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Population Genetics of Marine Organisms

by Dennis Hedgecock

From its inception, U.S. GLOBEC has been concerned with resolving the systematics and population genetic structures of organisms targeted for long-term field study. This concern reflects a growing interest on the part of biological oceanographers and fisheries scientists in the theory and practice of population genetics, particularly as enhanced by molecular biological methods. Recent expressions of this interest, among others, have been the National Science Foundation Fellowships in Marine Biotechnology, the National Research Council's Ocean Studies Board planning meeting, "Marine Biodiversity and the Ocean Environment," held at the University of California, Irvine, in April 1993, and the recent symposium at the 1993 CalCOFI Conference, "Genetics of the Fauna of the California Current." This article is a personal view of exciting new developments in marine population genetics research and their application to U.S. GLOBEC.

Major scientific questions being addressed by population geneticists working on marine animals can be grouped under five headings: (1) identification of morphologically cryptic, sibling species; (2) amount and spatial structure of genetic diversity within species; (3) temporal genetic change; (4) retrospective analyses of historical oceanographic collections; (5) phylogenetic and phylogeographic analyses; and (6) development of theory and statistics to aid in the analysis and interpretation of rapidly accumulating, molecular data.

Sibling Species

A major contribution of population genetic studies to marine biology has been the identification of biological species within morphologically defined taxa, including some that are well studied such as *Mytilus*, *Capitella*, and *Calanus* (reviewed by Knowlton 1993). These discoveries, which are often serendipitous by-products of research directed at other questions, could eventually increase marine biodiversity at the species level by an order of magnitude. A systematic investigation of the frequency of sibling species in various taxa appears warranted. Prudence dictates that the taxonomy of all U.S. GLOBEC target organisms be confirmed by both traditional and molecular methods and that voucher specimens be kept.

As a rule...we should not expect such studies [of spatial genetic variation] to yield conclusive information about the sources of recruits or the water masses bearing them.

Amount and Spatial Structure of Genetic Diversity within Species

The amount of genetic variation maintained in species is perhaps the most thoroughly studied aspect of marine population genetics. Early studies of protein polymorphism documented widely varying levels of

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genetic diversity among marine taxa, but causes of this variation are not entirely clear. Comparative studies of taxa differing in life-history or ecological traits have provided few compelling general explanations for the maintenance of different levels of genetic diversity in different taxonomic groups (Ward et al. 1992). Certainly, the amount of diversity measured for a particular taxon depends to a great extent on the particular type and set of genetic markers studied.

Spatial structure of genetic diversity or population subdivision is the topic of most interest to oceanographers and the U.S. GLOBEC community, because it is tied to the hope that the geographic sources of recruitment to marine animal populations might be identified by their genetic makeup. Indeed, "biotechnology" has in part been sold to this community as <u>the</u> solution to this important, mass transport problem. For most species of interest, those that comprise the zooplankton broadly speaking, this hope is not well founded in logic or fact.

Population genetic theory tells us that dispersal among geographic populations, even very low levels of dispersal on the order of a few migrants per generation, can eliminate the very genetic differences among geographic populations that are supposed to permit identification of provenance. Early studies of proteins established that species with dispersing, planktotrophic larvae had, as expected, much less geographic variation or population subdivision than species with poorly dispersing, lecithotrophic larvae (Burton 1983). The many genetic studies that have now been made of fish and invertebrate marine species with planktonically dispersing larvae have clearly shown them to be genetically quite homogeneous over very large regions, though not often over their entire geographic ranges. A common measure of population genetic differences is F_{ST}, the ratio of the variance of allelic frequencies among localities to the maximum variance that would obtain if each locality were fixed for one of the alternative alleles without change in mean allelic frequency. F_{ST} is generally much less than 0.05 for marine species with planktonic larvae.

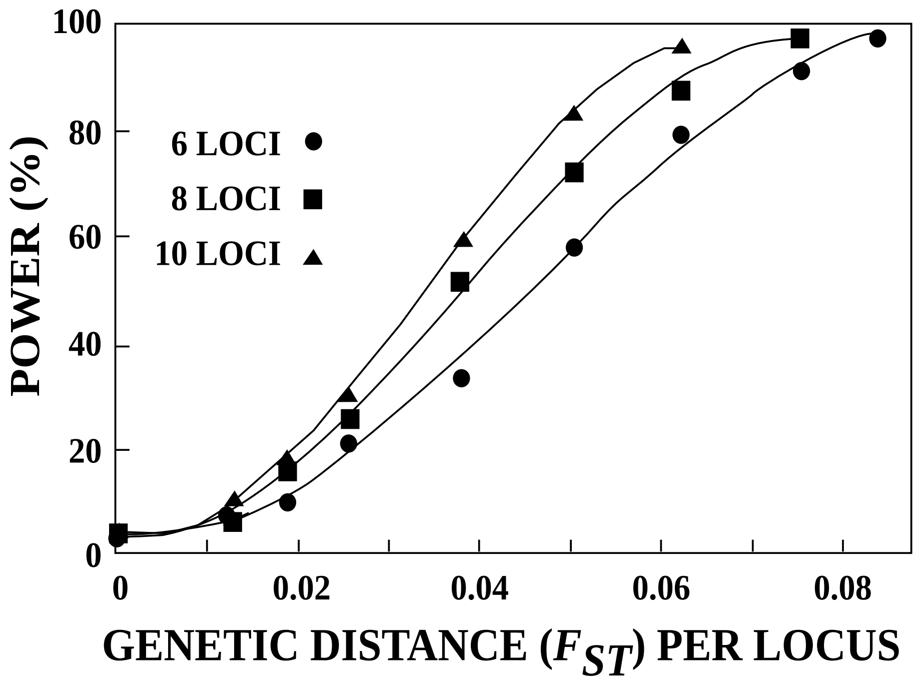

Figure 1. Power to detect a mixture of two populations (i.e. the probability of rejecting the null hypothesis when it is false), as a function of the average genetic distance (F_{ST}) between them (from Waples and Smouse 1990). Results are from 500 replicate computer simulations with sample size, N = 100, mean allele frequency q = 0.8 for each locus, and a population mixture ratio of 1:1. Note that F_{ST} for most marine animals with pelagic larvae is usually much less than 0.05, suggesting that a mixture would only be detected about 10-50% of the time. Power declines from that graphed with declines in sample size, mean allelic frequencies > 0.8, deviations from a 1:1 mixture, and time since a mixing/hybridization event.

The oceanographer's problem is to detect if a sample of zooplankton is a genetic mixture and if so, to determine the contributions of different geographic populations to the mix. This problem has been solved for certain mixed-stock fisheries, particularly for anadromous species; sophisticated statistical analysis of genetic data can identify source populations and their relative contributions to ocean salmon catches (Utter and Ryman 1993). These methods work well for salmon because anadramous source populations are identifiable in space and are genetically distinct, with F_{ST} values ranging up to 0.5; these same methods are not likely to work for the many marine species that lack obvious spatial genetic structure (Fig. 1).

