A Component of the U.S. Global Change Research Program

Dynamics of Open Ocean Populations
Report of a U.S. GLOBEC Workshop

U.S. Global Ocean Ecosystems Dynamics

Report Number 14

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This is a report of the U.S. GLOBEC Workshop on the Dynamics of Open Ocean Populations held in Woods Hole, MA, USA, at the Woods Hole Oceanographic Institution from 13-15 September, 1993. Laurence Madin and Michael Landry co-chaired the workshop and compiled and edited this report.

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I. EXECUTIVE SUMMARY

The purpose of the workshop was to explore questions of species diversity and community structure in open ocean pelagic environments with respect to potential global climate changes and their consequent effects. There were several reasons to consider GLOBEC questions in the open sea. If the apparent stability of oceanic communities is due to internal biological checks and balances, then this system might be more resistant to climate change than other more variable environments. However, if the stability of the ecosystem is due to the constancy of the physical environment, then blue water communities might be less resistant to perturbation than coastal systems. Disturbances of the population biology or community structure in the major ocean gyres by global climate change could constitute (or lead to) large scale changes in the biosphere.

In either case, we need to understand organismal and population responses to physical and biological forces, and re-examine them over the time scales of global climate change. At present very little is known about the life histories or population ecologies of zooplankton and fishes in the largest environment on Earth, and it is probably inaccurate to extrapolate from coastal to blue-water species.

A group of 22 participants from the U.S., Canada and France met for three days to discuss this topic and recommend research plans consistent with U.S. GLOBEC objectives. The first day was devoted to informal presentations on subjects ranging from plankton community structure to immunological methods for measuring growth rates. A goal of this discussion was to introduce new biochemical, molecular and genetic techniques that might be applicable to measurement of population dynamics and life history parameters of open ocean species that have previously been studied by more classical approaches. Following these talks, working groups were formed to discuss four topics:

- A. Population Characteristics and Genetics
- B. Distributional Patterns and Sampling Problems
- C. Biological Processes and Rates
- D. Physical and Biological Forcing.

Group A considered some of the physical and biological factors that maintain species diversity and community structure in oceanic environments, and whether these forces led to comparable communities in the central Atlantic and Pacific. They discussed the genetic composition of oceanic species, raising questions about gene flow and homogeneity, and the existence of phenotypic sub-populations adapted to more local ecological conditions. The group recommended time-series studies of physical and biological changes at fixed sites, focusing on a small number of target species. They cautioned that the taxonomic and genetic identity of the target species must be unequivocal, and that new methods might be needed to ensure that this is the case. They also stressed the importance of understanding behavior of the organisms.

Group B discussed questions of species distributions and sampling strategies. They began with consideration of how "open ocean" should be defined, and went on to compare the relative effects of changes in climate and circulation on communities in the centers of gyres *versus* the ocean margins. It was suggested that understanding the structure of open ocean plankton communities should begin with assessment of biomass distribution, then functional groups and finally species. This group also outlined criteria for targeting species to study in different oceanic regions over decadal time periods to seek evidence of climate change effects on population biology.

Group C was concerned with the biological processes that control population dynamics. They discussed possible differences in vital rates of oceanic *versus* neritic species, and the mechanisms by which climatic changes might act on those rates. There were questions raised about whether studies should focus on "typical" gyre environments, more productive margins, or other "hot spots". Problems of measuring biological rates of species dispersed in time and space were considered. This group recommended initial analyses of existing data on vital rates of oceanic *versus* nearshore species and efforts to develop new methods for measuring rate processes and sampling micro-scale distributions.

Group D debated the relative importance of physical *versus* biological forces in affecting population dynamics and community structure. They considered temperature and wind stress as two primary physical forces which might alter population biology via their effects on warming, stratification, advection, turbulence and circulation. Spatial and temporal distribution patterns brought about by these forces might be expected to constrain feeding, reproduction and dispersal of species. Principal biological factors acting on population dynamics were assumed to be food supply and predation, although the roles of disease and parasitism are not well understood. Understanding behavior of organisms relative to physical and biological forces was considered prerequisite to a study of possible climate change effects. This group recommended a re-sampling of the North Pacific gyre to compare community structure two decades later, and new, long time-series studies at other accessible oceanic sites.

The Workshop recommended a staged implementation of any Open Ocean GLOBEC program, going from retrospective and pilot studies to larger scale field programs. Central to the plan is selection of a small number of target species that have stable circumglobal distributions in several oceanic gyres and are tractable for process and population studies. Selecting species for open ocean studies that have (1) life histories that are known, (2) low genetic diversity, and (3) minimal physiological (non-genetic) variation, will maximize the opportunity for detecting environmental impacts of climate change in the different ocean regions. Target species would become the focus of population dynamics research conducted as time-series and transects in several parts of the world ocean. These efforts would be allied with other large programs that could provide data on global climate conditions.

