

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

EASTERN BOUNDARY CURRENT PROGRAM

A Science Plan for the California Current

U.S. Global Ocean Ecosystems Dynamics

Report Number 11

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This science plan for a U.S. GLOBEC program in the California Current System developed from initial discussions held at a small workshop in San Francisco in January 1993—P. Ted Strub and John Hunter, conveners. Subsequently, a rather large writing team, chaired by P. Ted Strub, was formed to produce this document. Contributors to this document were David Ainley, Jack Barth, Hal Batchelder, Tim Baumgartner, Loo Botsford, Tim Cowles, Jim Eckman, Peter Franks, Steven Gaines, Anne Hollowed, George Hunt, Ron Lynn, David Mackas, Mark Ohman, Bill Peterson, Tom Powell, Frank Schwing, Paul Smith, and Ted Strub.

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SECTION I—EXECUTIVE SUMMARY

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. This Science Plan suggests a number of hypotheses on how the coupled physical-biological system may respond to global climate change (some of these are highlighted in the box on the following page), 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 processes**.
- 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 interregional 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 differences in local, regional and basin scale forcing.

Example Predictions of Changes in the CCS
Associated with Global Climate Change*

- Decreased inflow from the north and total transport in the CCS (Peterson et al. 1993)
Potential Impact: Decreased zooplankton production and prey for higher trophic levels (fish) (Chelton et al. 1982)
- Increased intensity of upwelling, offshore transport and mesoscale activity (Bakun 1990, Hsieh and Boer 1992)
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 (Lasker 1975; Parrish et al. 1981; Bailey 1981; Farrell et al. 1991).
- Altered frequency and intensity of ENSO events (Meehl et al. 1993)
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; Manabe et al. 1991, 1992) and increased stratification of the water column (Peterson et al. 1993)
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.

* See Section IV for detailed discussions .

Products

A successful program in the California Current System will produce four consequents that we believe will not occur without this program.

- 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 system.
- 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 U.S. GLOBEC 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.

SECTION II—INTRODUCTION

The U.S. GLOBEC (Global Ocean Ecosystems Dynamics) program seeks to understand how global climate change affects the distribution, abundance, production and population dynamics of animals in the sea. One type of climate change is the natural variability on scales of years to centuries. Anthropogenic changes in atmospheric circulation, such as those caused by increased concentrations of greenhouse gasses, will cause additional changes in the ocean's temperature and current fields. Although the pattern and magnitudes of these changes are not known, scientists do know that during past glacial periods the locations of major ocean currents were significantly different from their present positions. Thus, the climatic changes associated with increased concentrations of greenhouse gasses are expected to include displacements and changes in the strength of ocean currents. These will cause significant local changes in climate and ocean conditions in coastal regions, displacing local species, disrupting the completion of life-cycles dependent on present-day conditions, altering behavior patterns and predator-prey interactions. All of these factors could lead to significant shifts in ecosystem structure and function. Different ecosystems having different trophic pathways and dominant species may result.

Initial U.S. GLOBEC efforts are focused on understanding and quantifying present-day physical forcing and the effects of natural climate variability on the population dynamics of selected target species. Zooplankton, including meroplankton and ichthyoplankton, are a prime focus of U.S. GLOBEC because they are transported passively by ocean currents and are thus susceptible to changes in ocean circulation. Zooplankton are also a key link between phytoplankton and higher trophic levels (such as fish), thus climate-driven variations can affect ecosystem structure through trophic pathways. Wherever possible, U.S. GLOBEC scientists will undertake retrospective studies, including paleoclimate and paleoceanographic research, to characterize past natural variability over time scales of decades to centuries. In addition, such work provides the longer-term (interannual to interdecadal) context for shorter-term (order of 5-7 year) process-oriented research. An integral part of U.S. GLOBEC is the development of coupled physical-biological process models, resulting in assessments and predictions of the impact of climate change on marine resources and marine ecosystems.

The Importance of the Populations within the CCS

Economic Value

The California Current System (CCS) provides an excellent opportunity to accomplish U.S. GLOBEC goals in a region vital to U.S. interests. It is important to the regional and national economies due to commercial and recreational use by a large population and is cherished for its aesthetic as well as economic value (U.S. GLOBEC Report No. 7).

Collectively, the Eastern Boundary Current (EBC) systems in the Pacific and Atlantic account for approximately 35% of the global marine fish catch. Marine fisheries on the west coast of the U.S. produced a direct, indirect or induced impact of \$4 billion on the economies of California, Washington and Oregon in 1992 (U.S. Dept. of Commerce, 1992; hereafter USDOC). Sportfishing and marine mammal watching yielded additional revenues. U.S. fishermen cannot now meet the demand for fish. As a nation, we exported \$3.4 billion and imported \$5.7 billion of fish in 1992. U.S. consumers bought 62% more fish this decade than two decades ago, 24% due to rising population and 38% due to increasing per capita consumption. The value of California seafood imports from other countries is eight times the value of its exports (Leet et al. 1992).

There are presently 40 stocks of living marine resources under management in the Pacific. Many of these stocks are fully or over-utilized; there are not sufficient data to evaluate the status of many others (USDOC). Commercially important fish in the CCS include the Pacific sardine, northern anchovy, Pacific mackerel, Pacific hake, salmon, rockfish, dover sole, sablefish and jack mackerel. There are also important recreational fisheries in all three west coast states. Significant invertebrate fisheries on the West Coast, include sea urchins, Dungeness crab and Pacific shrimp.

The long-term potential yield of fish stocks has traditionally been based on the assumptions that stock production in the recent decades of study are representative and that the essential climatic features that maintain stock production rates will stay the same. Reality often proves to be otherwise. One example is the sardine population in the CCS. Analysis of historical data now reveal that large-scale interdecadal climate change altered ocean conditions after 1945, which would have produced a natural decline in the sardine population even without fishing. This natural decrease was exacerbated, however, by uncontrolled fishing (Jacobsen and MacCall, in press). One of the prime goals of U.S. GLOBEC is to improve our understanding and ability to predict the vulnerability of living marine resources to natural and accelerated changes in the climate and to human pressures on those resources. This understanding should help to avoid prolonged decreases in populations of important species in the future.

Ecological Importance

The strong connection between the CCS and basin-wide oceanic and atmospheric circulation provide linkages to global scale climate changes, as evidenced by its well-documented response to the basin-wide, interannual El Niño/Southern Oscillation (ENSO) variability. A similar response to interdecadal basin (or global) scale variability has recently been recognized. On both time scales, major changes in population abundances and distributions of key species have been documented in response to changes in the oceanic circulation and physical environment. Moreover, the applicability of results in the CCS to other EBCs gives the study global significance. For example, biological and physical responses to ENSO in the Pacific EBCs which have strong changes can be contrasted with Atlantic EBCs where ENSO effects are weak (Bakun and Parrish, 1980). Apart from differences in ENSO response, the atmospheric forcing, circulation and zooplankton communities and pelagic fish stocks of the California Current System are similar to other eastern boundary currents of the world ocean: the Humboldt Current (Peru/Chile), Benguela Current (Southwest Africa), and the Canary Current (the Iberian Peninsula to Northwest Africa). These systems often have narrow shelves and are characterized by coastal upwelling, equatorward flow over a poleward undercurrent and a small number of species of dominant pelagic fishes (anchovy, sardine, hake, mackerel and bonito). Fluctuations and redistributions of anchovies, sardines and pilchards occur in all EBCs.

U.S. GLOBEC research on the northeast Pacific boundary currents can utilize a rich history of time-series, quantitative surveys of zooplankton and fish off British Columbia, Washington, Oregon, California and Baja California Mexico and coastal process-oriented surveys. These can be used to define better the relation between zooplankton production and regional-scale processes like transport and local-scale processes like predation, upwelling and isopycnal shoaling. We also need seasonal and regional comparisons of the impact of pico- and large phytoplankton production on zooplankton populations, since the productivity of the bacterio- and phytoplankton is transferred to the higher trophic stages via zooplankton. While upwelling of nutrient-rich water stimulates primary and secondary production, it also may transport zooplankton, and fish and

benthos larvae, out of their habitat or destroy the local aggregations of food on which they depend. Determining the relative importance of advective losses versus predation as dominant sources of mortality for planktonic populations is crucial. This issue, fundamental to population dynamic studies, has not been properly resolved for any marine planktonic population.

The impact of climatic change on zooplankton production depends on its persistence—short-term changes in the environment, such as occur during an El Niño, may not impact the production of fish having generation times of five years or longer. It is important that U.S. GLOBEC relate physical oceanographic features to the production of zooplankton on which sustained resource productivity depends. While the adult stages of the zooplankton are well known, most resource species rely on their immature stages for food. The genetics and population dynamics of the critical zooplankton species are not sufficiently well known to link physical oceanographic events and trends to secondary and fishery production dynamics.

Existing long-term data series, such as the CalCOFI dataset, and the paleoecological data from sediments, are valuable for examining ecosystem response to past climate variability. The longer data sets allow the identification of natural modes of variability, prior to any anthropogenic modification (e.g., fishing). This temporal variability, as well as the large degree of spatial variability within the present system, can be used to identify and examine the mechanisms by which the CCS responds to changes in forcing, which can then be applied to predict biological responses to scenarios of future climate change.

Program Elements

From discussions that began at a workshop in Bodega Bay in September 1991, four classes of studies (Program Elements), spanning different temporal and spatial scales, were identified that are needed to understand the mechanisms causing variability of CCS populations:

1. Modeling studies (addressing all scales)
2. Retrospective and comparative studies (seasonal-to-interdecadal scales)
3. Field process studies to include:
 - large-scale studies, focusing on latitudinal gradients, and
 - mesoscale studies, focusing on filaments, jets and eddies,
4. Long-term environmental monitoring

Modeling. The development, validation and improvement of biophysical ecosystem models will be conducted throughout the duration of the U.S. GLOBEC CCS program and forms its ongoing integrative element. Several types of models will be developed that integrate effects of important biological and physical processes affecting coastal populations. Biological subcomponents will be included in existing numerical circulation models, which will allow interaction of the biological and physical components. High resolution biophysical models will be constructed with more realistic representation of turbulence and fine structure in the vertical dimension. Population models will also be developed, which relate abundance and persistence of populations to varying physical and biological conditions.

Modeling studies will ultimately be used to test various climate change scenarios proposed in this Science Plan. This will mostly be accomplished by running the models in "stand alone" process-study experiments. By the end of the project, however, it is hoped that the models will be capable of being imbedded within coupled ocean-atmosphere GCMs, at least in a rudimentary fashion. This will allow a more complete

test of the ability of the models to hindcast the statistical properties of past climate and ecosystem variability and the probable effects of increased concentrations of greenhouse gasses in the future. To do this, there is a need for further research into the methods of imbedding fine resolution models within basin-wide or global models and in assimilating both biological and physical data, to correct for poorly known initial conditions.

Retrospective and Comparative Analysis. The goal of this component is to define and understand the characteristic modes of natural variability over seasonal to centennial time scales in both the CCS and other EBCs. This goal will be achieved through assembly, analysis and interpretation of retrospective time series for the CCS and analysis of existing contemporary data sets from other EBCs such as the Peru-Chile and Benguela systems. Integration of paleoecological information with the historical CalCOFI and other plankton data sets is a critical element in the goal to link the information developed from U.S. GLOBEC field studies to natural climate variability at longer time scales. Moreover, using retrospective analysis in a comparative mode, we can compare life history strategies of species whose range spans several regions of the CCS, or of a species complex which occurs in several EBCs.

A compelling reason for selecting the CCS for study is that extensive historical and paleoecological data sets exist which permit determination of the natural modes of variability at seasonal and longer time scales. Analysis of physical, zooplankton and fisheries data will permit a description of CCS dynamics during past ENSO cycles, and elucidate changes that occurred during the 1976-1977 "interdecadal-scale" shift from cool to warm phases. Analysis of paleoceanographic data may permit study of regime shifts back in time for the past two millenia. In the future, when (or if) the system switches back to the cool phase, as determined from the long-term monitoring program, the present process studies will serve as a comparison for future process studies in the CCS.

