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Recruitment Processes and Ecosystem Structure of the Sea

A Report of a Workshop

Prepared for the
Ocean Studies Board
Commission on Physical Sciences,
Mathematics, and Resources

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This report has been reviewed by a group other than the authors according to procedures approved by a Report Review Committee consisting of members of the National Academy of Sciences, the National Academy of Engineering, and the Institute of Medicine.

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In April 1985, the Ocean Studies Board requested NRC program initiation funds to enable the academic community to explore a program in recruitment processes (the factors controlling the variability in successive generations of marine animal populations). The rationale for this request was to examine the feasibility of a research initiative on this subject first identified in the long-range plan of the Advisory Committee of the Ocean Sciences Division of the National Science Foundation. The first Panel chaired by John Steele was convened in June 1985. Several informal meetings were subsequently held culminating in a second Panel meeting in August 1986, chaired by Brian Rothschild and Michael Mullin, at which this document was prepared.

We would like to acknowledge individuals who have participated in regional meetings or who have corresponded with us. The good points in this work owe to the contributions of our colleagues. These include Robert Carney, Louisiana State University; Michael Dagg, Louisiana Universities Marine Consortium; Darryl Felder, University of Southwestern Louisiana; John Fleeger, Louisiana State University; Scott Holt, University of Texas; Donald Hoss, National Marine Fisheries Service, Beaufort; Tom Leming, National Marine Fisheries Service, Pascagoula; Harriett Perry, Gulf Coast Research Laboratory; James Power, Louisiana State University; Nancy Rabalais, Louisiana Universities Marine Consortium; Richard Shaw, Louisiana State University; Joanne Shultz, Gulf Coast Research Laboratory; John Steen, Gulf Coast Research Laboratory; Eugene Turner, Louisiana State University; Richard Waller, Gulf Coast Research Laboratory; William Wiseman, Louisiana State University; Larry Atkinson, Old Dominion University; William Boicourt, University of Maryland; Michael Sissenwine, National Marine Fisheries Service, Woods Hole; Michael Roman, University of Maryland; Edward Houde, University of Maryland; Guritno Roesijadi, University of Maryland; Richard Strathmann, University of Washington; Warren Wooster, University of Washington; and Paul Smith, Southwest Fisheries Center, La Jolla, California.

EXECUTIVE SUMMARY

Over the last century, numerous changes in the species composition of the marine ecosystem have been recorded. The species involved often made up important components of the human food supply or species of fish and invertebrates eaten by the food fish. The economic and societal impacts of ecosystem change can be considerable, particularly inasmuch as the variation in species abundance could be driven by anthropogenic factors. As a consequence, the benefits that could accrue from an ability to understand and predict major changes in the abundance of marine organisms, and their ecosystems, on interannual and decadal time scales would be substantial. To push toward such an understanding, and to take advantage of the opportunities for disciplinary synthesis and cooperative programs, will require scientific planning for a coherent program on "Recruitment Processes and Ecosystem Structure --Biodynamics of the Sea" to begin now with the intent that the program be fully operational in the 1990s.

In developing the scientific plan, consideration needs to be given to the importance of recruitment processes, significance of global scales, coordination of effort, scales of studies, study locations, study organisms, the need to incorporate new tools, and the development of theory and models. The following observations arose from the workshop discussions.

1. Importance of Recruitment Processes. Since most marine animals share the common strategy of producing hundreds to millions

of offspring, the vast majority of which are bound to die before they mature, recent research on population dynamics has focused attention on early life history stages and the variability of their recruitment to adult stocks. Attention must be focused on the biological, chemical, and physical dynamics of the oceans that control recruitment processes and, in turn, ecosystem structure.

2. Significance of Global Scales. Ecosystem structure and recruitment processes must be considered globally because they are driven, in part, by the complex dynamic interactions of global atmospheric/ocean processes. The time is now ripe to begin to plan for this effort because planning is rapidly advancing for global programs and tools whose products should directly feed into the data base for regional recruitment process studies. These include the World Ocean Circulation Experiment (WOCE), the Tropical Ocean Global Atmosphere (TOGA) program, Global Ocean Flux Studies (GOFS), and the new generation of ocean color satellite sensors. The global effort would need to relate to the interaction between aquatic and terrestrial studies.

3. Coordination of Effort. The time is also ripe to advocate the involvement and leadership of U.S. academic ocean scientists in this effort. Recruitment dynamics is a major thrust proposed in the long-range plan of the Advisory Committee of Ocean Sciences Division of the National Science Foundation (NSF) and endorsed by the Ocean Studies Board. It has become important to the goals of federal agencies such as the National Oceanic and Atmospheric Administration

(NOAA) --including National Marine Fisheries Service and Sea Grant-- and the National Aeronautics and Space Administration (NASA) --as expressed in their new Earth Systems Science Initiative-- both nationally and in international organizations. In addition, there are opportunities for coordination with other national programs specifically oriented toward recruitment (e.g., Programme National sur le Determinisme du Recruitement [FNDR] and Institut Français de Recherche pour L'Exploitation de la Mer [IFREMER]).

4. Scales of Studies. Recruitment process studies will focus most profitably on the important components and dynamics of readily identifiable ecosystems, such as the examples outlined (Georges Bank, etc.), and will be directly concerned with fine scales (individual animals/turbulence) to mesoscales (breeding populations/eddies, fronts, etc.). It will be necessary to incorporate input from global and basin-scale atmospheric/ocean phenomena provided by other major global change programs (WOCE, TOGA, GOFS).

5. Study Locations. Most of the studies envisioned center on coastal oceans, where biomass and economic activities are concentrated, as opposed to the deep ocean basins. These studies will be intimately associated with the projected studies of coastal ocean dynamics, fluxes, and sediment transport, which are beginnning to be discussed in many federal agencies and academic forums.

6. Study Organisms. It is important to emphasize consideration of benthic and water column invertebrates, as well as fish populations. The structure of marine ecosystems is the manifestation of

the outcome of countless predator-prey interactions, most of which involve early life history stages of species at all trophic levels. This approach will assure the eventual development of an overall theoretical framework.

7. The Need To Incorporate New Tools. We advocate major investment in the variety of promising new technologies in environmental sampling and real-time analysis of densities of species by age and reproductive category that are emerging in biological oceanography, and the integration of these technologies with those of ocean physics and chemistry. The rapid application is foreseen of the powerful new tools being developed in the disciplines of molecular biochemistry and population genetics.

8. Theory and Model Development. A long-range effort is necessary to develop a new, comprehensive theoretical base linking ocean ecology, chemistry, and physics (biodynamic theory), designed to take advantage of the evolving atmospheric/physical oceanography models and the supercomputational power rapidly becoming available to academic scientists. The goal is to link physical and biological components in a new generation of models leading towards efficient and effective capabilties to predict animal population changes in the ocean.

INTRODUCTION

Numerous questions of scientific and societal significance regarding oceanic and coastal marine ecosystems and the way that they will be affected by human activity are stimulated by the long- and short-term variability in marine-populations. For instance, will the production of fish and zooplankton change in the next century as a function of changes in the physical environment, habitat modification, climate change, pollution, and resource-harvesting policies? Can the effects of changes in the ocean's biota for various decadal-length scenarios on climatic variability be observed and predicted? Is it possible to predict the population explosions such as that observed for a sardine off Japan or the triggerfish off much of the west African coast? Is it possible, likewise, to predict the sudden population collapses such as those experienced by herring, oyster, scallop, and crab populations? Can we explain and predict the dramatic changes in entire ecosystems as exemplified by the "gadoid outburst" or the Russell cycle in the North Sea? How can we explain the long-term changes in the abundance of major copepod populations in the North Atlantic?

