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A Coupled Individual-Based Trophodynamics and Circulation Model for Studies of Larval Cod and Haddock on Georges Bank

by Francisco E. Werner, R. Ian Perry, R. Gregory Lough and Daniel R. Lynch

This year, 1994, marks the 80th anniversary of the publication of a landmark paper in the study of marine fish population dynamics. In 1914, Hjort outlined two of the dominant hypotheses that continue to guide research into the causes of fluctuations in fish populations: 1) recruitment variability is governed by food-limitation of the larval stages; and, 2) recruitment variability is regulated by the supply of larvae (mediated by the physical circulation) to or from their appropriate distributional area. These hypotheses have been examined for cod and haddock on Georges Bank, with evidence suggesting food-limitation at times and for certain areas (Buckley and Lough 1987), and other studies finding that advection off the Bank is limited by the gyral circulation and the development of frontal zones on the northern and southern flanks (Smith and Morse 1985). However, these two processes have rarely been examined simultaneously.

Recent modeling efforts of Werner et al. (1993) and Lough et al. (1994) have focused on the Bank's circulation as it affects the distribution and transport of larvae spawned on the Bank. These studies identify a range of conditions (strength of physical forcing, spawning location, position in the water column, etc.) that result in larvae being retained on the Bank or advected to neighboring regions. We are extending our model-based studies to include trophodynamic aspects related to the feeding and growth of individual larvae within their broad-scale transport and distribution by the circulation. Our approach is to use an individual-based model (IBM) of larval fish trophodynamics coupled with a 3D circulation model on realistic topography. The essence of IBMs is a recognition that biological entities are not all equal (see Mangel and Clark, 1988; DeAngelis and Gross, 1992), and that variation can occur in egg quality, hatch size, prey encounter rates, prey capture success, predation risk, etc. Variation at each stage affects the ability of individuals to feed, grow, and survive. As a result, for example, the final frequency distribution of the sizes of survivors can be radically (and nonlinearly) different from the initial size distribution.

The core of our model is the ability to represent growth as the difference between the amount of food absorbed by a larva and the metabolic costs of its daily activities. This approach was introduced by Beyer and Laurence (1980 and 1981) in studies of winter flounder and Atlantic herring larvae. The food ingested is a function of such processes as the number of prey encountered, captured, eaten, and excreted, while the metabolic costs are a function of larval size, ambient temperature, swimming speed, etc. Larvae are assumed to die (of starvation) if their weight falls below a prescribed "death barrier". Using trophodynamic relationships derived from laboratory studies on the physiology and growth of Atlantic cod and haddock eggs and larvae, Laurence (1985) presented a model which included individual variation in hatch-size, prey density, prey size, and

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Coupled Model—(Cont. from page 1)
prey encounter rate.

We have extended Laurence's trophodynamic model by coupling it to a 3D circulation model on the realistic topography of Georges Bank. The circulation (Naimie et al. 1994) is used to derive trajectories for the transport of larvae (Werner et al. 1993), and their location each day determines the amount of food available based on the ambient prey concentration. At the present stage of model development, prey concentrations within appropriate size classes—which include *Pseudocalanus* spp. and *Calanus finmarchicus* eggs, nauplii, copepodite stages CI-CV and adults—are based on May plankton data from Laurence (1985) and February-March plankton data from Davis (1984 and 1987) and prescribed as "frozen" in time and vertically homogeneous within three regions of the Bank: northern flank, northeast peak, and the southern flank (Fig. 1). Present randomizations for individual larvae include the number of prey encountered each day (determined as a random deviate from a negative binomial distribution to represent prey patchiness; e.g., Winemiller and Rose 1993), and the success in capturing and ingesting the encountered prey (determined as a random deviate from a binomial distribution; Beyer and Laurence 1980). The contagion parameter in the negative binomial distribution, set to 1 in the examples shown here, defines the level of prey patchiness. Values on the order of 10 simulate encounters with randomly distributed prey and approximate a Poisson distribution (variance equal to the mean); decreasing values of the contagion parameter simulate greater patchiness (increased variance). In contrast to Laurence's formulation in which ingestion of a preferred prey size is considered, the prey biomass ingested by the larvae in our model is a combination of the eight specified prey items, with proportions of the ingested prey items determined by Kane's (1984) analysis of the gut contents of cod and haddock larvae.

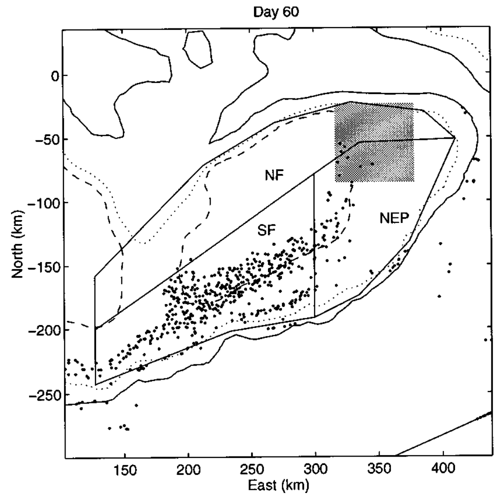

Figure 1. Particle locations on Georges Bank 40 days post-hatch (60 days post-spawn); the particles were fully passive. The flow field used to compute the particle trajectories is that described by Naimie et al. (1994) for climatological March-April conditions. The northern flank (NF), the Northeast Peak (NEP) and the southern flank (SF) prey (polygonal) regions/sectors are outlined; the spawning grounds are indicated by the shaded square. Isobaths are 60 m (dashed line), 100 m (dotted line) and 200 m (solid line).

Spawning is assumed to occur on the northeast peak, and the larvae drift passively southwestward with the circulation (Fig. 1). When all cod larvae are identical at hatch (specified here as the mean size at day 0 observed by Bolz and Lough 1988) and experience any of the prey densities prescribed within the three regions (deterministic case, Fig. 2), no larvae remain alive on the Bank after three days, with approximately a 10% loss of cod from the Bank during the egg stage due to the circulation. When the number of prey encountered and ingested by a larva are allowed to vary randomly about their expected values, such that (conceptually) some larvae encounter higher prey densities and some experience greater success at capturing and ingesting prey (stochastic

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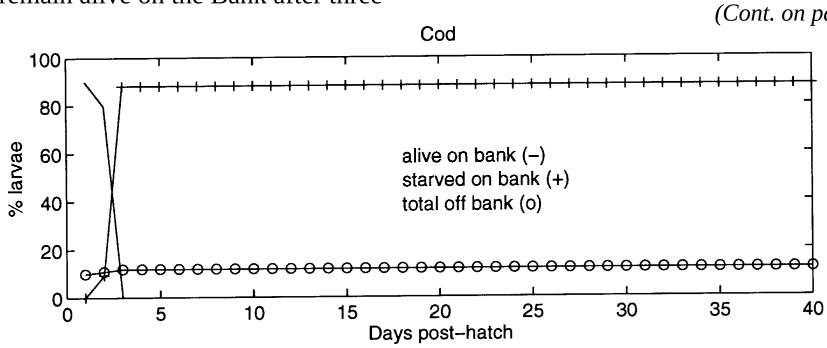

Figure 2. Post-hatch time history of the percentage of cod larvae alive and starved on-Bank, and advected off the Bank for the deterministic case.

