ment, but there is one specifically lagoonal feature. As they are often used for aquaculture and yields are generally related to primary productivity, lagoonal waters are frequently deliberately enriched to boost catches. Such enrichment varies from domestic organic wastes from the surrounding communities to commercial processed fish foods. Probably in the majority of such cases, however, the result of this nutrient injection has been eutrophication, loss of macrophytes, deoxygenation, and in several areas a change in the primary producers in the direction of a bacteria-dominated plankton and, across wide areas, benthos as well. In Mediterranean France, this all too frequent state of affairs is known as 'malaïgue'. Culture of mussels in the Thau Lagoon in France produces an input to the benthos of some 45 000 tonnes (dry weight) of pseudofecal material. Not surprisingly, at times of minimum throughput of water, malaïgues can cause mass mortality of the cultured animals and degradation of the whole habitat. Thus in Europe, malaïgues in the south, pollution in the Baltic lagoons (**Table 3**), and reclamation of those on the Atlantic seaboard have rendered the habitat especially threatened even at a continental level. For this reason they are now a 'priority habitat' under the European Union's Habitats Directive. Intensive lagoonal aquaculture also injects not only nutrients, but antibiotics, hormones, vitamins, and a variety of other compounds, and the wider effects of these are giving cause for concern.

See also

Crustacean Fisheries. Demersal Fishes. Eels. Eutrophication. Geomorphology. Macrobenthos. Mangroves. Molluskan Fisheries. Pelecaniformes. Phytobenthos. Primary Production Distribution. Salt Marshes and Mud Flats.

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LAGRANGIAN BIOLOGICAL MODELS

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Introduction

The Swiss mathematician Leonhard Euler (1707–1783) derived the formulations for describing fluid motion by either measuring the properties of the fluid at a fixed point over time or alternatively following the trajectory of a parcel of fluid as it is carried with the flow. The first of these is known as the Eulerian description of the flow, while the method following a material parcel or particle is known as the Lagrangian description after the French mathematician Joseph Lagrange (1736–1813). Most of the theory used to model ocean currents is posed in an Eulerian frame because of the difficulties in solving the momentum equations in the complicated matrices that arise in the Lagrangian form of the equations. However, it is often useful to use the Lagrangian frame of reference when considering the manner in which mixing occurs in turbulent flows such as those found in the oceans. It is also common to measure these flows by using drifters or floats that trace out oceanic currents. As shown below, the Lagrangian description is also conducive to handling models of marine populations in many cases. This is especially true when the models include quantities that structure the population, such as age, genetics, or physiological traits that depend upon the history of individual organisms that are carried in or swim through oceanic flows. Organisms that drift freely with the currents are termed planktonic, while those that can swim effectively are termed nektonic fauna. Here Lagrangian methods for considering populations of both plankton and nekton are given. Much f the detailed formalism can be found in Okubo (1980) (*see* Further Reading). The present discussion highlights the application of these methods to marine population dynamics.

Comparing the Eularian and Lagrangian Formulations

To understand the difference between the Lagrangian and Eulerian formulations, consider the population dynamic equations for marine organisms. If the *i*th population is made up of N_i individuals, one can write an equation for each individual. This will include each organism's position, $X_{\mathrm{m}}(t)$, as a function of time t. The total, or Lagrangian, derivative of $X_{\mathrm{m}}(t)$ with respect to time, $\mathrm{d}X_{\mathrm{m}}/\mathrm{d}t$, gives the individual's velocity, $\mathbf{V}_{\mathrm{m}}(t)$. This can be separated into the influence of the advection of the organism by ocean currents, $\mathbf{U}(X_{\mathrm{m}}, t)$, and a swimming contribution, $\mathbf{U}_{\mathrm{s}}(X_{\mathrm{m}}, \mathbf{B}, t)$, where $\mathbf{B}(X_{\mathrm{m}}, t)$ is a vector of behavioral clues. These clues involve both physical and biotic components of the environment. The acceleration of the individual organism is then derived by carrying out another differentiation in time (eqn [1]).