II. INTRODUCTION AND BACKGROUND

A. U.S. GLOBEC Objectives

The overall objective of the U.S. Global Ocean Ecosystem Dynamics (U.S. GLOBEC) Program is to understand the physical and biological processes that control the population dynamics of key populations of marine animals in space and time.

B. Importance of Open Ocean Ecosystems

U.S. GLOBEC efforts to date are focused on areas, like Georges Bank and the Arabian Sea, that are of a relatively limited spatial extent and are subject to strong, seasonal climatic forces which are likely to affect or control the dynamics of animal populations. Tropical and subtropical open ocean ("blue-water") environments are, in contrast, among the largest definable ecosystems on the planet. Moreover, they exist in less seasonally variable regimes, and may be controlled by the interplay of physical and biological forces on much different time and space scales than the ocean margins. The study of these systems may provide a valuable comparison to the more physically forced sites that U.S. GLOBEC will study, and could illustrate different kinds of physical-biological interactions.

C. Workshop Goals

The purpose of the workshop was to explore and identify some issues or situations concerning population dynamics of zooplankton or fish in the open ocean that could be the basis of comparison with regions that are physically and climatically dynamic. The primary goal was an intellectual one, to stimulate thought and discussion about problems in population ecology of oceanic animals, but it was also expected that specific questions for investigation within the GLOBEC (and perhaps JGOFS) frameworks would be identified.

Despite the fact that they cover much of the globe, the remote and dilute nature of blue-water environments has made them difficult places to study. Good time-series data on abundance, growth and distribution of populations will be difficult and expensive to collect in such regions. Thus, there was particular interest in including discussions of new biochemical and molecular techniques that might be applied to the assessment of biological constraints, such as genetics, feeding history, physiological condition, or growth rates, on the population dynamics of blue-water organisms. These approaches could be particularly valuable in open ocean environments where the logistics and resources for long-term sampling efforts are not likely to be available. To facilitate the transfer of new technologies to open ocean problems, the workshop sought to bring together a mixture of investigators, some with experience in blue-water environments and an appreciation for the special characteristics of the organisms that live there, and others involved in the development of new analytical or diagnostic methods. The emphasis was on individual-investigator scale problems and opportunities for collaborative research within the logistical umbrellas of existing or scheduled programs (e.g., JGOFS HOTS and BATS sites), rather than a new large program.

D. Workshop Structure

The three day workshop was held at the Woods Hole Oceanographic Institution from 13 to 15 September, 1993. Each of the 22 invited participants (Appendix 3) was asked to prepare a one-page summary of his/her research interests and perspectives in advance of the meeting. The first day was devoted to a series of half-hour presentations/discussions on topics of relevance to the whole group:

Community structure in the Central Pacific Gyre	J. McGowan
Tropical zooplankton populations	R. LeBorgne
Zooplankton community dynamics in the North Atlantic	E. Head
Research at HOTS and BATS sites	M. Landry & T. Michaels
Feeding biology of oceanic copepods	G. Paffenhöfer
Ecology of leptocephali in the open ocean	M. Miller
Population genetics of pelagic fishes	P. Graves
Molecular population genetics of zooplankton	A. Bucklin
Population regulation: physical and biological factors	H. Caswell
Cell proliferation and growth rate	M. Moore

The second day was devoted to working group discussions on four broad topics, with the participants divided for concurrent morning sessions and remixed for afternoon sessions (Appendix 2):

A. Population characteristics and genetics	A.M.
B. Distributional patterns and sampling problems	A.M.
C. Biological processes and rates	P.M.
D. Physical and biological forcing	P.M.

Working group progress reports and report writing were scheduled for the third day, and the meeting ended with a plenary session for discussing the working group summaries.

III. SUMMARIES OF WORKING GROUP DISCUSSIONS

A. Population Characteristics and Genetics

Chairperson: Ann Bucklin
Rapporteur: Michael Miller

ISSUES:

- How do food supply, competition and predation interact to maintain species diversity and community structure?
- Are oceanic species sensitive or resistant to environmental variation?
- Are oceanic populations genetically uniform, or are there ecological sub-populations with differing characteristics?
- Does diversity or community structure differ between the North Pacific and North Atlantic gyres?
- Can target species be selected for study from highly diverse communities?

CONCLUSIONS:

- Studies of populations in the subtropical gyres should be conducted for comparison with results from GLOBEC investigations in adjacent coastal regions.
- New methodologies are needed to address problems of taxonomy and genetics in the open oceans.
- Behavior-oriented studies are essential for understanding the dynamics of species in diverse assemblages.