Identification of sources and sinks of zooplanktonic populations is critical to understanding their distribution and abundance. It remains to be seen, however, whether the promise of greater resolution of individual and population genetic differences afforded by DNA analyses will make such identifications tractable. The fundamental limitation may be the dispersal biology of such species, which homogenizes the frequencies of alleles at all loci, be they DNA sequences or allozymes.

Nevertheless, studies of spatial genetic variation should be made for all U.S. GLOBEC target species as a part of a baseline population genetic description. Such studies may reveal exceptions to the general rule or they may reveal a previously unrecognized

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Genetics—(Cont. from page 2)

barrier to dispersal that has resulted in a major genetic subdivision. As a rule, however, we should not expect such studies to yield conclusive information about the sources of recruits or the water masses bearing them.

Temporal Genetic Change

Despite the generalization that marine species with planktonic dispersal are genetically homogeneous over large geographic regions, statistical comparisons of allelic frequencies among samples taken sometimes on scales of meters often indicate significant, "chaotic," microspatial heterogeneity embedded within the basin-scale similarity of allelic frequencies. Recent work on this paradox has focused attention on temporal genetic change in marine populations, which in the few studies conducted thus far appears to be as large or larger than geographic variation on basin scales (reviewed by Hedgecock 1994).

Microspatial heterogeneity and temporal change may be jointly explained by the hypothesis that a large variance in individual reproductive success results from a sweepstakes-chance matching of reproductive effort with spatio-temporal windows of oceanographic conditions conducive to spawning, fertilization, larval survival, and recruitment (Hedgecock 1994). According to this hypothesis, only small fractions (from 1/100 to 1/100,000) of spawning adults effectively reproduce and replace standing adult populations each generation, so that random genetic drift of allelic frequencies should be measurable in some populations. This prediction has been borne out by temporal studies of semi-isolated natural oyster populations. Amounts of genetic drift imply effective population sizes that are many orders of magnitude less than the simple abundance of adults. More detailed studies of larval populations are needed to test a second prediction that specific cohorts of larvae should show genetic evidence of having been produced by only a segment of the potential parental pool.

This hypothesis establishes a connection between oceanography and population genetics in the study of recruitment and may explain how local adaptations and speciation can occur in seemingly large, well-mixed marine populations. Temporal genetic studies are therefore germane to U.S. GLOBEC field studies.

Retrospective Analyses of Historical Collections

An exciting new technology for enzymatically amplifying specific DNA sequences from small and preserved biological samples, the polymerase chain reaction or PCR (Saiki et al 1988) can potentially be applied to the study of preserved material in large historical oceanographic collections such as those maintained at Woods Hole Oceanographic Institute and Scripps Institution of Oceanography. Molecular methods could aid in a more rapid systematic treatment of these collections and be used to establish genetic histories for particular species of interest. Geneticists urge that future collections be stored in alcohol rather than formalin, which can chemically degrade nucleic acids.

Phylogenetics, Phylogeography, and Paleo-oceanography

Molecular genetic analyses are being used to reconstruct genetic phylogenies at all taxonomic levels and for many phyla. The application of phylogenetic methods to molecular as well as organismal traits such as morphology, life history and behavior, will undoubtedly shed new light on the evolution and systematics of marine organisms. Comparisons of genetic divergence within and between closely related species across paleo-oceanographic barriers of known age, such as the arctic land barrier or the Isthmus of Panama, are useful for calibrating rates of molecular evolution and reconstructing the history of faunal exchanges. Ultimately such studies may provide the basis for development of biotechnological tools for rapid, automated classification of oceanographic samples and collections.

Within the past decade, the application of phylogenetic approaches to molecular variation within species has yielded new insights into population histories and a new conceptual framework for uniting the traditionally separate disciplines of systematics and population genetics (Avise et al. 1987). Studies of mitochondrial DNA in several species living along the Gulf of Mexico and Atlantic coasts of the U.S. have revealed concordant patterns of major genetic subdivisions. In all of these species, Gulf haplotypes give way to Atlantic haplotypes across a previously recognized biogeographical boundary in southeastern Florida. Gulf and Atlantic haplotypes represent clades that separated over a million years ago. Thus, "phylogeographic" patterns reflect the persistence of historical events in the gene pools of organisms. Such information is relevant to management and conservation efforts and begs for inter-disciplinary, paleo-oceanographic explanation. U.S. GLOBEC studies of species in the California Current may well encounter similar intraspecific, phylogeographic patterns of variation across the biogeographic boundary at Point Conception.

Data Analysis, Interpretation, and Archiving

Molecular methods are beginning to generate more information than can be presently handled by theory and statistical methods developed for the analysis of allozyme or early DNA-RFLP data. As the potential for resolving genetic individuality at the level of DNA sequences is realized, identification of relatedness and clustering of individuals into biologi-

(Cont. on page 11)

One Way to Estimate Egg Mortality Rates in Marine Copepods

by Bill Peterson and Wim Kimmerer

One of the goals of the U.S. GLOBEC program is to determine which factors control the recruitment of planktonic animals in the sea. For marine copepods, recruitment includes consideration of rates of egg production, rates at which individuals move through each development stage, and survivorship and mortality schedules.

We have just completed a study of processes controlling the recruitment of the marine calanoid copepod, *Temora longicornis*, in Long Island Sound (Peterson and Kimmerer, in press). In that paper we discuss factors controlling egg production, egg mortality and cohort survival rates. One of the remarkable results we wish to highlight in this article is that we found egg mortality rates to be extraordinarily high—no more than 10% of the eggs produced on any given day reached the first nauplius stage. Here we outline our method for calculating egg mortality rates, present some of the results of the analysis of our *Temora longicornis* data, and include results of analyses of some new data sets.

To estimate egg mortality rates, one needs four pieces of information (see Table below).
At steady state, the rate at which eggs (or any other developmental stage) pass through that stage is a function of the rate at which they enter the stage and the mortality rate, m, within the stage (Kimmerer, 1987). For eggs,

$$R_a = R_o\, e^{-ma} \qquad (1)$$

Parameter	Symbol	Units
egg production rate	B	eggs female^{-1}day^{-1}
female abundance	N_f	females L^{-1}
egg abundance in situ	E	eggs L^{-1}
egg development time	D	days

where R_a is the rate at which eggs pass through age *a*, R_o is the rate of egg production per unit volume, and m is the daily mortality rate. This can be integrated over *a* from 0 to D to obtain the number of eggs per unit volume,

$$E = R_o\, [(1 - e^{-mD}) / m)] \qquad (2)$$

substituting for R_o = (B) (N_f) and rearranging yields

$$E/BN_f = (1 - e^{-mD}) / m \qquad (3)$$

Mortality rate is determined iteratively from (3). The proportion of eggs surviving for one day is calculated from

$$S = e^{-m} \qquad (4)$$

Figure 1 shows the time series of mortality rate and proportion of eggs that survive each day. The median mortality rate for the first half of the study period (18 Feb-10 Apr) was 0.46 d^{-1} and for the second half of the study period (23 Apr-9 July) was 5.3 d^{-1}. The median percentages of eggs dying per day for the same two periods were 37% d^{-1} and 99% d^{-1}.