These questions are examples of those being addressed on a daily basis by scientists and decision makers. Unfortunately, because the questions are broad in scope and complex, clear answers are not as yet available despite their importance and despite the existence of relevant knowledge in population dynamics, population biology, and physical oceanography.

The panel believes that answers could emerge through a coherent long-term program that would (1) create a data base to test extant concepts and facilitate creation of new hypotheses, (2) create and extend theory to account for changes in population abundance as a function of both population density and the physical environment, and (3) interrelate relevant disciplines.

The substance of a coherent long-range program requires developing a predictive understanding of the mechanisms that regulate or otherwise affect reproductive success and, hence, population variability. The mechanisms involve predator-prey trophic relations and the way that the physical environment affects contact between predators and prey, the efficiency of predation, and the transformation of ingested prey into either reproductive or somatic biomass or catabolites.

Insights into these mechanisms require (1) enhancing our understanding of submesoscale physics, scales that appear to be most relevent to the trophic transactions among the organisms, (2) developing techniques to rapidly measure population densities of selected predatory and prey organisms, (3) assessing the physiological status of predator and prey to determine the effects of physical variability and population density upon trophic relations and reproductive capacity, and (4) developing techniques to determine changes in population genetic structure that could influence longer-term changes in population response to environmental change, this last being particularly essential to understanding the influence of climate-scale events upon population dynamics.

Many theoretical building blocks are accessible, and requisite observational techniques are defined and ready for intensive development. The integration of these building blocks and the undertaking of the observations necessary for theoretical enrichment will require a long-term effort, which can only be successful in a framework of a coherent program.

In considering such a program, it is appropriate to take account of the historical background of the study of recruitment processes, which is rooted in the late nineteenth century study of fisheries. Oceanographers began to investigate the causes for large interannual variations in the production of fish in the "great fisheries of Northern Europe." At that time, large fluctuations in fish-population abundance were related to the survival of very young fish born in each population, each year, and as these young fish would eventually be "recruited" to the adult population, the term <u>recruitment</u> came to be used to represent the number of young fish produced each year.

In the early years of recruitment research it was believed that fish recruitment variation depended on variations in larval feeding success or the advection of larvae into favorable or unfavorable environmental conditions. For many years, recruitment research seemed to concentrate on relatively intense surveys of ichthyoplankton abundance and field and laboratory studies of larval fish nutrition (see, e.g., Lasker and Sherman, 1981). However, it was realized only recently that the scope of these studies was too narrow and that consideration needed to be given to the more general subject of larval predators; the influence of larval nutrition and predation on population dynamics; and the effects of the physical structure of the sea on the population dynamics of the organisms of concern (Rothschild and Rooth, 1982).

In taking account of the major changes in populations and ecosystems, even this view seems too narrow. To address natural and anthropogenic causes of population variability it is necessary to attribute variability to a complex of specific causes. Because variability would not likely be attributable solely to phenomena associated with any single species, an understanding of the dynamics of species assemblages is required. Thus, the study of recruitment has evolved into the study of a much broader range of issues: the dynamics of a spectrum of marine populations (and not necessarily the fate of a particular life history stage); the linkages among populations; and the effects of the climate, the weather, and the physical structure of the sea on these relationships. It involves production ecology, population dynamics and biology, and ocean physics.

If studying of these processes were just beginning, the task would be formidable indeed. However, many major components of the problem are well known and define a structure that helps specify the nature of the relationships among the components and the particular areas that require intensified investigation. Once these inter-relationships are better explored, facilitation of research, even in areas that are relatively well known, can be better justified while areas that are less well known can be better identified and enhanced. For example, primary production, the population dynamics of fish, and mesoscale physics are relatively well known, while secondary production, the population dynamics of copepods, and the physics of turbulence are not well understood. The integration of biological, physical, and chemical oceanography demands interaction between biological, physical, and chemical oceanographers as the complexity of the involved processes is reflected by the different directions and time scales employed to address the various biological, physical, and chemical components.

Recent advances in oceanography serve to fortify the consensus that developing a program on recruitment processes and ecosystem structure--the biodynamics of the sea--is opportune. The consensus emerges from (1) conceptual and planning meetings held over the past several years (e.g., Fish Ecology I, II, and III); (2) initiation, continued implementation, and facilitation of national and international programs (United Kingdom, France, Norway, Denmark, Federal Republic of Germany, Japan, Spain, Netherlands, Australia, Poland, and the U.S.S.R.); (3) the accessibility of theoretical building blocks that can be used to tie together the population dynamics and population-biology studies with those of the physical and chemical environment; (4) the identification of various biological sampling techniques, which when given adequate funding could be used to fully implement acquisition of needed empirical data; and (5) the feasibility of making physical oceanography measurements on the sub-mesoscale range, not heretofore studied in detail.

Accordingly, this report recommends that the scientific planning of a coherent program, "recruitment processes and ecosystem structure of the sea," should begin immediately as theoretical and pilot studies and be fully implemented in the 1990s. This report describes the scope of the recruitment process problem, outlines an experimental framework, and concludes with specific observations on the societal significance of the problem.

THE SCOPE OF THE RECRUITMENT PROCESS PROBLEM

A working theory on recruitment processes would provide an explanation of the dynamics of the populations of the sea --the fluctuations in their abundance-- as well as the mechanisms that affect these increases and decreases.

Populations in the sea are for the most part statistically stable, which means that even though they fluctuate, they rarely increase at maximal rates for very long or become extinct. The statistical stability is maintained by strong feedbacks to increase populations when they are at low levels and to depress their growth at high levels of abundance. The stimulus for population increase is often related to the availability of food. Among the most simple interpretations, when a prey population is at a high level of abundance, its predators increase in abundance. In this context, predator-prey ratios are implicated in the increase or decrease of predator and prey biomass, and the proportion of biomass partitioned into reproductive material. In turn, this influences the numbers of young produced by subsequent generations and sets in motion the processes that affect population variability.

The ratio of predator to prey density that affects predator-prey dynamics is not the actual ratio of predator to prey, but the ratio of predator to prey that is "apparent" to the predator and the prey. This apparent predator-prey ratio can be strongly affected by the physical environment (i.e., light, temperature, and motion). There are two kinds of effects, which will be denoted as Type I and Type II effects.

In the case of Type I effects, the physical environment affects the performance of prey and predator per se. For example, an increase in temperature usually affects the basic physiology of both predator and prey, making the predator more efficient at capture, or the prey more or less efficient at escape. For Type II effects, the physical environment affects the contact rate between predator and prey (e.g., through changes in the intensity of turbulence) and accordingly modifies the apparent predator-prey ratio. Hence, Type I and Type II effects influence the apparent density of predator and prey and the reproductive capacity of the population. While such a framework is important, it is also necessary to take into account longer term considerations, which basically involve those genetic changes in populations that affect the response of organisms to environmental variability. For example, the influence of temperature on basic physiological variables or the capability of predators to capture prey, or prey to elude predators, is not necessarily constant but a function, inter alia, of the genetic structure of each organism and each population. The nature of the dynamic process can be affected by genetic factors in each genetically identifiable subpopulation responding with differential reproductive success to environmental variation, therefore, making genetic variability an important potential component of population dynamic variability.