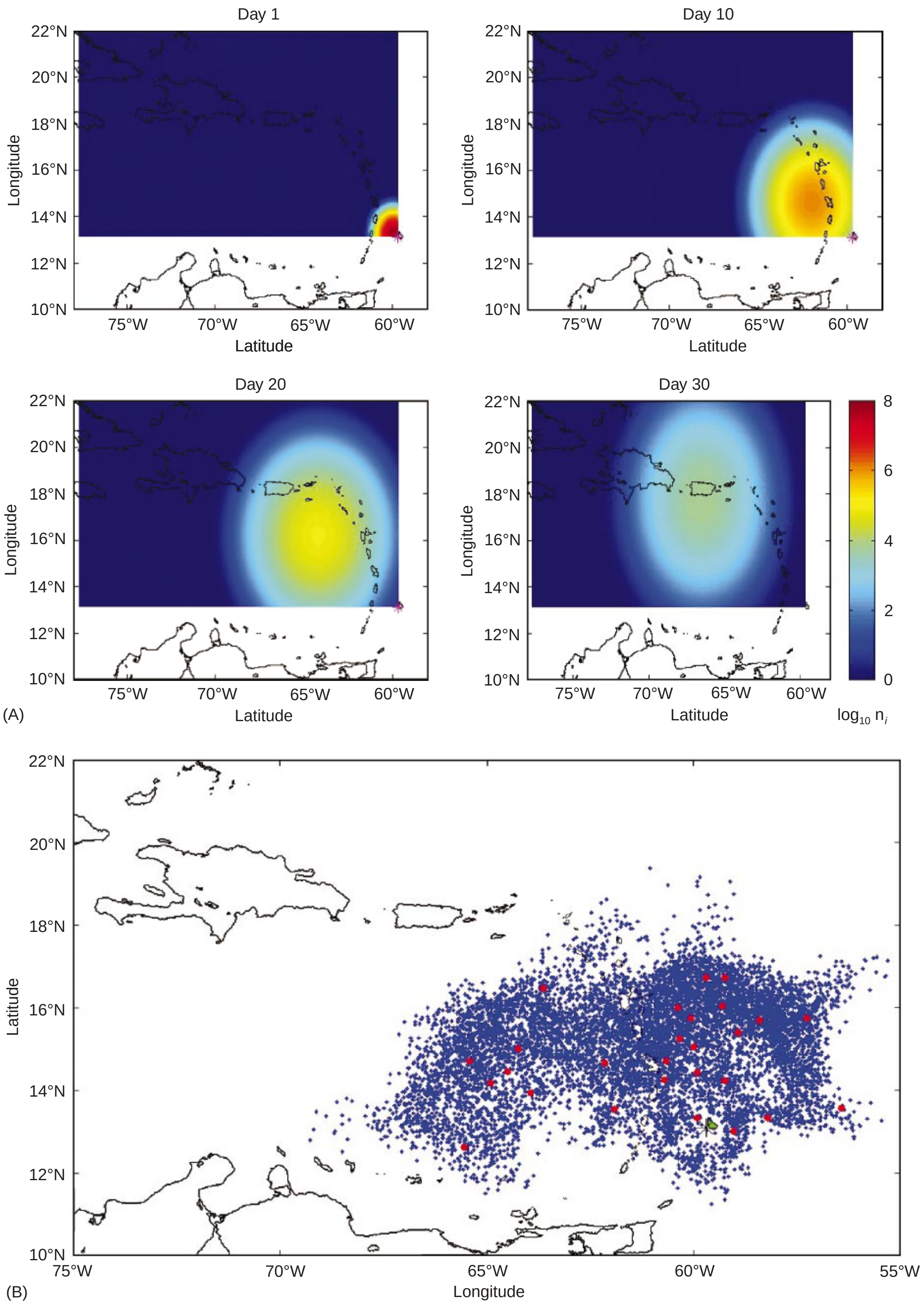
$$\frac{\mathrm{d}\mathbf{V}_{\mathrm{m}}}{\mathrm{d}t} = \frac{\partial \mathbf{U}}{\partial t} + \frac{\partial \mathbf{U}_{\mathrm{s}}}{\partial t} + \mathbf{U}\bullet\nabla\mathbf{V}_{\mathrm{m}} + \mathbf{U}_{\mathrm{s}}\bullet\nabla\mathbf{V}_{\mathrm{m}} = F(\mathbf{B}) \quad [1]$$