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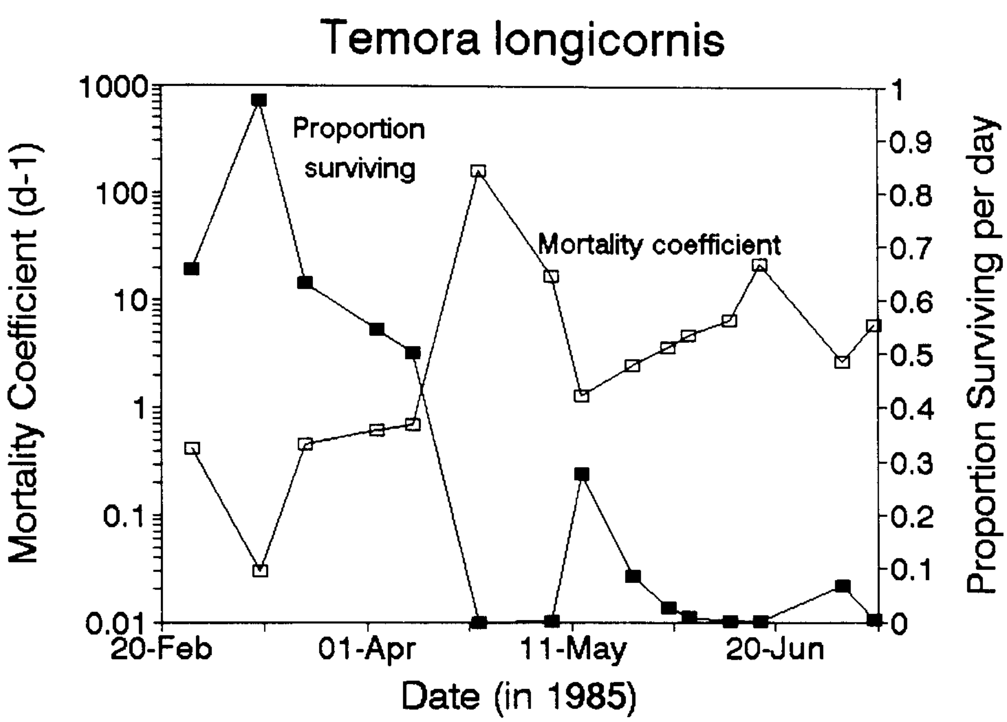

Figure 1. Temora longicornis*. Mortality coefficients (□) and proportion of eggs surviving each day (■), in Long Island Sound.*

Egg Mortality—(Cont. from page 4)

We are aware of three other data sets that could be used to calculate egg mortality rates: two of these data sets are published—Beckman and Peterson (1986) study of *Acartia tonsa* in Long Island Sound, and Van Rijswijk et al. (1989) study of *Temora longicornis* in the Netherlands, and one unpublished data set on *Calanus chilensis* off Chile, some of which were presented in Peterson et al. (1988). For Acart*ia tonsa* we found somewhat lower mortalities than in the *Temora longicornis* example above: mortality coefficients averaged -1.4 d^{-1} and survival, 48% d^{-1} (Figure 2). However for both the Van Rijswijk et al. (1986), and Peterson et al. (1988) data sets, we found positive mortality for most sampling dates. This means that there was either a surfeit of eggs or a deficit of females, a situation which could arise by advection of eggs into (or females away from) the sampling site. In both of these cases, the stations sampled were highly influenced by advection. The former was in a tidal creek in the Netherlands and the latter in the coastal upwelling zone near Talcahuano, Chile. Thus, the method we describe may only work in regions that are not highly advective, such as in Long Island Sound, fjords, and perhaps on submarine banks—such as Georges Bank or Agulhas Bank off South Africa—characterized by retention zones, or within a recirculating eddy.

A final note: it should be clear that one should not use the egg ratio method to estimate egg production rates in situ because the calculation is based on abundances of eggs and females in situ. Because of the possibility that eggs do not survive to hatch, the egg ratio method underestimates the true egg production rate by some unknown amount. Thus, the egg production data of Checkley (1980) and Peterson (1985), for example, should be interpreted with caution. *(Bill Peterson is a biological oceanographer and currently program manager of U.S. GLOBEC. Wim Kimmerer is a marine ecologist with Biosystems Analysis, Inc in Tiburon, California)*

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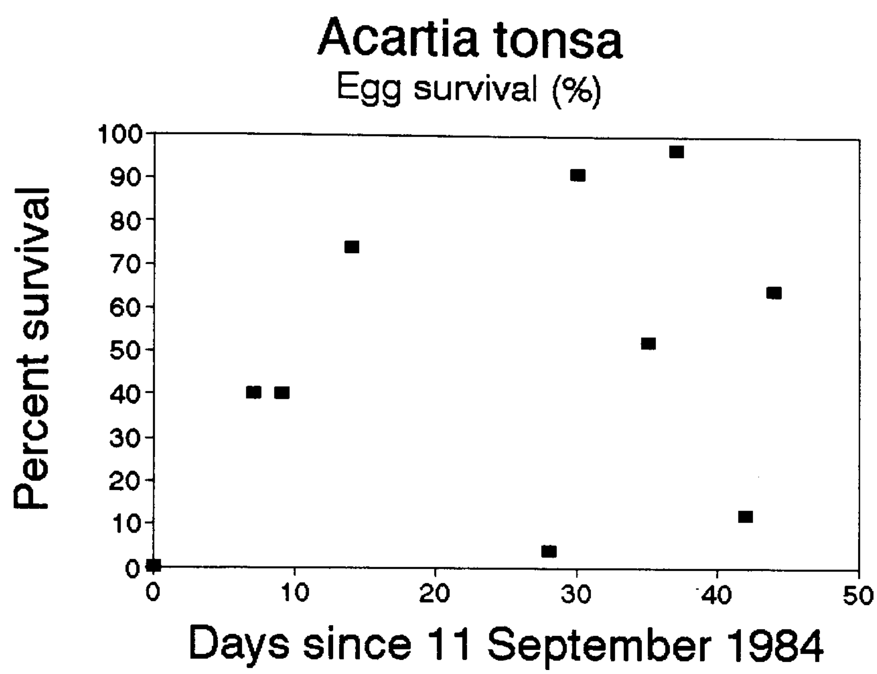

Figure 2. Acartia tonsa. Mortality coefficients for Acartia tonsa in Long Island Sound, calculated from data listed in Beckman and Peterson (1986).

(Editors Note: Technology Forum is intended to stimulate thought and discussion on diverse oceanographic technology issues. We welcome contributions on technological issues relative to ocean science, but particularly to U.S. GLOBEC.)

