishes a maximum carrying capacity for larval herring on the Maine coast. In a given year the number of larvae spawned, amount of food available to them, and the environmental conditions to which they are subjected will determine the extent to which this potential productive capacity is utilized.

SPECIAL SESSION ON RECRUITMENT

Graham and Sherman (MS 1986) also used a statistical model to relate recruitment at age two to indices of larval survival. The larval survival indices for a given year were calculated by taking the number of larvae surviving to early winter as a fraction of either the eggs spawned or of the 4+ spawning population multiplied by the rate at which the larvae died during the rest of the winter. A statistically significant correlation was demonstrated between these survival indices and the corresponding harvest of 2 year old fish. Departures from the resulting regression line (index vs. harvest) correlated with the hypothetical year class production of Georges Bank at age 2, an age group generally not found on the bank. This relationship compared with larval distributions suggested migration of larval herring from the bank to the Maine coast. Building on these models, this paper brings together aspects of the early life history and ecology of herring larvae within the environment of coastal Maine to develop an energy circuit model depicting the recruitment process.

Background Information

Figure 1 divides the Maine coast by setting a boundary which splits the Penobscot Bay into eastern and western halves. The position of this boundary is based on longstanding evidence that the climatological and oceanographic processes which govern the ecosystem in eastern and western Maine are of different intensity. These variations in intensity probably lead to qualitative differences between the ecosystems found in the two areas.

Solar radiation is usually greater in the western section than in the east due not only to the small latitudinal difference but also to the greater average cloudiness in the eastern sector (Gran and Braarud 1935). Bigelow (1927) showed greater vertical mixing along the eastern Maine coast than along the west. More recently, Yentsch and Garfield (1971) have evaluated this phenomena using satellite imagery. Garrett et al. (1978) related the extent of mixing throughout the Gulf of Maine to differences in tidal mixing. The average tidal height along the eastern Maine coast is about 25% greater than in the west. Differences in vertical mixing in the Gulf of Maine may in part be due to wind (Yentsch and Garfield 1971, Loder and Greenberg 1986). Saunders (1977) showed that the average wind stress along the eastern Maine coast is about twice that found along the western coast in most seasons. The character of waters along the eastern Maine coast may be modified by advection from the well mixed area at the mouth of the Bay of Fundy (Apollonio and Applin 1972, Brooks 1985, Townsend et al. 1986). The coastal topography around Mt. Desert begins to force streamlines offshore leading to the formation of a gyre around Jordan Basin (Brooks 1985) and a region of complicated flow at the mouth of the Penobscot Bay (Graham 1970). Townsend et al. (1986) have examined the significance of the unique oceanographic environment in eastern Maine to larval herring survival.

There is a considerable body of information describing the ecology and life history of herring larvae in coastal Maine. Eggs are deposited on the bottom in both the eastern and western sections of the Maine coast (see Figure 1, Eovar et al. 1973). Egg production is due primarily to fish age 4 and greater, although some herring recruit to the spawning population at age 3 (Anthony and Waring 1980). Spawning usually begins during late August in eastern Maine and in late September in western Maine (Graham et al., 1972), although spawning may occur as late as December (Graham, 1982).

After hatching the larvae are observed to accumulate in the vicinity of egg beds for a few days. These small larvae are subject to several oceanographic processes. They may be carried inshore immediately by tidal or wind driven dispersion or they may move along shore carried by the counter-clockwise circulation

of the Gulf to be dispersed into estuaries and embayments at a later time (Graham 1982, Townsend et al. 1986). The transport of larvae shoreward may extend as far as the tidal current systems remain intact (Graham 1972). A few larvae remain in the coastal current and are carried southwestward toward Massachusetts Bay.

Recently hatched larvae are subject to severe mortality as they concentrate on the spawning ground and attempt their first feeding (Graham and Chenoweth 1973). The breakup of this concentration and the transport of larvae southwestward improves their nutritional condition and survival (Townsend et al. 1986). Sherman (1970) showed that macrozooplankton concentrations are generally several times higher along the western Maine coast than along the eastern coast. In the estuaries and embayments the accumulation of larvae leads to a severe density dependent mortality (Graham 1982) followed by a less severe, but longer winter mortality. Comparison of the growth rate and mortality of several larval cohorts indicated that the high mortality suffered by small larvae is due in part to predation as well as food limitation (Graham and Townsend 1985). Temperature may be a significant factor in determining the magnitude of density independent mortality in the winter months (Anthony and Fogarty 1985, Graham and Davis 1971). Metamorphosis to the juvenile form occurs in the spring and the juveniles grow through the summer reaching a size sufficient for canning by the sardine industry during autumn. However, recruitment occurs primarily in the subsequent summer when the juveniles are at a most appropriate size for canning.

Model Development

The model to examine herring larval recruitment is divided into four cells numbered 1 through 4 in Figure 1. The dotted line drawn along the coastal headlands marks the boundary between estuarine and coastal waters. Physical transport processes move larvae along shore through cells 1 and 3, as well as shoreward from coastal to estuarine waters (cell pairs 1 and 2 and 3 and 4). The seaward boundary of the coastal waters is taken as the 100 meter isobath. The lines drawn normal to the shore form the eastern and western boundaries of the coastal water cells. The physical and biological basis for setting these boundaries has been outlined in the preceding presentation of background material.

Figures 2, 3, and 4 present the energy circuit models which depict larval herring recruitment along the Maine coast. The ecosystem components are the same within each cell and consist of storages representing phytoplankton biomass, P, zooplankton biomass, Z, small herring larvae 7 mm to 15 mm in size, S, and large herring larvae > 15 mm in size. Only small herring larvae are subject to physical transport processes. We assumed that the development of the caudal fin at about 15 mm (Blaxter 1962) would give larvae greater than this size more control over their movements making them less susceptible to passive physical transport. There is some evidence that larvae smaller than this size are able to adjust their height in the water column and thus they may have more control over their movements than in this model (Blaxter and Hunter 1982). Transports of phytoplankton and zooplankton may also be important but they are not of principal interest and including their transports would make the model much more complex.