The conceptual arrangement that was described above is shown in Appendix A, fig. 1, (see page 41) linking physical variables and biological transformations (e.g., the transformation of a prey into predator biomass and in turn the eventual conversion of predator biomass into predator eggs). Observations to quantify theoretically established biodynamics would need to involve (1) the physics, (2) the densities of organisms, (3) the trophic and reproductive status of organisms as indicated by physiological measurements, and (4) the genetic structure of the population.

In order to sharpen our view of the conceptual arrangement whereby populations increase or decrease as a function of their food resources, the way in which the apparent densities of the food vary as a function of motion, light, and temperature may be explored in terms of (1) the theoretical building blocks, (2) the physical oceanographic perspective, and (3) the biological oceanographic perspective.

THEORETICAL BUILDING BLOCKS

Scientific opportunities are to be found in bringing together components of established theory in population dynamics, population biology, and physical oceanography. At the same time, opportunities to utilize observations of large-scale environmental variability derived from satellites and various biological and physical sampling devices are in the offing.

A particular example is the possibility of linking physical and biological theory, as in the opportunities that exist to link optimal foraging theory (Pyke, 1984) with physical processes. Optimal foraging theory is based upon hierarchical partitioning of energy of biomass among biological processes at the individual-organism level. In the individual, energy consumed is either assimilated or eliminated as feces. The transformation of food resources into reproductive products only occurs when the food resources consumed are sufficient to exceed basal metabolic needs. Hence the individual that forages in such a way as to yield the greatest net rate of energy gain will produce proportionally more progeny; selection should favor that foraging behavior which is optimal in terms of energy gain. This body of theory has the potential to tie together and focus studies ranging in scale from the capture of single food items to the selection of genotypes with differing foraging behavior. It has already been used to explain and predict both size of organisms in, and trophic structure of, aquatic communities as a function of their productivities (Gerritsen, 1984).

Foraging theory can be drawn upon to define the lower limit of time scales of interest in biodynamics and to suggest upper limits. At low food abundances, food encounter rate limits foraging, and the natural time scale is the inverse of encounter frequency. Above some threshold encounter rate, the kinetics of digestion and assimilation become limiting, and the natural time scale is that of the time to pass through the gut (Penry and Jumars, 1986). Encounter rate is not just set by density of prey and predator behavior, but is also influenced by small-scale fluid motions, temperature, and ambient light, providing an example of an important opportunity to link biological and physical processes in a biodynamic theory.

One can point clearly to the success of the meshing of fluid dynamics with the study of primary production. Just as with optimal foraging approaches, knowledge of mechanisms at the individual level allows powerful prediction at the population level. Advances in knowledge of photoplankton physiology and upper mixed-layer physical processes have now produced much more accurate models of the physical and biological controls on primary production. It is time to bring similar approaches to the study of secondary producers.

Foraging success is undoubtedly an important component of successful recruitment, but it is not the sole determinant. Foraging theory has been modified (Pyke, 1984) to incorporate simultaneously the risks and potential gains of foraging in the presence of predators. A more inclusive approach, of which foraging theory could be considered a subset, is game (or risk-benefit) theory (Maynard, et al, 1973), where success is measured in terms of the strong constraint of progeny (i.e., reproductive fitness); a heritable behavior that results in the leaving of no progeny will quickly disappear. The approach links individual behavior (foraging) with environmental variables and genetic consequences. Application of such theory is usually aimed at defining Evolutionarily Stable Strategies (ESSs) toward which a population is predicted to evolve in the context of its physical and biological (including both predators and competitors) environment. In evaluating the adaptive value of vertical migration, a game theoretic approach might, for example, balance risks of expatriation due to vertical shear with benefits of predator avoidance.

Dispersal of planktonic larvae of benthic macrofauna has been examined from such a risk-benefit standpoint, and mechanisms for altering the extent of dispersal have been identified (e.g., Strathmann, 1974; Jackson and Strathmann, 1981). Several apply equally well to dispersal of holoplankton. These mechanisms (e.g., adjusting vertical distribution variance or spreading release time among members of a given brood) interact explicitly with the advective-diffusive structure of the ocean, and the models thus suggest a suite of linkages between environmental conditions and recruitment success. To date, such models have been used primarily with parameterizations of mean physical conditions for classes of environments. It would be informative to incorporate spatially and temporally varying conditions as measured with the latest instrumentation in mesoscale and microscale physical oceanography. Important issues involve the probabilities both of expatriation (outside environmental tolerances) and of exchange among patches with varying prey and predator abundances.

EXTENDING THE UTILITY OF OUR PHYSICAL UNDERSTANDING OF THE SEA

The utility of our physical understanding of the sea has been demonstrated in describing the vertical and horizontal structure of the ocean, the dynamics of both large and mesoscale events, and the relation between the ocean and atmosphere, for example. Of all the possible areas of application, one of the least known and perhaps one of the most fertile for inquiry involves the dependence of population dynamics upon the physical structure of the sea. Despite the dependence of population dynamics upon the physics, there are a number of questions purely in the physical realm that need to be addressed before questions of interaction can be pondered. These questions relate to the kinematics of particles as abstract representatives of living organisms or biologically active particulate matter, because, as explained previously, the contact rates among particles govern the trophic interactions, which in turn govern reproductive success and drive population-dynamic variability.

With regard to understanding the distribution of particles both as biological and as kinematic abstractions, our concern in the biodynamic context involves our abilities to describe and understand kinematic and other physical properties on scales pertinent to planktonic trophic and dispersive relations. These include the scales over which plankton are horizontally advected "over the ground" and scales that involve the position of plankton relative to one another, which thus affect their encounter rate and hence their foraging success. Put another way, we are concerned with the effect of environmental kinematics on the maintenance or dissolution of patches of organisms, the relative position of the patches, and the relative positions of the organisms in the patches.

The appropriate space and time scales appear to range downward spatially from the mesoscale and temporally, from weeks to days or less. The lower bounds of the range depend upon the particular organisms of concern. Great progress has been made in modeling mesoscale motions in the coastal ocean. Although studies of the interaction of plankton with the small-scale physical environment are few, laboratory and in situ techniques are available, and a concerted effort could produce a suite of models testable by field studies. Recent advances in observational techniques for measuring kinematics on small to microscales have allowed improved resolution in the vertical relative to the horizontal.

The simultaneous measurement of physical (including optical) and biological variability has been accomplished in a few recent experiments such as ODEX and BIOWATT. These studies have concentrated variously upon questions concerning temporal and spatial variability in particulate matter and optical properties (the latter program concerns primary productivity as well). However, no comparable studies have addressed the problems of secondary productivity or larval recruitment of particular species. Furthermore, there are currently few (if any) data concerning the four-dimensional (space and time) variability of physical and biological parameters on horizontal scales ranging from a few meters to 50 km. The relevant spatial and temporal scales for physical processes in relation to biodynamics are illustrated in Figures 2A and 2B (see pages 42 and 43) and are highlighted in Appendix B (see page 41).