New 3-D Acousto-Optic Instruments for Small Scale Oceanic Measurements

by Jules Jaffe, Ed Reuss, Andrew Palowitch, Duncan McGehee and Girish Chandran

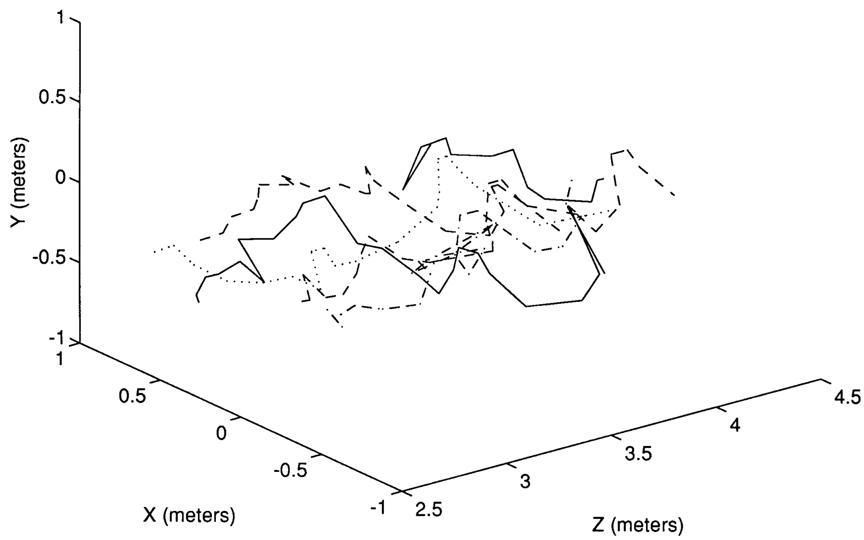

Figure 1. Six target tracks, reconstructed from an FTV sonar image.

Over the last several years, our research group in the Marine Physical Laboratory at Scripps Institution of Oceanography (SIO) has been developing several new underwater imaging systems for measuring both spatial and dynamic characteristics of underwater organisms. Our primary goal has been to create what we consider to be a "next generation" of ocean technology. To us, this means cameras that have fast repetition rates and good spatial resolution. We have been developing both sonar technology as well as optical methods in an effort to resolve phenomena on scales ranging from centimeters to meters (McGehee and Jaffe, 1993; Palowitch and Jaffe, 1992; Palowitch and Jaffe, in press). These include fine scale distribution of phytoplankton, behavior of zooplankton, interactions between zooplankton, and interactions between zooplankton and phytoplankton. We now have several working prototypes. In this article we describe our progress to date.

The use of sonar systems to look at zooplankton is certainly not new and various researchers have concentrated their efforts on using these tools both for broad survey and size characterization. Currently, two commercial systems, one manufactured by Biosonics (Seattle, WA) and the other by Simrad (Norway) are routinely used in both echocounting and echointegration studies. Although much has been learned from data processed from both of these systems, neither can count or track multiple organisms at high frame rates when target densities exceed even moderate amounts. Our efforts in developing new sonar systems have been dedicated to creating a system which has the capability of resolving, in both space and time, single organism tracks. From a technical point of view, the solution to this problem is clear: multibeam sonar imaging systems with high repetition, or frame, rates.

The system that we have designed to achieve the goal of both finer spatial resolution and more frequent sampling in time utilizes two arrays of eight sonar transducers each, to create a three-dimensional image of "targets" in the field of view of the sonar. One aspect of sonar imaging systems, similar to the type that we designed, is that the two cross range dimensions

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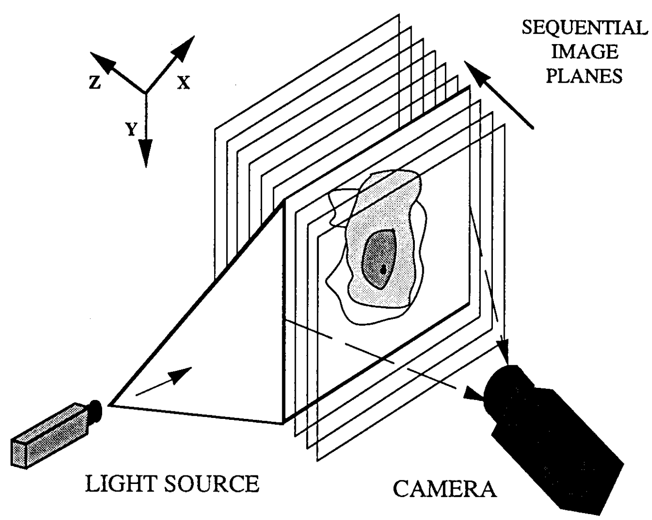

Figure 2. Components of the light stripe imaging system.

Acousto-Optics—(Cont. from page 6)

have fixed resolution in angle rather than distance. Our system, FTV (for Fish TV) has beams which are approximately 2 degrees by 2 degrees. In the third direction, range, the resolution is determined essentially by the "effective" pulse length. We are currently using a pulse which provides a range resolution of approximately 3 cm. The system operates at a frequency of 450 kHz.

At a distance of 4 meters, the system has resolution cells which are about 15 cm x 15 cm x 3 cm. The repetition rate of the system is variable, but can be as high as five frames s^{-1}. Since the system has eight two-degree by two-degree beams, it images a "wedge" of space which is 16 degrees by 16 degrees. The depth of the wedge can also be varied to a range as large as 20 meters. Presently, we have tested the system to a range of four meters; at this distance, a single 0.5 cm sized animal can be localized and tracked in three dimensions.

During the past year, the system has undergone numerous field tests. In one instance, we operated the system mounted on a Phantom IV ROV from the SIO RV *Robert Gordon Sproul*. The system was utilized to depths of 80 meters. Two deployment modes were used. In one mode, the ROV was raised and lowered in the water column to measure both the amount of scatterers and also their 3-dimensional spatial distribution. In the other mode, the system was kept at a fixed depth so that the trajectories of various targets could be measured. Figure 1 shows the result of processing 42 frames of data and the resultant trajectories of 6 euphausiid-like targets that were tracked simultaneously within the field of view of the system.

We have also been experimenting with some new methods which utilize structured lighting in order to characterize three-dimensional distributions of chlorophyll-a. Although structured lighting has been used before in underwater surveys, our idea to use it to map 3-dimensional distributions of phytoplankton appears to be novel. As illustrated in Figure 2, the technique consists of scanning a stripe of blue light, parallel to the image plane of a sensitive digital CCD camera. The resulting fluorescence induced from the incident illumination is then recorded. The stripe is then moved to a slightly different position, adjacent to the first beam, where another picture is taken, and so on. The resulting set of 2-dimensional images are then processed with an algorithm which computes the chl-a concentration in the 3-dimensional volume by taking into account the attenuation and the emission of light due to both the water and the chl-a.

Computer simulations and laboratory experiments performed with a two component system consisting of water and chl-a, indicate that the technique can resolve chl-a concentrations as low as 0.1 mg m^{-3} in volumes as large as a cubic meter with a spatial resolution of 1 cm. That is to say, a 1 cubic meter volume can be resolved into volumetric elements of 100 x 100 x 100 one centimeter cells. The primary limitation of the technique is the "low" level of light emission due to the fluorescence when compared with the relatively high attenuation of water in the emmited, or red wavelength. Other setups, which use only scattered light, and not the fluoresced emission may theoretically be used to image larger volumes.