∇ is the spatial gradient operator and F is the gravitational and viscous forces imposed on the organism as well as behavioral responses, i.e., swimming. Notice that the Lagrangian derivative on the left leads to a set of Eulerian terms that involve spatial gradients in the fluid velocity and the behavioral clues on the right side of the equation. This equation fully expresses the motion of an individual. To the equation describing the organism's motion, a set of state relations must be added expressing changes in its physiological state, its age or stage, and the probabilities of its death and reproduction to explain population dynamics. Such a model considering the conditions of each individual explicitly in a population is called an individual-based model (IBM).

Individual-based models provide a method for understanding behavior and small groups of organisms as discussed below. For large populations, however, the number of equations involved becomes impossible to handle. It is therefore common to introduce the concept of organism density, $n_i = N_i/A$, where N_i is the number of individuals and A is a given areal measure. The density of the *i*th taxon is then measured in numbers per square kilometer of ocean surface area. This leads to a continuous spatial field equation. It is typical to consider the mean field of population density and perturbations about it so $n_i = \langle n_i \rangle + n_i'$. Here the first term is the mean population density and the second the perturbations (or variance) about the mean; the mean is over the population. The same separation can be done for the velocity components such that $\mathbf{U} = \langle \mathbf{U} \rangle + \mathbf{U}'$ and $\mathbf{U}_{\mathrm{s}} = \langle \mathbf{U}_{\mathrm{s}} \rangle + \mathbf{U}_{\mathrm{s}}'$. Equation [1] above involves products of velocity components with each other such that the contributions to the mean motion of the population and therefore its average spread will involve both the mean velocities and correlations between velocity perturbations. In the field equations these correlation's between fluctuations in the turbulent fluid velocity or swimming behavior will lead to turbulent and behavioral diffusion. It is typical to introduce diffusivities, K for the turbulence and K_{s} for the behavioral related dispersion. There is also a correlation between the variations in the environmental factors, including the distance to members of the same species that come into effect given $\mathbf{B} = \langle \mathbf{B} \rangle + \mathbf{B}'$. The resulting field equation for the expected mean density of an organism is then given by eqn [2].

$$\frac{\mathrm{d}n_i}{\mathrm{d}t} = \frac{\partial n_i}{\partial t} + \mathbf{V}_m\bullet\nabla n_i = F(\mathbf{B}) + \nabla[(\kappa + \kappa_{\mathrm{s}})\nabla n_i] \quad [2]$$

The κ are inside the spatial gradient operators to denote that they are functions of space. Taking the κ_{s} term all the way inside the ∇ operators allows density or schooling effects on population density


Day 1
Day 10
Day 20
Day 30
22°N
20°N
18°N
16°N
14°N
12°N
10°N
75°W
70°W
65°W
60°W
Latitude
Longitude
8
6
4
2
0
$\log_{10} n_i$
(A)
55°W
Longitude
Latitude
(B)

through behavioral preferences for nearest neighbor distance. The results of the field model versus the Lagrangian model following individuals can lead to impressive differences (**Figure 1**).