<u>Text of Chair/Rapporteur's Report:</u>

The Issues

Open ocean regions, like the central Pacific gyres, are environments of high spatial homogeneity and temporal stability. Zooplankton communities in such regions are extraordinarily diverse, with a preponderance of rare species. Mechanisms controlling the dynamics of these communities are poorly understood, and, in fact, extremely difficult to investigate. For instance, numerous salp species co-occur in time and space; feeding nonselectively and not obviously food limited. An analogous situation exists for copepods (Hayward and McGowan, 1979). How can competition for food be demonstrated in a stable system without evidence of habitat partitioning? The role of predation in stabilizing such systems is also unclear. Testable hypotheses for the regulation of population size and community structure of open ocean zooplankton do not currently exist.

The "sensitivity" of open ocean organisms to variations in the physical environment and climatic fluctuations was discussed at length Our initial thought was that populations from environments that normally experience little variation in physical parameters should respond strongly to environmental perturbations. Enormous changes in the census size of Antarctic euphausiids, for instance, follow relatively small changes in sea surface temperature (SST) (Quetin and Ross, 1984). On the other hand, plankton in the central Pacific gyre appear to be markedly insensitive to temperature fluctuations (McGowan and Walker, 1985). Moreover, since vertical gradients in temperature overwhelm horizontal and temporal variations in such systems, it is difficult to hypothesize circumstances in which small changes in SST will significantly impact the population dynamics of vertically migrating species.

We also considered the influence of oceanic circulation on diversity and abundance of animal plankton in the open ocean. Although large scale circulation patterns are clearly a dominant influence in oceanic plankton distributions and dynamics, logistical difficulties preclude any attempt to characterize gyre-scale patterns of ocean circulation. Since circulation patterns directly affect and determine patterns of sea surface temperature, we agreed that temperature was a useful indicator of environmental fluctuation, and that the relationship between temperature and the dynamics of open ocean populations and communities should be examined.

With regard to the genetics of open ocean plankton and fish, the primary question is one of partitioning. It seems unlikely that genetically distinct sub-populations remain isolated within gyres. However, gyre populations may be ecologically partitioned as individuals become physiologically and reproductively suited to local conditions over short time periods. Physiological variation may be highly significant in ecological terms even if genetic homogeneity of the gyre population is maintained by periodic mixing. Appropriate markers of non-genetic variation within species populations include: functional differences in enzymes that are not reflected in allozymic variation (see Graves et al., 1983) and variations in regulatory genes (e.g., cytochrome P450) that may be important in adapting individuals to local conditions. There may also be genetic determinates of behavior that allow behavioral switching according to local conditions. Studies might focus on vertical migration, which may be under both genetic and behavioral control (Bollens and Frost , 1989).

Although gyre populations are likely to be genetically homogeneous, there may be significant genetic structuring at larger spatial scales (e.g., between populations in the North and South Pacific Central gyres). The genetic cohesiveness of amphitropical species should be examined. Molecular clock approaches may be cautiously applied for estimating time-since-divergence, and to investigate the likelihood of gene flow between populations in different gyres during periods of global warming and cooling.

Hypotheses

- The recently recorded change (rise) in temperature in the North Pacific has altered population sizes, dominance structure (rank order of abundance), and diversity in the Central Pacific gyre.
- Populations in systems having continuity of circulation and stability of environmental variables are genetically unstructured. However, species may exhibit significant variations among "ecological" populations in physiological and functional characteristics driven by natural selection.
- Species diversity, population sizes, and dominance structure differ between the North Atlantic and North Pacific Oceans.

Recommended Approaches

Time-series measurements are highly desirable, but their shiptime requirements may be prohibitive. GLOBEC can achieve a modified time-series approach by repeating the cruise tracks of previous field studies in the North Pacific and North Atlantic. In the North Pacific, a transect between Hawaii and Kodiak, Alaska was studied in 1960, 1963 and 1980. Another analysis of this transect would provide the basis for a comparative study and evaluation of decadal variations in population abundance, species diversity, and dominance structure. In the North Atlantic, a similar result could be achieved by repeating a transect between the Canary Islands and Iceland.

Methodological Hurdles/Needs

GLOBEC will require taxonomists trained to discriminate widely distributed species groups so that introduced species can be recognized. Geographic locale cannot be used as a taxonomic character, in the face of increasingly frequent, especially anthropogenic, species exchanges between ocean basins. New methods of taxonomic discrimination will also be required, to facilitate rapid identification and quantification of species abundances in oceanographic samples. GLOBEC should investigate all possible ways of automating zooplankton enumeration, particularly for larval and juvenile stages that cannot be easily resolved morphologically. Biochemical, molecular, optical and acoustic approaches should be examined.