Large Scale and Mesoscale Process Studies. The California Current can be divided into four regions, with each separated by a more-or-less distinct physical and/or biological boundary. From north to south they are: Region I (North of 43°N) extends from the southern British Columbia south to the vicinity of Cape Blanco, OR-Cape Mendocino, CA; Region II (35°N to 43°N) includes northern and central California, from Cape Mendocino to Point Conception; Region III (30°N to 35°N) is the Southern California Bight south to Punta Baja, Mexico and regions offshore; and Region IV (south of 30°N to 23°N), is Baja California from Punta Baja to Cabo San Lucas.

Mesoscale dynamics are interesting because they dominate much of the physical and biological dynamics of the CCS and because they differ in each of these regions as a result of regional differences in wind stress, intensity of coastal upwelling, coastal morphology, shape of the coastline, freshwater inflow, and the influence of advection, turbulence and buoyancy. There are also regional differences in planktonic, benthic and fish assemblages, the timing of plankton production cycles, and the reproductive activity of fishes. Since climate-controlled changes in large scale atmospheric and oceanic forcing have a major impact on mesoscale activity, a field research effort focused on this spatial scale is critical. Thus, regional differences in physical-biological linkages provide a natural laboratory for comparing potential changes in marine populations due to climate variability and climate change.

Monitoring and Observations. U.S. GLOBEC intends to augment existing monitoring programs and to initiate new programs as funding levels permit. A long-term environmental monitoring system should be designed to provide greater temporal resolution of ecosystem response to natural event-scale and seasonal variability, interannual variability due to ENSO, and long term climate variations. Monitoring is also

intended to provide the long-term context for the short-term process-studies; regions/locations monitored will be selected to coincide with locations of mesoscale process studies and, if possible, long records of historical data. To the extent possible, monitoring of environmental variables will include real-time reporting of the data, allowing rapid response to unusual events.

Time and Space Scales

Research within these four program elements will address two ranges of time scales, seasonal-to-interannual and decadal-to-centennial, and two space scales, mesoscale and large-scale. The central questions are articulated in the box below in terms of these scales. Below, we discuss temporal scales.

Central Questions*

Seasonal-to-Interannual Variability in Biological Responses

- How will climate change alter California Current ecosystems, through changes in the length, strength and timing of cyclical interannual variations, especially ENSO events?

Decadal and Longer Variability in Biological Responses

- What is the nature of the biological response in Eastern Boundary Currents to demonstrated, basin-scale, interdecadal changes in ocean-atmosphere coupling?

Mesoscale Variability in Biological Responses

- How are biological processes and the characteristics of planktonic populations affected by mesoscale features and dynamics in the CCS?

Latitudinal Gradients in Biological Responses

- How are recruitment, retention/transport, predator/prey relations, and life history strategies of planktonic stages impacted by latitudinal variability in the large-scale atmospheric and oceanic forcing in EBC ecosystems?
- How do differences in mesoscale activity in the four regions of the CCS affect the recruitment dynamics, vital rates, and life histories of resident marine animal s?

* See Section V for detailed discussions.

Seasonal-to-Interannual Variability. Longer term climatic changes in a region often consist of the effects of changes in the nature of the seasonal and interannual variability. Seasonal variability may be defined by even shorter events, such as the relatively rapid transition to upwelling conditions over much of the California Current in spring, or a sequence of events, such as the strength and frequency of winter storms. Interannual variability may, in turn, consist of changes in the timing of these seasonal transitions or in the accumulated effects of these sequences. Thus, although U.S. GLOBEC is primarily interested in the effects of longer-term climatic changes, the biophysical mechanisms responsible for those changes occur initially at the event scale. Within the CCS, the interannual physical and biological variability with the most severe economic and ecological effect is associated with the ENSO cycle. During the 1982-83 event, fish catch

per unit effort off California was reduced by 30% and the overall loss to North American fisherman was estimated at \$200 million. Much of our understanding of the response of marine organisms to ENSO is either anecdotal or so qualitative that it has little value for prediction. Because ENSO is one of the best documented and well-understood modes of climate variability, examination of the physical and biological response at this time scale is singled out for careful study. In addition, interaction of the ENSO time scale with the decadal (and regime shift) time scale will be given some emphasis. The program described previously—consisting of (1) monitoring of physical variables, plankton and nearshore organisms along selected transects and at coastal sites within the CCS; (2) development of coupled regional physical-biological diagnostic models to study physical and ecosystem response to ENSO forcing; and (3) process work on vital rates, such as reproduction, growth and mortality, or key populations—is well suited to address the ENSO time scale.

Decadal-to-Centennial Variability. At longer time scales, time series of sea surface temperature (SST) near the coast display distinct multidecadal periods of relatively cool and warm conditions, punctuated by the ENSO warm events (Miller et al. 1994a). SST observations at high latitudes have a periodicity of about 20-30 years which seems to be linked to atmospheric pressure anomalies; analysis of sediment cores from anoxic basins reveal a 60-70 year cycle in the relative dominance of sardine and anchovy over the last 1500 years. The direct observational time series, extending back 50-100 years, resolve one cycle of this pattern in the physical environment and ecosystem structure, with warming around 1925, cooling around 1948, and warming again around 1977. Coincident with the warming surface ocean temperatures in the mid-1970's is a notable decrease of zooplankton biomass in Region III and an increase in the sardine population in Southern California. The strength of springtime northerly winds diminished during this period and there is evidence that the large-scale ocean-atmosphere circulation changed.

From these observed changes, it is reasonable to assume that interdecadal fluctuations in ocean climate create changes in habitat that tend to favor certain species over others. Through retrospective analysis, descriptions of the system under different conditions in the past will be produced by making use of (1) the CalCOFI data base to compare cool regime conditions before 1977 with warm regime conditions after 1976, and (2) paleoceanographic data on fish scale and other biological debris in cores from anoxic basins to study the frequency of these shifts during the past 2000 years. The monitoring system put in place over the course of this 7-8 year program will continue into the future and provide continuity between the past and present observations and those made in the future, possibly within different phases of interdecadal cycles.

Recommendations for Initial Activities

In this science plan we emphasize the broad questions which need to be answered and the hypotheses which need to be tested in order to increase our understanding of how the distribution and abundance of animal populations in the CCS is affected by past and present climate variability and how ecosystem structure may be altered by global warming and global climate change. The **CENTRAL QUESTIONS AND GOALS** are discussed in Section V (page 33) in the context of the time and space scales of interest. The program elements, summarized above, are discussed in Section VI (page 37), **POTENTIAL COMPONENTS OF A CCS STUDY**. Clearly, the entire large, four-dimensional California Current, with its many habitats and species, cannot be sampled with sufficient resolution to determine its internal response to physical forcing at many points in time and space. The challenge is to design a program that takes advantage of the existing spatial and temporal variability to isolate the mechanisms likely

responsible for determining the fates of populations within a climatically-changing ecosystem.

This Science Plan will form the basis for several Announcements of Opportunity (AO) for research on relationships between climate variability, physical and ecosystem dynamics, and climate change in the California Current. The first AO is expected to be released in the fall of 1994, and will call for proposals on some or all of the following activities, depending upon the level of funding available.

1. Modeling activities.
2. Retrospective data analysis and comparative EBC studies.
3. Augmentation to existing and initiation of new monitoring programs.

These efforts are discussed more fully in Section VII (page 61).

SECTION III—OCEANOGRAPHIC SETTING

The Physical Setting

Regional Divisions

The California Current system spans more than 25 degrees of latitude along the west coast of North America (Figure 1). We divide the CCS into four regions--each is forced by somewhat different physical processes (see also Parrish et al. 1981). As a result, each region harbors a somewhat different ecosystem structure. The four regions are broadly defined, from north to south, as follows:

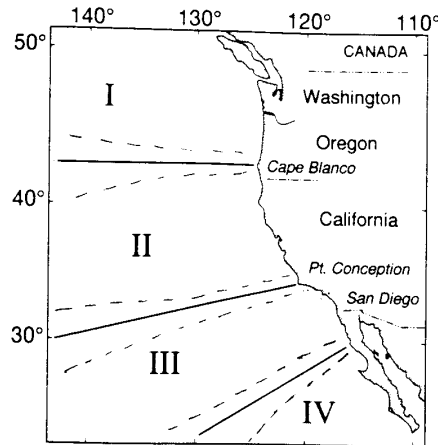
- Region I. Vancouver Island, Canada to Cape Blanco (Oregon, 50°N-43°N);
- Region II. Cape Blanco to Point Conception (California, 43°N-35°N);
- Region III. Point Conception to Punta Baja in northern Baja California (the Southern California Bight and offshore waters, 35°N-30°N);
- Region IV. Punta Baja to Cabo San Lucas (Baja California, 30°N-23°N).

Each of these regions is characterized by differences in wind stress, intensity of coastal upwelling, coastal morphology, freshwater inflow, large scale-advection and the level of mesoscale activity (Figure 1). Although we identify the boundaries by geographic features, above, the boundaries between these regions can be diffuse and some are known to change in response to interannual events, such as ENSO, and other long-term climate variation. In some cases, these same boundaries (or entire regions) also separate biological provinces (see below).

Large Scale Features

The CCS contains three major currents: the equatorward California Current, the poleward Davidson Current, and a poleward Undercurrent. In the long-term average of dynamic height, the California Current appears as a slow, equatorward flow that extends southward from the trans-Pacific flow of the West Wind Drift. The poleward Undercurrent is a sub-surface current, trapped along the continental slope (Huyer, 1983; Chelton, 1984; Hickey, 1979,1989). Poleward flow extends to the surface next to the coast from October through February and this surface poleward flow is referred to as the Davidson Current.

These currents and other more transient features of the CCS can be identified by unique water mass properties (Hickey 1979). California Current water is cool, fresh and high in dissolved oxygen and nutrients. The northward flowing poleward Undercurrent transports water of relatively high temperature, salinity and nutrients and low dissolved oxygen from equatorial regions. Subtropical water to the west and Equatorial Pacific water to the south are warmer and have lower dissolved oxygen and nutrients. Jets and meanders in Region II are often associated with upwelled water that is generally cool, salty, nutrient-rich and oxygen poor on the inshore edge of the jet (with opposite characteristics on the offshore edge) (Huyer et al. 1991).



	Region I	Region II	Region III	Region IV
Storms	Winter storms frequent and strong	Moderate winter storms	Fewer winter storms	Infrequent storms from tropics
Winds	Seasonal wind stress reversals	Winds mostly upwelling favorable	Minimum in longshore wind stress	Modest and persistent longshore wind stress
Upwelling	Moderate upwelling in spring / summer	Strongest upwelling in spring / summer	Weak upwelling	Modest upwelling year-round
Freshwater input	Significant freshwater input	Minor freshwater input	Negligible freshwater input	Negligible freshwater input
Coastal relief	Relatively smooth coastline	Major coastal promontories	Concave coast, islands, subsurface basins	Several major promontories
Shelter/Nurseries	Major estuaries / nursery grounds	A few major bays, estuaries	Sheltered bight, major nursery	Several sheltered bays
Circulation	Moderate advection, mesoscale activity	Extreme advection, mesoscale activity	Strong local recirculation, longer residence times, weak mesoscale activity, stronger stratification, major water mass mixing	Moderate advection, mesoscale activity
Productivity	Primary productivity strongly seasonal	Primary productivity strongly seasonal	Damped seasonality in primary productivity	Moderate seasonality in primary productivity
Zooplankton biomass	Zooplankton biomass strongly seasonal (Copepods commonly overwinter at depth)	Zooplankton biomass seasonal	Modest seasonality in zooplankton biomass	Damped seasonality in zooplankton biomass
Spawning	Patchy spawning by epipelagic fish	Latitudinal minimum in spawning by epipelagic fishes	Latitudinal maximum in spawning by epipelagic fishes	Patchy spawning by epipelagic fish

Figure 1. Generalized regional variations in physical and biological processes within the CCS. The boundaries between regions I, II, III, and IV are only approximate and vary over time. The generalizations regarding Region III apply primarily to the Southern California Bight.

Mesoscale Features

Satellite images of sea surface temperature (SST) and ocean color, (Figures 2 and 3), and fields of sea surface height from altimeter data have revealed a rich structure of jets, filaments and eddies, especially in Region II in summer. These mesoscale features are superimposed on the slow, generally southward flow that is often shown as the typical eastern boundary current structure (Wyllie, 1966; Levitus, 1982).