The diffusion model in **Figure 1A** using the equations above lead to a finite probability of finding organisms everywhere in a domain immediately. The Lagrangian treatment limits an organism's spread to the fastest velocities present, so that it takes a finite time for spread. It is important to note, however, that there must also be population losses that are more abrupt than simple exponential decrease of the population across habitat boundaries. This occurs in most population parametrizations such as a logistic growth with linear mortality to achieve realistic population distributions. In the real ocean, while it takes much longer than in the analytical diffusion model, the Lagrangian motions will still lead to a finite possibility of finding organisms everywhere in the domain at large timescales, unless mortality is properly treated.

Simple Models in the Lagrangian Frame

The most important issue in modeling marine populations is providing an accurate depiction of the physics, the biology, and the intricate biological/physical interactions that occur. These are represented in the equations above by mean quantities acting on means or perturbations and then by correlations between both physical and biological perturbations. One use of the Lagrangian description of motion is to simulate these interactions along a fluid trajectory in the case of the plankton (**Figures** 2 and 3). In this case a simple meandering current and its impact on populations is envisioned. The calculation involved is a simple integration that in **Figure 2** reveals the basic response without biological nonlinearities. In **Figure** 3 the impact of a primary production response as seen in **Figure 2** on a density-dependent population conceals a set of more interesting patterns, including extinction. The situation in **Figures 2** and 3 involves dynamics that allow exact calculations, i.e, in this case simple integrations of the functions without any use of numerics. This sort of analysis is recommended for testing more complicated cases where numerical methods become a major issue. Essentially these simple applications use the Lagrangian frame of viewing advection as a means of allowing simple calculations of population dynamics. The Lagrangian frame becomes indispensable when structured populations are considered.

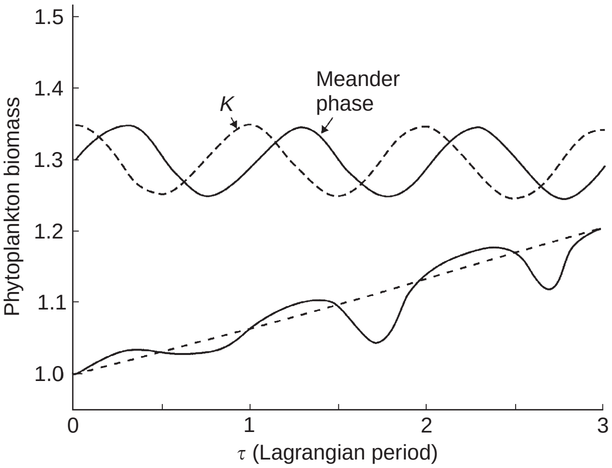


Figure 2 Response of phytoplankton to a simple meandering current. The meander is assumed to set up a simple sinusoidal series of upwelling (high) and downwelling (low) at meander crests and troughs, respectively, that provide nutrients upon the upwelling phase. The model assumes logistic phytoplankton response to a sinusoidal carrying capacity (K) and is solved analytically by simple integration of the Lagrangian equation in time. The forcing function involves linear response to a cosine shown in the figure.

Simulations of Populations with Demographic Structure

The Lagrangian description of the path that biological entities follow through the ocean environment becomes the only feasible method for treating population dynamics where the detailed history of the populations' interaction with the physical environment and other populations are important. Early works in this area include the plankton models of Wolf and Woods following the details of mixed layer and thermocline development in the

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Figure 1 **(Left)** (A) Simulation of larval reef fish drift from Barbados using the mean flow into the eastern Caribbean and a κ of $5000\,\mathrm{m}^2\,\mathrm{s}^{-1}$ at 1, 10, 20, and 30 days after spawning. A typical larval mortality rate $\mu = 0.2$ (or ~ 18% per day) is applied to larval abundance (N_i). (B) Lagrangian simulation of the same case with trajectories computed from an oceanic general circulation model at day 30 (Cowen *et al.*, 2000). The survivors are indicated by red dots after applying the same $\mu = 0.2$. Note that none are on suitable island habitat after 30 days. For the diffusive case (A) there is a finite probability of finding larvae well beyond the range of any of the simulated trajectories. In this case the mortality is truncated by the 30-day duration of planktonic behavior in the fish's assumed development, i.e., after this time there is assumed recruitment to an island or death.