Direct observation of the behaviors of open ocean plankton will be required to understand population and community dynamics, since these organisms generally behave unnaturally in contained, experimental systems. GLOBEC should continue to encourage development of *in situ* observation techniques, including video imaging and photography.

Conceptual Problems

U.S. GLOBEC strategies for the study of nearshore planktonic ecosystems may not be appropriate for the open oceans. In particular, identification of "key" species will be problematic. In a community of numerous rare species, few can impact community and trophic interactions by numerical fluctuations. How do we select target species in such systems?

Opportunities

The approach of JGOFS is particularly useful for integration with open ocean GLOBEC studies, because of the time-series analyses at fixed sites near Bermuda and Hawaii. Hydrographic, meteorological data, and samples of zooplankton, and perhaps fish, from these sites should be examined to describe temporal patterns of variation in open ocean environments.

Comparisons among open ocean, margin, and coastal areas may reveal unique characteristics and dynamics of open ocean ecosystems. Three regional GLOBEC studies border central gyres—the Northwest Atlantic (Georges Bank) Study, the Eastern Boundary (California) Current Study, and the Nordic Seas (Mare Cognitum) Study—and will provide useful information for comparisons.

A semi-submersible Deep-Sea Observatory (DSO) may also be useful for time-series observations in the open ocean (Wiebe et al. 1993). The DSO would provide a platform for blue-water diving for observational studies. Collection of biological samples could be achieved by trawling from work boats sited at the Observatory.

B. Distributional Patterns and Sampling Problems

Chairperson: Richard Harbison
Rapporteur: Loren Haury

ISSUES:

- How do we define "open ocean"—by geography, hydrography or biology?

- Are climate signals and species responses likely to be stronger at the edges than in the middle of gyres?
- Is advection more important in the centers of the gyres or at the edges?
- In what order do we best gain information about community structure—biomass, functional groups or species?
- What sampling methods—nets, acoustics, ROVs, submersibles—are needed to investigate the biology of oceanic populations?

CONCLUSIONS:

- Comparative studies should focus on a few "target species" for parallel studies in different regions.
- The selection of target species should be based on literature and pilot studies focusing on distributional patterns and experimental tractability. In particular, target species should include organisms with circumglobal distributions, congeners from different oceans, and different genera with similar functional roles.
- It is essential to quantify life history parameters and population dynamics of target species over time and space relative to variations in the physical environment.

<u>Text of Chair/Rapporteur's Report:</u>

Given limitations in our present knowledge of open ocean systems and how to identify "key" species in them, the GLOBEC objective was redefined in community terms:

> *To understand the underlying physical and biological processes that control the dynamics of key communities of marine animals in space and time.*

Including studies of blue-water communities as part of GLOBEC will make programmatic conclusions more global and robust because the major ocean basins are the largest habitats on Earth. They are characterized by different biological and physical regimes which may respond differently, perhaps oppositely, to changes in global climate.

Identification of Target Species

Knowledge of community structure must begin with information on species compositional abundance, biomass, functional groups, and size distributions. Biological and physical factors will confound the interpretation of climatic effects on the diverse and poorly-studied species of the open oceans. Since the fauna of the open ocean is so diverse, selection of a few key species is precluded. Therefore, we use the term "target species", which has the additional advantage of not being semantically loaded. Investigations need to focus on a few target species whose distributions and basic biologies are reasonably well known. The target species will serve as a focus for research efforts. In order to understand their place in the open ocean ecosystem, other species that interact with them will also need to be studied. The process of identifying potential target species for study should begin early with literature surveys and preliminary studies focused on the following selection criteria:

- Species that are now believed to have circumglobal, cosmopolitan distributions.
- Closely related species in the same genera from different oceans.
- Species from different genera which appear to fill similar functional roles in different ocean systems.

- Closely related species that may be splitting environmental regions (to compare with globally distributed forms).
- Species that can be sampled quantitatively and relatively easily.
- Species with identifiable life history stages.
- Species that are abundant and present all, or most, of the time.
- Species that are tractable for experimental work.
- Species which exhibit various behaviors (e.g., vertical migration) which might be impacted by changes in the physical or biological environment.

While modest funding of a literature search would be useful for acquiring historical information, including previous results of a time-series nature, distributional studies and life history data, the work must also include pilot studies, ideally with international cooperation, in the major ocean basins. Most previous work in the open ocean has not collected critical information about the physical environment or species biology (smaller size classes, life stages) with modern collecting techniques. Preliminary work also needs to be done on culturing organisms and establishing methods to obtain rate estimates and other needed information to understand the dynamics of populations.