Seasonal Variability

Region I experiences the strongest winter storms with moderate summer upwelling. Region II experiences less intense winter storms than Region I. Following a 'spring transition', winds in Regions I and II become upwelling favorable, strongest is Region II (Huyer et al., 1979; Strub and James, 1988). Winds are weakest in the Bight (inshore part of Region III). Winds are moderately upwelling favorable all year in Region IV. A conceptual diagram of the seasonal surface currents is shown in Figure 4 (based on Hickey, 1979; 1989; Lynn and Simpson, 1987; and analysis of Geosat altimeter heights, Strub, unpublished). This shows the development of an equatorward jet off North America in spring next to the coast and the offshore movement of the jet in summer and fall, as the northward Davidson current develops next to the coast in winter. Inshore of the region occupied by the equatorward jet in spring and summer, colder and richer water is found. This is shown by satellite images of SST and pigment concentrations (Figures 2 and 3), as well as by field data (Brink and Cowles, 1991; other papers same volume).

Interannual Variability

The major source of interannual variation in the Pacific Ocean is the ENSO cycle. Effects of this variability reach the CCS by two mechanisms: oceanic and atmospheric. During the warm phase of ENSO, the oceanic signal propagates poleward from the equator, and is manifested as an increase in northward transport, a deepening of the thermocline and a rise in surface temperature and sea level (Simpson 1983; Huyer and Smith 1985; Rienecker and Mooers 1986). SST variability associated with the ENSO cycle also cause changes in the position and strength of the atmospheric pressure (and wind) patterns which affect the California Current region (Philander, 1990). Since the ENSO cycle has periods of 3-7 years it can be expected to contribute to much of the variability seen over the 5-7 years of a U.S. GLOBEC study.

Decadal Variability

Time series of physical and biological measurements in eastern boundary currents exhibit nonstationary properties—changes in temperature, accompanied by shifts in ecosystem structure, occur on a time scale of 30-50 years. Shifts in state have been documented for the mid-1940s when the system switched from warm phase to cool phase, and for winter 1976-77 (Miller et al. 1994a) when it switched from cool to warm phase (see Fig. 9). The 1977 shift is particularly well documented because atmospheric, sea surface and subsurface data were sufficient to demonstrate the basin scale nature of the shift. There is growing evidence that warm phase/cool phase shifts in the California Current are linked to the intensity of the Aleutian Low (Trenberth 1990; Graham, 1994; Miller et al., 1994b; Trenberth and Hurrell, 1994). A deepening of the Aleutian Low seems to result in more vigorous cyclonic circulation of the North Pacific subarctic gyre, and a deepening of the mixed layer in the North Pacific subtropical anticyclonic gyre.

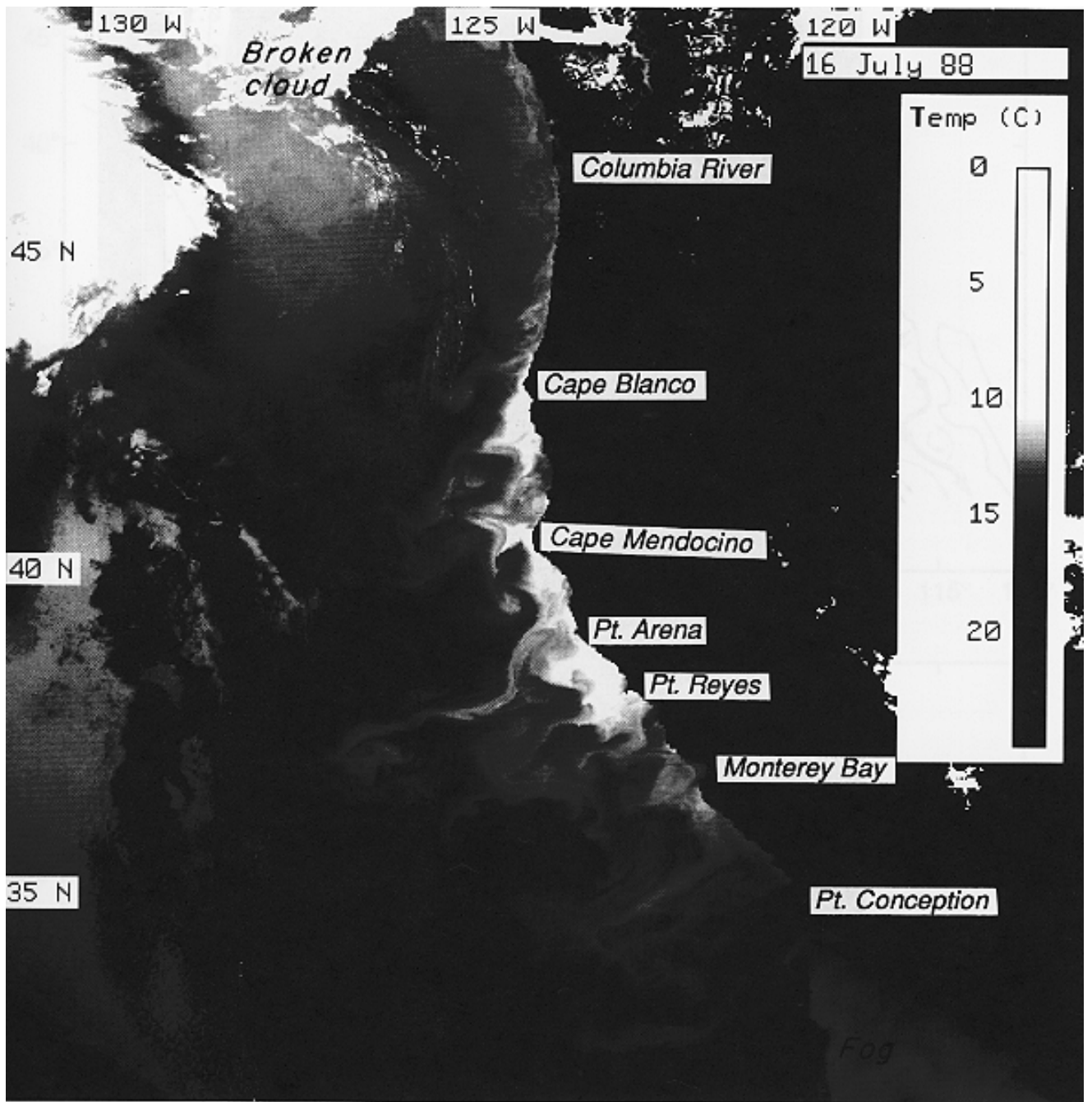


Figure 2. Surface temperature from the AVHRR satellite sensor on 16 July 1988 (from Strub et al., 1991).

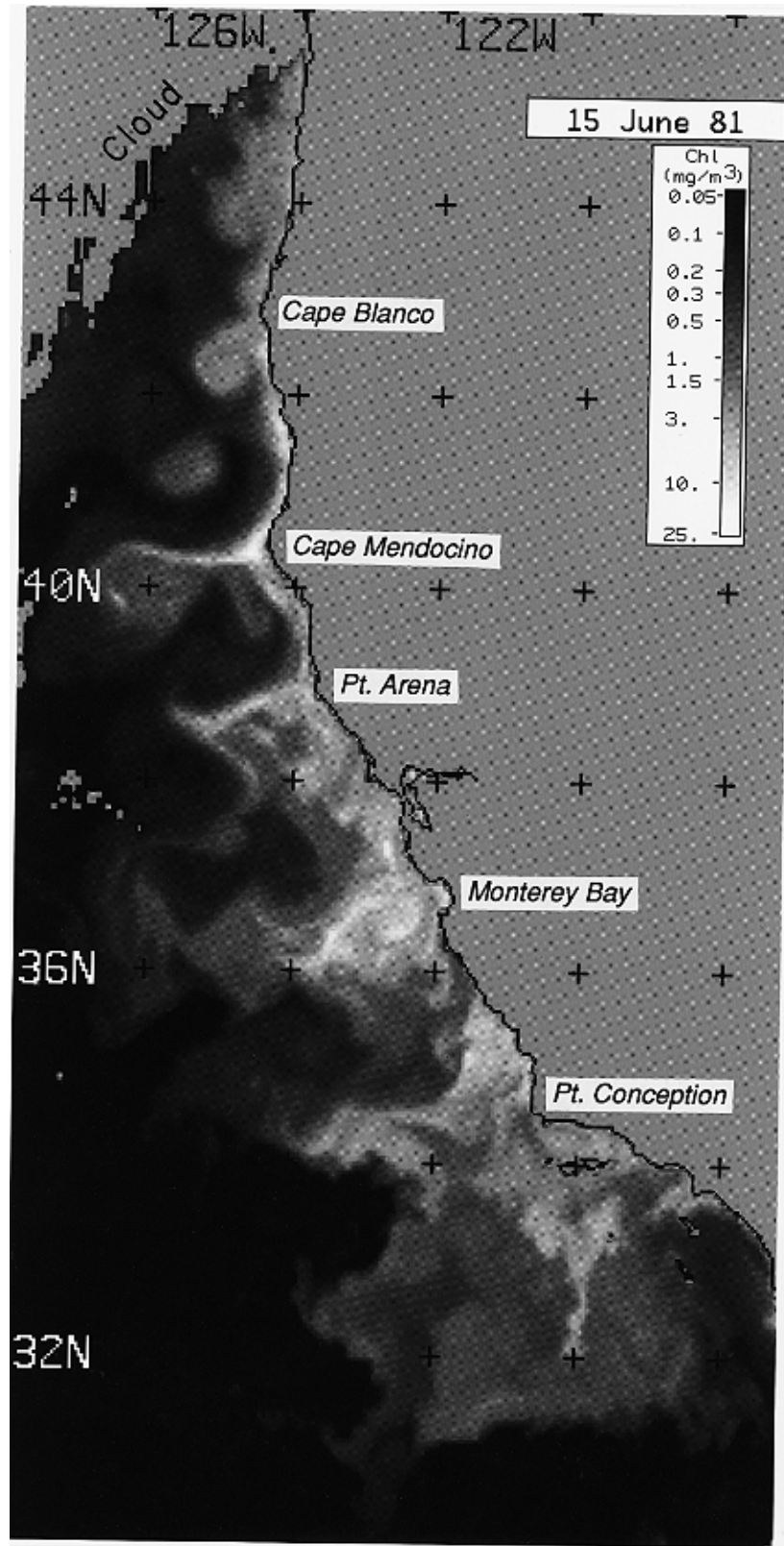


Figure 3. Surface chlorophyll content estimated from the Coastal Zone Color Scanner (CZCS) on 15 June 1981 (from Strub et al. 1991).