In the model phytoplankton production is controlled by solar insolation alone. This is not unreasonable for the light limited waters of the eastern section (Campbell and Wroblewski 1986) and may also be appropriate for the western section as well during most of the fall and winter. The zooplankton component includes both macro and microzooplankton which feed on the phytoplankton and in turn are eaten by small and large herring larvae and other predators. Small herring larvae are allowed to feed on the microzooplankton only (Sherman and Honey 1971) and large larvae are allowed to utilize the entire zooplankton biomass. Small

larvae develop into large larvae and both sizes of larvae are lost to density dependent predation. In the coastal waters small larvae are input to the model upon leaving the yolk sac stage inflow J in Figures 2-4. The yolk sac larvae were input to the

model as a sinusoidal pulse centered on late September in the east and on mid October in the west (Figure 2). Temperature was considered to be an important variable controlling the growth and mortality of large larvae within the estuaries (Anthony and Fogarty 1985). Larvae that remain in the coastal waters were not considered to be vulnerable to negative winter temperature effects because it was reasoned that they could always find cooler temperatures by seeking deeper water. Both temperature, J , and solar insolation, J , are input to the model as monthly average values from September to April.

Figure 2 shows that advective transport through the coastal cells is driven by the counter-clockwise current in the Gulf of Maine, J , and by northeast winds J which act to augment the transport in the coastal current (Greenberg 1983, Day 1958). Water enters the eastern coastal section around Gran Manan carrying with it a small concentration of herring larvae S .

Larvae are transported between the eastern and western sections but some water and larvae move offshore at the Penobscot Bay. Further down the coast water and a few larvae move southwestward out of the western section toward Massachusetts Bay.

Tidal dispersion acts to move small herring larvae shoreward under the assumption that the coastal current forms a seaward reflecting boundary whereas the estuaries and embayments act as absorbers of herring larvae. Fletcher (1985) has demonstrated through a random walk analysis of fish movements along a barrier screen that boundary conditions similar to those given above lead to a greater probability of fish moving toward the absorbing boundary. Thus, the physical factors which control water movements in the coastal waters of Maine supply boundary conditions which result in the inshore movement of larvae from chance alone. Wind driven transport will also have a shoreward bias given these boundary conditions. Tidal transport J is

entered as a constant for each section of the coast, whereas wind driven transport J is entered as a monthly mean from September to December.

Methods

Energy circuit modeling (Odum 1971, 1983) was used to characterize the process by which larval herring are recruited in coastal Maine waters. This modeling methodology consists of a number of steps which ultimately lead to the computer simulation of an ecological system. The first step in the modeling process is to bring several experts in a field together with the modeler to assemble the facts which are known about a problem. Through a process of iteration between the modeler and the experts a complex model is created which includes all processes thought to be important in determining the outcome of a problem. The second step is to evaluate the model with the data at hand. In this step data gaps in the information base are identified. Also in this stage the model is further refined and simplified based on the information obtained from model evaluation and further iterations between the experts and the modeler. The third step is to take the aggregated and simplified model and translate it first into a set of equations and then into a computer program. Finally the model is run on the computer and the real world process is simulated. Different techniques such as sensitivity analysis can now be used to investigate the problem at hand. The computer analysis culminates in the validation of the model with

one or more independent data sets. In this paper we present the first two steps in the process of modeling herring larval recruitment in coastal Maine waters which lays the foundation for computer simulation and analysis at a later date.

Results

Evaluation of the herring larval recruitment model (shown in Figures 2-4) constitutes the results for this study. The forcing functions, storages, and pathways in the model are defined and evaluated below. A description of how the function or value was calculated along with the necessary assumptions and references is given.

Forcing Functions

J_i is the monthly average solar radiation received on a horizontal surface from September to April. List (1984) gives the following formula:

$$Q = Q_0 (0.61S + 0.35) \quad (1)$$

for the calculation of the average solar radiation, Q , given the fraction of possible direct solar radiation, S , and the solar radiation received on cloudless days, Q_0 . The NOAA local

climatological data sheets for Portland, ME were used to obtain an estimate of S in the western coastal section. A monthly comparison of S for the years 1949 to 1952 between Portland and Eastport ME showed that the fraction of possible solar radiation received in Eastport was 0.03 less than in Portland for Sept. and Oct., 0.12 less than Portland from Nov. to Feb., about equal to Portland in March, and 0.06 less than Portland in April. Values of S measured in Portland were adjusted by the fractions given above to reflect the greater average cloudiness of weather in the eastern coastal section. Q_0 was estimated from List (1984) using

latitude 44 degrees and 30 minutes for the eastern sector and latitude 43 degrees 50 minutes for the western sector along with the assumption that the atmospheric transmission coefficient is 0.9 on cloudless days. Sunlight was entered into the model as a continuous function from September to March or April with the monthly mean values centered midway through the month.

J_i is the volume transported each day by the tide. The salt balance equation was used to estimate a tidal exchange coefficient of 0.62 for the eastern half of the Penobscot Bay from data in Meade (1970). The tidal embayments along the eastern coast of Maine were assumed to have similar exchange properties. The tidal prism of the eastern Maine estuarine area outlined in

Figure 1 is $3.23 \times 10^9 \text{ m}^3$. The volume exchanged per tide is then $2.0 \times 10^9 \text{ m}^3$ times 1.93 tides per day gives about $3.9 \times 10^9 \text{ m}^3 \text{ d}^{-1}$ transported by the tide in the eastern sector. In the western sector the salt balance equation was used to estimate tidal exchange coefficients of 0.03 for the Sheepscot estuary and 1 for the western Penobscot Bay from information given in Garside et al. (1978), Meade (1970), Haefner (1967), and Apollonio and Applin (1972). If Casco Bay has exchange characteristics similar to the eastern embayments, an area weighted average along the western coast gives a tidal exchange coefficient of 0.7. By a calculation similar to that used for the eastern coast this exchange coefficient gives a tidal transport of $2.7 \times 10^9 \text{ m}^3 \text{ d}^{-1}$ for the western coastal section.

J_C is the volume transport of the current along the Maine coast. The average current speeds of the counter-clockwise circulation from September to April along the eastern and western coastal sectors were taken from Bumpus and Lauzier (1965). The cross sectional areas of the three vertical sections from shore to the 100 meter isobath which form the boundaries of the eastern and western sections in Figure 1 are Gran Manan, $2.0 \times 10^6 \text{ m}^2$; Vinalhaven, $2.0 \times 10^6 \text{ m}^2$; and Cape Porpoise $1.3 \times 10^6 \text{ m}^2$. If the current speed from 0 to 20 meters is constant and then decays linearly to the bottom we have a depth averaged current speed of 2100 m d^{-1} for Gran Manan and Vinalhaven and 2250 m d^{-1} for Cape Porpoise. The volume transport into and out of the eastern coastal section is about $4.2 \times 10^9 \text{ m}^3 \text{ d}^{-1}$ and the volume transport out of the western sector is $2.9 \times 10^9 \text{ m}^3 \text{ d}^{-1}$. We assume that the difference between these two transports moves offshore at the boundary between sections.