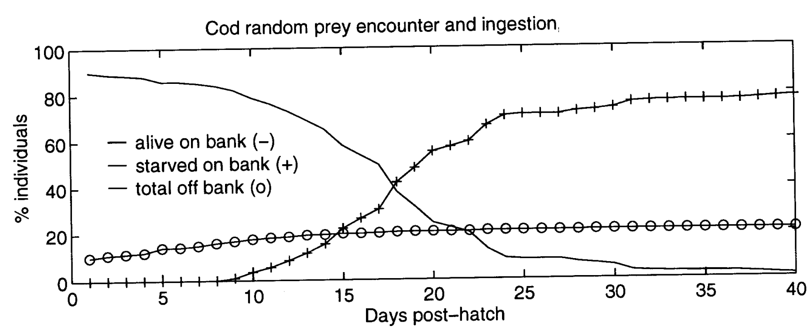

Figure 3. Post-hatch time history of cod larvae with random prey encounter and ingestion, showing the percentage of larvae alive and starved on-Bank, and advected off the Bank.

Coupled Model—(Cont. from page 2)

case, Fig. 3), the results are quite different. A small percentage of larvae now survive for the entire 40 day simulation with a marked increase in the mortality due to starvation on the Bank between 15-25 days post-hatch. However, at the food densities defined in the model, all larvae remain very small (less than 5 mm in length or 50 µg in weight) after 40 days. The proportion of larvae lost off the Bank due to the circulation is about 20%, most of which occurs within the first 15 days post-hatch.

To achieve the growth rates (in weight) of about 10% per day that have been observed for cod on Georges Bank over the first two months by Bolz and Lough (1988) required a five-fold increase of the densities of the smallest prey items (eggs, nauplii, and copepodite stages C-I and C-II), illustrating the sensitivity of prey availability at first feeding. This factor is within the range of variability for estimates of zooplankton prey densities on Georges Bank, particularly during spring (Lough 1984). A survival rate of about 50% on the Bank was obtained in the deterministic case, with approximately equal losses due to starvation and advection off the Bank (Fig. 4), while in the stochastic case, on-Bank survival of about 70% was obtained, with almost all losses due to advection of larvae off the Bank, i.e., with less than 1% loss due to starvation. The trajectories and the amount of time spent in the various regions by the surviving larvae are also important in determining growth rates and larval sizes to day 40. For example, the resulting size distribution of cod larvae at the end of the deterministic simulation (Fig. 5) arises from the differing lengths of time spent by the larvae in the northeast peak and southern flank regions. The largest larvae (corresponding to those between 1500-3000 µg in Fig. 5) are those that spent the longest time in the northeast peak region, which was assigned to have a high proportion of small prey. The smaller larvae (associated with the mode centered at roughly 200 µg) are those that spent 20 days or more in the southern flank region, which had a lower proportion of small prey.

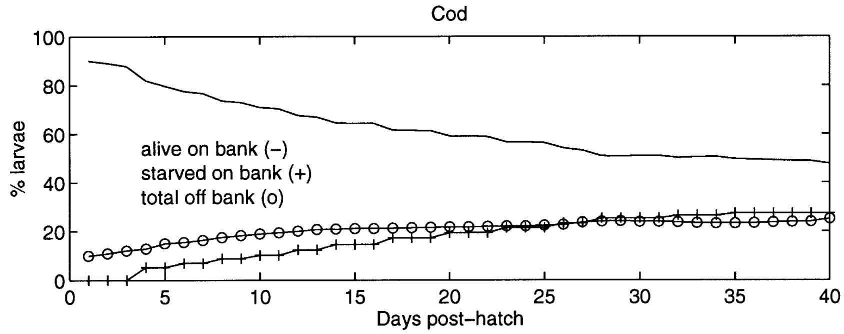

Figure 4. Post-hatch time history of cod larvae in the deterministic case with a five-fold increase of egg, nauplii, C-I and C-II prey items showing the percentage of larvae alive and starved on-Bank, and advected off the Bank.

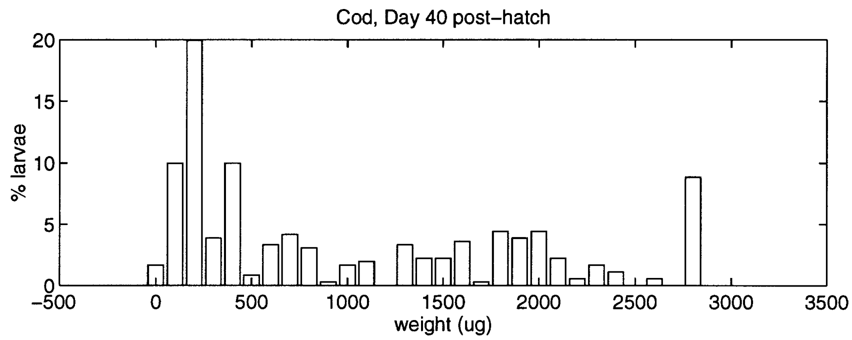

Figure 5. Weight distribution (µg) at day 40 for live cod larvae in the deterministic case with a five-fold increase of egg, nauplii, C-I and C-II prey items.

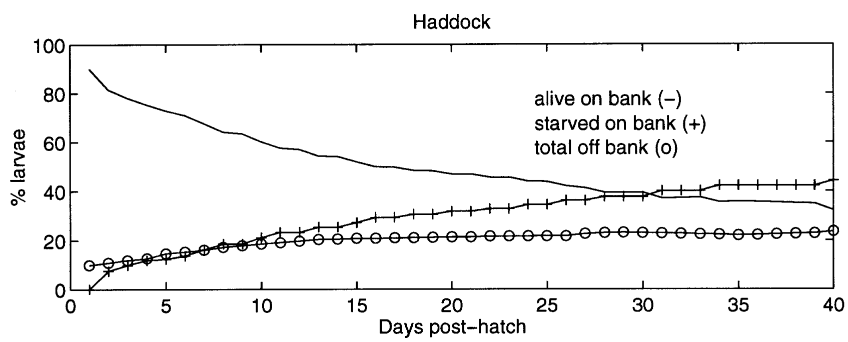

Figure 6. Post-hatch time history of haddock larvae in the deterministic case with a fifteen-fold increase of egg, nauplii, C-I and C-II prey items showing the percentage of larvae alive and starved on-Bank, and advected off the Bank.