Figure 3 shows the results of a lab experiment designed to characterize the system's capability in measuring chl-a concentration in a 3 component system. As illustrated, unfiltered seawater drawn from the SIO pier (chl-a

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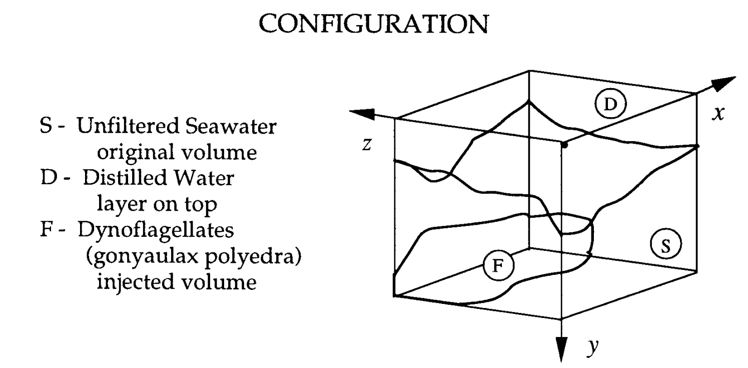

Chl *a* Concentrations (mg Chl a/m^3) Fluorometer Values				Calculated Voxel Values Near Sample Point (mg Chl a/m^3)
Sample	Before	Sample Point	After	
S	1.06	10,10,1	1.85	0.85 - 1.75
D	0.00	5,1,4	0.08	0.01 - 0.03
F	2.18	5,11,11	1.67	1.53 - 3.60

Figure 3a. Schematic diagram of the three-dimensional light imaging experiment and a table of results.

Acousto-Optics—(Cont. from page 7)

concentration of 1.06 mg m^{-3}) was injected with a volume of dinoflagellate culture measured at 2.18 mg chl-a m^{-3}. Then, a volume of warm distilled water was floated on top of the seawater. A 12 cm x 12 cm x 12 cm volume in the center of a larger test volume was selected for imaging. Serial section images were collected using the technique described above and then reconstructed. The accompanying 3-dimensional rendered volume (using Sunvision software) shows a projected view of the 3-dimensionally reconstructed volume. As illustrated in the figure and the accompanying table, good quantitative agreement was obtained between samples obtained from the volume and the calibrated samples.

In summary, we have presented two "new" types of imaging systems. We believe that the availability of this technology presents many opportunities in that they provide a view of the ocean that has never before been available. Both systems are aimed at obtaining the three-dimensional information (e.g., relationships of predator to prey and herbivore to food) which is important to the goals of the U.S. GLOBEC program. Perhaps one of the most exciting and new opportunities concerns our plans to use both systems together so that both animal trajectories as well as distributions of phytoplankton can be measured to learn about foraging strategies. *(The authors are members of the Underwater Imaging Group (headed by J. Jaffe) of the Marine Physical Laboratory at SIO).*

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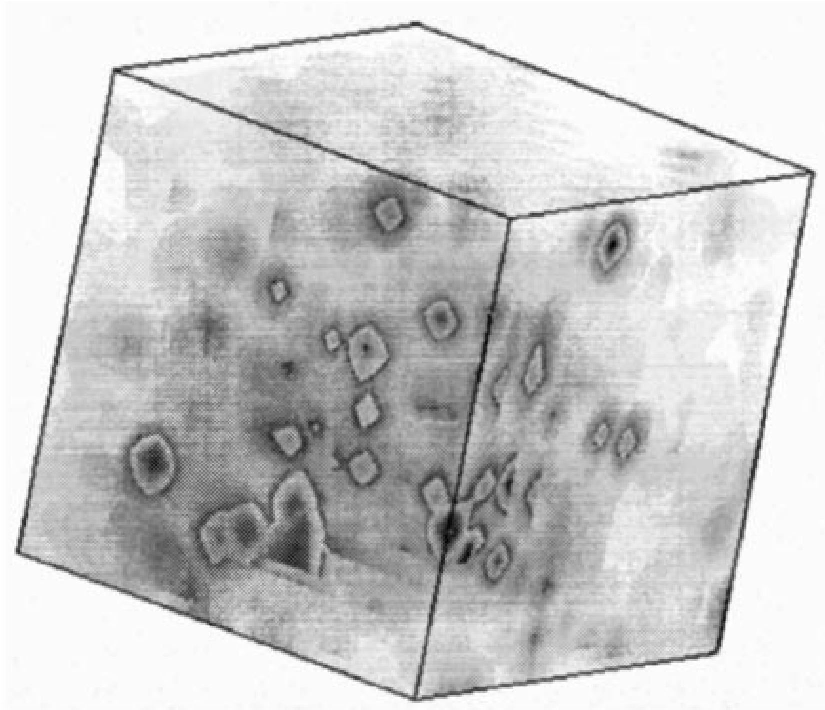

Figure 3b. Three-dimensional rendered volume of the inferred chl-a concentration.

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1994

19-22 April: Eleventh Annual PACLIM Workshop, Pacific Grove, CA. (Contact: W. Dean, U.S. Geological Survey, Box 25046, MS 939 Federal Center, Denver, CO 80225 (Phone: 303-236-5760; FAX: 303-236-0459; Internet: dean@sedproc.cr.usgs.gov)

5-9 June: International Association for Great Lakes Research (IAGLR) 1994 Annual Conference, Windsor, Ontario, Canada. Contact: G. Haffner, Great Lakes Institute, University of Windsor, Windsor, Ontario, Canada N9B 3P4 (Phone: 519-253-4232; FAX: 519-973-7050)

6-8 June: GLOBEC.INT Southern Ocean Implementation Meeting, Bremerhaven, Germany. Contact: Victor Smetacek, Alfred Wegener Institute, (Phone: 471-4831440; Fax: 471-4831149; Omnet: V.SMETACEK)

9-10 June: U.S. GLOBEC Scientific Steering Committee meeting, Corvallis, OR. Contact: H. Batchelder, Division of Environmental Studies, University of California, Davis, CA. (Omnet: H.BATCHELDER; Internet: hpbatchelder@ucdavis.edu; Phone: 916-752-2332; FAX 916-752-3350).

12-16 June: ASLO and PSA 1994 Joint Meeting, Miami, FL. Contact: A. Szmant, MFB, RSMAS, University of Miami, 4600 Rickenbacker Cswy, Miami, FL 33149 (Phone: 305-361-4609; FAX: 305-361-4600; Omnet: A.SZMANT; Internet: aszmant@rsmas.miami.edu)

14-16 June: International Symposium on Global Trends in Fisheries Management, Seattle, WA. Contact: E. Pikitch, School of Fisheries, WH-10, University of Washington, Seattle, WA 98195 (FAX: 206-685-7471)

20-24 June: Small Pelagics and Climate Change (SPACC) meeting, La Paz, Baja California, Mexico. Contact: J. Hunter, NMFS/NOAA, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038-0271 (Phone: 619-546-7127; FAX: 619-546-7003; Internet: john_hunter@ccgate.ssp.nmfs.gov)

22-25 June: The Crustacean Society Second Summer meeting, Portland, ME. Contact: L. Watling, Darling Marine Center, University of Maine, Walpole, ME 04573 (Phone: 207-563-3146; FAX: 207-563-3119; Omnet: MAINE.CMS)