J_W is the volume transport by the wind. The average monthly wind velocities were obtained from the local climatological data for Portland. Wind stress was calculated as in Saunders (1977). Saunders' data showed that the average wind stress is usually greater along the Maine eastern coast than along the western coast, but in autumn this difference is small. Therefore, Portland wind data are used for both the eastern and western sectors in the model. An Ekman transport velocity at the surface was calculated using the formulas in Sverdrup et al. (1942) (pp. 493 and 496) with an average water depth of 60 m for the Maine coast and latitude 44 degrees. For an eleven year average autumn wind speed of 3.6 m s^{-1} the depth of frictional resistance to the wind is about 30 m using formula XIII, 81 in Sverdrup et al. (1942). The linear dimension of the two coastal sections is about 145000 meters giving a cross sectional area for transport of $4.35 \times 10^6 \text{ m}^2$. The calculated values for Ekman transport velocity at the surface were depth averaged to 30 m and multiplied by the calculated cross sectional area to obtain transport volumes. These volumes were decreased by one half because roughly half of the autumn winds along the Maine coast result in Ekman transport velocities at the surface which are directed inshore (see Figure 5).

J_{NE} is the additional longshore volume transport generated by the interaction of northeast winds with the southwestward flowing circulation and the Maine coastal topography. All days with resultant wind velocities of at least 1.8 m s^{-1} and wind direction from 30 to 60 degrees were recorded from the local climatological data for Portland. Ekman transport velocities at the surface were calculated as above. The effects of wind were checked by reference to Greenberg (1983) who used a mathematical model to show that a 0.5 dyne cm^{-2} wind stress could develop a southwestward flowing circulation averaged along the Maine coast of about 12 cm s^{-1} . The calculated surface Ekman transport velocity for a similar wind stress was about half of the velocity produced by Greenberg's model. The calculated transport velocities were doubled to reflect the interactive effect of northeast wind with the Gulf of Maine topography as shown in Greenberg's model. These velocities were depth averaged and multiplied by the width of the shelf to the 100 m isobath times the depth of frictional resistance to obtain an estimate of the additional southwestward volume transport by the northeast wind.

J is the sea water temperature in the estuarine waters of the Maine coast. Sea water temperature at Boothbay Harbor, Maine was obtained from Welch and Churchill (1984).

J_{Y1} is the influx of yolk sac larvae from eggbeds along the Maine coast. Graham et al. (1973) supply data which were used to estimate the distribution of herring spawning from Cape Cod to Gran Manan. We used the quantity of larvae < 10 mm found in each section of the coast from September to November of 1971 and 1972 as a fraction of the total larvae spawned in the autumn of each year to estimate the fraction of the Gulf of Maine herring population which spawned in the different coastal sections in each year. We found that about 50% of the Gulf of Maine herring population spawns in Massachusetts Bay or on Jeffrey's Ledge whereas the additional 50% spawn along the eastern and western Maine coast. We assume that 25% of the population spawns in the eastern section and 25% in the western section of the Maine coast. The number of eggs produced in each sector was obtained by taking the VPA estimates of 4+ stock size from Fogarty and Clark (1983) and multiplying by the age specific fecundity data of Morse and Morris (1981) then dividing by four to obtain the egg production in each sector of the Maine coast. Mortality in the egg stage is estimated at about 10% Caddy and Iles (1973) and mortality of the yolk sac stage is assumed to be another 10%.

-2

Numbers of yolk sac larvae were converted to mgC m⁻² sea surface assuming a 7 mm average size for the larvae and using Chenoweth (1970) to estimate dry weight, then multiplying by 0.55 C:dry weight ratio and dividing by the area of the coastal section.

Storages

P₁ is the amount of phytoplankton in the water. Measurements of chlorophyll a in the coastal water were taken from Apollonio and Applin (1972). An average carbon to chlorophyll ratio of 45:1 was used (Parsons and Takahashi 1973). Chlorophyll is assumed to be present in significant quantities to an average depth of 25 m in the estuarine waters and to a depth of 50 m in coastal waters. An average of Apollonio and Applin's September, 1971 transects through the eastern and western areas gives 6.2 gC m⁻² for the western estuaries; 6.4 gC m⁻² for the western coastal area; 3.7 gC m⁻² for the eastern embayments; and 8.3 gC m⁻² for the eastern coastal section.

Z₁ is the amount of zooplankton in the water. No zooplankton data were available for 1971, therefore, we chose to use the 1968 zooplankton measurements from the data which K. Sherman obtained along the Maine coast from 1964 through 1968 (Sherman 1966, 1968, 1970) because this year was most similar to 1971 in sunlight and temperature characteristics. Since Sherman used 0.366 mm mesh nets which did not sample the microzooplankton we adjusted his volumes according to the observations of Beers and Stewart (1969) by adding their maximum 43% of macrozooplankton volume to the zooplankton measured in our eastern sector. We added 25% of the macrozooplankton volume measured in the western sector to account for the microzooplankton there, because the data of Bigelow et al. (1940) indicated that planktonic protozoans are more abundant in the eastern sector than in the western sector in fall. The zooplankton biomass in the western estuaries is estimated to be 149 mgC m⁻² of which 36 mg is microzooplankton; in the western coastal area there are 350 mgC m⁻² of which 99 mg are microzooplankton; in the eastern embayments there are 28 mgC

\bar{m} of which 10 mg are microzooplankton; and in the eastern coastal area there are 42 mgC m^{-2} of which 15 mg are microzooplankton. Conversions from displacement volume to mgC were made using the formula of Wiebe et al. (1975).

S and L, respectively, are the amounts of small (7-15 mm) and large (>15 mm) herring larvae present in the water. Data from Graham et al. (1972) were used to evaluate these storages. The number of larvae per 1000 m^3 were converted to mgC m^{-2} using Chenoweth (1970) assuming an embayment depth of 40m, a coastal depth of 60m and a carbon to dry weight ratio of 0.55. From these data there are 2.2 mgC m^{-2} of small herring larvae and 1.8 mgC m^{-2} of large herring larvae in the eastern coastal waters in early September, 1971. In the western coastal sector there are 0.024 mgC m^{-2} small herring larvae and 0.91 mgC m^{-2} of large herring larvae. From Granam (1982) and Graham et al. (1972) we estimate that larval biomass per m^2 of sea surface within the eastern embayments is about 10% of the coastal biomass in coastal waters in September. We estimate are 0.22 mgC m^{-2} of small herring larvae and 0.18 mgC m^{-2} of large herring larvae in the eastern embayments in early September, 1971. Similarly we assume that the western estuaries hold 10% of the herring larval biomass present in the western coastal waters. Therefore, we have 0.0024 mgC m^{-2} small herring larvae and 0.091 mgC m^{-2} large herring larvae in the western estuarine waters.