Methodology

Methodological constraints, particularly the need for easy, quantitative sampling, set limits to the kinds of animal populations that could be studied in the open ocean ecosystems. There was some discussion on the desirability of including commercially-important, open-ocean fishes, such as tuna, in the effort. However, the technical problems of sampling the various life history stages of large, long-lived, migratory stocks over meaningful temporal and spatial scales are daunting. The sampling gear of choice for U.S. GLOBEC open ocean studies would most likely be instrumented zooplankton nets (e.g., MOCNESS design), fished obliquely in the mid- to upper water-column. This would presumably constrain the potential target species to robust forms (e.g., crustaceans, squids, fish and salps as opposed to more delicate gelatinous forms) within the size range that can be reasonably collected with such systems (e.g., smallest developmental stage not less than 50 μm and upper size limited by ability to avoid net capture). Pilot studies should use other strategies and technologies -- ROVs, submersibles, moorings, acoustics, video -- to establish the effectiveness of sampling the populations of interest and to determine large-scale horizontal and vertical patterns in species and biomass distributions. Further, target species cannot be studied in isolation; one must know their predators, prey, competitors, symbionts and parasites as well. Therefore, a variety of sampling methods will be required, since no single method of sampling can provide biologically meaningful qualitative and quantitative information over a range of spatial and temporal scales (Harbison, 1983).

Problems

Several concerns provoked considerable discussion in this working group and probably warrant even further consideration. First, it was not entirely clear what is meant by "open ocean" and "blue water" environments, how they differ from one another, and where their boundaries stand with respect to the ocean margins. While the group tended to focus on the subtropical gyres as the likely locations of a "blue water " research effort, they are clearly only part of the open ocean, most of which is poorly studied and some of which may be more relevant for global change investigations. Even so, it was difficult to cleanly distinguish the blue water fraction of the oceans from all others by species, spatial and temporal patterns of variability in biology and physics, stratification, or light. Second, we wondered about problems associated with following the life histories of populations in advective environments, particularly the interplay between vertical structure in currents and migratory behaviors. It is not inherently clear that advective problems are less severe in the open ocean. Lastly, we considered whether studies of blue-water populations ought to be focused on the cores of ocean gyres, where advective problems may be minimal and there is a greater likelihood of populations approximating stable age distributions (a great advantage in determining life tables in population dynamic studies). The alternative, or complementary, approach would be to study the "edges" of ocean regions, where the dynamics of species are more temporally and spatially variable, but where the "signals" from climatic changes may be more clear.

Opportunities

Certain advantages (logistics and basic measurements of lower trophic levels) link GLOBEC blue-water studies to JGOFS time-series stations in the North Pacific (HOTS) and North Atlantic (BATS) subtropical gyres, In addition, WOCE lines and CPR tracks provide opportunities for more spatially extensive sampling schemes.

C. Biological Processes and Rates

Chairperson: Ann Durbin
Rapporteur: Hans Dam

ISSUES:

- What are the vital rates (birth, growth, death) for open ocean populations, and how do they differ from those of coastal organisms?
- What are direct and indirect effects of climate change on organisms and their vital rates?
- How should populations be studied when cohorts cannot be recognized or tracked?
- Is the stability of the North Pacific gyre real and typical, and if so, what maintains it?
- Should studies focus on the "typical" open ocean, or on "hotspots" of biological activity?
- What new approaches to rate measurements are needed?

CONCLUSIONS:

- It is desirable to conduct preliminary retrospective analyses of existing data and samples.
- We need to develop new methods for measuring process rates as part of existing efforts in GLOBEC, JGOFS, and individually- funded studies.
- In addition, we must work towards new technologies that will improve microscale sampling and analyses.

<u>Text of Chair/Rapporteur's Report:</u>

The Issues

Previous analyses of community structure in the subtropical North Pacific gyre (McGowan and Walker 1979, 1985) have raised two questions -- Why are there so many species in the open ocean? and, What preserves the stability of such pelagic communities (i.e., is the stability real?)? These issues are linked in the Energy-Stability-Area theory of biodiversity (Wilson 1992).

If blue-water communities are stable and the sizes of animal populations within them vary little with time, then birth and death rates will be largely in balance. Knowledge of these vital rates is extremely limited for small oceanic crustaceans (e.g., Petit 1982, Dessier 1985), though not so bad for fish species (Longhurst and Pauly 1987). Thus, important goals for blue-water GLOBEC studies would be to determine vital rates (birth, death, development) of animal populations in the open ocean, and to compare these rates to those of nearshore animals at similar temperatures. The latter goal is particularly timely in light of the recent suggestion that growth rates of copepods can be estimated directly from ambient temperature (Huntley and Lopez 1992). The implication that food may not be limiting to growth in nature should be evaluated experimentally for organisms inhabiting regions of the oceans which represent the extremes of high temperature and low apparent food density -- the blue-water gyres.