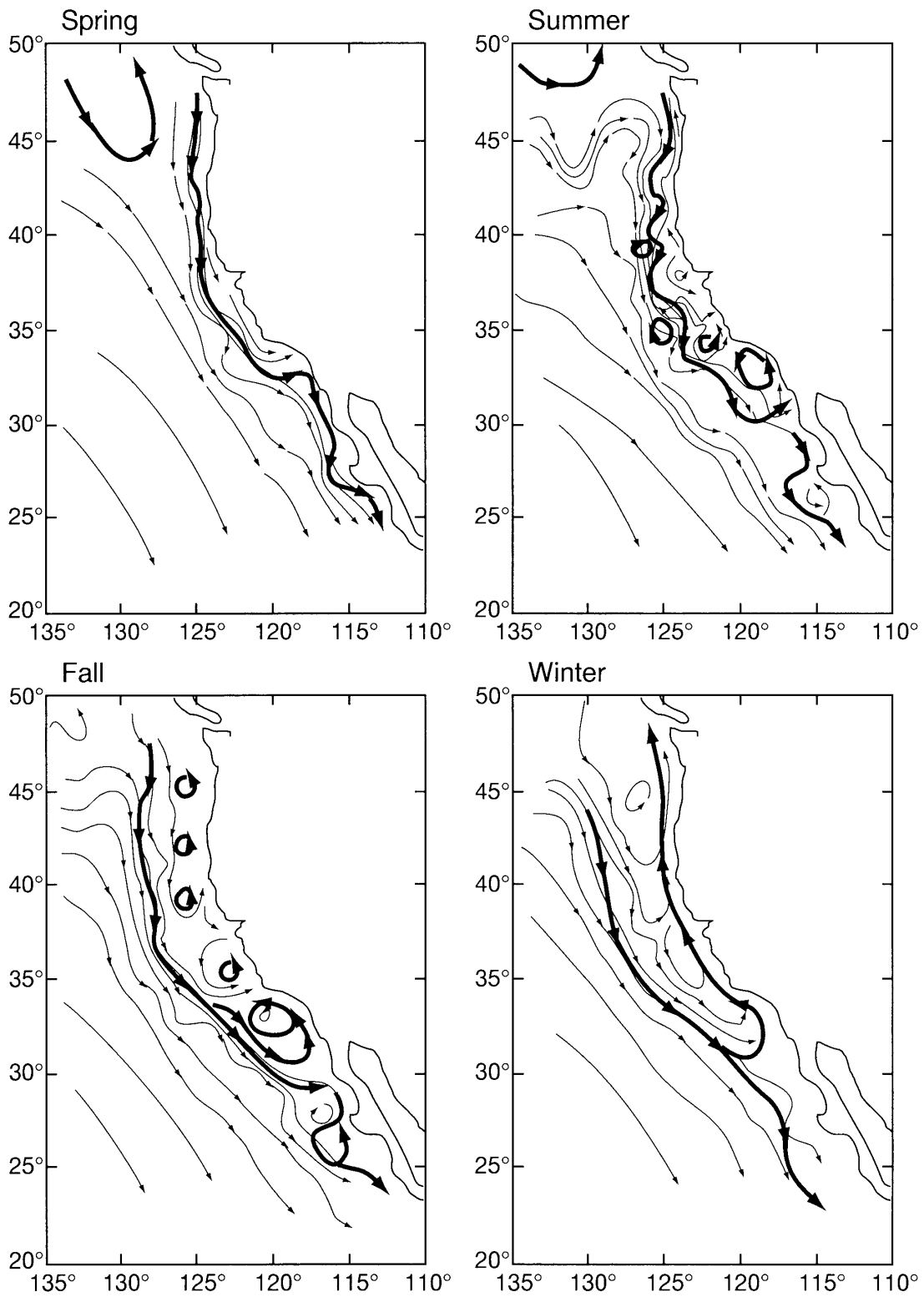


Figure 4. Schematic of the seasonal circulation of the CCS. (from Strub, unpublished)

The Biological Setting

The four regions of the CCS, defined above from physical attributes, have many unique biological characteristics. A more detailed and referenced discussion of these regional differences is found in Section VIII and is only briefly summarized here.

Regional Division

Region I—Vancouver Island to Cape Blanco. Phytoplankton biomass and production are strongly seasonal. Zooplankton species are primarily of subarctic affinity and are also highly seasonal. Many of the common copepods overwinter in deep water and have seasonally restricted growing seasons. There are several major estuaries that serve as spawning and nursery grounds for fish. Some pelagic fish spawn in Region I.

Region II—Cape Blanco to Point Conception. Primary production is strongly seasonal, and can be elevated in mesoscale jets and eddies. Cape Blanco (to Cape Mendocino) is the approximate southern boundary of Subarctic zooplankton species; in Region II the dominant zooplankton fauna consists primarily of Transition Zone species and no Region II endemics are known. Zooplankton biomass varies seasonally. There are a few major estuaries. Region II is the latitudinal minimum in spawning by epipelagic fishes.

Region III—Point Conception to Punta. Baja. Primary production shows damped seasonal variation, which is often exceeded by interannual variations. The zooplankton is a mixture of Transition Zone species with warm water taxa introduced from the south and the west. An example of Pt. Conception as a distributional boundary for two euphausiid species can be seen in Figure 5. Zooplankton biomass shows relatively small amplitude seasonal variability. Copepods may show both overwintering at depth and continuous reproduction. Region III is the latitudinal maximum in spawning by epipelagic fishes.

Region IV—Punta Baja to Cabo San Lucas, Southern Baja California. There is modest seasonality in primary production, much of which may be localized in major upwelling centers. The zooplankton assemblage is a mixture of some Transition Zone and other cool water species with Equatorial and Eastern Tropical Pacific fauna. Zooplankton biomass shows damped seasonality. Fish spawning tends to be geographically localized.

Boundary Shifts

Variability Due to ENSO. The boundaries between regions are approximate and may shift during episodes of strong transport from the south, such as during ENSO events (Fig. 6, Brinton, unpublished) or intervals of strong transport from the north (Chelton et al. 1982). Distributional shifts, such as the northward displacement of the cool water, coastal euphausiid *Thysanoessa spinifera* during ENSO events can alter food webs. For example, both silver salmon and certain pelagic birds depend on *T. spinifera* in the Gulf of Farallones, off San Francisco Bay, and the northward displacement of their primary prey in the 1982-83 ENSO altered feeding success. In addition to geographic displacements associated with ENSO's, ENSO-induced decreases in zooplankton biomass (McGowan 1985) and shifts in relative abundances of gelatinous and crustacean zooplankton (Smith 1985) have been documented. These ENSO variations, and other interannual signals, can generate much of the biological variability in the CCS.

Decadal Scale Shifts. Major biological shifts in the CCS have been documented for the recent warm period (beginning in 1977; see Fig. 9), including a five-fold drop in zooplankton abundance within the Southern California Bight (Roemmich and McGowan 1994; Fig. 7) and recovery of depleted Pacific sardine stocks (Barnes et al. 1992). We do

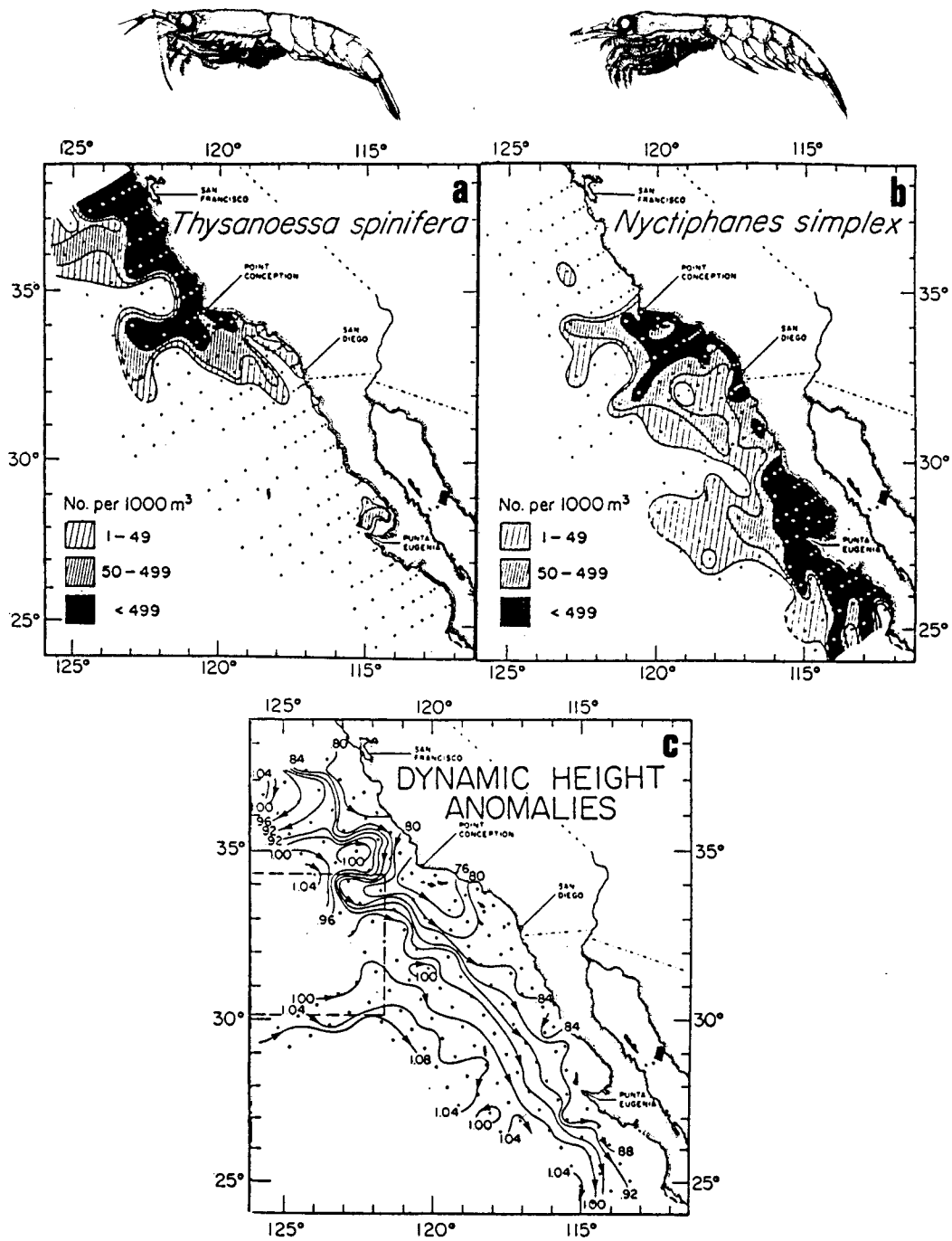


Figure 5. Point Conception as a faunal boundary. (A) The cool water euphausiid *Thysanoessa spinifera*, introduced from the north and (b) the warm water euphausiid *Nyctiphanes simplex*, introduced from the south. Note the pronounced influence of the mesoscale eddies located west of Pt. Conception (see panel C) on the local distributions of euphausiids. (From Brinton 1981 and Haury et al. 1986.)

Thysanoessa spinifera

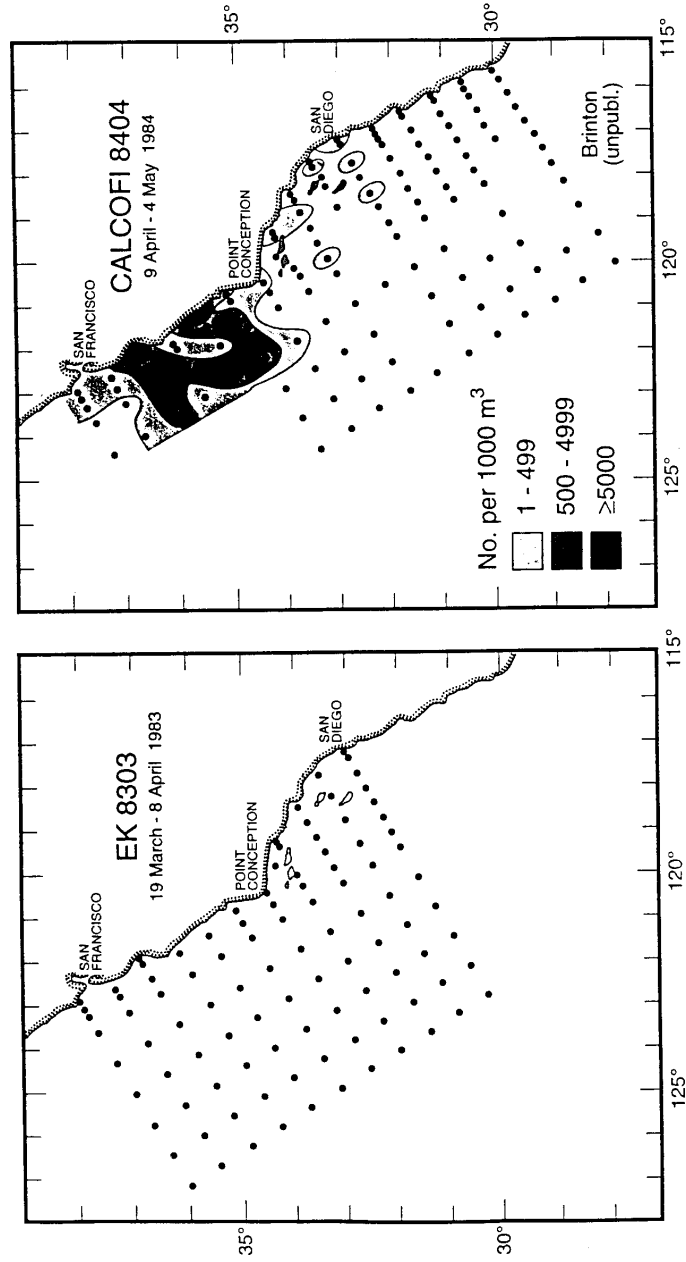
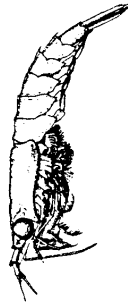


Figure 6. Change in the abundance of the euphausiid, *Thysanoessa spinifera*, in central and southern California during the warm phase of an ENSO. Left panel is from cruises done in spring 1983 when waters were much warmer than normal. Right panel is from a spring CALCOFI cruise in 1984, following a return to more normal (non El Nino) conditions. (from Brinton, unpublished)

not know how these are related to spatial boundaries in the CCS. However, during this same period, zooplankton biomass in the subarctic Pacific has doubled (Brodeur and Ware 1992) as has that of squid (Brodeur, in prep), suggesting major shifts in productivity of the subarctic gyre (increased) and California Current (decreased) during the present warm regime.