Pathway flows

$k P_{oi}$ is the amount of solar radiation absorbed by the ecosystem. This value is calculated by taking the difference between the incident solar radiation J_{oi} and the albedo J_{Ri} , estimated as 10% for latitude 44 degrees (Von Arx 1962). J_{oi} and J_{Ri} are 4720 Cal $m^{-2} d^{-1}$ on September 1, 1971 for the western sector and J_{oi} and J_{Ri} are 472 Cal $m^{-2} d^{-1}$ leaving 4248 Cal $m^{-2} d^{-1}$ to be absorbed by the western ecosystem. J_{oi} and J_{Ri} are 4570 Cal $m^{-2} d^{-1}$ in the eastern section, J_{oi} and J_{Ri} are 457 Cal $m^{-2} d^{-1}$ leaving 4113 Cal $m^{-2} d^{-1}$ to be absorbed by the eastern ecosystems.

$k P_{Ji}$ is the phytoplankton gross primary production in coastal and estuarine waters. From Garside et al. (1978) an average rate of 3 mgC mg Chl $a^{-1} h^{-1}$ primary production from summer to winter was calculated for the Sheepscot estuary. Assuming that this rate is typical of September primary production along the Maine coast and adding in 10% for phytoplankton respiration (Steeman Nielson and Hansen 1959), we have 464 mgC $m^{-2} d^{-1}$ gross primary production in the western coastal waters, 450 mgC $m^{-2} d^{-1}$ in the western estuarine waters; 602 mgC $m^{-2} d^{-1}$ gross primary production in the eastern coastal

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waters and 268 mgC m⁻² d⁻¹ in the eastern embayments.

^{21 1}
k_P is the loss of phytoplankton biomass through respiration, sinking, and predation by animals other than zooplankton. This loss is taken as the difference between gross primary production and zooplankton grazing.

^{31 1 1}
k_{PZ} is the phytoplankton grazed by zooplankton. We assume that macrozooplankton graze 20% of their body weight per day and microzooplankton graze 60% of their weight per day (Parsons and Takahashi 1973). Western coastal zooplankton graze 110 mgC m⁻² d⁻¹; western estuarine zooplankton graze 44 mgC m⁻² d⁻¹; eastern coast zooplankton graze 15 mgC m⁻² d⁻¹; and eastern estuarine zooplankton graze 10 mgC m⁻² d⁻¹.

^{41 1 1}
k_{PZ} is the food assimilated by zooplankton. The zooplankton assimilation rate is assumed to be 70% (Steele 1974).

^{51 1}
k_Z is the loss of zooplankton biomass through respiration and predation other than by herring larvae. Zooplankton respiration is calculated from the equations of Ikeda (1970) using an average body size of 1 mg for large zooplankton and 0.1 mg for small zooplankton. This gives 10 mgC m⁻² d⁻¹ zooplankton respiration in the western coastal area; 4 mgC m⁻² d⁻¹ in the western estuarine area; 1.2 mgC m⁻² d⁻¹ in the eastern coastal area; and 0.8 mgC m⁻² d⁻¹ in the eastern embayments. Secondary production by zooplankton is calculated using a yearly F:B ratio of 7:1 for macrozooplankton and 25:1 for microzooplankton (Cohen and Grosslein 1986). For the zooplankton storages in the model, secondary production is 1.54 mgC m⁻² d⁻¹ in the eastern coastal ecosystem, 11.6 mgC m⁻² d⁻¹ in the western coastal ecosystem, 1.03 mgC m⁻² d⁻¹ in the eastern embayments, and 4.6 mgC m⁻² d⁻¹ in the western estuaries. The loss zooplankton biomass to predation other than by herring larvae can now be calculated by difference.

^{61 1 1}
k_{ZS} is the amount of zooplankton biomass eaten by small herring larvae. Small herring larvae (11 mm average size) search about 1.5 l h⁻¹ (Blaxter and Hunter 1982) and have a capture rate assumed to average 50% over the interval from 7 to 15 mm. If these larvae feed only on microzooplankton during daylight hours they can ingest a maximum of 0.07 mgC m⁻² d⁻¹ in the eastern coastal area; 0.007 mgC m⁻² d⁻¹ in the eastern embayments; and 0.02 mgC m⁻² d⁻¹ in the western coastal area and 0.0007 mgC m⁻² d⁻¹ in the western estuaries.

^{71 1 1}
k_{ZL} is the amount of zooplankton biomass eaten by large herring larvae. Large herring larvae (17 mm in the east and 22mm in the west) search an average of 7.5 l h⁻¹ and have a capture

rate of 95% (Blaxter and Hunter 1982). Large larvae ingest $0.19 \text{ mgC m}^{-2} \text{ d}^{-1}$ in the eastern coastal area; $0.019 \text{ mgC m}^{-2} \text{ d}^{-1}$ in the eastern embayments; $0.26 \text{ mgC m}^{-2} \text{ d}^{-1}$ in the western coastal area; and $0.011 \text{ mgC m}^{-2} \text{ d}^{-1}$ in the western estuaries.

k_{ZS} is the assimilation of small larvae. Blaxter and Hunter (1982) note that growth averages 40% of ration and 45-51% of the energy assimilated. Thus, assimilation is between 80 and 90% of ingestion. We assume that assimilation is 90% for small larvae. Small larvae assimilate $0.063 \text{ mgC m}^{-2} \text{ d}^{-1}$ in the eastern coastal area; $0.0063 \text{ mgC m}^{-2} \text{ d}^{-1}$ in the eastern embayments; $0.018 \text{ mgC m}^{-2} \text{ d}^{-1}$ in the western coastal area; and $0.0006 \text{ mgC m}^{-2} \text{ d}^{-1}$ in the western estuaries.

k_{ZL} is the assimilation of large herring larvae. Using an assimilation rate of 90% there are $0.175 \text{ mgC m}^{-2} \text{ d}^{-1}$ assimilated by large herring in the eastern coastal area; $0.0175 \text{ mgC m}^{-2} \text{ d}^{-1}$ assimilated in the eastern embayments; $0.23 \text{ mgC m}^{-2} \text{ d}^{-1}$ assimilated in the western coastal area and $0.01 \text{ mgC m}^{-2} \text{ d}^{-1}$ assimilated by large larvae in the western estuaries.