Although the first step is to quantify vital rates of animal populations, the ultimate goal, for reasons of intellectual satisfaction and predictive capability, would be to understand what regulates these rates. With regard to potential effects of climate change, exposure to elevated temperatures leads generally to reductions in mean body size within populations or to changes in zooplankton community structure from larger to smaller species (Moore and Folt 1993). Climate change may also affect ocean circulation and hydrography, thus altering the growth environment (e.g., temperature, mixed layer depth, nutrient fluxes) of primary producers. This may lead to changes in production rates or phytoplankton community structure that will alter trophic transfer to higher levels, indirectly impacting the dynamics of consumer populations.

The controversy over "bottom-up" (resource competition) *versus* "top-down" (predation) controls of population abundances was discussed in terms of open-ocean communities. It may be difficult to determine density-dependent effects on population size when birth and mortality rates are in balance (as could be the case for stable age distributions). In the case of stable populations, birth rates may be more easily determined, and mortality assessed indirectly. The favored approach for studying the dynamics of temperate coastal zooplankton—tracking cohorts—may not be adequate in tropical and subtropical regions because species reproduce more or less continuously through time. Moreover, following cohorts through time in a spatially extensive region would be extremely difficult (but see Dessier 1985). An alternative approach would be to assume that the populations exhibit stable age distributions. Information on vital rates can then be derived from life tables constructed from snapshots of the population at a single time. It would be essential to demonstrate that the stable-age assumption is met before embarking on studies of key species in the open ocean.

Because population dynamics is by nature a field that deals with questions of demography, the first priority would be to concentrate on the study of vital rates (birth, growth, death) of populations. Quantifying and understanding physiological processes (e.g., ingestion, respiration and excretion) through the energy balance approach should be a second priority that can also aid in measurements of species growth rates (LeBorgne 1982) and can provide a mechanistic understanding of growth at the organismal level.

Methodology

In principle, the methods required and the conditions to be met for successful studies of open ocean species would be similar to those used in any study of population dynamics. For instance, identification and enumeration of all stages within a species would be essential. Thus sampling methods (whether they be nets, pumps or direct observation with video cameras or submersibles) should be designed with this goal in mind.

On the other hand, traditional incubation methods for estimating growth rates (e.g., Peterson et al. 1991) may not be adequate for fragile oceanic species. These methods are also extremely time consuming and require extraordinary care in animal handling. Furthermore, incubation methods must assume that the animals experience their natural food resources. Therefore, innovative approaches that obviate the need for incubations need to be developed. Some of the promising approaches are: the oocyte maturity index of reproduction (Runge 1987); biochemical indices of growth and metabolism (RNA:DNA, citrate synthase activity, BRDU incorporation into DNA, PCR amplification of mRNA—see reviews by Buckley and Bulow 1987, Buckley and McNamara 1993, Crawford 1993); and indices of age (otolith rings for fish and lipofuscin for invertebrates, Sheehy 1992).

Opportunities

U.S. GLOBEC has funded several studies to evaluate biochemical and molecular indices of growth, and some answers from those studies may be available before a GLOBEC open-ocean study is designed. Collaboration with existing JGOFS studies may be advantageous provided that the different programmatic emphases (JGOFS interest in community level and biogeochemical relevant phenomena *versus* GLOBEC interest in species level issues) can be reconciled. Moreover, existing data sets from other oceanic localities (e.g., Station Papa, India, BATS and HOTS sites) should be considered.

D. Physical and Biological Forcing

Chairperson: Gustav-Adolf Paffenhöfer
Rapporteur: Anthony Michaels

ISSUES:

- How does wind stress affect mixing and turbulence, and hence distributions and vital rates of organisms?
- How do temperature and temperature variability affect warming, advection and overturn and, thereby, influence animal populations?
- How does spatial heterogeneity produced by turbulence affect feeding, reproduction and dispersal?
- How does bottom topography indirectly affect surface distributions or aggregations of organisms?
- What are the roles of parasites and disease in regulating animal populations relative to food supply and predation?
- What are the roles of behaviors that aggregate organisms in environmental gradients relative to life functions?

CONCLUSIONS:

- Long time-series of physical and biological variables are needed at the JGOFS HOTS and BATS sites and elsewhere.
- The North Pacific gyre should be re-sampled to evaluate changes in community structure on decadal scales.

Text of Chair/Rapporteur's Report:

Physical Factors and Variables

Meteorological forcing from wind stress results in the displacement of surface waters, turbulence and mixing. Depending on the strength of the winds, these effects can reach to depths of tens of meters, not only affecting the vertical and horizontal distributions of zooplankton, but also their population birth, death and growth rates (Wroblewski 1980, Paffenhöfer et al. 1994).