The sensitivity of haddock to low prey densities and its contrast with cod is illustrated in Figure 6 where the results of a fifteen-fold increase of the prey field is shown. Growth rates close to those observed for Georges Bank haddock (Bolz and Lough 1988) were achieved at these prey densities, which also produced a 30% survival rate of haddock larvae on the Bank (Fig. 6). No haddock survived on the Bank in the deterministic case when the prey concentration was increased by a factor of ten. The effect of random prey encounter and prey ingestion at these increased prey densities (not shown)

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Marine Birds in the California Current Ecosystem: Contributions to U.S. GLOBEC's Goals

by William J. Sydeman and David G. Ainley

One of U.S. GLOBEC's principal goals is to forecast how climate change will influence the population biology of marine organisms. Linking measurements of physical oceanography (such as the intensity of yearly upwelling) with demographic parameters (such as growth, mortality, and reproduction) of marine species is required to understand the potential effects of climate change on animal populations. Moreover, a third link, information on oceanic habitat use, foraging ecology, and diet of marine animals is needed to develop mechanistic relationships between environmental conditions and population dynamics. These types of data are extremely rare, available for only a handful of marine species worldwide.

A Top-Down or Bottom-Up Approach?

In the California Current Marine Ecosystem, a 24-year time-series on 12 species of seabirds from the Farallon Islands provides one of the most detailed datasets available on upper trophic-level predators in marine systems. Although U.S. GLOBEC has selected zooplankton as featured organisms, the effect of climate change on upper trophic-level animals is important and tractable. Moreover, as integral components of the marine system which are highly visible to an environmentally conscious human population, and as consumers responsive to variation in prey (fish and zooplankton) populations, seabirds can tell us much about the status of the marine environment and certain key zooplankton and fish species.

Our research program, designed to provide mechanistic understandings of seabird population ecology as affected by local prey populations and remote ocean climate was initiated in 1971. At the onset, we knew that long-term research would be needed to adequately assess temporal variability. Our study site, Southeast Farallon Island, is a small granitic island 47 km west of the Golden Gate Bridge where we have staffed a field station daily in a joint venture with U.S. Fish and Wildlife Service. Here, marine birds number in the hundreds of thousands. Each year, we have collected data on the physical environment (such as wind strength and direction and seawater salinity and temperature) and ecology of the birds (including foraging effort and diet, egg and clutch size, reproductive success, adult and juvenile survivorship, chick growth, and annual population size). Studies of foraging ecology indicate that the birds sample a 4000 km^2 area from Point Reyes to Santa Cruz and out 100 km from the coast. Within this region exist two recurring upwelling plumes/eddies, one produced off Point Arena and Point Reyes, and the other off Point Año Nuevo. Birds at this site are therefore exposed to ocean structures of great interest to U.S. GLOBEC.

Through collaborative efforts with NMFS biologists (Tiburon Laboratory) and oceanographers (PFEG), we have investigated causal relationships among physical variables and seabird diet and demography. As an introduction, it is instructive to illustrate values of sea-surface temperature (SST) taken by PRBO staff at the Farallones throughout the study period (Fig. 1). First, SST has generally increased from the early 1970s to the early 1990s; a polynomial regression of monthly mean SST against year was significant ($P < 0.05$). Second, interspersed within the long-term record are obvious warm-water years associated with the 1982-83, 1986-87, and 1992-93 ENSO events (shown by a cubic spline). Other warm water conditions in 1973, 1976, and 1978 are also evident, but their peaks are suppressed in this graphic owing to the calculation of an anomaly statistic based upon grand monthly means for the entire study period. The trends in SST are consistent with those of shore sites along the California coast.

In relation to sea temperature, we examined the timing of reproduction for each species using the mean date of clutch (egg-laying) initiation.

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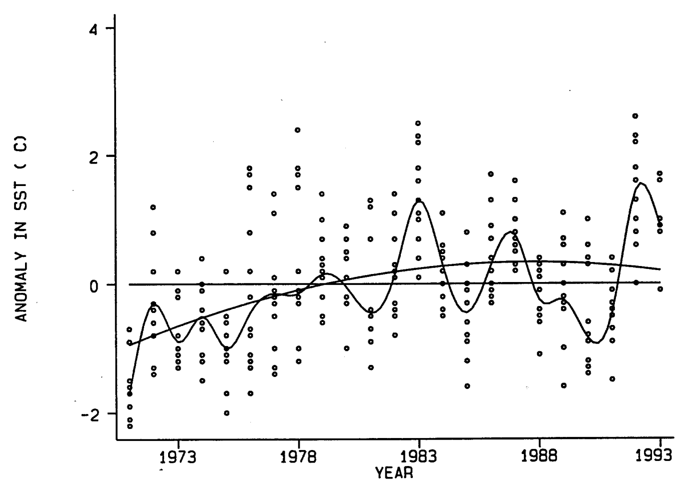

Figure 1. Sea-surface temperature (SST) at the Farallon Islands from 1972 - 1993. Monthly anomalies are plotted with a quadratic regression line, showing long-term trends, and a cubic spline, illustrating interannual variability.

Birds—(Cont. from page 4)

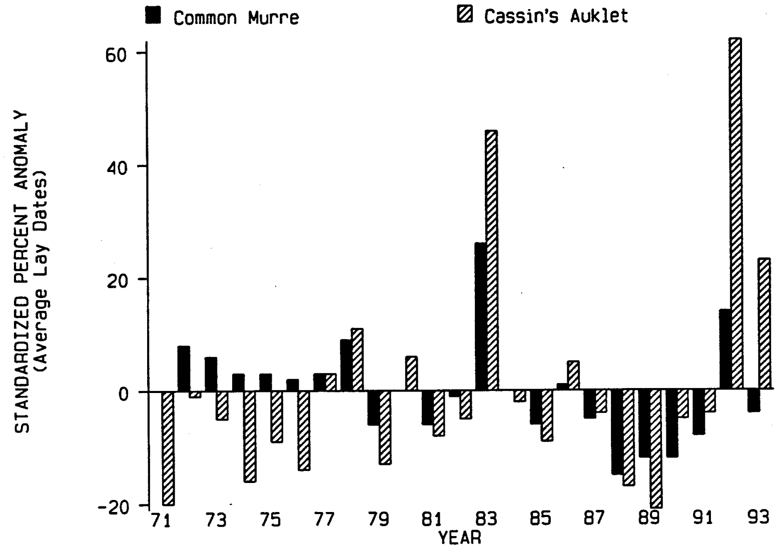

Figure 2. Annual variability in the timing of egg-laying for the Common Murre and Cassin's Auklet breeding on the Farallon Islands.

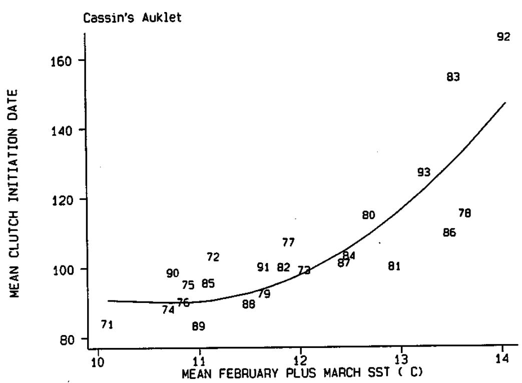

Figure 3. The relationship between SST and mean egg-laying dates for Cassin's Auklet on the Farallon Islands, 1971-1993. A significant curvilinear regression line is presented (F=25.92, P<0.001, r^2=0.72).