Longer term, interdecadal scale variations in zooplankton abundance in parts of Region III of the CCS have also been observed. Roemmich and McGowan (1994; Fig. 7) document a long term decline in zooplankton biomass within the Southern California Bight that began approximately at the time of the mid-70's warming event in the CCS.

Life History Traits

The large-scale latitudinal differences in intensity of coastal upwelling, primary productivity, and cross-shore transport in the CCS correspond to regional differences in dominant life history traits of marine invertebrates and fishes. There is a strong tendency for the spawning activity of motile fishes to be centered in Region III (the Southern California Bight and region immediately offshore); over 90% of the epipelagic fish biomass (principally hake, sardine and anchovy) in the southern sector of the CCS spawns in Region III (Ware and MacFarlane, 1989). Pacific hake (*Merluccius productus*), for example, occur as adults off northern Washington and British Columbia but undertake southward migrations along ca. 15° of latitude to spawn in Region III. Parrish et al. (1981) suggest that Region II is a hazardous region for spawning of epipelagic fishes because of intense off-shore advection of larvae, many of which are lost to the population. The concentration of fish spawning activity in regions of the CCS with longer residence times and reduced offshore transport (Region III) is consistent with the member-vagrant hypothesis of Sinclair (1988), which supposes that pattern and abundance of a population is spatially defined by the size and location of spawning and early life-history areas, themselves defined by physical conditions permitting life-cycle closure. Parrish et al. also suggest that those species that do spawn in Region II employ life history strategies that reduce the risk of offshore transport of the larvae, such as live-bearing by rockfishes, anadromous spawning by salmonids, demersal spawning in protected waters by herring, lingcod and littoral fishes, and deep-water spawning by some pleuronectids and sablefish. Marine holozooplankton that are restricted to the nearshore in Region II may employ vertical migration behavior and ontogenetic changes in vertical distribution that interact with vertical current shear to reduce offshore transport and increase their residence time in the coastal zone in a manner shown for *Calanus marshallae* (Peterson et al., 1979; Peterson 1980; Wroblewski, 1982) for Region I.

Sedentary adults of marine benthic invertebrates clearly cannot undertake the spawning migrations of motile fishes. Although spawning of marine benthic invertebrates may not be localized to one region of the CCS, recruitment success to the nearshore marine benthos can be. Roughgarden et al. (1988), for example, suggest that the recruitment success of intertidal barnacles along the central California coast is strongly influenced by cross-shelf transport of larvae, which may be controlled by onshore-offshore displacement of alongshore fronts. Recruitment is favored when the fronts are nearshore and act as a barrier to offshore dispersal. In Region I, however, where cross-shore transport is less intense (and onshore flow associated with downwelling occurs for part of the year), the supply of larvae is thought to be capable of saturating benthic substrates. Where the supply of larvae is saturating, adult-adult interactions or predation on the bottom may be the most important determinants of population growth and benthic community composition (Paine, 1984). Similarly, topographically controlled nearshore circulation can regulate recruitment success both in space and time. Recruitment of purple sea urchin (*Strongylocentrotus purpuratus*) larvae to the benthos is influenced by

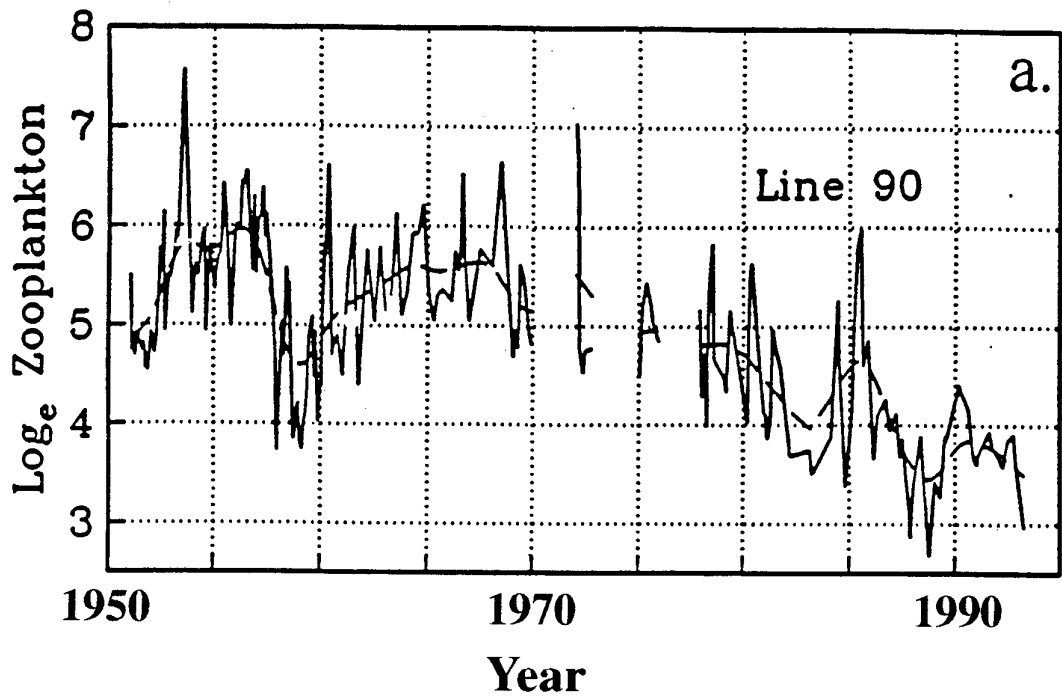


Figure 7. Time series (1950-present) of zooplankton volumes from stations along CalCOFI transect line 90. Line 90 extends onshore-offshore within the center of the California Bight (Region III). (from Roemmich and McGowan, 1994)

latitudinal variations in the presence of topographic features such as capes and headlands. Such features tend to be sites of strong offshore transport and thus reduced nearshore larval supply, resulting in infrequent events of successful recruitment (Ebert and Russell, 1988). Wing et al. (in press) have shown how upwelling relaxation can lead to northward, onshore transport and subsequent recruitment of crab species in Region II. Concentration of larvae in upwelling shadows in the lee of promontories, with subsequent northward transport may provide a retention mechanism in the face of strong southward currents during upwelling.

Satellite images reveal that zones of enhanced phytoplankton biomass extend further offshore in Region II than elsewhere in the CCS, in a rich variety of mesoscale features including eddies, jets, and coastal filaments (Strub et al., 1991). While experimental evidence suggests that copepod lipid reserves and egg production may increase in response to the enhanced food supply in coastal filaments (Smith and Lane, 1991), the ultimate fate of this elevated copepod secondary production is not known.

The life history traits of sibling species of marine copepods differ in the north and south of the CCS. *Calanus pacificus*, for example, shows seasonal diapause at depth in Region I (in Puget Sound, Osgood and Frost, 1994), but in Region III only one fraction of the *C. pacificus* population undergoes diapause (Longhurst, 1967; Alldredge et al., 1984) while another fraction shows continuous year-round reproduction in near-surface waters (Mullin and Brooks, 1967). Similar differences in diapause response are known for a population within a region: the *Calanus marshallae* population in Dabob Bay, a fjord at the northern end of Region I, produces a single generation which begins in February and goes into diapause in May. The population which resides in shelf waters off Oregon and Washington (also Region I) passes through multiple generations, beginning in January/February and extending through September.

Comparative studies of conspecifics in different parts of their range are likely to lead to improved understanding of both the proximate cues and ultimate advantages of different life history traits. These studies will provide the basis for the development of predictive models of population growth under different scenarios of a changing ocean climate.

Genetic Considerations

Many key species of holozooplankton, fish, and benthic invertebrates are distributed widely throughout the CCS. Examples include the calanoid copepod (*Calanus pacificus*), the Dungeness crab (*Cancer magister*), the red sea urchin (*Strongylocentrotus franciscanus*), and several clupeid fish (northern anchovy, *Engraulis mordax*; Pacific herring, *Clupea pallasii*; and Pacific sardine, *Sardinops sagax caerulea*). Because of the broad geographic extent of the CCS, it is possible that such widespread species will be genetically variable among populations in different regions, although the broad dispersal of planktonic stages will act as a strong evolutionary force promoting genetic homogeneity. It is important that U.S. GLOBEC resolve the systematics and population genetic structures, both spatially and temporally of organisms targeted for long-term field study. Exciting new techniques have been developed for characterizing genetic variation, amplifying DNA sequences from single, microscopic individuals, and measuring rates of migration among populations; these techniques should be applied to key taxa in the CCS.

Isolation of subpopulations, particularly in regions of steep environmental gradients, can lead to genetic differentiation of populations through local adaptation or genetic drift. There are clearly large environmental gradients among regions of the CCS, however, subpopulations of most marine species are unlikely to be isolated from one another due to the large scale dispersal of planktonic stages. The ensuing gene flow associated with this

dispersal should homogenize the genetic composition of populations over large regions (Burton 1983, Gyllensten 1985, Hedgecock 1994a). Comparisons of life histories and vital rates for many widespread species have found significant differences among regions of the CCS. U.S. GLOBEC studies must determine if genetic variation contributes to this geographical variation in key traits. Genetic studies will need to resolve whether species thought to range widely in the CCS are indeed single species or instead sibling species, whose morphological similarity masks underlying genetic differences. Similarly, population genetic studies will need to characterize the amount of spatial genetic variation within species. Such studies could reveal exceptions to the expectation of spatial homogeneity (e.g., some evidence exists for differentiation of northern and southern populations of *Calanus* ; Bucklin and Kann, 1991), or they could reveal previously unrecognized barriers to dispersal (e.g., Avise et al. 1987, Burton 1994).

Temporal genetic change via recruitment appears to be as large or larger than geographic variation on broad spatial scales (Johnson and Black, 1984; Hedgecock, 1994a, 1994b). Molecular methods could be applied to preserved zooplankton (such as in the CalCOFI collections) to establish time-series estimates of genetic structure and variation for targeted taxa. Moreover, population genetic studies are also important for estimating effective population size—i.e., an estimate of the number of individuals that successfully reproduce—which has recently been shown to be surprisingly small, often many orders of magnitude less than adult abundance (Hedgecock, 1994b). If so, this establishes a link between oceanographic processes and population genetic structure which might be exploited to help explain how local adaptations and speciation can occur in seemingly large, well-mixed marine populations.

Understanding how widely distributed species respond evolutionarily to climatic variation over a broad geographic range may provide important clues to predict how distributions may be altered by climate change. It is equally important, however, to understand how more narrowly distributed species may respond to climate change, because they may respond first or be most seriously affected by future climate change.

SECTION IV—THE CLIMATE CONTEXT

Predictions from Historical Data

The CCS exists within the context of basin-wide oceanic circulation patterns that determine its internal structure (temperature, salinity, nutrients, stratification) and affect its currents through inflow and outflow across its boundaries (Pares-Sierra and O'Brien 1989). "Local" surface wind forcing is also large scale in nature, since it is directly linked to the North Pacific high pressure system over the ocean, the thermal low over western North America (in summer) and the Aleutian low pressure system and storm tracks in winter. In the California Current, there are known, large biological changes associated with both the spatial and temporal patterns of physical circulation. Thus, it is not surprising to find strong covariability between physical and biological processes in the CCS and the large-scale atmospheric and oceanic circulation patterns that vary over event to decadal time scales (Peterson 1989).

Several long time series have been used to document the natural physical and biological variability in the CCS. These include shore-based and merchant vessel measurements (~100 years); subsurface biological and physical measurements from the CalCOFI data set (45 years) and additional surveys from specific regional projects (various dates); fish otolith collections (documenting annual growth over the past 60-100 years); and high resolution varved sediments from the Santa Barbara Basin (fish scales, diatoms, foraminifera and radiolaria over the past 1500 years). These time series show distinct quasi-periodic variability in the physical and biological components of the ecosystem, with interannual to interdecadal time scales. Moreover, ocean warming has already been measured in the California Current using hydrographic time-series data from the CalCOFI program. Roemmich (1992) documented a general ocean warming of ca. 0.8°C and a rise in sea level between 1950 and 1990 along the southwest U.S. coast. The data indicate that the warming was greatest in the upper 100 m, but was significant to depths of 300 m.