Temperature variability has direct and indirect effects. Diurnal cycles of insolation can warm the surface waters during the day resulting in surface advection sometimes in excess of 15 cm s^{-1}, as well as vertical current shear (Weller et al. 1985). Seasonality in ocean heating and wind stress result in deep convective overturn of the water column in some temperate regions like the North Atlantic, but not in others, like the Subarctic Pacific, which has a permanent halocline. Macrozooplankton assemblages in these open ocean regions are dominated by species adapted to the local physical forcing -- e.g., *Calanus finmarchicus* in the North Atlantic *versus Neocalanus* spp. in the Subarctic Pacific.

The formation and displacement of eddies with widely ranging signatures also occurs in the open ocean, thus creating temporary subprovinces which change over time with horizontal advection (e.g., Gulf Stream rings). Differential advection with depth, accompanied by diel vertical migration can result in wide dispersal of populations and assemblages of zooplankton (Riley 1976).

Richard Feynman called turbulence the subject of top research priority in physics. In the ocean, there is good evidence of large-scale turbulence at the surface due to wind forcing and current shear, but little empirical evidence on the occurrence of mm to cm scale turbulence. Semiquantitative observations, however, indicate that feeding schools of juvenile and adult fish create short-term (< sec) bursts of turbulence resulting in heavy predation mortality on copepods (Kils 1992). It may be that significant small-scale turbulence in the ocean originates from biological activity.

Bottom topography (ridges) seem indirectly to cause aggregations of vertebrate predators in the euphotic zone; the effects of these rises on zooplankton have been documented (McGillivary 1988 thesis, and others) but thorough studies are lacking.

Internal waves occur in most parts of the oceans and should at least temporarily effect vertical distributions of zooplankton directly and possibly indirectly by redistribution of potential food organisms.

Biological Factors and Variables

The main biological factors affecting population dynamics of zooplankton are thought to be food quantity and quality (Lampert 1986, Kleppel 1993) and predators (Landry 1976). Not so much is known about the significance of diseases and parasites. There are, however, reports on widespread effects of parasites on salps (hyperiid amphipods, e.g., Laval 1980) and on copepods (Ianora et al. 1987).

Aggregations are of great significance for the dynamics of populations, whether the aggregations are the animals themselves, or their predators or prey (e.g., Omori and Hamner 1982). Anywhere in the ocean zooplankton form some type of loose or tight aggregation, be it early juveniles in an upper mixed layer (e.g., Paffenhöfer 1983) or older stages in deep layers, tight patches of calanoid or cyclopoid copepods behind obstacles (e.g., Hamner and

Carleton 1979), or near the seafloor (Ueda et al. 1985). Tight aggregations of cells occur over extended periods of time in the open ocean (Cowles et al. 1993). These features are often less than 1 m thick and represent environments in which zooplankton would not be food limited. Migrating zooplankton which are otherwise in a nutritionally dilute environment, particularly in the open ocean, need to locate and exploit such discontinuities. Aggregations are also thought to reduce predation or enhance feeding success (schools *versus* individual fish, Kils 1992). Traditional sampling will not locate such aggregations of potential food or predators. As shown by Kils (1990) for fish schools and their ciliate prey in nearshore regions, quantification of predator-prey interactions in space and time are essential for understanding how and where physical and biological forcing affect the population dynamics of zooplankton in the open oceans.

Recommendations

Long-term time series studies are needed for open-ocean populations. Target species should be selected with an emphasis on those which co-occur in at least two different open ocean provinces. Population rate processes of target species must be assessed at an adequate frequency, coupled with the measurement of relevant physical and biological variables. Study options include:

- Revisiting historical locations, such as the North Pacific gyre.
- Exploiting opportunities in existing high time-series programs: BATS, HOTS.
- Establishing low technology time-series at new sites adjacent to blue-water gyres.
- Conducting short-term (minutes to hours) *in situ* studies (similar to Kils 1990, 1992) to obtain an understanding of aggregate formation and dissipation, and the fates and behaviors of individuals within small aggregations.

IV. WORKSHOP SUMMARY AND RECOMMENDATIONS

The Workshop recommended a stepwise implementation, from modest, single-investigator efforts to large scale field programs starting about 5 years from now. It was agreed that "open ocean" would mean the temperate, subtropical and tropical central regions of the world oceans, including the borders of gyres and with emphasis on the epipelagic zone. It was agreed to concentrate on zooplankton or fishes >100 µm in size.