18-22 July: GLOBEC.INT Strategic Planning Meeting, Paris, France. Contact: GLOBEC.INT Secretariat, CBL, University of Maryland, P.O. Box 38, Solomons, MD 20688 (Phone: 410-326-7211; FAX: 410-326-6987; Internet: freise@cbl.umd.edu)

19-22 July: The Oceanography Society Pacific Basin Meeting, Honolulu, HI. Contact: TOS, 1124 Wivenhoe Way, Virginia Beach, VA 23454 (Phone: 804-496-8958; FAX: 804-496-8960; Omnet: OCEANOGRAPHY.SOCIETY)

15-18 August: ICES Symposium on Zooplankton Production: Measurement and Role in Global Ecosystems and Biogeochemical Cycles, Plymouth, U.K. Contacts: R. P. Harris, Plymouth Marine Laboratory, or J. C. Gamble, Sir Alister Hardy Foundation for Ocean Science, Prospect Place, Plymouth PL1 3DH, UK (Omnet: PML.UK or J.GAMBLE.CPR; Phone: + 44 752 222772; FAX +44 752 670637)

19 August: GLOBEC International and ICES Cod and Climate Change Mini-symposium, Plymouth, U.K. Contact: B. Rothschild, CBL, University of Maryland, Solomons, MD; Phone: 410-326-7289; FAX: 410-326-6987; Omnet: B.ROTHSCHILD; Internet: broth@cbl.umd.edu)

22-24 August: ICES/GLOBEC.INT Aggregation Workshop, Charlottenlund, Denmark. Contact: Michael St. John or Brian MacKenzie, Danish Institute for Fisheries and Marine Research (Phone: 45-339634; FAX: 45-3393434; Internet: msj@fimdfh.fim.dk (M. St. John) or brm@fimdfh.fim.dk (B. MacKenzie))

6-8 September: First International CEOS Meeting, Monterey, CA. Contact: R. Mendelssohn or P. Cury, PFEG, P.O. Box 831, Monterey, CA 93942 (Phone: 408-656-3311; FAX: 408-656-3319)

22-30 September: ICES Annual Meeting, St. John's, Newfoundland, Canada. Contact: ICES Secretariat, Palægade 2-4, DK-1261, Copenhagen, Denmark (Phone: 33 15 70 92; FAX: 33 93 42 15; Omnet: ICES.DK)

6-7 October: U.S. GLOBEC Scientific Steering Committee meeting, Washington, DC. Contact: H. Batchelder, Division of Environmental Studies, University of California, Davis, CA. (Omnet: H.BATCHELDER; Internet: hpbatchelder@ucdavis.edu; Phone: 916-752-2332; FAX 916-752-3350).

10-14 October: International symposium on the assessment, yield, and long-term sustainability of large marine ecosystems of the Pacific. Qingdao, China. Contact: Q.

(Cont. on page 11)

Calendar—(Cont. from page 10)

Tang, Yellow Sea Fisheries Research Institute, 19 Laiyang Road, Qingdao 266003 P.R. China (FAX: 0086-532-270702; Phone: 0086-532-2869103)

15-17 October: GLOBEC.INT Workshop at Annual PICES Meeting, Nemuro, Japan. (Contact: PICES Secretariat or GLOBEC.INT Secretariat, see other items on calendar)

15-24 October: Third Annual Meeting of the North Pacific Marine Science Organization (PICES), Nemuro, Hokkaido, Japan. Contact: PICES Secretariat, c/o Institute of Ocean Sciences, P.O. Box 6000, Sidney, B.C., Canada V8L 4B2 (Phone: 604-363-6366; FAX: 604-363-6827; Internet: pices@ios.bc.ca; Omnet: PICES.SEC)

24-28 October: Symposium on the Biology and Ecology of Northwest Atlantic Cod, St. John's, Newfoundland, CANADA. Contact: Symposium Organizer, Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, Newfoundland A1C 5X1, CANADA (Phone: 709-772-2051; FAX: 709-772-6100)

26-28 October: International Symposium on North Pacific Flatfish, Anchorage, AK. Contact: B. Baxter, Alaska Sea Grant College Program, University of Alaska Fairbanks, Fairbanks, AK 99775-5040

1995

May (tentative): Living Resources of the Azov-Black Seas and their Rational Use, Kerch, Crimea, Ukraine. Contact: V. Yakovlev, Director, YugNIRO, 2 Sverdlov Street, Kerch 334500, Crimea, Ukraine (Phone: (06561) 210-65; FAX: (06561) 215-72; Internet: jug!niro@mastak.msk.su)

12-16 June: ICES International Symposium on Fisheries and Plankton Acoustics, Aberdeen, Scotland. Contact: E. J. Simmonds, Marine Laboratory, P.O. Box 101, Victoria Road, Aberdeen, Scotland AB9 8DB, United Kingdom (Phone: +44 224 876544; FAX: +44 224 295511) ΔΔΔ

Genetics—(Cont. from page 2)

cally meaningful groups become challenging problems. Given the density of population genetic information in the future, such computations will likely require routine use of supercomputers. There is need also to develop new theory for gene phylogenies at the intraspecific level so that the causes of discordant phylogeographic patterns among different classes of molecular markers can be interpreted. Finally, genetic and organismal information from U.S. GLOBEC studies should be entered into perpetual data sets that can serve as the basis for detecting long-term trends or shifts in biodiversity. *(Dennis Hedgecock is with the Bodega Marine Laboratory, University of California, Davis, and is a former member of the U.S. GLOBEC Scientific Steering Committee.)*

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Utter, F. and N. Ryman. 1993. Genetic markers and mixed stock fisheries. Fisheries, 18, 11-21.

Waples, R. S. and P. E. Smouse. 1990. Gametic disequilibrium analysis as a means of identifying mixtures of salmon populations. American Fisheries Society Symposium, 7, 439-458.

Ward, R. D., D. O. F. Skibinski, and M. Woodwark. 1992. Protein heterozygosity, protein structure, and Taxonomic differentiation. Evolutionary Biology, vol. 26, M. K. Hecht et al. (Eds.), Plenum Press, pp. 73-159. ΔΔΔ

Boom and Bust May Be the Norm in Nature, Study Suggests

New York Times Article, March 15, 1994

Unperturbed environments can see wild swings.

By CAROL KAESUK YOON

From sudden plagues of locusts to mysterious declines in sought-after creatures like the Dungeness crab, the booms and busts of nature have puzzled researchers. A new study suggests that scientists may sometimes have difficulty finding an environmental cause for these fluctuations simply because there is not one.

In the study published last month in the journal Science, researchers at the University of California at Davis found evidence that many animals, even when they are unperturbed by unusual weather or any other alterations in their environment, can undergo wildly unpredictable changes in their numbers.

Using a very simple computer model inspired by the life cycle of the Dungeness crab, the researchers found that instability and change are the rule for these animals rather than the exception, that their population numbers whirl along through time, never settling down, even after tens of thousands of generations. The results, they say, suggest that nature is more unpredictable and unstable—and difficult to study—than researchers had guessed.