k_{S1} is the respiration of small herring larvae and natural mortality of small herring larvae. The respiratory rates for small larvae of size 0.15 mg were estimated from De Silva and Tytler (1973). Respiration of small larvae in the eastern coastal area was $0.14 \text{ mgC m}^{-2} \text{ d}^{-1}$; in the eastern embayments it was $0.014 \text{ mgC m}^{-2} \text{ d}^{-1}$; in the western coastal waters it was $0.0015 \text{ mgC m}^{-2} \text{ d}^{-1}$ and in the western estuaries respiration was $0.00015 \text{ mgC m}^{-2} \text{ d}^{-1}$. Natural mortality of the small larvae in the eastern section was prorated by size of the larvae present. Larvae < 10 mm in size were assigned a mortality of 29% d⁻¹ (Graham and Chenoweth 1971) and larvae between 10 and 15 mm were assigned a daily mortality of 5% (Oiestad and Moksness 1981, Lough et al. 1985). The loss of larval biomass through natural mortality in the eastern coastal section was $0.16 \text{ mgC m}^{-2} \text{ d}^{-1}$. Similarly the loss of larval biomass within the eastern embayments is $0.016 \text{ mgC m}^{-2} \text{ d}^{-1}$. The loss of small larval biomass through mortality in the western section was $0.006 \text{ mgC m}^{-2} \text{ d}^{-1}$, and in the western estuaries it was $0.0006 \text{ mgC m}^{-2} \text{ d}^{-1}$.

k_{L1} is the respiration and natural mortality of the large larvae. Respiratory rates for large larvae of weight 1.1 mg were calculated from De Silva and Tytler (1973). The respiration of larvae in the western coastal waters was $0.08 \text{ mgC m}^{-2} \text{ d}^{-1}$, in the eastern embayments it was $0.008 \text{ mgC m}^{-2} \text{ d}^{-1}$, in the western coastal waters it was $0.04 \text{ mgC m}^{-2} \text{ d}^{-1}$, and $0.004 \text{ mgC m}^{-2} \text{ d}^{-1}$ in the western estuaries. An average natural mortality for the

k_{12} large larvae was estimated at $3\% \text{ d}^{-1}$ (Graham and Davis 1971, Lough et al. 1985). The loss of biomass through natural mortality in the eastern section was $0.054 \text{ mgC m}^{-2} \text{ d}^{-1}$, the loss in the eastern embayments was $0.0054 \text{ mgC m}^{-2} \text{ d}^{-1}$, this loss in the western coastal section was $0.027 \text{ mgC m}^{-2} \text{ d}^{-1}$, and in the western estuaries it was $0.0027 \text{ mgC m}^{-2} \text{ d}^{-1}$.

k_{12} is the loss of small herring larvae through growth into large larvae. Assuming an average growth rate of 0.25 mm d^{-1} (Graham and Townsend 1985) it will take about 16 days for the average small larvae to become a large larvae. $0.14 \text{ mgC m}^{-2} \text{ d}^{-1}$ of small larvae become large larvae in the eastern coastal area; $0.014 \text{ mgC m}^{-2} \text{ d}^{-1}$ of small larvae in the eastern embayments become large larvae; and $0.0015 \text{ mgC m}^{-2} \text{ d}^{-1}$ of small larvae in the western coastal area become large larvae.

k_{13} $J(S_{1,3} - S_{2,4})$ is the net transport of herring larvae shoreward by the wind. The net shoreward wind transport in September, 1971 was $1.6 \times 10^9 \text{ m}^{-3} \text{ d}^{-1}$ which gives $0.02 \text{ mgC m}^{-2} \text{ d}^{-1}$ transport of small larvae into the eastern embayments, and $0.0003 \text{ mgC m}^{-2} \text{ d}^{-1}$ as the transport of small larvae into the western estuaries.

k_{14} $J(S_{1,3} - S_{2,4})$ is the net transport of herring larvae shoreward by the tide. The tidal transport of larvae shoreward in the eastern sector is $0.05 \text{ mgC m}^{-2} \text{ d}^{-1}$ and the shoreward transport in the west is $0.0006 \text{ mgC m}^{-2} \text{ d}^{-1}$.

k_{15} $S(J_C + J_{NE})$ is the influx of herring larvae from waters around Gran Manan. The concentration around Gran Manan is assumed to be about 0.44 mgC m^{-2} from Graham et al. (1971). There are $0.01 \text{ mgC m}^{-2} \text{ d}^{-1}$ of herring larvae entering the eastern coastal section around Gran Manan.

k_{16} $S(J_C + J_{NE})$ is the loss of herring larvae from the eastern sector to the western sector and is calculated from the model to be $0.05 \text{ mgC m}^{-2} \text{ d}^{-1}$.

k_{17} $S(J_C + J_{NE})$ is the amount of herring larval biomass which is transported into the western sector from the eastern sector and is calculated to be $0.035 \text{ mgC m}^{-2} \text{ d}^{-1}$. The remainder is carried seaward off the Penobscot Bay.

k_{18} $S(J_C + J_{NE})$ is the biomass of larvae transported out of the western sector toward Massachusetts Bay. This number is calculated from the model to be $0.0045 \text{ mgC m}^{-2} \text{ d}^{-1}$.

Discussion

The energy circuit models shown in Figures 2 to 4 may aid us in understanding herring recruitment in a number of ways. First the evaluated models provide a source of information about the relative importance of the various environmental factors and ecological processes which affect herring larval recruitment. The proposed model structure forces us to think in holistic and quantitative terms about how herring recruitment really works and whether or not this particular formulation of ideas is plausible. Finally, the modeling process helps us to identify aspects of the recruitment problem which are not yet entirely understood. Several points taken from the models will be discussed in order to improve our understanding of herring recruitment in Maine waters. We hope that some of these insights will be found applicable to herring recruitment in general.

One prominent aspect of the Maine coastal environment is the large difference between the physical forcing variables in eastern and western Maine. From the model evaluation we found that tidal transport is 44% greater in eastern embayments than in the western estuaries. Wind stress on the water surface differs markedly between east and west in all seasons except autumn. Solar insolation is 12% greater in the western coastal area from November through February than in the east. The amount of longshore transport is probably somewhat greater for the eastern shelf than for the western shelf (45% more as evaluated in this model). Perhaps the principal ecological difference observed as a consequence of differing environmental conditions in the eastern and western coastal waters is the paucity of zooplankton in the eastern waters and the relative abundance of zooplankton found in the west (Sherman 1970, Townsend et al. 1986). In contrast there was relatively little difference in the food available within the coastal and estuarine areas at least for 1971, the year we evaluated.