To fully evaluate the biophysical interactions, we need to know the probability of a patch of predators coming within "striking distance" of its prey. Since "striking distance" will vary with the motility and perceptive capabilities of the predator, we need to resolve different scales for different species interactions. We expect that the appropriate scales range from about 1 m or less up to about 10 km (large patch size). At this time, we still do not understand what range of scales is actually important, especially at the small-scale end. An intensive biological modeling effort will be required (given substantial kinematic and physiological input) to resolve these questions. The crucial measurements to obtain will be four-dimensional estimates of the velocity deformation field, which will contribute to the determination of encounter frequencies on time scales of seconds to about one day. The approximately 10 km and downward range of horizontal spatial scales has only recently begun to be intensively studied by physical oceanographers, yet is crucial to our quantitative understanding of species interactions. Larger space/time scales can become important when the question of genetic difference is significant, since the generation length becomes a significant scaling factor.

BIOLOGICAL VARIABILITY

Predicting and explaining the mechanisms of secondary production is one of the most critical problems in biological oceanography. A major difficulty in this field has been the seemingly extraordinary variability associated with secondary production data. Since a significant proportion of this variability owes to physical processes, a better understanding of the physics on appropriate scales will do much to resolve the high variabilty.

To provide linkages for physical and biological concepts, process-oriented population dynamics models are being used to develop notions that not only take account of the system as a whole but also account for recruitment mechanisms: (1) the trophic interactions; (2) the way that these affect egg production; and (3) the way that the year class of eggs affects the number of subsequent spawners and the causal rather than the correlative effects of the physical processes on these mechanisms (see, e.g., Rothschild, 1986).

Recent progress in biological oceanography is setting the stage for addressing these problems. For example, the Gulf-Stream Warm Core Rings Program has generated important insights into the nature, kinematics, and temporal variation in biological production in entrapped, semidiscrete, mesoscale parcels of water as they affect both the offshore and the onshore transport of larger parcels of water, enhancing the exchange of the biota and biological active material between the two regions. These broad descriptions need to be supplemented with additional studies of recruitment mechanisms.

Dynamics of benthic organisms are an important component of recruitment studies. In their pelagic phases the physical setting is the same as for the typical water column organisms. However, in the vicinity of the bottom boundary layer, special features need to be taken into account such as the zero-motion interface between the water column and the substrate. Particularly important questions in benthic dynamics involve the contributions of larval transport, habitat choice, and post-settlement mortality to the spatial variation in the abundance of adults. Also important are the physical limits on the capability of larvae to detect cues related with water movement and to use the movement to arrive at favorable places, and determination of cues to favorable substrate utilized by larvae.

These process models, studies of biological production in eddies and the dynamics of benthic organisms have opened the door to new possibilities and techniques. For example, satellite imagery offers the possiblity of appreciating not only the effects of variability but also the magnitude, scales, and dynamics of the temporal and spatial distribution of biomass. Satellite imagery by itself, however, is as yet insufficient to study individual species, the fundamental units of concern. However, the opportunity is now afforded to develop critical-mass blocks of funding to utilize, in a more focused way, the techniques that have recently been identified to measure the distribution, density, and capability of organisms to reproduce and to change genetically. These techniques involve advanced sampling vehicles such as submarines and towed samplers; satellite imagery for the study of biomass variability; both discrete-volume samples and acoustic and optical devices to estimate plankton density by size category; computer-based plankton identification methods for rapid identification of planktonic forms; a large array of biochemical and biotechnological techniques, many of which have not been fully utilized, and mesocosm facilities for conducting experiments in contained volumes of water.

There are fundamental differences in the ways in which we attempt to explain patterns and variability in these systems (Steele, 1985). While terrestrial ecologists concentrate on "internal" mechanisms such as competition and predation, marine ecologists also emphasize the impact of "external" environmental variability, particularly in the context of recruitment. This generates a basis for the divergence in interpretation, arising from significant differences in the marine and terrestrial environments, particularly the character of the temporal variability and the consequent evolution of organisms and communities. Such comparisons would not only lend valuable insights into the variable responses of terrestrial and aquatic systems to environmental change but also provide an important opportunity to transfer theory and techniques long established in terrestrial studies to aquatic studies and vice versa, raising the possibility of enriching our understanding of the response of both aquatic and terrestrial organisms to environmental change.

EXPERIMENTAL APPROACH

The study of recruitment processes and ecosystem structure will require substantial theoretical development to link the sometimes seemingly diverse concepts of biodynamics. While each region will have its own special setting and its own problems of specific interest, a single general approach would serve to coordinate activities among regions. This approach involves (1) identifying regions for study and appropriate species for study, (2) describing and interpreting the physical structure on dynamically important scales, (3) monitoring changes in density of selected predator and prey organisms, (4) assessing the physiological status of the organisms to determine the effects of physics and population density, and (5) determining the role of food quality in influencing larval growth and survival; (6) the study of behavioral mechanisms pertinent to settlement and prey-predator interactions; and (7) assessing genetic change.

The following sections discuss these components as well as the specific case of benthic-water column processes. Many approaches and methodologies are identified, mainly to point out the range of available approaches. It should be emphasized that it will be necessary in any specific regional study to carefully analyze the alternative methodologies and to select those that provide the most efficient techniques for the problem at hand.

CRITERIA FOR SELECTION OF REGIONS AND SPECIES FOR STUDY AND DESCRIPTION OF REGIONAL POINTS OF DEPARTURE

Criteria need to be developed to select regions and species for study. In this section some possible criteria are mentioned and some preliminary thoughts are provided on the Georges Bank, Gulf of Mexico, and the California Current region as points of departure for applying the experimental approach described above.

For selection of regions, the criteria involve both physical and biological considerations. On the physical side, it is important to consider the complexity of the processes; the role of horizontal and vertical variability, and whether bottom topography has an important effect on the physics. With respect to the selection of species, it is important to determine the extent to which all life stages can be quantitatively sampled and efficiently identified; to be able to measure the behavior of the organisms with respect to food, predators, and habitat selection; to be capable of evaluating environmental stimuli on scales relevant to the individual organism; to determine intrapopulation variation in physiological status, viability, and reproductive capacity; and finally to sample the population on a time scale that adequately samples intragenerational and intergenerational changes (perhaps 10 times per generation and over 3 to 10 generations).

A background document on candidate regions would do much to organize and open for dialogue the critical region and species selection process. For example, some regions have important, long term, time series of environmental and biological features. These are extremely useful in interpreting past and future trends and would be used in deciding which regions are candidates for study. The document would describe what is known about the biodynamics of the region. Although many well-studied regions are described by overview papers, this document would need to focus specifically on recruitment processes. A typical outline might include what is known about the population dynamics of the organisms, the physics (on appropriate scales), and the interaction between the physics and the population dynamics. The document would then include appendixes on theoretical developments and experimental design, keeping in mind that both the pilot and operational phases need to be dominated by a logical framework or overview model, which will be continuously improved and updated.

REGIONAL "POINTS OF DEPARTURE"

This section contains observations on Georges Bank, the Gulf of Mexico, and the California Current, which can be considered as points of departure for the application of the experimental approach.