Interannual variation in the timing of nesting for the Common Murre (*Uria aalge*) and Cassin's Auklet (*Ptychoramphus aleuticus*) indicated significant delays during ENSO 1982-83 and 1992-93 (Fig. 2). Other time trends are also evident in these results: Common Murre nesting chronology has become progressively earlier throughout the study period ($P < 0.05$). Both murres and auklets feed extensively on the euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* during the pre-nesting period (PRBO, unpublished data). Thus, there may be a relationship between a seasonal increase in the availability of these organisms and the onset of reproduction among the avian predators. For the auklet, we have regressed the average February plus March SST against the mean egg-laying dates for the population (Fig. 3). Results indicate earlier reproduction during years with low SST during winter ($P<0.05$); a similar result was obtained for the murre. Earlier egg laying generally translates into more productive seasons, which may eventually lead to variation in population size. Murres, and especially auklets, also likely track interdecadal temporal variation in oceanic conditions (c.f. Ainley and Lewis 1974) recently identified for anchovy and sardine populations in the California Current (e.g. Baumgartner et al. 1992). Also awaiting are analyses comparing diet composition and physical measurements, such as SST and other measurements of oceanic upwelling, to investigate a causal link between upwelling, prey availability, and timing of breeding.

Lastly, chick production in most seabirds is directly correlated to the availability of prey through the spring and summer. Of the 12 species of breeding birds on the Farallones, only 2 (both storm-petrels) show little response to annual variability in marine productivity. The most variable, and hence sensitive species to marine conditions, were those having greater reproductive effort (i.e. clutch size > 1 egg) (Fig. 4). Data provided for the Brandt's Cormorant (*Phalacrocorax penicillatus*) and Western Gull (*Larus occidentalis*) show declines in reproductive success during all ENSOs and other warm-water years (1978, 1989, 1990). For the cormorant, highly successful reproductive years equal in magnitude and frequency to negative ones also are evident. ENSO events drive many warm-water oceanic anomalies in the California Current (Quinn et al. 1987), but the seabird data indicate that other forces, related to the intensity and geographical extent of the Aleutian Low Pressure system may alter wind patterns, corresponding upwelling regimes, and the food web of central California (Ainley, Sydeman, and Norton, in press).

Intermediate between the large- and small-scale ocean conditions and the birds are the species of mid trophic levels which are of particular interest to U.S. GLOBEC: zooplankton and pelagic fishes. The availability of mid trophic level species has a direct effect on the productivity of marine birds and provides a mechanistic link between ocean climate and marine bird populations. For example, the availability of juvenile rockfish (*Sebastes* spp.) in central California, as determined by biologists from the NMFS Tiburon Laboratory (W. Lenarz and S. Ralston, unpublished data), correlates strongly with annual reproductive success for the Brandt's Cormorant (Fig. 5) and Western Gull (Sydeman et al. 1991). Rockfish, mainly *Sebastes jordanii*,

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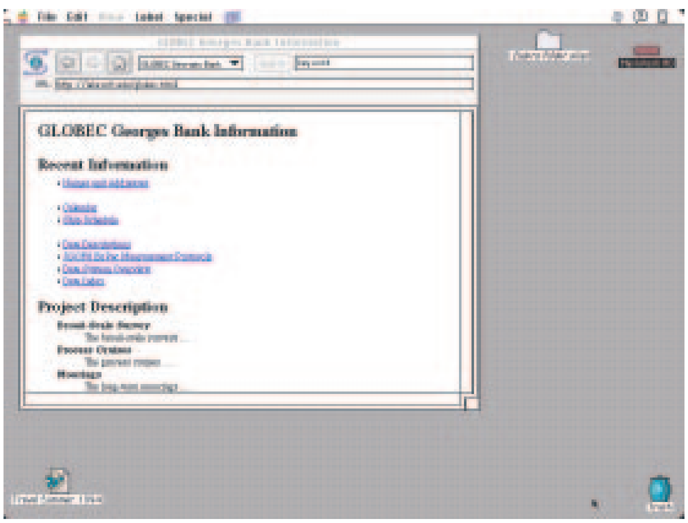
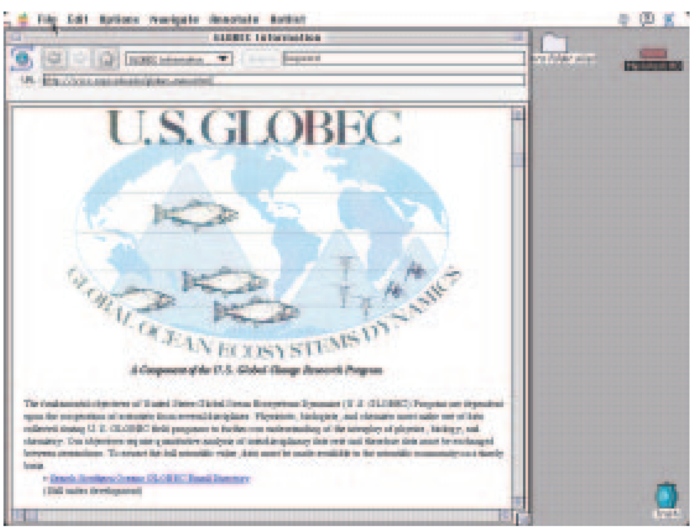
(Editors Note: Technology Forum is intended to stimulate thought and discussion on diverse oceanographic technology issues. We welcome contributions on technological issues relative to ocean science, but particularly to U.S. GLOBEC.)

GLOBEC and the World-Wide Web

The World-Wide Web (WWW) is a distributed global information system that is based on the hypertext transfer protocol (HTTP). WWW documents can contain links to other documents on the same or other servers on the network. WWW sites and documents are identified by Uniform Resource Locator (URL). A hypertext link in a document is indicated by underlining or another form of highlighting. Activating the link opens the associated document. Documents on the WWW are not restricted to being text only—sound including speech, images, and video can also be accessed. URLs can also point to information in other (non-HTTP) formats on the internet—e.g., to files on an anonymous File Transport Protocol (FTP), Gopher or Wide Area Information (WAIS) server. Access of resources on the WWW requires a client program designed for the purpose.

Mosaic is a WWW client with multimedia capabilities developed by the National Center for Supercomputing Applications (NCSA) at the University of Illinois. Versions of NCSA Mosaic are available for Macintoshes, PCs running Windows, and UNIX workstations running X-windows.





Top: Mosaic access of U.S. GLOBEC's Georges Bank information page at http://lake.mit.edu/globec.html.
Bottom: Mosaic access of the GLOBEC Southern Ocean information page at http://www.ccpo.odu.edu/globec_menu.html

GLOBEC is only just beginning to take advantage of the capabilities of the WWW. Two (there may be others) sites have implemented Mosaic servers partially directed toward GLOBEC information. The first of these is at the Massachusetts Institute of Technology [URL site http://lake.mit.edu/globec.html (top figure)] and is providing information about the U.S. GLOBEC projects underway on Georges Bank in the Northwest Atlantic. Browsers of that site can presently obtain addresses of the Georges Bank PI's, ship schedules, etc. Eventually cruise reports from the broad-scale and process cruises on Georges Bank will be on-line. The second GLOBEC Mosaic server is at Old Dominion University's Center for Coastal Physical Oceanography [URL site http://www.ccpo.odu.edu/globec_menu.html (bottom figure)] and is principally directed towards GLOBEC's planning and activities in the Southern Ocean. It presently also has available the U.S. GLOBEC Data Policy document (U.S. GLOBEC Report No. 10) for on-line browsing.