The largest source of variability at the interannual (2-10 year) time scale is the ENSO cycle. Following the warm phase in the tropics, the observed effects at mid-latitude reach the coastal ocean by both an oceanic and an atmospheric path, causing warming of the upper ocean and deepening of the thermocline. The oceanic path occurs along the eastern margin of the basin, where Kelvin waves propagate poleward, depressing the thermocline and resulting in anomalously warm temperatures (Rienecker and Mooers, 1986; Simpson 1983). Increased advection from the south has also been measured directly by current meters (Huyer and Smith, 1985). The atmospheric path is usually slower, resulting in an anomalously strong Aleutian low that may be displaced to the south and/or west and a weaker North Pacific high that may be displaced to the south. The change in atmospheric pressure and storm tracks results in wind-driven currents that transport warmer water onshore. Upwelling in summer does not necessarily weaken but its effects (cold SST and higher pigment concentrations) appear trapped closer to the coast than during other phases of the ENSO cycle (Fiedler, 1984). The boundaries between the regions in the CCS (Figure 1) have been observed to shift during these warm phases causing northward shifts in the distributions of species and their spawning patterns (Percy and Schoener, 1987; Wooster and Fluharty, 1985). Onshore and northward shifts of predators create unusually high mortality rates for herring and salmon smolt. Primary production, phytoplankton stocks, and thus food resources for zooplankton are reduced due to reduced nutrient supply. Seabird reproduction in some regions is also impacted by the disappearance of their euphausiid prey (Ainley and Boekelheide 1990). Thus, a number

of physical and biological parameters are strongly affected during the warm phase of the ENSO cycle, although the effects may differ among the different regions.

On longer time scales, time series of SST display distinct multidecadal periods of relatively cool and warm conditions, punctuated by the ENSO warm events. SST observations at higher latitudes display a periodicity of about 20 years that may be linked to long period tides (Royer 1993) or atmospheric pressure anomalies (Emery and Hamilton, 1985; Trenberth, 1990). Sediment cores reveal a 60-70 year cycle in the relative dominance of sardine and anchovy over the last 1500 years (Baumgartner et al., 1992) and the direct observational time series (50-100 years) resolve one cycle of this pattern in the physical environment as well as the ecosystem structure—warming around 1925, cooling around 1948 and warming again around 1976 (Hollowed and Wooster, 1992). Shifts from one state to another (warm to cool or vice versa) are often accompanied by concomitant shifts in biological conditions, as abundances, distributions or compositions shift.

The most recent shift is particularly well documented. Coincident with the change in SST was a notable decrease of zooplankton biomass in Region III (Roemmich and McGowan, 1994) and an increase in the sardine population in Southern California (Barnes et al. 1992). The strength of springtime northerly winds diminished during this period and there is evidence that the large-scale ocean-atmosphere circulation changed after 1976 (Trenberth, 1990; Graham, 1994; Miller et al., 1994b; Trenberth and Hurrell, 1994). From these observed changes, it is reasonable to assume that interdecadal fluctuations in ocean climate, such as those modeled by Miller et al. (1994a, 1994b), create changes in habitat that tend to favor certain species over others on similar time scales. Analysis of the ecosystem response to these interdecadal changes in forcing is especially promising in the CCS, due to the exceptional time series available from the region.

Predictions from Models

Added to these natural modes of variability will be anthropogenic effects, such as the changes in climate expected to be caused by increased concentrations of greenhouse gasses. Ideally, the design of observational programs intended to determine the likely effects of climate change on marine animal populations in the CCS would be based on clear, well-understood directions and magnitudes of the changes expected in the physical environment. Unfortunately, the global coupled ocean-atmosphere models (general circulation models; GCMs) that have been used to examine atmospheric and oceanic circulation responses to increased concentrations of greenhouse gasses (hereafter referred to as carbon dioxide; CO₂) have spatial resolutions too coarse (approximately 250 km grid spacing) to represent the details of coastal ocean circulation or wind forcing. Moreover, the effects of vertical ocean circulation dynamics and cloud cover are either poorly understood or inadequately included in existing GCMs.

Despite such shortcomings, coupled GCMs may provide broad indications of global warming induced changes in the large-scale Pacific Basin atmospheric and oceanic circulation and internal ocean structure, from which we can hypothesize physical and biological changes in the CCS. For example, coupled GCMs suggest that an atmospheric doubling of CO₂ will increase land-sea temperature differences (Trenberth, 1993), intensify equatorward winds in summer and lead to stronger coastal upwelling (Bakun, 1990). Other studies point out that the effects will be more complex and regional than a simple increase in wind strength everywhere (Hsieh and Boer, 1992). Trenberth (1993) discusses implications from the coupled global models and suggests that: (1) the western

coast of North America is expected to warm by 1-1.5°C by the year 2030; (2) northern regions will warm more rapidly than equatorial regions, decreasing the strength of the mean atmospheric circulation; (3) monsoonal circulation will intensify as the land heats more than the ocean, supporting Bakun's (1990) hypothesis; (4) the hydrologic cycle will strengthen by approximately 10%, implying greater extremes of evaporation and precipitation; and (5) ENSO cycles will continue to exist and to produce greater extremes of flood and drought in the tropics (also found by Meehl, et al., 1993).

On the oceanic side of the coupled GCMs, gradual CO₂ doubling causes temperatures in the ocean at mid-latitudes to increase by 2°C at the surface, 1°C at 500 m and 0.5°C at 700 m. Thus, both temperature and stratification increase in the upper water column (Bernal 1993). At higher latitudes, heating is only 1.5°C at the surface but it extends deeper. Manabe et al. (1991) show this warming to be slightly less in the NE Pacific than in the zonal mean, with values of 1-2°C at the surface.

With respect to forcing by winter storm winds, the model results suggest either no change or a decrease of storm activity at mid-latitudes. Stevensen and Held (1993) show changes in the zonal atmospheric circulation that includes weakening of the subtropical jet on its equatorward side and strengthening of the jet on its poleward side (north of 45°N), i.e., a northward shift in the jet. They find the Atlantic storm track to be weakened and imply no change in the Pacific storm track, although they caution against over-interpreting the details of the coarse resolution model results. In fact, many of the authors of the present generation of climate models caution us about the high level of uncertainty that exists in the model results. Keeping this caution in mind, several possible effects of climate change on the circulation and ecosystem dynamics of the CCS can be hypothesized from these model results, in some cases supported by observations.

Predictions from First Principles

One simple prediction of the response of the CCS to global climate change is that the **boundaries between distinct physical and biological regions will move** (Fields et al. 1993), as noted during ENSOs. This could occur due to changes in large-scale wind forcing or meridional advection. Given the prediction of increased upwelling-favorable winds in summer under global warming scenarios, it is possible that the CCS-wide increase in upwelling and mesoscale activity might move or blur the boundary between present Regions II and III (e.g., between the region offshore of the Southern California Bight and the region off central California). Another simple prediction is that changes in the large-scale atmospheric circulation and the predicted increase in land-sea temperature differences could **change the strength, timing or even the occurrence of the spring transition**. Spawning by many species having pelagic larvae occurs synchronously with blooms of phytoplankton in some regions of the CCS. Successful reproduction and fledging of young in some bird populations of the CCS is tied to the timely availability of large amounts of appropriate food resources near the rookery. Changes in water temperature and/or wind patterns that alter the timing and location of blooms of phytoplankton or spawning (reproduction) of animals may compromise the synchronicity necessary to assure successful recruitment. In the extreme, such changes could result in the failure of resident species and replacement by other species having life history strategies favored by the changed conditions.

In regions where the Bakun hypothesis is correct, **greater upwelling and increased stratification will create stronger upwelling fronts and jets as well as increased vertical shear within these jets**. Since the growth rate of baroclinic instabilities is proportional to vertical shear they should be more unstable, leading to greater mesoscale

activity in summer. Finally, through Ekman balance there will be an increase in average offshore transport at the surface, with compensating onshore flow below to feed the increased coastal upwelling. At the same time, mean southward transport in the core of the CCS is predicted to decrease due to: 1) a decrease in the inflow to the CCS from the north as the strength and position of the West Wind Drift is altered by latitudinal-dependent global warming; 2) a decrease in the mean atmospheric circulation and thus ocean forcing; and, 3) little change in storm-driven flow entering along the western open boundary of the EBC region. If thermocline depths and stratification do not change with global warming in part or all of the CCS, the Bakun hypothesis suggests increased nutrient delivery to surface waters which should increase primary production and increase phytoplankton and higher trophic level biomasses.

Peterson et al. (1993), however, argue that **global warming will cause the thermocline and nutricline to be depressed** along the west coast of the Americas. Through analogy with the warm phase of ENSO, they argue that the net result of increased upwelling-favorable wind stress and a depressed nutricline will be greater upwelling, offshore transport and turbulent mixing, but decreased nutrient concentrations in the mixed layer. Even in the absence of a depressed thermocline in the eastern Pacific, an increase in stratification creates the possibility that much of the onshore flow compensating the offshore surface flow may come from above the nutricline, also reducing nutrient levels in the mixed layer. Reduced nutrient levels in the mixed layer would impact phytoplankton productivity and species composition and perhaps lengthen food chains, resulting in reduced fish biomass.

Climate Change Scenarios

Table 1 summarizes hypothesized physical changes that might occur in the CCS as a result of greenhouse gas-induced climate change. While the directions of the hypothesized changes are of interest in their possible impacts, they are in most cases tentative and should not limit the scope of planned investigations. The hypotheses are most useful in identifying which physical and biological parameters should be measured and which biophysical mechanisms might be of greatest importance.

Direct Effects of Climate Change

Lateral Boundary Conditions

Inflow from the West Wind Drift (WWD)—Hypothesis: decrease. This may decrease, if heating of the higher latitude Alaskan gyre is deeper than farther south, weakening the north-south gradient in dynamic height across the WWD. Increased precipitation in the Alaskan gyre may enhance this slightly. However, the position of the WWD could also shift north or south, changing the proportion of the transport that flows into the CCS as opposed to the Alaskan gyre. The coupled models appear to indicate a northward shift of the atmospheric jets and a weakening at mid-latitudes, which may move the WWD northward and/or weaken it further, reducing the inflow to the CCS.

Table 1. Hypothesized physical changes in the CCS under a global warming scenario.

<u>Physical Process</u>	<u>Hypothesized Change</u>
1. Intensity of west wind drift	Decrease
2. Location of west wind drift	Shifts further north
3. Freshwater input	Increase in region I, decrease elsewhere
4. Coastal wind stress	Incr. summer, no change - decr. winter
5. Mean sea surface temperature	Increase in all months
6. Stratification	Increase
7. Mean transport of CCS	Decrease
8. Alongshore transport upwelling jets	Increase
9. Turbulent mixing	Incr. summer, no change - decr. winter
10. Transport in eddies and meanders	Increase
11. Offshore transport	Increase
12. Vertical transport (upwelling)	Increase
13. Mixed layer depth	Unknown
14. Winter storm frequency	Fewer
15. Winter storm intensity	Less intense
16. Timing of spring transition	Unknown

Storm-driven inflow along the western boundary—Hypothesis: No change or decrease. As discussed above, several factors may affect the strength of storms, changing the strength of the mean northward winds over the western portion of the CCS and the onshore Ekman transport into the CCS. Stephenson and Held (1993) suggest that present models do not indicate a strong change but the weaker overall circulation suggests a decrease in storm winds at mid-latitude.

Outflow to the south—Hypothesis: decrease. By simple continuity, if there is less inflow at the north and no change along the western boundary, the outflow will decrease. This might be slightly altered during summer, if the increased upwelling draws water from beneath the main current into it or if the stronger upwelling produces a stronger jet that can pull more water into the system from the north. During the warm phase of ENSO's, there is a transient northward flow associated with the poleward propagation of the equatorial signal, but there would not necessarily be an analogous northward flow due to gradual heating.