GEORGES BANK SHELF PROTOTYPE EXPERIMENT

Recruitment studies on Georges Bank can be based on the considerable information already available from studies under way that suggest that recruitment on Georges Bank is biologically controlled by interspecific and intraspecific predation. The studies are focused on the influence of variations in stratification and recirculation on retention, growth, and survival of haddock and cod and their predators and prey in relation to the "spring bloom" and interannual variability in recruitment success. The data base includes information on abundance estimation of eggs and larvae and mortality rates for developmental stages during the first year of life. Biochemical indices (e.g., RNA/DNA ratios) have been developed to measure the physiological condition or health of eggs and larvae in relation to changes in hydrographic conditions and prey densities. Oceanographic observations have shown that cod and haddock larvae are carried southwestward from spawning areas on northeastern Georges Bank to the southern side of the bank by the Georges Bank gyre during the "spring bloom." The juvenile stages are found later in the year (autumn) concentrated on the northern side of the bank. The movement around the bank occurs through some as-yet undefined temporal and spatial synchrony among the annual production cycle of phytoplankton and larval prey, including adaptive behavior of the larvae and juveniles of the copepods *Calanus* and *Pseudocalanus*.

The circulation over the western part of Georges Bank includes a recirculation of about 10 to 30 percent of the water from the south side around to the northern part of the bank. The adaptive mechanism that allows for the fish to be advected around the bank is not understood and requires study of the predator-prey field at the 1-mm to 20-km scale in an experimental design that will allow for studies of linkage from microscale to the mesoscale biodynamic events that control recruitment.

The results of the Georges Bank study will be closely compared to gadoid recruitment studies to be conducted by Norwegian scientists on the Arcto-Norwegian cod in the Norwegian Sea and Barents Sea ecosystems, and studies of cod and haddock recruitment to be conducted by Canadian scientists on the Scotian Shelf. The Norwegian experiment will include the testing of hypotheses that assume that recruitment is controlled principally by environmental events involving advection from spawning grounds in the West Fjord to nursery grounds in the Barents Sea. The Canadian study will also be focused on evaluating the importance of advective processes on the growth and mortality of early life stages of cod and haddock. The Canadian and Norwegian studies will employ new technologies for measuring changes in ocean physics in relation to the availability and abundance of the prey field of fish larvae. All three studies (Georges Bank haddock, Arcto-Norwegian cod, and Scotian Shelf haddock and cod) are to be conducted within a mesoscale network of standardized biological productivity and hydrographic measurements of the upper water layers. These studies will be coordinated with interested European scientists through the International Recruitment Experiment Steering Group of the International Council for the Exploration of the Sea (ICES).

GULF OF MEXICO

Many fishes and invertebrates spawn in the coastal ocean and then must be transported as larvae into estuaries or other nearshore habitats, where much of their growth and development occurs. Such environmentally transgressive species are especially prominent in the fisheries of subtropical and tropical regions of the world. They constitute the large majority of harvested biomass in the Gulf of Mexico, including the most valuable (penaeid shrimp) and most abundant (menhaden) of the U.S. fisheries. The population dynamics of these environmentally transgressive species depend on (1) the interaction of physical and biological processes in the coastal ocean that affect growth and survival of larvae; (2) the physical advective processes and biological behavior that govern transport to the juvenile habitat inshore; (3) the growth and survival of juveniles; and (4) the offshore migration and successful spawning of adults. Phenomena that are thought to be critically important for successful completion of life cycles include: (1) the association of larvae with density fronts, such as the Mississippi and Atchofalaga river plumes, which provide concentrated food resources; (2) the degree to which larvae and postlarvae can move across the density front associated with the well-developed coastal boundary layer; (3) the tidal and meteorologically forced exchanges between the coastal boundary layer and estuaries; and (4) refuge from predators and the food resources provided by the coastal habitat. All of these involve physical forcings on small and large scales (e.g., turbulence, advection, salinity patterns, and water level).

Improved understanding of the controls on population dynamics of environmentally transgressive species is offered by coordinated biological and physical studies. Development of predictive capabilities is important in projecting the effects of such global or continental changes as the rise of mean sea level resulting from atmospheric warming (which may inundate wetlands and alter circulation characteristics of estuaries), altered climatic patterns (which might result in increases or decreases of freshwater runoff), and nutrient enrichment resulting from altered land use and waste disposal (which may already be implicated in large-scale hypoxia on the continental shelf of the northern Gulf of Mexico).

CALIFORNIA CURRENT EXPERIMENT

A conceptual investigation into the recruitment of clupeoid fish populations off Southern California and Baja California has been designed to determine (1) the production of eggs and larvae over a spawning season within the geographical limits of the northern anchovy population, and (2) differential recruitment from month to month within a spawning season as deduced from a comparison of the birthdates of larvae and juveniles that survive at least one month, with the rate of production of youngest larvae as a function of date. The design is based on several years of study of sardine and anchovy by the Southwest Fisheries Center and includes multidisciplinary studies to determine the environmental and biological conditions that may cause differential survival.

Several new techniques have made such projects possible. Foremost is the ability to determine accurately the ages of individual young fish by counting daily rings on their otoliths. Also, a precise histological method is now available to determine whether individual larvae are starving in the sea. An immunological test is also available to determine whether predation occurs on fish eggs and young larvae by invertebrates. For anchovies, a method of biomass assessment based on egg production has been developed. With concurrent oceanographic and ecological information, these techniques provide the data needed to test, on a large population, the current density-dependent and density-independent hypotheses concerning recruitment. The basic concept is applicable to a variety of important fishes. Developers of the program believe that insights into the recruitment processes of a variety of species in the same habitat are possible, since different species may recruit quite differently in the same environment. The approach is essentially comparative in nature, in that the same field measurements can be done in regions where similar groups of species are dominant, e.g., the upwelling regions of Spain and Portugal, Ecuador and Peru, Chile, and northwest and southwest Africa. In this way, a data base comparing both different species and different habitats will accumulate much faster than could be obtained by one country alone. Since fisheries statistics are collected by all these countries, information on the strength of each year class will be available as a check on the predictions arising from the oceanographic and ecological sampling.

International work along these lines, sponsored by the Intergovernmental Oceanographic Commission of UNESCO, has started off Galicia, Spain, and proposals have been written by Peru, Ecuador, and

Chile. In the United States, NOAA may support this program at the Southwest Fisheries Center starting in 1990. This represents an opportunity for academic scientists to do important and related work in the context of a larger program. It will be desirable to expand the range of techniques used to determine starvation, poor condition, growth, and ability to avoid predation. Studies of the distribution, abundance, and feeding energetics of predators on larvae, including their parents, will be important in assigning causes of mortality. Detailed measurements of offshore transport, especially by mesoscale features and water column stability, as functions of time and location (i.e., not just large-scale averages) will be essential. Both the abundances of food organisms and the horizontal and vertical variations in abundances of food organisms should be measured, and, ideally, estimates of the secondary production of these food organisms should be made to link fish recruitment to a trophodynamic view of the ecosystem.

An unusual opportunity for cooperation between academic and NOAA/NMFS scientists is thus in view, combining comparative and detailed studies on particular species with an ecosystem perspective.

PHYSICAL MEASUREMENTS AND MODEL BUILDING

At the outset, it will be necessary to better define the relation of biodynamics to physics at various scales. Present physical instrumentation allows mapping of time and space over the scales suggested in Appendix Figures 1 and 2. Biological sampling is more difficult, owing in part to the need for improved technology, especially in regard to the individual species and life stages, so equivalent resolution will not be available for their concentrations, much less their productivity. Hence, much progress will depend upon modeling using the physical and biological data with their disparate resolution. Substantial information on particle-fluid interaction is available in the chemical engineering and the geological literature and is applicable to the initial stages of the modeling effort.