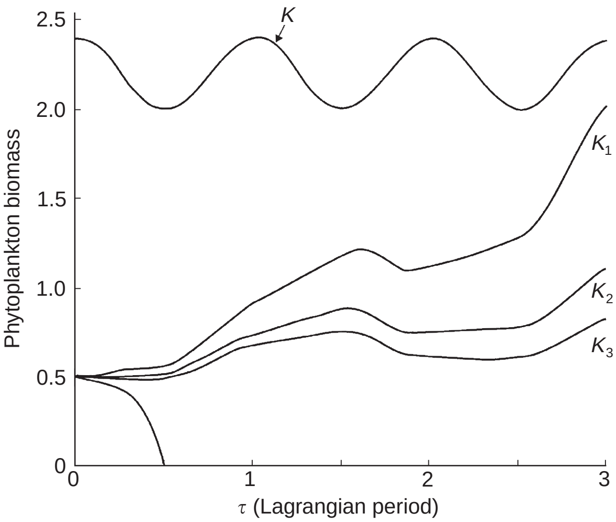

Figure 3 A calculation of the zooplankton response to the phytoplankton distribution in a meander like that treated in **Figure 2**. Here the integration in time along trajectories is slightly more complicated but still analytical. The zooplankton response is parametrized by a Hollings type 2 curve such that the time dependence of zooplankton (*Z*) is governed by the equation below.

$$\frac{dZ}{dt} = r\frac{ZP}{K_0 + P} - dZ$$

Here *r* is a growth rate, *P* is the sinusoidal phytoplankton field, K_0 is a half-saturation term, and *d* is the death rate for *Z*. The pattern of the carrying capacity, *K* is shown at the top of figure. Four different *K*s are shown with different magnitudes K_1–K_3 and fourth that goes extinct. See Olson and Hood (1994) and the literature cited there for further discussion of meander impacts on marine ecosystems.

North Atlantic over many seasons and the work on zooplankton in the coastal environment by Hoffman *et al.* The problem becomes that the Lagrangian frame (i.e., following individual trajectories of individuals or individual subpopulations) is the only way to track the biological dynamics where the past history plays a major role in determining the present dynamics. These historical parameters may involve the past history of nutrient or forage availability, the temperature and salinity encountered over the development of the organisms, or the past history of selection on the genetic structure of populations when reproduction occurs.

As an example of a structured population simulation in a turbulent ocean gyre, a simulation of a population of physiologically and genetically structured pelagic copepods is described. The population is based on the properties of *Nanocalanus minor*, a copepod found in the subtropical gyre in the North Atlantic. The model is designed to consider the dynamics behind the mitochondrial DNA patterns found in this population in the Gulf Stream. The Gulf Stream and its recirculation gyre are treated as a circular flow with superimposed turbulence. The copepods are simulated as subpopulations, each carried on Lagrangian particles advected in this flow. The populations are subject to a carrying capacity, $K = K_0 + K' \sin(\theta/2)$, that is high in the northern Gulf Stream and low in the oligotrophic southern portions of the gyre. The population has variable growth rates that are controlled genetically. The growth potential is determined by the statistics of the local breeding subpopulations and by selection induced by competition at a given location and time for food.