Freshwater input at the coast—Hypothesis: increase in the Pacific Northwest. The increase in the strength of the hydrologic cycle implies an increase in precipitation in the Pacific Northwest, which enters the ocean primarily in the Columbia River and through the Straights of Juan de Fuca. This would slightly increase the stability in the top 1-20 m of the ocean, north of approximately 43°N. A change in storm track location and strength could alter this effect (i.e., if more storms are diverted into the Gulf of Alaska).

Surface Winds

Alongshore wind stress, mixing power and wind stress curl—Hypothesis: increase in summer, no change or decrease in winter. This is based on the Bakun (1990) hypothesis and the fact that the mixing power (proportional to the cube of the wind speed) and the curl of the wind stress in the 100-200 km next to the coast also increase when the strength of the southward winds increases. The lack of change or decrease in winter is based on the prediction of no change or decrease in storm activity (Stephenson and Held 1993).

Timing and persistence of the spring transition—Hypothesis: unspecific change. The occurrence of the spring transition in winds in the Northeast Pacific is part of a rapid large-scale expansion of the North Pacific High, which coincides with a reorientation of the jet stream, similar to a brief (approximately 10 day) blocking event (Strub and James, 1988). This may involve the interaction of the atmospheric circulation and the seasonally developing land-sea temperature difference, with pressures over the land dropping as the continent heats. The weakening of the strength of the atmospheric circulation and the increase in the land-sea temperature difference seems likely to change the strength, timing or even existence of the spring transition, but no guess is offered on the form this change may take.

Mean temperature and stratification—Hypothesis: increase in both. The hypotheses are based on the mean model results, since it is unlikely that the present coarse-resolution models represent the local conditions in the CCS. Given the mean upward slope in the thermocline from west to east, the mean change in temperature and stratification may be more representative of the deeper ocean and thus weaker than that produced by the Stouffer et al. (1989) model. Given the coarse resolution of the model, it is possible that the model misses important differences between the CCS and the mid-ocean.

Indirect Effects of Climate Change

Transport

Mean alongshore transport—Hypothesis: decrease. The argument is same as for outflow to the south (above).

Transport in alongshore upwelling jets—Hypothesis: increase. Upwelling converts vertical density differences to horizontal differences across a front. If both the ambient vertical stratification and wind-driven coastal upwelling increase, stronger fronts will be created, with stronger alongshore jets. Stronger turbulent mixing may deepen or widen these jets, reducing velocities, but transport will still be greater.

Transport in mesoscale meanders and eddies—Hypothesis: increase. If the previous hypothesis is correct, the stronger horizontal density gradient in the upwelling front implies greater geostrophic shear in the jets. This will make them more unstable, leading to greater meandering of stronger jets and subsequent eddy activity.

Offshore transport—Hypothesis: increase. One of the robust findings of Ekman theory is that the vertically integrated wind-driven transport is in good agreement with the simple Ekman calculation. This has specifically been tested, and confirmed, over the shelf of eastern boundary currents under upwelling conditions (Lentz, 1992). Thus, where Bakun's hypothesis is correct, there will be increased average offshore transport at the surface, with compensating onshore flow below and upwelling along the coast. There will also be increased transport in the offshore portions of the meandering jets, if their strength increases as hypothesized.

Vertical transport (upwelling)—Hypothesis: increase. Upwelling at the coast will increase with increased summer winds, as stated above. Upwelling over the region between the coast and 100-200 km offshore will increase due to increased wind stress curl. Upwelling due to the internal dynamics of eddies and jets will increase with the increase in mesoscale activity. Whether this upwelling draws water from above or below the pycnocline is a crucial question.

Movement of Regional Boundaries—No hypothesis. As stated earlier, one simple prediction for the response of the California Current System is that the boundaries between the physical and biological regions will shift latitudinally. This could occur due to changes in large-scale horizontal advection (north-south) or due to changes in the surface forcing (mostly winds) and the resultant circulation patterns. Movement of these boundaries has been observed during El Niños, possibly caused by the increase in northward transport, by storm-driven onshore transport of warmer water, or both.

As an example of the kind of changes that could occur if upwelling-favorable winds increase in summer as a result of global warming, we offer this scenario. If the physical boundary between Regions I and II off southern Oregon is caused by the presence of Cape Blanco, the location of this boundary would not be expected to change. The hypothesized increased in wind stress, mesoscale activity and upwelling might, however, make the Southern California Bight look more like Region II, moving the boundary between Regions II and III to the south and changing the nature of the Bight. This could have severe impacts on the pelagic species that presently use the Bight as a nursery. This is offered only as an example, not as a prediction. One of the questions to be answered by the research suggested by this science plan is the extent to which these boundaries

have changed in the past during normal climate variations and whether their movement will increase or decrease as a result of global climate change.

Vertical Structure—Hypothesis: Increase in stratification, decrease in mixed-layer nutrients. The vertical structures of temperature, density and nutrients are important parameters for biophysical interactions and offer an example of the complexity of those interactions. Changes in these structures depend upon a mix of factors: 1) the ambient structure of the deep ocean (especially stratification, depth of the thermocline and nutricline); 2) the degree of vertical turbulent mixing (depending on wind mixing power and stratification); and, 3) the strength of upwelling. The predictions of stronger ambient stratification and stronger winds in summer, lead to an increase of upwelling, but changes in the depth of the mixed layer depend on the relative balance of mixing power and stratification. If the increased wind mixing is capable of penetrating the increased stratification and creates a mixed layer as deep as found at present, the overall water column must still be more stable, resulting in a greater density jump at the bottom of the mixed layer. If the wind penetrates farther, the density jump will be even greater. This raises the possibility that much of the onshore flow compensating the offshore surface flow may come from above the thermocline and nutricline, reducing nutrient levels in the mixed layer. Three-dimensional dynamical models of the coastal ocean are needed to determine the effect of specified changes in winds and stratification. Those models must have realistic parameterization of turbulence to determine the effect on nutrient distributions.

Basin-scale circulation patterns may also affect the vertical structure of density and nutrients. Peterson et al. (1993) argue that the basin-wide density structure under global warming scenarios will resemble conditions during the warm phase of ENSO cycles. They argue that: 1) the warm pool in the western Pacific will expand eastward and reduce the fetch over which trade winds travel between the cool eastern tropical Pacific and the warm pool; 2) the reduced fetch (similar to the Atlantic) will result in less inclination of the thermocline from west to east and a deeper thermocline and nutricline in the eastern Pacific; and, 3) the present west to east tilt due to equatorial dynamics extends to at least 30°N, implying that deeper thermoclines and nutriclines will be found at temperate latitudes, although less strongly off North America than off South America. If the thermocline and nutricline are depressed by global warming along North America, the net result of increased upwelling-favorable winds will be greater upwelling, offshore transport and turbulent mixing, but decreased nutrient concentrations in the mixed layer, similar to El Niño conditions. They further discuss the implications of these conditions for: 1) recruitment of different species of fish and benthic invertebrates (less favorable for sardine/anchovy); 2) predator/prey interactions (fewer pelagic fish, more euphausiids); and, 3) food web energy dynamics (longer food chains, less fish biomass, and an increased energy supply to the benthos). Although one may disagree with many of their arguments about individual mechanisms or interactions, their discussion serves as an example of the complexity of the interactions and feedbacks involved in determining the complete biophysical response of eastern boundary currents to changing environmental conditions.

SECTION V—CENTRAL QUESTIONS AND GOALS

The goal of U.S. GLOBEC is to understand the linkages between climate variability and long-term change, and the distribution and abundance of animal populations, including many that are important to society. The CCS offers an excellent opportunity to accomplish this goal. In the CCS we can exploit known spatial and temporal variations in physical processes and biological responses to project population trajectories under different scenarios of climate change. We can utilize: 1) the present latitudinal variations within the CCS; 2) interannual (periods of 2-10 years) temporal variability within the CCS, especially as linked ENSO cycles; 3) the extensive historical data sets within the CCS, which can be used to identify natural modes of variability; and, 4) present day differences between the CCS and other EBCs, to examine ecosystem responses to differences in the strengths of local and basin-scale forcing.

The central, over-riding question that drives the proposed U.S. GLOBEC study of the California Current System is:

How will the distribution, abundance, and life history characteristics of marine animal populations respond to climatically driven changes in the CCS?

More Specific Questions

The central question can be expressed as a series of more specific questions that reflect the broad range of spatial and temporal scales in which physical-biological couplings in the CCS are manifested. Within each category we pose, as examples, several even more specific questions. It should be noted that these questions are not meant to be exhaustive, but rather to provide the reader with guidelines for the types of questions that might be investigated during a program examining the impact of climate change on EBC ecosystems.

Interannual Variability in Biological Responses

• **How will climate change alter California Current ecosystems, through changes in the length, strength, frequency and timing of ENSO cycles and other interannual variations?**

- What are the natural modes of variability and covariability between components of the ecosystems in the CCS on interannual and longer time scales and what is the relation between these modes, past climate variability and potential future climate change?
- Is the response to perturbed forcing during ENSO events more complex than simple expansions and contractions of range? Can these more complex changes serve as analogs for responses to longer climatic changes?

The latter question encompasses long time frames as well as short, and therefore relates to issues discussed below under "Interdecadal Variability" as well. The ENSO cycle and especially warm phase (El Niño) events may serve as useful proxies for examining ecosystem responses to longer-term, more gradual climate change because of their dramatic impacts on both the physical environment and biological populations of the CCS. A U.S. GLOBEC study of the CCS should be prepared to determine how ecosystem responses to warm ENSO events differ between regions of the CCS. Finally, given the relatively short-term physical impact of warm ENSO events (1-3 years), one

might be able to address the following questions: How does the generation time of marine animals influence the impact of warm events? How does the recovery rate of populations perturbed by an ENSO event differ for benthic versus pelagic populations? How would these populations be affected by changes in the frequency or intensity of warm ENSO events?

Interdecadal Variability in Biological Responses

- **What is the nature of the biological response in Eastern Boundary Currents to demonstrated, basin-scale, interdecadal changes in ocean-atmosphere coupling?**

- Are there rapid shifts between well-defined, quasi steady-state bio-physical regimes on time scales of decades to centuries or is there a more continuous progression of ecosystem structure?
- How do the different Regions (I-IV) of the CCS respond—similarly or differently—to these interdecadal shifts?

Among the uncertainties encompassed in these questions are: Do interdecadal shifts in climate lead to modification in timing or intensity of mesoscale activity which affects recruitment, retention/transport, predator-prey relationships, or life history strategies of plankton, nekton and benthic species? Are interdecadal shifts triggered by ENSO activity? How would a sustained (centennial-scale) global warming trend interact with natural interdecadal-scale ecosystem variability in the EBCs?

Mesoscale Variability in Biological Responses

- **How are biological processes and the characteristics of planktonic populations affected by mesoscale features and dynamics in the CCS?**

- What physical forcing determines the strength, frequency and location of mesoscale jets and eddies?
- How and to what extent do zooplankton use the small-scale three-dimensional circulation near mesoscale fronts and eddies to modify an otherwise passive transport?
- How do differences in local transport between small and large upwelling centers impact the survival of larvae and recruitment to the adult population?

The important biological processes include primary production; growth, mortality and the genetic composition of zooplankton (holoplankton, meroplankton and ichthyoplankton); transport, retention and recruitment; and links between secondary production, especially reproductive output, and the subsequent recruitment success of fish and benthos.

Mesoscale physical processes expected to control these biological variables, and subject to change with changing climate, include frontal dynamics, locally intense cross-shelf transport, eddy recirculation, stratification and vertical shear. The patterns of behavior (vertical and horizontal swimming) by which plankton use mesoscale features to modify their transport need to be understood in order to incorporate this behavior into individual based biophysical models. Only by realistically including the interaction of the mesoscale circulation with the behaviorally-modified transport of larval populations will the models be able to predict the consequences of changes in the mesoscale circulation which may accompany climate change.

Latitudinal Gradients in Biological Responses

- **How are recruitment, retention/transport, predator/prey relations, and life history strategies of planktonic stages impacted by latitudinal variability in the large-scale atmospheric and oceanic forcing in EBC ecosystems?**
- **How do differences in mesoscale activity in the four regions of the CCS affect the recruitment dynamics, vital rates, and life histories of resident marine animal populations?**
 - What forces maintain the physical boundaries between regions and determine their locations?
 - How sharp are the bio-physical (including genetic) gradients across the boundaries between the present regions and what maintains those biological boundaries?
 - What life history strategies result in increased zooplankton productivity and successful recruitment of fish and invertebrates in the different regions now and how will climate change impact presently successful strategies and populations?