In order to make progress on the physical determinants of recruitment processes, horizontal current variability and physical parameters that affect biological processes (e.g., motion, light, and temperature) will need to be understood (at least kinematically) on the previously largely unresolved scale range between the microscale (1 cm to 5 m) and the mesoscale (10 to 100 km) with time resolution of a day or less. The panel envisions a sequence of nested studies down to and including 10 km squares in the horizontal. Of particular interest is the question of how particle interactions vary with regard to environmental inputs (e.g., stratification, winds, proximity to strong currents). A thorough kinematical study of a "box" would require velocity profiles, hydrographic mapping, and microstructure measurements from the surface to about 200 m. The panel envisions a multiship survey using Doppler log, GEK, towed body, thermistor chain, and other underway measurements to be supplemented by satellite remote sensing as well as Lagrangian and possibly Eulerian current measurements. It will be crucial to complete the small-scale surveys as quickly as possible and to allow numerous repeat surveys over short time intervals. Examples would include underway mapping of light, fluorescence, beam transmission, particle counts, nutrient chemistry, and surface phytoplankton and zooplankton. It should be emphasized that combinations of existing technology rather than development of new systems can be utilized to make these measurements.

ESTIMATING THE DENSITY OF ORGANISMS

Ecosystem structure theory requires accurately estimating the densities of predator and prey. The standard tools for density estimation, environmental sampling, and analysis in biological oceanography have not changed fundamentally over the past one hundred years. They are still based on nets, trawls, dredges, and box cores, which take minutes to hours to deploy and retrieve and weeks to years to analyze in detail in the laboratory. Modern physical, chemical, and geophysical oceanography disciplines have invested substantial resources in the development of new technologies that emphasize speed, intercompatibility, and near-real-time data analysis. These efforts have resulted in the realization of operational tools.

TECHNOLOGICAL FACTORS

Biological oceanography is at the threshold of this new era. Modest investments have been made in a variety of new directions, and promising technologies are within sight. However, a fundamental problem is that many present sensors detect some property (e.g. pigment composition, or size as determined by electrical impedance) which is not species-specific, while the fundamental units of study for understanding recruitment are the age groups of populations of particular species. The requirement now is not for new inventions, but an investment of resources, an order of magnitude greater than currently assigned, to convert the expensive prototypes to the economical, operational, state-of-the-art commercial equipment.

Examples of such sampling/analysis tools include the following:

1. a. Multifrequency acoustic sonars capable of resolving the density of particles in a size frequency spectrum from less than 0.1 mm upwards, in a "plankton/CTD" configuration, for profiling and towed modes; and the computer hardware and algorithms capable of providing real-time shipboard analysis.

   b. Surface and moored Doppler acoustic instruments to measure water current strength and direction and plankton biomass concentrations and movement.

2. a. "Plankton cameras" capable of profile/towed modes to record visual images of particles for subsequent calibration of acoustic data.

   b. Laser/video systems to record particle movement in 3-D in a form available for near-real-time analysis.

c. *In situ* laser-based pattern recognition systems for automated real-time density and taxonomy information.

3. a. Multispectral satellite-borne color sensors to discriminate quantitatively the range of photopigments on large space scales.

   b. Shipboard flow cytometer/cell sorters to evaluate and differentiate physiological and biochemical attributes of cell populations in the environment.

4. Automated rapid image analysis of particles from bacteria upwards to efficiently process hundreds to thousands of samples in the laboratory and on shipboard.

ASSESSING AGE AND PHYSIOLOGICAL STATUS OF ORGANISMS IN NATURAL POPULATION

Recent advances in biochemistry and molecular biology have not really been brought to bear in a systematic way on the problems related to recruitment processes, and marine ecosystem structure. There are two points of concern. The first concerns the determination of an organism's age, and the second concerns the monitoring of biological transformations that reflect the progress of the conversion of ingested material into reproductive material, and the third, factors that influence reproductive success.

With respect to age determination, much of the currently available population dynamics methodology requires an explicit or implicit knowledge of the age of the organism. In some organisms, age is determinable through an examination of hard parts (such as in fish larvae). But for other organisms, such as copepods, age can only be inferred from size, a method that may often be unsatisfactory since size is highly dependent upon variations in growth, which may not relate to age. There is, thus, a considerable demand for techniques that might be useful in age determination, and these would most likely arise in the fields of biochemistry and molecular biology.

With respect to monitoring biological transformations (see Figure 1) of ingested material, a number of methods are currently available, others are beginning to be developed that may be even more useful, and in some cases there is a need to develop sensitive, accurate, and practical techniques to address the problems associated with recruitment. Of the variety of techniques, studies of the regulation of the rate of fish and invertebrate growth and the development of reproductive tissues are important parts of the biodynamic transformations and provide examples of what can be accomplished.

With respect to reproductive tissue, spermatogenic and gametogenic capacity is also another critical component of the biodynamic transformation. While standard procedures of counting changes in gamete concentration and measuring gonad weight are useful indices for estimating reproductive capacity in some instances, they are nevertheless crude measures, destructive by nature, and very time consuming. There is a need to develop sensitive, rapid molecular methods for estimating these parameters. Vitellogenin is particularly useful in assessing the reproductive status of oviporous vertebrates. Reproductive capacity of individuals with different phenotypes within and between populations can have a tremendous impact on differential recruitment into populations. It has also been shown that rate of development and hatching of several fish species is directly related to genetic background. Early hatching often increases an individual's ability to compete for food. Genetic background can be studied relative to hatching time by fertilizing eggs in vitro and scoring the genotypes of individuals as they hatch. Such studies can provide significant insight into the genetics of the recruitment process.

DETECTION OF GENETIC VARIATION

Genetic transformations are in a sense more fundamental than the simple ingestion and metabolic transformations. In order to place these studies in a biodynamic perspective, one needs to know the following: (1) To what extent do various subpopulations contribute to a given population? (2) Is genetic mortality the same or different between various life stages within and between populations? (3) What is the magnitude of genetic exchange between breeding stocks? (4) Does the genetic composition of populations change in concert with catastrophic crashes or expansions? (5) What is the role of genetic background in differential growth, development, and reproduction? The answers to these and related questions hinge on one's ability to detect differences between stocks and variation among individuals of a population. While morphological characters are sometimes useful in such studies, they are often inadequate for the needs of population biologists. During the last two decades, the introduction of electrophoresis coupled with histochemical staining for the identification of allelic electromorphs has uncovered a wealth of genetic variation at the molecular level. These methods have been useful for studying some species, but the lack of such genetic variation in a host of important commercial species has dampened its wide application to problems of stock assessment and recruitment. This was partly due to the fact that such methods grossly underestimated the extent of genetic variability due to their inability to detect isopolar amino acid changes in protein structure and inability to detect nucleotide changes in the DNA that are not reflected in the protein sequence.

Recent advances in biotechnology and the commercial availability of restriction enzymes and other molecular tools have made it possible for population biologists to examine changes in DNA, allowing us to address a host of previously hidden genetic variability. Not only do these methods allow one to study a broader array of gene diversity, but the sensitivity of these techniques makes it possible to study egg and juvenile stages as well as tissue biopsies of adults.