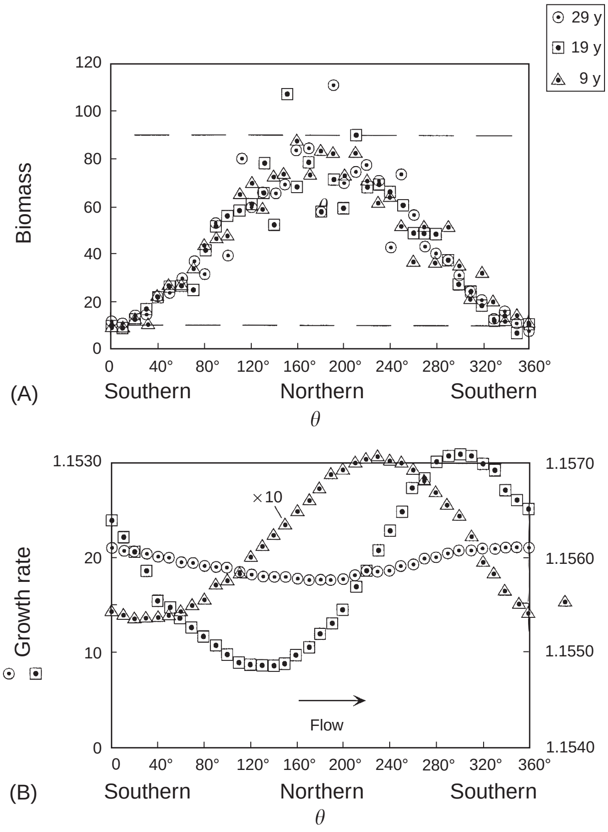

Figure 4 (A) Biomass of copepods per m^2 of surface area as a function of distance (θ) around the gyre, at 10-year intervals. Gyre circulation time is 3 years. The carrying capacity at the northern and southern ends of the gyre are indicated by dashed lines. Note that mixing can cause a region to exceed the carrying capacity. The variation in populations is largest at the highest carrying capacity. (B) The mean growth rate (biomass per day) in different segments around the gyre at the three times. The scale at 9 years is 10 times that for the later times (scale at right). Growth rate is going slowly to a constant or fixed state as expected from population genetics grounds. The distribution of growth rates matches the cosine nature of the carrying capacity distribution, but is fully advective in the sense that these patterns advect with the mean flow around the gyre. The direction of this drift is indicated by an arrow.

Selection is local since there is not an optimal growth rate in the sense that it pays to have a high reproductive potential in the northern gyre under low population densities. The offspring of such a population are inevitably at a disadvantage, however, when advected into the southern oligotrophic reaches of the gyre. Since the resulting genetic and physiological attributes at a location depend upon the past history of all of the subpopulations contributing to the interaction at a given time, this sort of simulation becomes computationally impossible in a Eulerian frame. The population distributions in **Figure 4**, done in a Lagrangian simulation, takes only an hour on a laptop computer. The details of a suite of such simulations are currently being compared to population density and gene sequences.

Conclusions

The use of Lagrangian particle-following simulations in modeling population dynamics allows several advantages over Eularian fixed-grid calculations. For simple models the advantage is that the population equations can be simply integrated in time. As new techniques for tracking fluid parcels and therefore planktonic trajectories or individual large pelagic fish or whales become more available, models using real trajectories will become possible. The other advantage that direct Lagrangian simulation of turbulent dispersal of organisms has is that it overcomes the problems that advection/diffusion schemes have with population densities at large distances from their source. Finally, the largest promise in Lagrangian simulations is their use in models that explicitly treat the demographic traits of populations. With the ever-increasing realism in physical models of the marine environment and Lagrangian population models, new insights into marine population dynamics are possible.

See also

Plankton Viruses. Population Dynamics Models.

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LAND–SEA GLOBAL TRANSFERS

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Introduction

The interface between the land and the sea is an important boundary connecting processes operating on land with those in the ocean. It is a site of rapid population growth, industrial and agricultural practices, and urban development. Large river drainage basins connect the vast interiors of continents with the coastal zone through river and groundwater discharges. The atmosphere is a medium of transport of substances from the land to the sea surface and from that surface back to the land. During the past several centuries, the activities of humankind have