Table 1 shows the relative importance of various physical and ecological processes affecting small herring larvae along the Maine coast in early September. In general biological processes are controlling larval concentrations except for the important physical transport of small larvae into the estuaries and embayments and the movement of larvae with the longshore current from the eastern to the western coastal section. Growth dominates mortality in the western waters which are rich in zooplankton. Growth in the eastern waters is much slower and mortality is more important in controlling the biomass of larvae. Tidal and wind driven transport of herring larvae are, in general, more important than advective longshore transport. However, the most important process controlling herring larval distributions in the western section at this time of year is the transport of small herring larvae from the east. In contrast the transport of larvae into the eastern sector from the Bay of Fundy is very small. This process is not well understood and its elucidation is one of the objectives of a current joint Canadian-US research program. The dominant process controlling the biomass of small herring larvae in the east is hatching and the subsequent input of post yolk sac larvae to the eastern coastal sector.

A similar analysis of the ecological processes controlling the abundance of large larvae showed that growth exceeded mortality in all areas (see Table 2). Growth of large larvae was greater in the eastern area than in the western as expected from the distribution of food items. Mortality was about the same in both areas, but input to large larvae from the development of small larvae was much greater in the eastern sections than in the western. The large larvae in western coastal waters were growing somewhat faster than those in the western estuaries.

The turnover times given in Tables 1 and 2 are based on the assumption that small larvae average 11 mm in size and large larvae average 22 mm in size. In September 1971 this was true for the large larvae in the west and for the small larvae in the east. However, small larvae in the west really averaged 8 mm in

size and the average large eastern larva was really only 18 mm in length. When feeding rates of the smaller larvae are used, we found that growth of small herring larvae in the western coastal area just balances mortality, while in the western estuaries mortality of 8 mm larvae would exceed growth. The 18 mm large larvae in the east actually can only break even on the low zooplankton concentrations rather than grow as indicated by Table 2. Thus, large larvae within an increment will be nutritionally better off and small larvae worse off than indicated in Tables 1 and 2. If the biomass of microzooplankton is underestimated in the model these results on larval feeding would be modified to give greater growth and higher survival. This number is not well known and future research should be directed toward increasing our knowledge of zooplankton concentrations in Maine coastal waters.

Calculation of advective transport along the coast indicated that 30% of the water that leaves the eastern sector exits the coastal waters off the Penobscot Bay. This water and the larvae contained in it are probably caught up in the counter-clockwise eddy that often occupies this area. After a variable lag time these larvae may then be released to the western coastal area by turbulent dissipative processes. Alternatively, they may be swept offshore and caught up in the gyre around Jordan Basin (Brooks 1985). There is some evidence that the former alternative is more likely (Graham 1970, 1982), but further work is needed to clarify the physical oceanographic processes that control water movements in this area to resolve the problem.

Figure 2 shows that northeast winds are modeled so that they increase advective transport along the Maine coast (Day 1958, Greenberg 1983, Csanady 1974). There is considerable year to year variation in the frequency of northeast winds in autumn along the Maine coast, and they were originally thought to be an important factor determining the residence time of herring larvae off the coast. Evaluation of this effect indicated that over a 120 day period from September to December transport by the northeast wind accounts for no more than 5 times the daily transport by the coastal current. This value is uncertain and the model will be used to test the effects of northeast wind for different efficiencies of transport generation.

Temperature is modeled as a major factor determining the survival of large herring in the estuaries during winter (Graham and Davis 1971, Anthony and Fogarty 1985). Temperature is modeled as a push-pull interaction; that is, temperature stimulates both anabolic and catabolic processes (Odum 1983). This formulation of temperature can explain the apparently contradictory correlation results of Anthony and Fogarty (1985). They observed a positive correlation of the Sept. to Mar. mean winter temperature with herring recruitment when comparing the highly productive years during the 1950's with later years. However, in the 60's and 70's they found a negative correlation between the mean and minimum temperature from Jan. to Mar. and herring recruitment. In the model higher winter temperatures will stimulate both growth and respiration; therefore, if food supply is low mortality will increase at higher temperatures. In contrast if higher water temperatures in the fifties were associated with increased solar radiation along the Maine coast and in consequence greater winter productivity; winter growth could balance or exceed the mortality associated with warmer water and result in greater herring survival.

The relationship between solar insolation as the basis of biological productivity and herring recruitment is further explored in Table 3. The correlation coefficient of a linear regression of 2 year old harvest on average autumn solar insolation is 0.346. Nevertheless, if we assume that there is some relationship between the potential biological productivity in a given year and herring recruitment and that the years 1976 and 1981 represent years with little or no recruitment from Georges Bank we can speculate on the possible influence of Georges Bank herring on the Maine 2 year old harvest (Graham and

Sherman MS 1986). The years 1966 and 1970 are both much higher than can be accounted for by productivity on the Maine coast. Nineteen seventy should have been a bad year based on potential productivity alone. Nineteen sixty six should have been a good year for herring but not nearly as good as it turned out to be. Nineteen sixty nine is anomalously low but this was a bad year on Georges Bank as well (Anthony and Waring 1980). The low herring production in this year may have resulted from low autumn productivity combined with high winter water temperatures. When both solar insolation and water temperature are compared for the years listed in Table 3, only 1969 has low insolation combined with high winter water temperatures. Conversely, 1976 which was a good year had very high autumn productivity and low winter water temperature.

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Table 1. A comparison of of small herring larvae turnover times generated by various ecological and physical processes when all other factors are held constant.

Type of Process	Turnover Time in Days			
	Eastern Section Coast	Eastern Section Estuaries	Western Section Coast	Western Section Embayments
Physical Process				
Inshore transport	31	3.1	27	2.6
Longshore transport out	44	----	53	----
Longshore transport in	220	----	0.7	----
Ecological Process				
Growth	35	35	1.3	3.8
Hatching	0.9	----	----	----
Mortality	7.3	7.3	3.2	3.2

Table 2. A comparison of of large herring larvae turnover times generated by various ecological processes when all other factors are held constant.

Ecological Process	Turnover Time in Days			
	Eastern Section Coast	Eastern Section Estuaries	Western Section Coast	Western Section Embayments
Growth	10.2	10.2	4	9.1
Development	12.8	12.8	606	606
Mortality	13.8	13.8	13	13

Table 3. The relationship between the average autumn solar insolation at Portland ME, winter water temperature at Boothbay Harbor and the Maine harvest of 2 year old herring 2 years later for years with and without possible inputs from the Georges Bank stock.