Central to the plan is selection of a small number of target species having stable circumglobal distributions in several oceanic gyres and tractable for process and population studies. Selecting species for open ocean studies that have (1) life histories that are known, (2) low genetic diversity, and (3) minimal physiological (non-genetic) variation, will maximize the opportunity for detecting environmental impacts of climate change in the different ocean regions. Target species would become the focus of population dynamics research conducted as time-series and transects in several parts of the world ocean. These efforts would be allied with other large programs that provide data on global climate conditions.

The proposed implementation plan includes:

1. **Retrospective analyses.**

   - A literature review to summarize patterns of biomass distribution, species diversity, and community structure in the Atlantic, Pacific and Indian ocean gyres. This would identify a preliminary pool of target species.
   - An analysis of existing data or samples from the central Atlantic, Indian and/or South Pacific to look for patterns of species distribution, diversity and dominance to compare with the North Pacific gyre.

2. **Pilot scale studies.** These are small efforts conducted at single sites (i.e., JGOFS time-series sites), from platforms of opportunity, or on dedicated cruises. Their goals include selecting final target species.

   - A comparison of new and conventional sampling techniques to establish the best ways to sample all life stages of target species.
   - Sampling in different ocean basins to establish distribution patterns of potential target species. A north-south transect in the North Atlantic could provide data complementary to those from the North Pacific gyre.
   - Sample collection for genetic analyses to establish the boundaries of populations within or between ocean basins.
   - One or more cruises should repeat earlier (1960-1980) transects in the North Pacific gyre to compare species abundance and diversity patterns over the past three decades.
   - Develop and/or evaluate emerging techniques for measuring process rates (e.g., growth, reproduction, mortality, energetics) on the target species.
   - Establish, with international cooperation, land-based sites in parts of the temperate and tropical ocean where simple measurements of climate and hydrography could be made and samples of zooplankton or fishes taken over long time periods.

3. **Dedicated Open Ocean Programs.** These would be larger-scale studies aimed at the target species over 1-2 year time periods. The nature and scope of these efforts would be dictated by results of the pilot studies and available funding. Emphasis would be placed

on establishing population characteristics and dynamics rather than bioenergetic processes, although the latter might play a supporting role. Micro- and meso-scale physical characteristics of the environment would need to be investigated simultaneously with the biological studies. In order to assess responses to global scale climate change, key population parameters and vital rates for the target species would have to be studied again after 5-20 years.

V. LITERATURE CITED

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Appendix 1.—WORKSHOP AGENDA

<u>September 13</u>

0800 - Continental Breakfast
0830 - Madin/Landry: **Welcome and Introduction**
0900 - McGowan: **Community structure in the Central Pacific Gyre**
0930 - LeBorgne: **Tropical zooplankton populations**
1000 - Break
1030 - Head: **Zooplankton community dynamics in the N. Atlantic**
1100 - Michaels/Landry: **Research at BATS and HOTS sites**
1130 - Paffenhöfer: **Feeding biology of oceanic copepods**
1200 - Lunch (Buttery)
1330 - Miller: **Ecology of leptocephali in the open ocean**
1400 - Graves: **Population genetics of pelagic fishes**
1430 - Bucklin: **Molecular population genetics of zooplankton**
1500 - Break
1530 - Caswell: **Population regulation: physical and biological factors**
1600 - Moore: **Cell proliferation and growth rate**
1630 - open
1700 - Adjourn

<u>September 14</u>

0800 - Continental Breakfast
0830 - **Working Groups A and B**
1030 - Break
1230 - Lunch (*in situ*)
1330 - **Working Groups C and D**
1500 - Break
1730 - Adjourn
1900 - Dinner at Landfall restaurant, Woods Hole

<u>September 15</u>

0800 - Continental Breakfast
0830 - **Oral summaries from Working Groups**
1000 - Break
1030 - **Working Group report writing**
1200 - Lunch (*in situ*)
1300 - **Opportunities and Implementation - General Discussion**
1500 - Adjourn

Appendix 2.—WORKING GROUP ASSIGNMENTS

TUESDAY MORNING 0830-1230

A. Population characteristics and genetics

Bucklin [Chair]
Miller [Rapporteur]
Boehlert
Caron
Caswell
Durbin
Graves
McGowan
Moore
Young

B. Distribution patterns and sampling problems

Harbison [Chair]
Haury [Rapporteur]
Dam
Head
LeBorgne
Michaels
Paffenhöfer
Powell
Steele
Torres

TUESDAY AFTERNOON 1330-1730

C. Biological processes and rates

Durbin [Chair]
Dam [Rapporteur]
Bucklin
Caron
Graves
Head
LeBorgne
Miller
Moore
Torres

D. Physical and biological forces

Paffenhöfer [Chair]
Michaels [Rapporteur]
Boehlert
Caswell
Harbison
Haury
McGowan
Powell
Steele
Young

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