"It's an important finding," said Dr. Robert May, the Royal Society Research Professor at Oxford University, who is considered a pioneer in introducing chaos theory to ecology. "It's an important insight clarifying the magnitude of the job ahead of us."

'Such Complex Behavior'

Dr. Simon Levin, the Moffett Professor of Biology at Princeton University and director of the Princeton Environmental Institute, called the results fascinating. Because the model was based on "one of the simplest equations you could write down, I wouldn't have expected such complex behavior"

Researchers found that knowing how these populations change over a few or even a few hundred generations allows no insights into the populations' past or future behavior. This presents a thorny problem for field ecologists and natural resource managers. Aiming to understand and often to control population fluctuations in the wild, these scientists may be at a loss because they often have just a few summers to do their work.

Inspired by the biology of the Dungeness crab the researchers modeled a world in which one might expect simplicity if ever it were to be found. Along a theoretical coast, adults produce young, which disperse from one of hundreds of subpopulations to others, where the young form new groups of adults, which produce young the next year, and so on. When there are too many or too few adults in one subpopulation, that group produces fewer juveniles for the next generation. But the environment never changes.

Despite the model's simplicity, over time the total number of individuals along the coastline fluctuated wildly.

Most disturbing of all, total population numbers could remain steady for thousands of generations, then without warning suddenly boom or crash. They could even cycle nicely up and down, then revert to chaotic behavior—and back and forth—over as many as 20,000 generations. Because no environmental changes are allowed in the model, the only causes for the increases and decreases are the internal dynamics of the population, like migration or competition for food or space.

"We were very surprised by what came out," said Dr. Alan Hastings, a professor and the chairman of the division of environmental studies at the University of California at Davis who wrote the paper with Kevin Higgins, a graduate student. And with environmental perturbations added, Dr. Hastings predicted, the chaotic behavior would last even longer.

Though inspired by the biology of the Dungeness crab, whose young can disperse widely along a coast, researchers said these dynamics could be expected of any quickly reproducing animal with a sedentary life phase and

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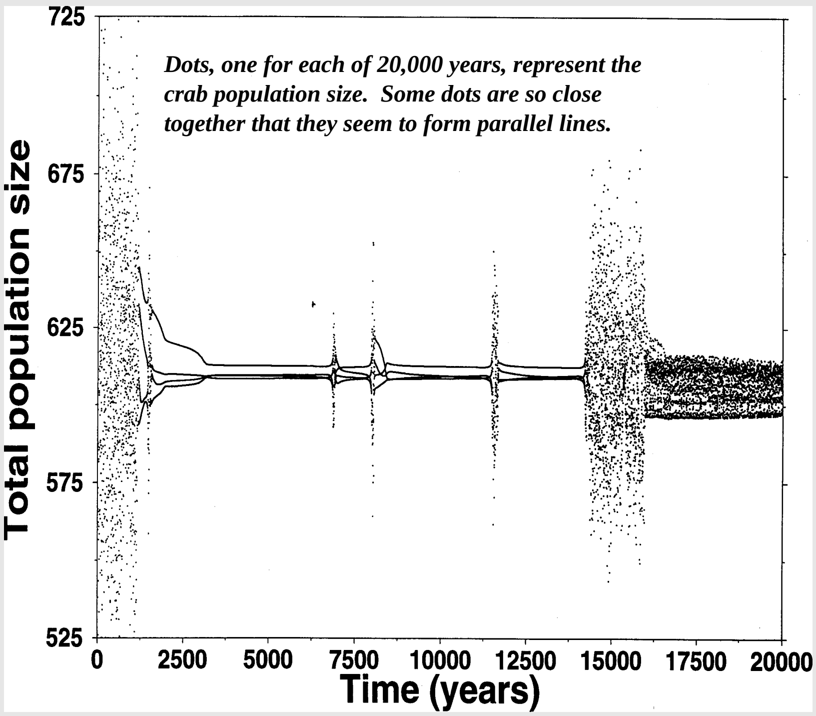
The work described by the Times article is part of a larger U.S. GLOBEC project to understand the population dynamics of organisms with pelagic larvae. The overall aim has been to combine the mechanism of larval movement and settling, as affected by the California Current, with dynamics of populations distributed along the Pacific coast. The ultimate goal is to understand the population dynamics of species such as the Dungeness crab and sea urchin in space and time. Thus our modeling efforts have focused on two different time scales: the scale of a few months corresponding to larval movement within a given year, and the time scale of years (or many years) corresponding to population dynamics, with larval movement, i.e., redistribution, as an input.

In our attempts to understand population dynamics over the scale of many years, we have uncovered behavior of unforeseen complexity, which will change our view of the dynamics of species distributed along coastlines, as described in the accompanying reprinted news article. We strongly believe that the more descriptive modeling approaches we have used are absolutely necessary within the context of a program aimed at understanding specific systems such as the California current—the uncovering of general principles is needed to understand specific models of complex systems.—*Alan Hastings, University of California, Davis, CA.*

Natural Population Variations: Simple Assumptions, Complex Results

To make this computer model of the varying population of crabs, only a few assumptions are fed into the program: 1. Intermediate numbers of adults produce the most larvae, with few adults producing few larvae and many adults also producing few larvae, because of competition and cannibalism. 2. The adults die after reproducing. 3. Most larvae remain near their point of origin, with fewer and fewer of them moving farther and farther away. The results show the high degree of natural volatility, environmental forces aside, in a population.



Boom and Bust—(Cont. from page 12)

a dispersing life phase, including many marine creatures, insects and even some small mammals like mice or voles.

"Of course from a pest insect point of view, it's a real problem," said Dr. William Murdoch, a population ecologist at the University of California Santa Barbara. "If this is really what real populations are like, it presents a big difficulty in analyzing and predicting how they're going to behave. It makes things even harder than they were before."

Useful Study, Despite Questions

Dr. Louis W. Botsford, a professor of wildlife and fisheries biology at the Davis campus, said that while it remains unclear how to translate the findings into management practice, the study is useful since it provides a new potential explanation for the mysterious booms and busts to which many marine creatures are subject.

For example, he said, in the late 1950's, the crab population in central California declined from a catch of 12 million pounds a year to less than 1 million pounds. On the other hand, in the last few years, lobster catches in Maine have been about 50 percent higher than usual for no obvious reason, reaching a high for the century in 1990.

Researchers said they have tended not to focus on populations' unpredictable and transient behavior but on their anticipated end-point behavior, that distant time when populations become more stable, reaching some equilibrium. But the new study suggests that for some animals, it can take so long to reach any kind of stability that there is no point in worrying about the end state.

The study is the latest in a growing body of work that is forcing ecologists to turn away from their comforting equilibrium models of the world. Nature, the data seem to insist, is in a state of constant flux and turmoil.

"The important message," said Dr. Peter Turchin, a research ecologist at the Southern Forest Experiment Station in Pineville, La., "is that the transient behavior becomes the end point, so to speak. So instead of focusing on long-term equilibrium behaviors, we should pay a lot of attention to how they get to that point. That may be more important."

It's Not all Bad

Some biologists cautioned that the new study, while a useful tool for understanding how populations might behave under some conditions, does not mean all populations are doomed to instability. How much of a role these dynamics play in the real world, they said, remains to be seen.