The U.S. GLOBEC Scientific Steering Coordinating Office at the University of California, Berkeley, will implement a U.S. GLOBEC Mosaic server this fall. It will contain HyperText Markup Language (HTML) versions of all published U.S. GLOBEC Reports, newsletters (including the issue you are reading now), and other miscellaneous documents (e.g., minutes of the Scientific Steering Committee meetings). It may also contain Postscript formatted versions of some of these documents, which can be downloaded to a client and subsequently printed. This Mosaic site will also provide links to all other known GLOBEC Mosaic sites. We are interested in learning from the experiences of others who have already established Mosaic servers. We also welcome comments and suggestions about what kinds of information would be useful to have electronically available.
Please direct comments to halbatch@violet.berkeley.edu or by mail to the U.S. GLOBEC office in Berkeley.

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Open Ocean Issues Discussed at Workshop

The purpose of the workshop was to discuss potential effects of global climate change on the species diversity, biomass, and community structure of open ocean pelagic environments. There are several reasons to consider GLOBEC questions in the open sea. First, is the issue of stability. 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 climatic perturbation than coastal systems. Second, because of the sheer size of open ocean ecosystems—ca. 60% of the surface area of the Earth—climate-driven changes of population biology or community structure, could have profound influences on the biosphere. To determine whether open ocean and nearshore pelagic environments respond differently to potential climate change will require increased understanding of organismal and population responses to physical and biological forces. U.S. GLOBEC is planning studies of the coupling of biological response to physical forcing in several nearshore environments (Georges Bank, California Current). This workshop addressed similar issues, but in open ocean environments. Such effort is needed for two reasons: first, very little is known about the life histories or population ecologies of zooplankton and fishes of open ocean gyres, and second, it is probably invalid to extrapolate knowledge gained from coastal species to blue-water species.

Twenty-two participants from the U.S., Canada and France met in Woods Hole, MA for three days in September 1993 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, four working groups were formed: A) Population Characteristics and Genetics; B) Distributional Patterns and Sampling Problems; C) Biological Processes and Rates; and, 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 behaviors 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. Criteria were developed for selecting candidate species, or groups of species, which could be studied in multiple oceanic regions over long enough periods to seek evidence of the effects of climate change.

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

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Birds—(Cont. from page 5)

comprise about 70% of the cormorant's diet during reproduction (Ainley and Boekelheide 1990, Sydeman and Pyle, unpubl. data); thus, it is not surprising that the availability of rockfish explained approximately 65% of the variation in cormorant reproductive success between 1983 and 1992. Importantly, these data provide a mechanistic explanation for how remote oceanic forcing during the ENSOs of 1983 and 1992 effects cormorant reproductive success locally.

The "top-down" perspective provided by seabirds provides a broad picture of how environmental conditions affects food web structure and energy transfer upward from lower trophic levels. Seabirds provide important up-to-date, quality information on the physical environment, and biological production in lower trophic levels. Furthermore, seabirds may also provide a means of assessing present fishery management regimes in the context of sustainability. Merging the top-down and bottom-up approaches will provide a powerful tool to understand ecosystem structure and food web dynamics as mediated by intermediate trophic levels. *(W. J. Sydeman is Director of Farallon Research at the Point Reyes Bird Observatory (PRBO) and a PhD student at the University of California, Davis. D. G. Ainley is Director of Marine Studies at PRBO.)*

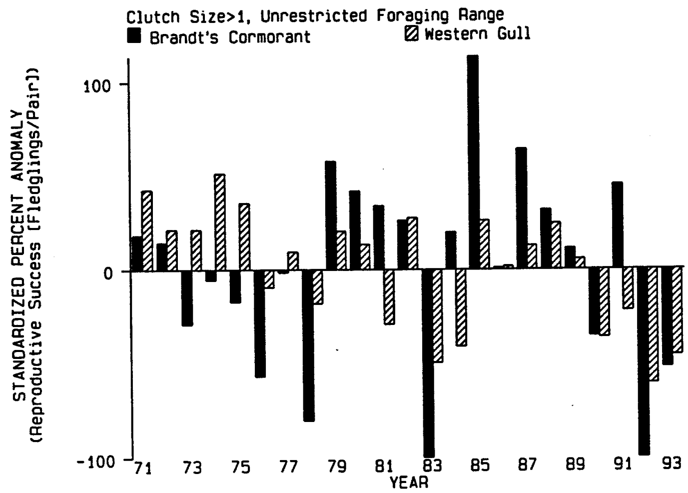

Figure 4. Anomaly in annual reproductive success of the Brandt's Cormorant and Western Gull on the Farallon Islands, 1971-1993.

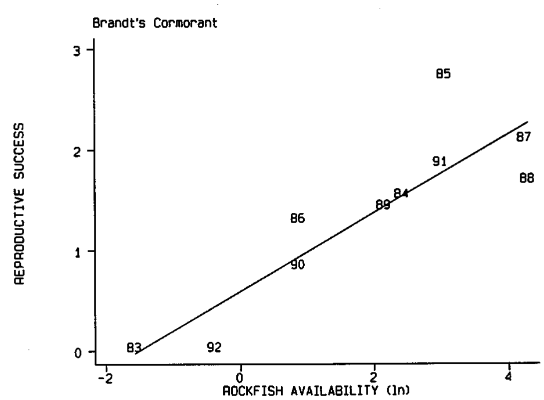

Figure 5. The relationship between annual productivity of Brandt's Cormorant and the availability of juvenile rockfish (Sebastes spp.), as determined by NMFS Tiburon Laboratory (W. Lenarz and S. Ralston, unpublished data), 1983-1992.

Acknowledgements

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U.S. GLOBEC Calendar

1994

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: halbatch@violet.berkeley.edu; Phone: 510-642-7452; FAX 510-643-6264).