Year	# 2 Year Olds 6 X 10	Insolation		Temperature °C
		-2 Cal m	-1 d	
Georges Bank Years				
1965	268	2890		2.1
1966	877	2957		1.2
1967	216	2870		1.0
1968	183	2767		2.4
1969	62	2643		3.0
1970	339	2493		1.5
1971	155	2883		2.3
1972	175	2720		2.6
1973	172	2907		3.7
Post Georges Bank Years				
1976 (little if any)	323	3060		2.0
1981	113	2706		3.3

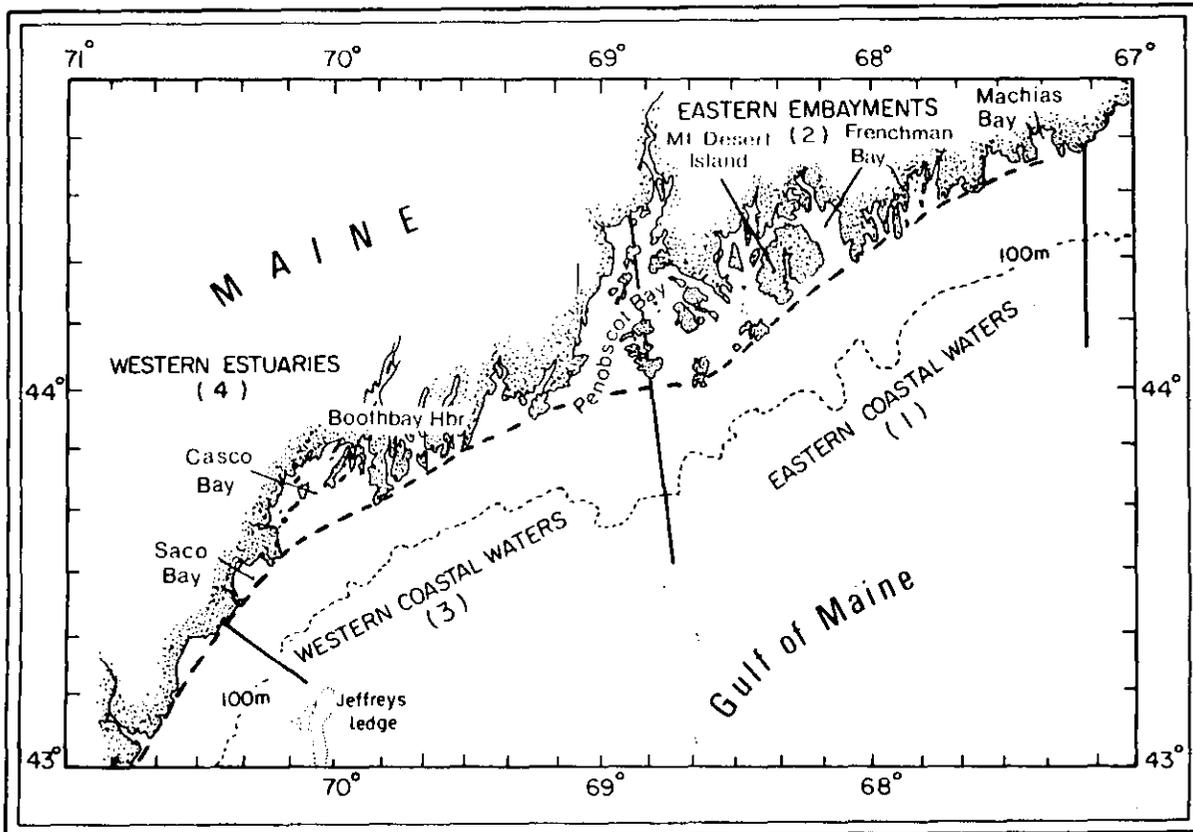


Figure 1. A map of the Maine coast showing the four model cells numbered 1 through 4. Estuarine ecosystems are separated from the coastal ecosystems by the dotted line along the headlands.

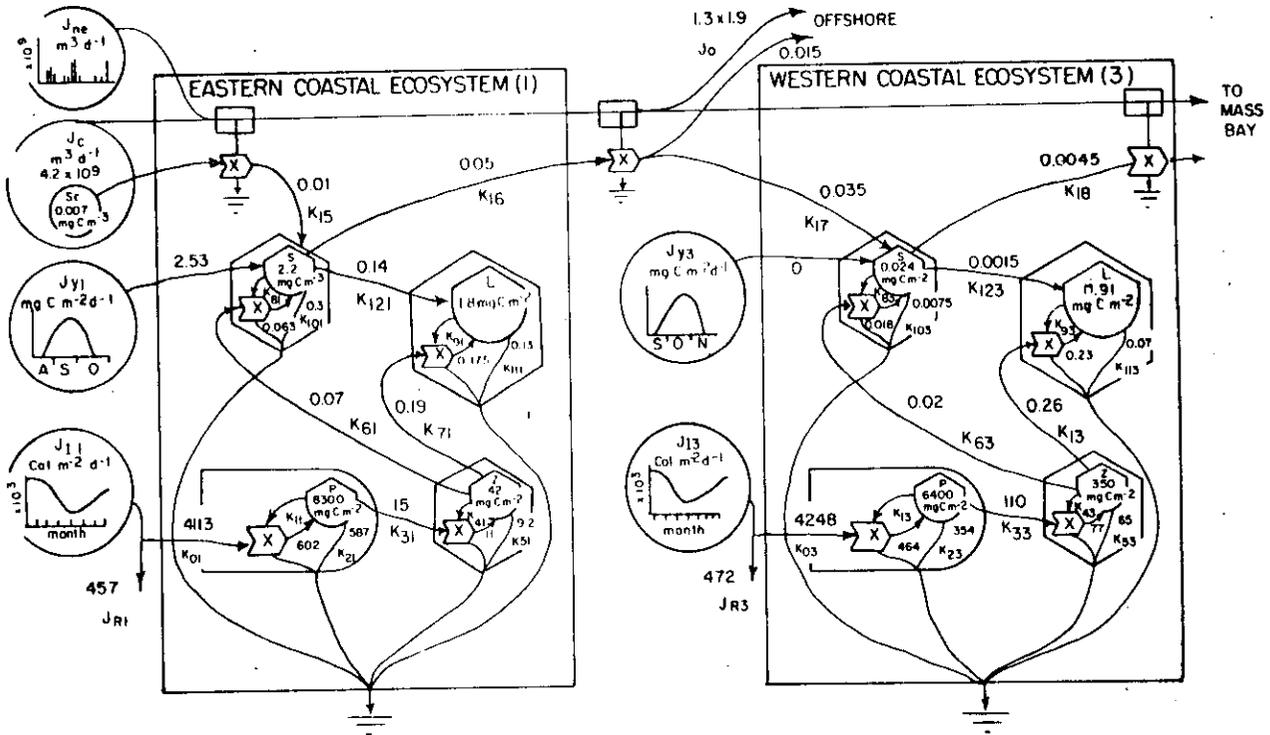


Figure 2. An evaluated energy circuit model showing the coastal ecosystems linked through longshore transports.