In any case, the news that nature is more unpredictable and unstable than researchers had thought is not necessarily all bad.

"The recognition that systems are not at or very close to equilibrium certainly complicates the world view of some people who are trying to manage systems," Dr. Levin said. "On the other hand, I think it's a hopeful fact for people managing for biodiversity maintenance."

He explained that it is just this kind of instability and transience that keeps species that might dominate under stable conditions from being able to do so, allowing many more species to persist. "The overall consequence," he said, "is the maintenance of much higher levels of diversity by orders of magnitude because of a constant regeneration of opportunity."

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International Symposium on Fisheries and Plankton Acoustics

This symposium, organised by the International Council for the Exploration of the Sea (ICES) will be held at the Aberdeen Conference and Exhibition Center, Aberdeen, Scotland from 12-16 June 1995.

Objectives and Scope

Acoustics has been used extensively for observation and measurement in oceans, lakes, and rivers. Scales of study extend from a few centimetres to hundred of kilometres, and from individual organisms to entire populations of fish or plankton. Acoustics provides a means to obtain continuous observation and assessment of underwater resources. There are many common problems and requirements in the use of underwater acoustics for aquatic studies. This Symposium will provide a forum for the presentation and discussion of a wide range of topics relevant to the use of acoustics for the study of fish, shellfish, micronekton, and plankton. This will be the fourth in a series of Symposia on acoustics sponsored by ICES, with previous ones being held in Bergen in 1972 and 1982 and in Seattle in 1987.

The 1995 Symposium will review and discuss the developments in technology and understanding of acoustic methods in the aquatic environment. Particular emphasis will be on improvements in techniques, development of technology, assessment of current problems, and identification or future directions for study. Papers reporting ongoing research, as well as those identifying areas for development, are invited on the following themes:

1. Acoustic survey design and data analysis methods for pelagic and demersal fish stocks and for survey techniques which combine data from different sources. Methods for estimating precision, bias in acoustic surveys, and the effects of spatial or temporal change. The use of ancillary variables such as water temperature, salinity, or plankton distributions in survey design and data analysis. Papers which only report survey results will not be included in plenary sessions, but those dealing with the validation of survey results will be welcomed.

2. Near-boundary problems. Studies of near-surface and sea bed measurement problems, including investigations of both aquatic organisms and their habitat. Acoustic observation and classification of sea or river bed in relation to biological phenomena. Observation of fish in situations where the interference between echoes from targets and boundaries is important.

3. Multi-dimensional acoustics, including studies with instrumentation specifically designed for 3D observation and methods that require reconstruction using data from electronic and mechanical scanning systems or sequential observation. Observations on fish schools, and spatial relationships between predators and fish.

4. Signal classification and identification procedures, including both acoustic observation methods and statistical techniques for classification of targets. Object size and shape characterization from systems. Wideband or multi-frequency methods particularly for target sizing and species identification.

5. Biology, including acoustic observation of behaviour, and studies of physiology using acoustics. The effects of sound on fish, including explosive shock waves and infra-sound, studies of fish hearing and the sounds generated by fish.

6. Target-strength measurement, data collection, methodology, and analysis techniques, and the use of models. Target-strength studies of fish, plankton, and micro-nekton. Target-strength distributions and relationships with target aspect and behaviour.

7. Validation and comparison of acoustic and other methods of assessment of fish, micro-nekton, and plankton.

Preference will be given to recent innovative research or validation of established methods. Papers on particular topics whether on techniques, technology, methodology, analysis, or results will be included in the same sessions.

Structure and Organization

The Symposium will be organized in consecutive plenary sessions, arranged by defined topics, at which contributed papers will be presented and discussed. Papers will be limited to a maximum of two per author and there will be a maximum of 100 presented papers. In addition a number of poster sessions will be organized for contributions more suited to this method of presentation. These sessions will be introduced with brief descriptions of each poster. The Symposium will be conducted in English.

Manuscripts

A Second Announcement and call for papers will be issued in early 1994 giving full instructions on the submission of titles, abstracts, and manuscripts, including the deadlines for publication. It is intended that selected contributions will be published, following peer review by ICES.

Participation

The Symposium, for which there will be a nominal registration fee (to be specified in the Second Announce-

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Acoustics Symp.—(Cont. from page 14)

ment), will be open to all interested scientists who announce their participation to the Convener by not later than 31 March 1995. Further information on the venue, hotel accommodation, and other practical matters will be provided following announcement of participation. Those wishing to be included on any subsequent mailing lists should notify the Convener.

For further information, publication, registration and accomodation please contact the convenor:

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First International CEOS Meeting

The Climate and Eastern Ocean Systems (CEOS) program will hold its first international meeting in Monterey, California on 6-8 September 1994. The meeting is being sponsored by the National Oceanic and Atmospheric Administration (NOAA) and the Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM). CEOS is a cooperative international research effort studying the potential effects of climate change on the living resources of the highly productive eastern ocean upwelling ecosystems and on the ecological and eonomic issues directly associated with such effects. One goal of the program is to attempt to separate local short-term changes in the resources or dynamics of these upwelling systems from long-term, climatic global changes. It was planned from the inception of CEOS to have meetings, such as the one planned for Monterey, to provide a forum for the exchange of results and ideas. Contacts for additional information are the organizers, Roy Mendelssohn and Philippe Cury, both at PFEG, P.O. Box 831, Monterey, CA; Phone: 408-656-3311; Fax: 408-656-3319). ΔΔΔ

SPACC Meeting

At their January 1994 planning meeting, the Steering Committee of GLOBEC.INT recognized SPACC, a project on "Small Pelagics (fish) and Climate Change", as a new element of the GLOBEC International Program. The objective of SPACC is to better understand the impact of climate change on pelagic fish population dynamics through comparisons among ecosystems supporting these populations. The goals are to:

- describe the characteristics and variability of the physical environment, zooplankton population dynamics and their effect on pelagic fish stocks such as sardines, anchovies, and sprats in key ecosystems

- improve existing knowledge on the nature and causes of long-term changes in these ecosystems.

The program is multidisciplinary involving climatologists, paleoecologists, physical and biological oceanographers, modelers, geneticists and fishery scientists. The scientific approach is to conduct comparative studies of biophysical processes in the sea using direct field measurements, analysis of long-term time series and paleoecological techniques.

A meeting will be held in La Paz, Baja California, Mexico from June 20-24, 1994 to develop a science plan on how SPACC will be implemented. Local host for the meeting is Dr. Daniel Lluch-Belda (Phone: 52-112-53633; Fax: 52-112-53625). For further information about this meeting contact one of the co-chairs (John Hunter, NMFS, La Jolla, CA, Phone: 619-546-7127, Fax: 619-546-7003, Internet: john_hunter@ccgate.ssp.noaa.gov; or Jürgen Alheit, Baltic Sea Research Institute, Rostock University, D-18119 Warnemunde, Germany, Phone: 49-381-5197208, Fax: 49-381-5197440) ΔΔΔ

U.S. GLOBEC

GLOBAL OCEAN ECOSYSTEMS DYNAMICS

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