10-14 October: International symposium on the assessment, yield, and long-term sustainability of large marine ecosystems of the Pacific. Qingdao, China. Contact: Q. 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: PICES-GLOBEC Workshop at Annual PICES Meeting, Nemuro, Japan. Contact: PICES Secretariat (next calendar item) or 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)

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

29-31 October: Management of the Mesopelagic Resources of the Gulf of Oman and Arabian Sea, Muscat, Oman. Contact: R. Shotton, Interim Tech. Secretary, WGM, FIRM, FAO, Via delle Terme de Caracalla, 00100 Rome, Italy (Phone: 396 5225 6481; FAX: 396 5225 3929; Internet: ross.shotton@fao.org)

14-19 November: Towards Sustainable Use of Oceans and Coastal Zones, Second International Conference on Oceanography, Lisbon, Portugal. Contact: G. Kullenberg, Secretary IOC, UNESCO, 7 Place de Fontenoy, 75700 Paris, France (Phone: 33 14 56 83 983; FAX: 33 14 05 69 316; Omnet: G.KULLENBERG)

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)

19-24 June: PICES Workshop on the Okhotsk Sea and Adjacent Areas, Vladivostok, Russia. Contact: Pices Secretariat, c/o Institute of Ocean Sciences, Sidney, B.C., Canada. V8L 4B2 (Phone: 604-363-6366; FAX: 604-363-6827; Internet: pices@ios.bc.ca)

21-26 September: ICES Statutory Meeting: Special Theme Session on Intermediate-Scale Physical Processes and their Influence on the Transport and Food Environment of Fish, Copenhagen, Denmark. Contacts: B. MacKenzie, Danish Institute for Fisheries and Marine Research, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark (Phone: +45-3396-3403; FAX: +45-3396-3434; Internet: brm@fimdfh.fin.dk) OR Francisco E. Werner, University of North Carolina, Chapel Hill, North Carolina 27599-3300, USA (Phone: 919-962-0269; FAX: 919-962-1254; Internet: cisco@hydra.chem.unc.edu)

Synopsis of the First SPACC Planning Meeting

The objective of International GLOBEC's Small Pelagic fish And Climate Change program, (GLOBEC SPACC) is to identify linkages between the driving physical forces that control population growth of small pelagic fish populations. The long range goal is to forecast how changes in the pattern and intensity of these forces, caused by elevated greenhouse gases and global warming, will alter the productivity of small pelagic fish populations. Toward that end, fifty-four scientists met in La Paz, Mexico in June 1994 to begin developing a science plan for GLOBEC SPACC. Attendees represented interests in the fields of physical and biological oceanography, numerical modeling, zooplankton ecology, remote sensing technology, paleoecology, genetics, early life history of fishes, and population dynamics. The scientists recognized that the GLOBEC SPACC goal requires highly multi-disciplinary, cooperative research and approached this challenge with enthusiasm. They also recognized the need to work together on shared stocks. They expressed their interest in developing regional (e.g. Humboldt Current, California Current, Patagonian Shelf, Baltic Sea, Mediterranean) as well as national SPACC projects.

The great stocks of sardines and anchovies, and other small pelagic fishes, account for about one third of the world's yield of marine fish and are of key economic importance in many nations. Production of these stocks depends upon a delicate balance of physical ocean processes. When environmental conditions in the ocean are optimal, great year classes result and populations grow rapidly. The optimal environmental window for small pelagic fish depends upon a triad of physical factors: enrichment processes that lead to the production of the zooplankton upon which the young stages depend for food; concentration processes that aggregate foods and thereby increase their availability to growing larvae; and retention processes that keep the young in their favored nursery habitat. Without a doubt, global heating will alter this triad of physical processes since all are functions of atmospheric forcing, ocean circulation, and fresh water inflow—all of which are expected to be altered by climate change.

Many present day populations of small pelagic fishes display a complex pattern of vital rates indicating adaptation of subpopulations to local habitat conditions. Some subpopulations are tiny with maximum biomass less than 20,000 mt while others reach millions of metric tons. These subpopulations experience different environmental conditions and are natural models of how marine populations react to environmental change. No group of marine populations is better suited for examining the linkage between physical forcing and population dynamics and structure than the small pelagics because of their world wide distribution, long time series in abundance, presence in the paleoecological records, and the wealth of information on their ecology and dynamics. Finally, the dominant small pelagic fish species shifts over decades in most systems. Changes in species dominance is due presumably to subtle changes in the suitability of the habitat. Shifts in dominants often occur nearly simultaneously in different regions of the world's oceans suggesting that atmospheric teleconnections may be important.

A common theme of the meeting was that significant advances could be made by comparing zooplankton production systems and the vital rates of small pelagic fishes in different ecosystems. Participants felt that within a zooplankton assemblage, a limited number of key species may exist that show strong links to larval and adult fishes. Advances in understanding will require recognition and description of these links, and perhaps monitoring or detailed examination of trophic and food web relations. The concept of an optimal environmental window for wind stress and other environmental variables was given considerable attention at the meeting, not only in the context of fish life history, but in the context of zooplankton production as well. Key in this regard is the extent that the optimal windows for zooplankton overlap those of small pelagic fish.

Core Elements of SPACC

The core program for SPACC process research includes: 1) daily somatic growth of larval and juvenile fish; 2) the daily production of zooplankton over the growth period; 3) circulation and vertical structure on population scale; and 4) numerical modeling to link the first three elements. The rationale for these choices was clear. Since SPACC is a GLOBEC-INT program, one or more of the dependent variables must directly affect population growth of small pelagic fish. Somatic growth, mortality, and reproductive effort are the obvious choices. Of these, daily growth rates estimated from increments on otoliths from larval and juvenile fish provide the most information at the lowest cost. If daily somatic growth is the measure of the response of fish to their environment, then measurements of the daily production of their zooplankton food supply is essential. Circulation and vertical structure of the sea must be known to understand how enrichment, concentration, retention/transport mechanisms work. A variety of models (e.g., circulation and bioenergetics) are needed to interpret and link elements.

Modeling functions as a research tool that provides a framework for hypothesis testing by putting disparate field measurements into a common framework. It is needed to

(Cont. on page 11)

SPACC—(Cont. from page 10)

summarize accumulated information, provide the linkage between historical data sets, retrospective studies, and field process studies, and develop predictions regarding the effects of climate change. A variety of models are needed, ranging from energy budget models of key species to physical models of regional circulation and mixing dynamics. Especially valuable are models that bridge the interface between biology and physics.

Temporally continuous monitoring of ocean dynamics is essential for SPACC process studies because environmental events throughout the year could be critical to the survival and growth of young fishes and production of their zooplankton forage. Intermittent information provided by research cruises must be temporally and spatially supplemented using satellite imagery of sea surface temperature, cloud cover and ocean color; coastal station records of wind, sea level, and salinity; and, low-cost subsurface observations.

The spawning habitat of most small pelagic fishes is bounded by a front or pycnocline between warm and cool water or between saline and fresher water. This perhaps was the only common denominator among the diverse array of spawning habitats reviewed at the meeting. These boundaries may provide water column stability, nutrient enrichment or concentration of food particles at the interface. The mechanism by which these boundaries provide benefits to the survival of the early stages of pelagic fishes need identification. To determine the role of these boundaries requires contemporaneous measurements of flow fields and larval distributions.

Determining how the local habitat of small pelagic fishes is affected by climatic variability was central to the meeting. In particular, to determine whether the dynamics of populations are due to local events or large scale climatic forcing. A consensus developed that retrospective analysis of the sedimentary records of anaerobic marine deposits could provide the long time scale data needed to characterize climate variability. In addition to providing a history of population abundance of small pelagic fishes (inferred from fish scale abundance in sediments), ecosystem histories could be developed from the sedimented remains of plants and other animals, and from chemical components. Interpretation of such paleoecological records is greatly improved by accurate description and understanding of the process of sedimentation at a site (e.g., sediment trapping). The scales of physical forcing can be studied using historical time series of biological and physical data. Evidence is mounting that ecosystems supporting small pelagic fish populations undergo productivity changes of decadal frequencies which are expressed, inter alia, by "regime shifts" of clupeoid populations. The causal mechanisms need identification, perhaps using new methods for analysis of time series of phytoplankton, zooplankton, fish, and physical data.