Perhaps the most useful of these DNA methods, at the present time, is the use of endonuclease restriction digestion of mitochondrial DNA (mtDNA) followed by electrophoresis and the construction of mtDNA restriction maps. Because mtDNA is maternally inherited, individuals within and between populations can be studied and various matriarchal lineages can be followed geographically, including contributions to new lineages, genetic exchange between stocks, and magnitude of contributions by a particular population to a fishery. Moreover, these "molecular tags" can be used to determine each component of the questions posed at the beginning of this section. These and other evolving methods such as repetitive DNA segments of genomic coding regions hold great promise for future studies of recruitment, stock assessment, and evolution of marine species.

LITERATURE CITED

Chelton, D.B., P.A. Bernal, and J.A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40:1095-1125.

Dickey, T.D., and D.A. Siegel. 1986. Physical, optical, and biochemical temporal variability in the Eastern North Pacific. Submitted to Prog. Ocean.

Gerritsen, J. 1984. Size efficiency reconsidered: a general foraging model for free-swimming aquatic animals. Am. Nat. 123:450-467.

Jackson, G.A., and R.R. Strathmann. 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development. Am. Nat. 118:16-26.

Lasker, R., and K. Sherman. 1981. The early life history of fish: recent studies. Rapp. P.-v. Reun. Cons. Int. Explor. Mer 178:607 pp.

Maynard Smith, J., and G.R. Price. 1973. The logic of animal conflict. Nature 246:15-18.

Penry, D.L., and P.A. Jumars. 1986. Modeling animal guts as chemical reactors. Am. Nat., in press.

Pyke, G.H. 1984. Optimal foraging theory: a critical review. Ann Rev. Ecol. Syst. 15:523-575.

Rothschild, B.J. 1986. Dynamics of Marine Fish Populations. Harvard University Press, Cambridge, Mass., in press.

Rothschild, B.J. Biodynamics of the Sea. Manuscript in preparation.

Rothschild, B.J., and C. Rooth (eds.) 1982. Fish Ecology III. A foundation for REX. A Recruitment Experiment. University of Miami Technical Report No. 82008, 389 pp.

Steele, J.H. 1985. A comparison of terrestrial and marine ecological systems. Nature 313:355-358.

Strathmann, R.R. 1974. The spread of sibling larvae of sedentary marine invertebrates. Am Nat. 108:29-44.

APPENDIX A

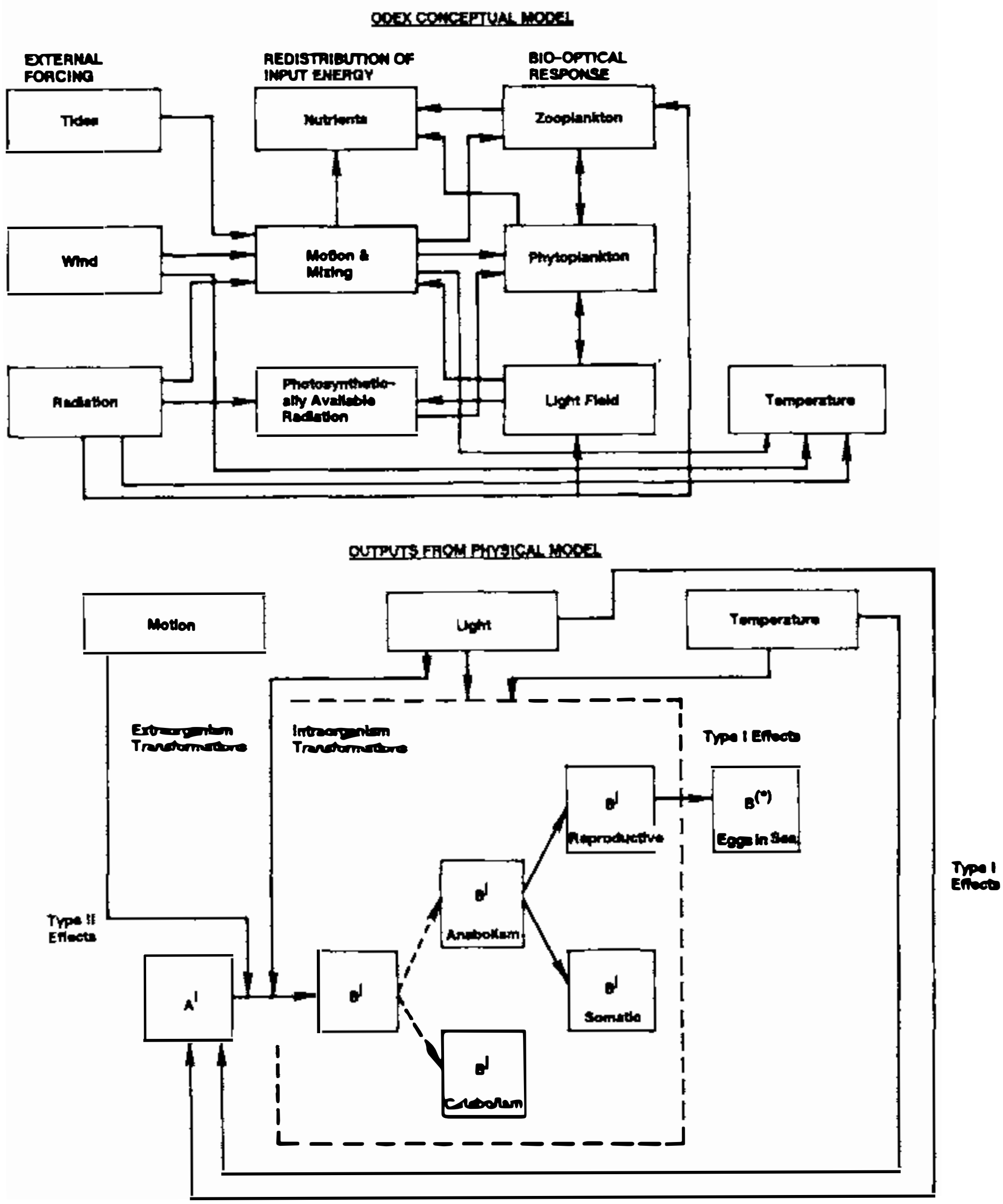

FIGURE A.1 Example of linkages between a schematic of a conceptual physical model and a biological transformation model. The physical model is modified after Dickey and Siegel (1986). The biological transformation refers to a single organism A^i. The superscript refers to its genetic subpopulation. A^i is consumed by predator B^j. A^i is thus transformed into anabolic, catabolic, reproductive, and somatic products, and eventually into eggs in the sea. The eggs in the sea have a variety of genetic attributes. The physics affect both the extra- and the intra-organism transformations (from Rothschild, manuscript in preparation).

APPENDIX B

Some of the more important spatial and temporal scales of interest for biodynamics in relation to physical scales of variability are presented below and are illustrated in Figures B.1 and B.2.

Spatial:

1. Individual larva/food encounter probability scale. This scale may range from size of the larva to the distance between the larva and its prey (millimeters to meters).

2. Horizontal larval patch scale. This is the horizontal extent of a given larval aggregation which would presumably be related to the scale of the larval prey and roughly to the scale of phytoplankton patchiness. Guessed scales range from 10's m to 10's km. The inter-patch scale (horizontal) may be 100's m to 100's km.

3. Vertical larval patch scale. The scale of maximum vertical extent of larvae would be 100 to 200 m. The vertical scale of variability in the patch would probably be roughly equivalent to that of phytoplankton (m's to 10's m).

4. Community scale. This scale is the horizontal regional extent of a given fishery (e.g., Georges Bank, coastal California, North Sea).