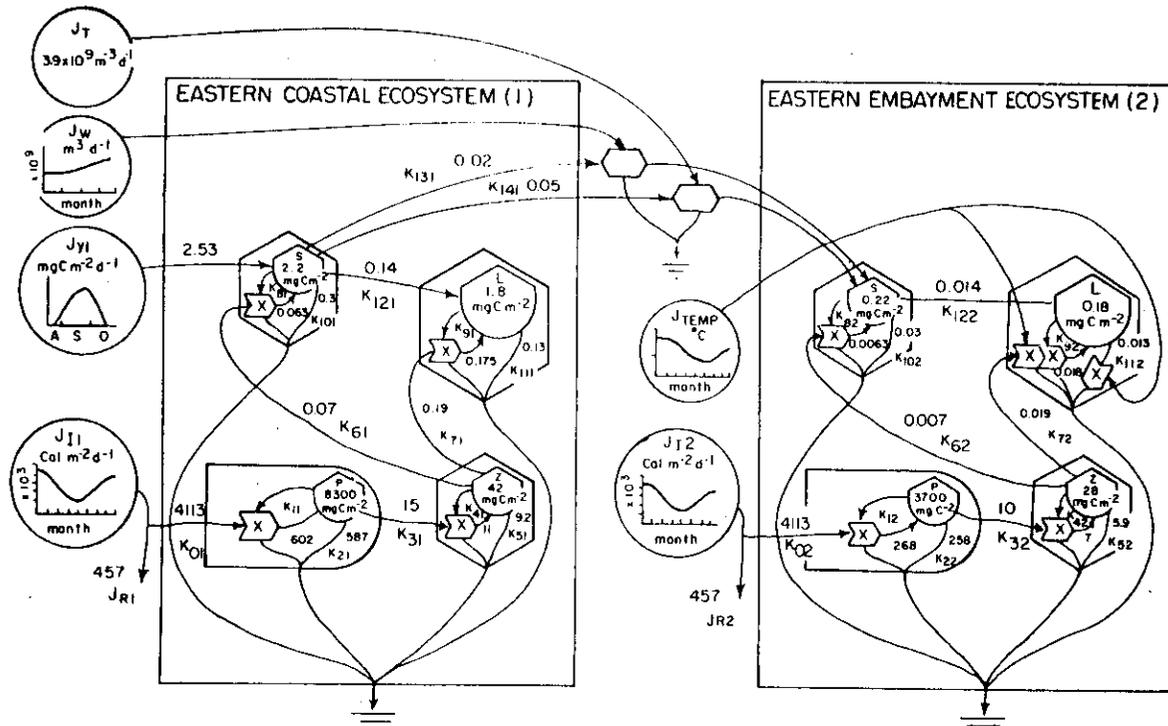


Figure 3. An evaluated energy circuit model which shows the eastern coastal and embayment ecosystems and the physical processes which link them.

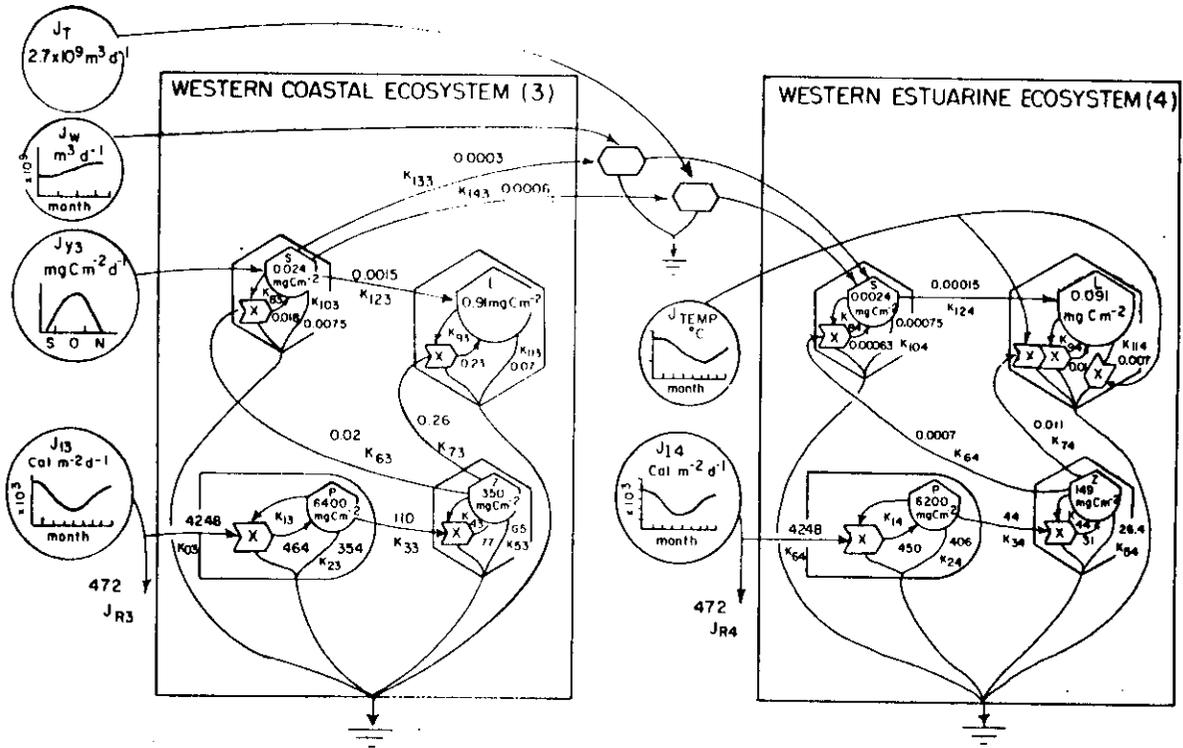


Figure 4. An evaluated energy circuit model which shows the western coastal and estuarine ecosystems and the physical processes which link them.