SPACC is in a position to address the systematics and population genetics of small pelagic fishes in the world's oceans using modern molecular methods. For many of the small pelagics, it is unclear where species and population boundaries begin and end. Moreover, climate change may rapidly influence the genetic and demographic structure of small pelagic fish populations because they are relatively short-lived and feed at the top of a short but unstable plankton-based food chain. Modern molecular methods may be useful in examining genetic diversity between and within populations, and perhaps also through time (using scale DNA).

GLOBEC-INT leadership in SPACC could assist in program development and technology transfer. GLOBEC-INT could aid program development in a region, or country, by providing support for regional workshops where participants from different universities, institutes, and fishery agencies could be encouraged to cooperate to develop and implement a SPACC study. A TEMA (training, education, and mutual assistance) component must be developed within SPACC to provide training for making routine measurements, using advanced oceanographic equipment, and interpreting data. Cited examples include training in: 1) modern methods of measuring zooplankton production; 2) determining back-calculated daily larval growth using otoliths of juvenile fish; 3) using advanced gear such as undulating samplers; and, 4) interpreting the data obtained from ADCPs and satellites. *(This article abstracted from documents provided by John Hunter of the NMFS—La Jolla. Dr. Hunter is a former member of the Steering Committee of U.S. GLOBEC, a current member of the organizing committee of GLOBEC International, and co-chaired the SPACC workshop.)*

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GLOBAL OCEAN ECOSYSTEMS DYNAMICS

U.S. GLOBEC NEWS

U.S. GLOBEC NEWS is published by the U.S. GLOBEC Scientific Coordinating Office, Department of Integrative Biology, University of California, Berkeley, California 94720-3140, telephone (510) 642-7452, FAX (510) 643-6264. Correspondence may be directed to Hal Batchelder at the above address. Articles, contributions to the meeting calendar, and suggestions are welcomed. Contributions to the meeting calendar should contain dates, location, contact person and telephone number. To subscribe to U.S. GLOBEC NEWS, or to change your mailing address, please call Hal Batchelder at (510) 642-7452, or send a message to Internet address halbatch@violet.berkeley.edu, or write to the address above.

U.S. GLOBEC NEWS Staff
Hal Batchelder
Tom Powell

U.S. GLOBEC Poised to Study California Current Ecosystem

The physical and biological dynamics of the California Current System (CCS) are sensitive to natural climate variability on time scales ranging from seasonal to interdecadal, and spatial scales from local to basin-wide. Ecosystem structure is closely coupled to variations in physical forcing, thus sensitivity of the coupled physical-biological system to climate variability implies great sensitivity to climate change. U.S. GLOBEC has produced a Science Plan that suggests a number of hypotheses on how the coupled physical-biological system may respond to global climate change, and lays out a plan for how U.S. GLOBEC will study the CCS with the overall goal of producing predictions and integrated assessments of ecosystem response to climate change.

The Research Program

GOAL: ***To understand the effects of climate change on the distribution, abundance and production of marine animal populations in the CCS.***

APPROACH: ***To study the effects of past and present climate variability on marine animal populations and to use this information as a proxy for how the CCS may respond to future global warming and global climate change.***

Program Elements

• Provide a quantitative description of ecosystem dynamics and assess ecosystem response to climate variability in the CCS by developing, validating and applying regional models that couple ocean physical processes to biological proceses.

• Determine the modes of natural variability at seasonal-to-interannual-to-interdecadal time scales by conducting retrospective analysis of environmental, satellite, plankton, fisheries and paleoecological data sets from the California Current and other Eastern Boundary Current (EBC) systems.

• Examine climate variability and ocean and ecosystem responses, especially as it relates to El Niño—Southern Oscillation (ENSO) cycles by initiating long term monitoring and observation programs.

• Describe and compare interegional differences in mesoscale dynamics and life history strategies of key species to understand effects of El Niño/La Niña events on ecosystem structure using focused process-oriented field studies within the distinct regions of the CCS.

Time and Space Scales

The CCS offers excellent venues for climate studies because the climate signals are strong and pervasive, and because regional differences are great. The U.S. GLOBEC research program will focus on variability at several scales:

• Seasonal-to-interannual variability in physical and biological dynamics;
• Decadal variability as related to possible regime shifts;
• Spatial variability along latitudinal and longitudinal gradients; and,
• Physical and ecological differences between the CCS and other Eastern Boundary Current ecosystems, to examine ecosystem response to

(Cont. on page 13)

Possible Changes in the CCS Associated with Global Climate Change

• Decreased inflow from the north and total transport in the CCS
Potential Impact: Decreased zooplankton production and prey for higher trophic levels (fish)

• Increased intensity of upwelling, offshore transport and mesoscale activity
Potential Impact: Decreased survival and recruitment to coastal fish and invertebrate populations because of increased offshore transport of larvae and/or dispersion of prey organisms.

• Altered frequency and intensity of ENSO events
Potential Impact: More frequent and stronger disruptions of “normal” conditions, favoring different species adapted to disturbed environments; periodic warmer than average temperatures; perhaps regime shifts.

• Increased average sea surface temperature (1-2°C) and increased stratification of the water column
Potential Impact: Shifts in major biogeographic boundaries; altered recruitment rates of coastal species through changes in the effectiveness of larval transport; increases in warm water predators altering mortality patterns and rates.

Calif. Current—(Cont. from page 12)
differences in local, regional and basin scale forcing.

Products

A successful program in the California Current System will produce the following:

• The development and/or significant improvement of a number of coupled biophysical models. These models will increase our ability to integrate biological and physical observations in coastal ecosystems in general and specifically in the CCS.

• The data sets assembled and collected during the program, including historical data sets, data from the mesoscale process studies and data from the monitoring activities.

• An improved monitoring system created during the program by augmenting existing systems with new elements.

• The experience gained by students and investigators in the use and interpretation of the combination of models and data. The training of students and other professionals in model use and interpretation is critical, if the activity begun during this program is to continue at the level necessary to reach the long-term goal.

The program in the California Current System will continue to move us toward our long-term goal of producing models that provide integrated assessments of the effect of environmental variability and climate change on ecosystems in the CCS and other marine ecosystems in coastal environments.