Temporal:

1. Individual's time scale. Primary time scales of importance for an individual are the diurnal light cycle and those associated with advection and mixing events (food encounter time scale).

2. Standing stock time scales. The primary time scales of importance for the standing stock are seasonal and interannual.

It is important that the connection in both time and space be made for the individuals and the standing stock as a whole.

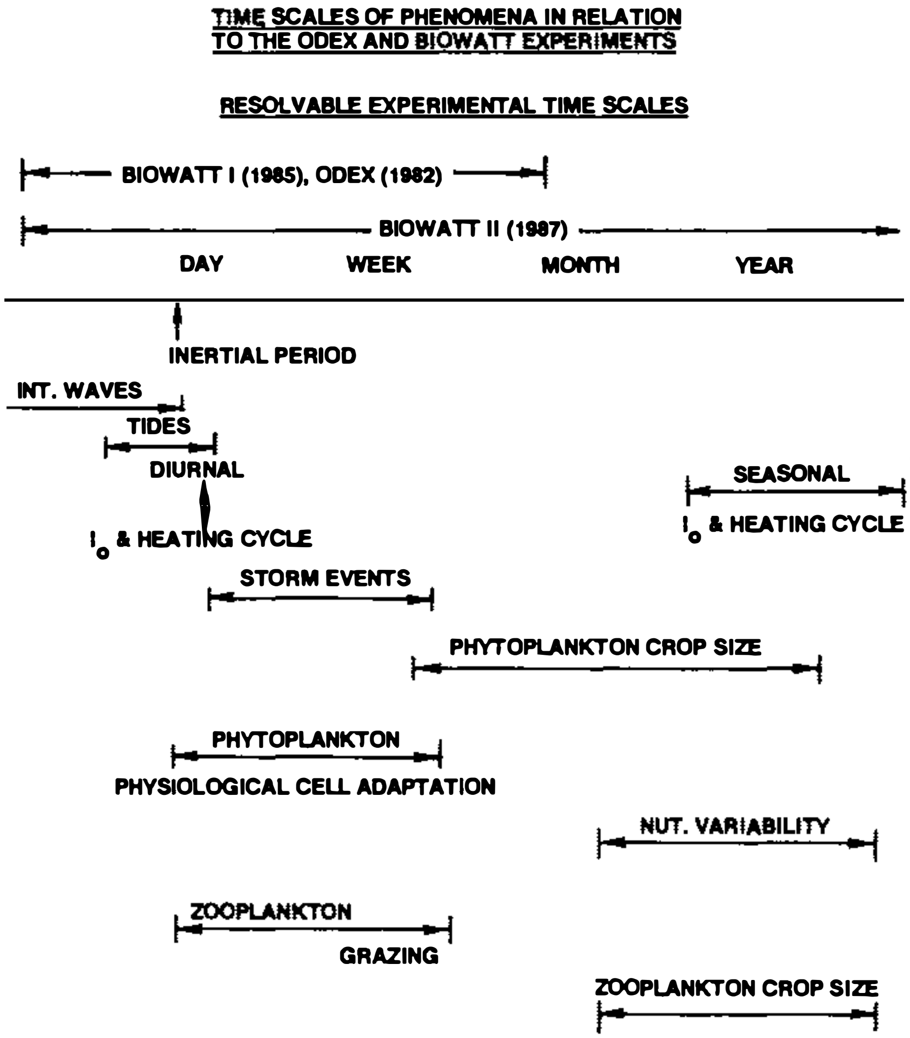

Figure B.1. Here, "int." means internal; "nut" means nutrient; and "I_o" means solar insolation.

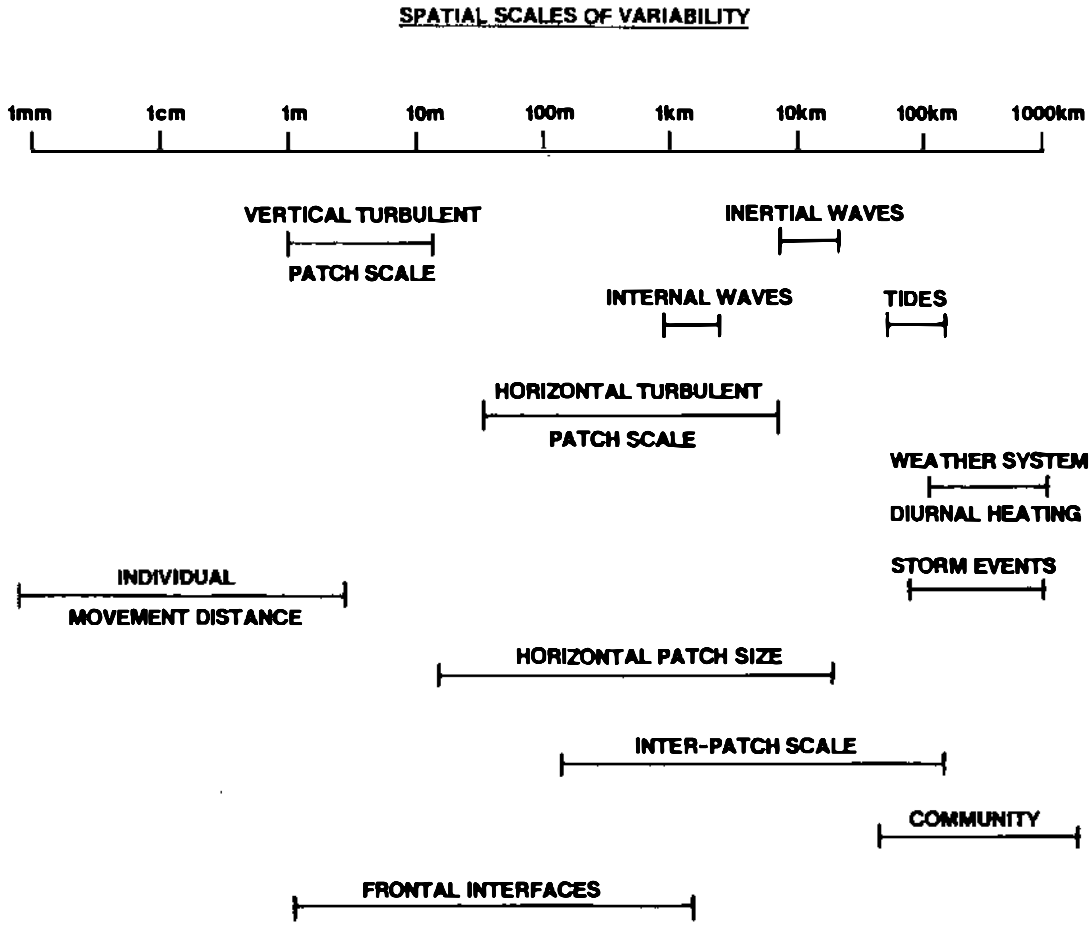
SPATIAL SCALES OF VARIABILITY
1mm
1cm
1m
10m
100m
1km
10km
100km
1000km
VERTICAL TURBULENT PATCH SCALE
INERTIAL WAVES
INTERNAL WAVES
TIDES
HORIZONTAL TURBULENT PATCH SCALE
WEATHER SYSTEM DIURNAL HEATING
INDIVIDUAL MOVEMENT DISTANCE
STORM EVENTS
HORIZONTAL PATCH SIZE
INTER-PATCH SCALE
COMMUNITY
FRONTAL INTERFACES

Figure B.2