If the monitoring and field programs are designed correctly, the data sets collected should provide quantitative assessments of ecosystem structure during a period of five or more years that is likely to span a warm ENSO event. The connection to the larger basin scale variability will be provided by data collected in the tropical Pacific Ocean, e.g., that collected by the Tropical Ocean—Global Atmosphere (TOGA) and World Ocean Circulation Experiment (WOCE) programs. Within the CCS, the models will integrate the observations to provide a more complete picture of the biophysical interactions, while the data sets will continue to provide information useful in continued model validation and improvement. In this iterative fashion, the data sets and models will continue to increase our understanding of the way in which CCS ecosystems respond to large-scale environmental variability, long after the formal end of the program. The monitoring system should also continue to be useful in providing new information, as well as in ongoing model improvements. Some of the biophysical models will be imbedded within coupled ocean-atmosphere climate general circulation models (GCMs) in order to test their ability to reproduce the statistics of the historical and paleoecosystem time series, allowing further identification of model weaknesses and further model improvements. Along with the historical physical, zooplankton and fisheries data, they will permit a description of CCS dynamics and ecosystem response during several past ENSO cycles and the most recent interdecadal regime shift in the mid-1970’s. When confidence in the biophysical models is established, they can also be imbedded within operational forecast models to provide short and medium range forecasts to the National Marine Fisheries Service (NMFS).

The models and monitoring systems will ultimately allow NOAA to provide managers and policy makers with better information on the role of environmental variability and climate change in determining abundances of living marine resources. Many marine populations in EBCs are especially vulnerable to collapse during El Niño events and other interannual to interdecadal extremes. The U.S. GLOBEC program will provide a more thorough scientific basis for assessments of the potential impact of El Niños on living marine resources. In addition, the research will provide scientific information needed to analyze the economic impact of ENSOs on marine resources.

Information on the response of the system to decadal variability will also be valuable to managers. EBCs are known for their spectacular fishery collapses, such as the Monterey sardines (1940s) and the Peruvian anchoveta (1970s). Such collapses seem to be an inevitable consequence of inadequate understanding of the resources of the ecosystems. We need (1) improved resource management models based on understanding of qualitative state shifts; and, (2) improved capability to recognize and predict state shifts. It is doubtful that adverse fluctuations in the stocks and related industries can be avoided entirely, but if management were armed with the above knowledge and acted appropriately, it should be possible to reduce the severity and duration of the downturns and their resultant economic and social hardships.

In summary, the models, data sets and monitoring systems developed in this program will directly benefit society. The models will stimulate future scientific inquiries, and will identify the most important components of key ecosystems—those which most require close, continued observation. The models represent the ongoing, integrative element of the program. They are the important beginning of operational, climatic ecosystem modeling—the ultimate need of society in order to understand and manage such ecosystems. This will be the legacy of the U.S. GLOBEC program in the California Current System. *(This article excerpted from the Executive Summary of U.S. GLOBEC Report No. 11, A Science Plan for the California Current)*

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Coupled Model—(Cont. from page 3)

was the same as that illustrated in Figure 3 for cod: a few haddock larvae persisted on the Bank for 30 days post-hatch, but they were extremely small in size (less than 5 mm in length or 30 μg in weight).

This preliminary sensitivity analysis demonstrates the significant differences that can arise in starvation mortality, growth rates, and losses due to advection off the Bank when individual variability is introduced in just two parameters: the number of prey encountered per day and the success at capturing and ingesting those prey. These results also suggest the extent to which spatial variability in prey distributions can influence the growth rates and resulting size distributions of larvae in different regions of Georges Bank. Variability in other parameters, such as the size distribution of larvae at hatch, undoubtably play a role. These results are also consistent with Laurence's (1985) original conclusion that haddock are more dependent on high densities of small prey items than are cod. While our trophodynamic relationships follow those of Laurence (1985), our model results also incorporate field-derived estimates of prey concentrations and distributions, and the observed prey sizes in the stomach contents of cod and haddock larvae.

In these examples we have considered only the effect of horizontal variations in prey concentration on larval growth. Analogous effects arising from vertical variations in the prey field concentration are likely and expected. Field studies have shown that stratification on Georges Bank can significantly influence the feeding and survival of larval cod and haddock (Buckley and Lough 1987). Up to 50% of haddock larvae (mean size 11.2 mm) from a well-mixed site in spring 1983 on Georges Bank had RNA/DNA ratios in the range observed in the laboratory for starved larvae. These field observations provide support for the hypothesis that haddock larvae require higher prey densities than cod and seem more adapted to spring conditions when prey are concentrated by stratification. A study of stratification variability on Georges Bank and its effect on larval fish is currently underway (U.S. GLOBEC News No. 3, 1993).

Our results suggest that two key aspects requiring detailed attention are an improvement in the spatial and temporal specification of the prey field, and better treatment of the details of the encounter rate and ingestion success of larvae with prey. Specifically: (1) The model's requirement of increasing the prescribed prey concentration by five to fifteen-fold to achieve growth and survival of larvae observed in the field is consistent with the range of (aggregated) prey concentrations reported by Lough (1984) and Buckley and Lough (1987). Increased prey aggregations of this magnitude were found in the vicinity of a pycnocline. Their studies also found that the mean depth of the larvae and/or the peak densities of larvae generally coincided vertically with the highest prey biomass indices, suggesting a larval behavioral component not considered in our calculations. In this regard, one of the crucial parameters in the model is the concentration of prey separated into size categories, and especially those sizes appropriate for the smallest larvae. Ideally, this parameter should be known in detail horizontally and vertically throughout the Bank, but in practice it is poorly known at some locations and unknown at most places. Analyses of historical small-mesh plankton samples and new information collected during the U.S. GLOBEC-Georges Bank field program should help provide additional details. (2) The different results between deterministic and stochastic simulations suggests the model is sensitive to small-scale prey distributions and to the ability of larvae to capture prey. Further work is needed to develop better representations of these processes, e.g., by including turbulence-dependent encounter rates (Rothschild and Osborn 1988) in place of the randomization routines, and laboratory studies to investigate capture success with different prey types and larval fish condition.

In conclusion, the ability to couple a larval fish trophodynamics model with a detailed model of the physical circulation on realistic topography, both of which operate at the scale of individual larvae, is providing a new tool for the development and exploration of the critical hypotheses regulating the variability of marine fish populations on Georges Bank. *(F. E. Werner (University of North Carolina), R. I. Perry (Pacific Biological Station, Nanaimo), R. G. Lough (NMFS—Woods Hole), and D. R. Lynch (Dartmouth College) are U.S. GLOBEC funded investigators working on Georges Bank.)*

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(Cont. on page 15)

Coupled Model—(Cont. from page 14)

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Werner, F. E., F. H. Page, D. R. Lynch, J. W. Loder, R. G. Lough, R. I. Perry, D. A. Greenberg, and M. M.

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Open Ocean—(Cont. from page 7)

other accessible oceanic sites.

The workshop participants recommended a staged implementation of an Open Ocean GLOBEC program, beginning with retrospective analysis and proceeding to pilot studies and 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. Known biological and genetic characteristics of these species could be accounted for, so that environmental effects in different regions could be clearly seen. 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. (*This synopsis of the U.S. GLOBEC Open Ocean Workshop was prepared from a draft report of the meeting, developed by Larry Madin and Mike Landry, who co-chaired the workshop in Woods Hole. A final report of the workshop discussions and recommendations will be published later by U.S. GLOBEC*).

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Coupled Model—(Cont. from page 15)

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