Because large-scale forcing and mesoscale physical variability differ markedly between regions of the CCS, the response of marine organisms to this spatial variability provides a useful indicator of how physical and biological conditions at a single site will respond to changing climatic conditions.

Approach to Answering the Questions

Questions regarding the impact of climate change on the CCS ecosystem are best addressed using a combination of modeling, field work, monitoring and retrospective data analysis. Our recommended approach to answering the questions is to identify and understand the most important links, at present and in the historical record, between the physical processes of the CCS and key population and ecosystem properties. Subsequently, this understanding will be applied to predict the responses of these populations to climate change. Identification of the most important biological-physical couplings is essential to both modeling and field efforts, since it is impossible to include every detail of an ecosystem in any tractable study.

The foundation of this approach will be the study of spatial and temporal variability in biological processes of the CCS, relative to physical processes of the CCS that might control biological variability. To help identify the physical processes to which population dynamics in the CCS are most sensitive, we recommend several initial activities (modeling, retrospective and comparative studies) in advance of new field studies. To aid future field studies, initial activities should also include technology development. These activities are discussed briefly in Section II, and in more detail in Section VII. New field studies will then be directed toward understanding the dominant processes responsible for present-day and historical distributions and abundances of populations (and their genetic composition), patterns of transport and recruitment of critical life stages of both fish and benthic species, and trophodynamics. Once the relevant processes are identified and their mechanisms are better understood, they can then be incorporated into quantitative, descriptive biological-physical models. The accuracy of these models can be evaluated in part by their abilities to hindcast historical time series and also predict present-day spatial variability. We expect this research to lead to a new generation of prognostic biophysical models, which will continue to be improved as they are used operationally and in research activities. They should be available for use with the next generation of coupled

ocean-atmosphere GCMs, which will have higher resolution and provide boundary conditions for the prognostic ecosystem models. The ultimate goal is to understand the relevant processes and linkages enough to develop operational, prognostic biophysical ecosystem models that, when coupled with GCMs, can be used to assess (and predict) the impact of potential climate change on the status of living marine resources within the CCS.

SECTION VI—POTENTIAL COMPONENTS OF A CCS STUDY

General Description

In this section methods are suggested as likely ways of answering the key questions driving the U.S. GLOBEC CCS program (Section V). Five program elements are identified that are deemed critical to addressing the important questions regarding the impact of climate change on marine animals in the CCS. These elements are:

- Modeling studies
- Retrospective and comparative studies
- Large scale spatial studies
- Mesoscale spatial studies
- Monitoring

Modeling, retrospective and comparative studies, and monitoring should begin as soon as possible (1995), with field work following by approximately two years. Within each element discussed below, we state the goals to be achieved in that element, the relevance to climate change, and provide more detailed questions and hypotheses that relate to the key questions driving the study.

We avoid developing a detailed implementation plan at this time, full of specifics about sampling strategy (e.g., target species, study sites). Instead we suggest several important scientific questions and possible ideas for the methodology needed to address them. This format should encourage investigators to apply their own knowledge, insight and ingenuity to craft a proposed research plan that lays out the methodologies to be followed to answer the key questions, using this document as a guide rather than a template. Certainly it will not be logistically (i.e., fiscally) possible to examine all the key problems described below, and we do not claim to have exhaustively listed all potential major elements of a CCS research program.

Some Criteria for Ranking Species Importance for Study in the U.S. GLOBEC California Current Program

- Likely to be impacted under hypothetical climate change scenarios
- Economically or ecologically important, either as a dominant member of CCS communities or through interactions with other species
- Has larval planktonic stage or is holoplanktonic
- Evidence that life history variability is linked to environmental variability
- Widely distributed within CCS, providing opportunity for latitudinal comparisons
- Life-histories and/or ecological interactions representative of many other species
- Demonstrated evidence of long-term shifts in abundance. (CCS, other EBCs or in models)
- Distribution associated with physical features and/or faunal boundaries
- Analogous species occur in other ecosystems (EBCs, etc.)
- Has existing long-term record of abundance (e.g., CalCOFI or paleoecological)

Consistent with this philosophy, we chose not to identify key or target species at this time. The following criteria will be used to select key species for study. Obviously, no one species or assemblage can fit all of the criteria; these are merely guidelines to be used

in assessing the relative merit of any proposed target species, rather than an absolute set of conditions that must be satisfied.

The table below lists criteria deemed useful in ensuring that the appropriate physical components (forces, processes and features) are selected for study. Physical processes of study must relate to the goal of U.S. GLOBEC—i.e., understanding how climate change and its effect on the physical system will impact marine animals. Physical processes that impact growth, survival and recruitment of marine populations are appropriate for investigation.

Some Criteria for Selection of Physical Forces/Processes/Features
that Impact Marine Populations

- Currently a significant factor within one or more regions, in terms of:
 - Dispersing or aggregating target species or prey
 - Impacting growth rates/life history of target species
- Would be impacted under hypothetical climate change scenarios in a way that could affect target species
- Exists in different regions, but varies in importance, timing, etc. (indicates covariance, potential climate change effects)—links to variability in biology between regions

Modeling Studies

While all of the elements of the U.S. GLOBEC CCS program are necessary to its ultimate success, modeling is the central element in two senses. First, the models integrate the information obtained by the other elements. Second, the models represent the central deliverable products of this program, although they are expected to continue in their evolution and use long after the formal program is over.

Modeling studies of the relevant physics and biology in the CCS will be used to investigate how changes in global climate will affect the forcing and physical characteristics of EBCs and how the distribution and abundances of animal populations will respond to changes in that forcing. Models of the relevant physics and biology can integrate information from a variety of sources into a common context and link biological and physical information of various temporal and spatial scales. While the ultimate goal of the modeling studies is to predict and assess likely consequences of global climate change on marine animal populations, they can also be used to accomplish important intermediate objectives. These include hypothesis testing, sensitivity experiments, planning and evaluating field research.

Questions related to large-scale physical changes are probably best examined using coupled ocean-atmosphere GCMs. Determining aspects of local atmospheric forcing and the oceanic response may require regional (perhaps nested) ocean-atmosphere models. Questions related to changes in local oceanic circulation will require regional-scale ocean circulation models. These regional-scale models may stand alone while being forced at their boundaries, but some aspects of the CCS response to global climate change will require active coupling between regional-scale models and oceanic GCMs.

Developing and implementing the biophysical models required to predict the biological consequences of climate change are major goals of U.S. GLOBEC and will be based on two approaches. The main objective will be to expand numerical circulation models to

include biological subcomponents which interact with the physical environment and the other biological subcomponents. High-resolution models, with more realistic representations of the turbulence and fine structure in the vertical are considered on one end of the scale, while regional models, nested within basin-scale models are found at the other end. A second approach will be to merge more realistic ocean circulation models of transport and dispersal into sophisticated biological metapopulation models. The ability to assimilate both biological and physical data into models is desirable.

Modeling studies should be initiated before any field sampling and can be used in retrospective and comparative studies of EBC systems. Modeling efforts should be conducted in conjunction with each field study, including mesoscale biophysical studies within regions of the CCS and large-scale regional biophysical comparison studies. Ultimately, the modeling studies are critical to accomplishing U.S. GLOBEC's goal of projecting the consequences of global climate change on marine populations.

Goals and Objectives

The overall goal of the modeling component of the EBC study is to **assess and predict the likely consequences of global climate change on the distribution, abundance, vital rates and life history of key marine animal populations**. Other objectives include:

- Development and validation of physical models to predict spatial and temporal features of mesoscale circulation, including the impact of wind fields and buoyancy fluxes.
- Development and validation of biological models that incorporate pertinent physics to predict abundances, growth, mortality, transport and recruitment of holoplankton, meroplankton and ichthyoplankton (H-M-I).
- Development of regional circulation models to study differences in physical forcing, processes, features and ecosystem response between regions.
- Coupling regional-scale biophysical models with basin-scale general circulation models (GCMs) to predict changes in CCS H-M-I population levels in response to large-scale changes in physical forcing.
- Evaluation and improvement of the accuracy of the physical and physical-biological models via a multi-year field program, retrospective and comparative studies, and ongoing monitoring.
- Use these models to 1) test hypotheses (e.g., to investigate what physical and biological processes are essential for successful life history strategies), and 2) to evaluate the sensitivity of a specific region to changes in forcing or between-region exchange for the purposes of planning field studies.

Relevance Of Modeling

Biophysical models are one tool needed to address the question of how climate change may affect marine populations in eastern boundary current regions. While we don't know the specific changes in atmospheric circulation and oceanic large-scale temperature and velocity structure that will result from climate change, models provide the necessary tools for examining the response of biophysical systems to hypothesized changes in forcing. For each of the hypothesized changes in atmospheric and/or ocean circulation listed in

Section IV, a model experiment can be designed to examine the response of the CCS. Considerable model development, evaluation and improvement are needed before such model experiments can be interpreted with confidence, which necessitates the early initiation of modeling activities. The interaction between the modeling and the observational efforts during the project will be crucial to the success of the program.

Furthermore, for each hypothesized biophysical mechanism, a series of numerical experiments can be designed to assess whether the proposed dynamics are consistent with all available information. Models also allow the examination of a variety of scales of biophysical interaction. By understanding fine-scale interactions and then synthesizing this information for use in larger-scale coupled biophysical models and in sophisticated metapopulation models, a framework is established for diagnosing the response of marine populations to climate change. Finally, models provide an important tool for PREDICTING the consequences of climate change.

Questions and Hypotheses

The following questions can be addressed with modeling studies, in conjunction with the field work, monitoring and retrospective data analysis elements of this program.

- What effects of climate change on EBCs will GCMs predict if coupled with regional models?
- What are the predicted biological responses to climate change on a regional scale?
- How are mesoscale patterns and processes in EBCs (physical and biological) expected to be modified by plausible climate change scenarios and what are the consequences for the animal populations in these regions?

Methods

Numerical circulation models on different scales have recently been applied to the CCS, reproducing many of the observed physical features (Haidvogel et al. 1991). Progress in physical models that realistically incorporate mixed-layer dynamics has also provided hope for investigating the physical response of the CCS to changes in forcing due to global climate change. However, much remains to be done in developing and validating models that span the wide range of physical scales necessary to link local populations to large-scale environmental changes. That development and validation is best done, we believe, within a program which has the ultimate goal of application to real biophysical problems, since those applications themselves often reveal model behavior at odds with observations. Initial biophysical models include the combination of models of individual plankton growth and mortality with circulation models. Perhaps the most advanced models are those of Hofmann et al. (1991) who provide a first-order explanation of the vertical distribution of holoplankton along an upwelling filament, that of Botsford et al. (1994) which shows how the influence of varying wind-driven flow, water temperature, and vertical migration on larval transport and development influence recruitment and the consequent population dynamics of benthic CCS species, and that of Tremblay et al. (1994) which demonstrates how the pattern and magnitude of larval exchange on a submarine bank are sensitive to various aspects of larval biology (growth, mortality) and three-dimensional flow fields. Although the state of the art is still primitive, the techniques and modeling experience exist to make further progress on coupling biological subcomponents to physical circulation models on a variety of spatial and temporal scales. Initial research on linking separate adult populations of planktonic species through larval dispersal has revealed the usefulness of studying such metapopulations in order to

understand the response of marine populations in the CCS to physically-induced variability. Parallel progress on all of these modeling fronts will provide a powerful tool for translating the results of field and retrospective studies into better understanding and predictions.

U.S. GLOBEC should undertake four types of modeling efforts, relevant to scientific issues of the CCS:

- A. Coupled (mesoscale) biological-physical models that resolve fronts, mixed-layer dynamics and diurnal time scales.
- B. Regional-scale coupled biological-physical models capable of assimilating available observations (e.g., remote sensing data, buoy data).
- C. Regional biological-physical models linked with a basin-scale GCM.
- D. Modeling efforts that investigate the response of biological metapopulations to spatially and temporally varying physical forcing.

Additional background related to these modeling initiatives can be found in Section 3.6.2 of the U.S. GLOBEC Report on Climate Change and the California Current Ecosystem (U.S. GLOBEC 1992; Report No. 7). Although the primary focus of U.S. GLOBEC research will be on secondary production, fish and zooplankton population dynamics (the latter to include both holoplankton and meroplanktonic larvae of targeted benthic species), the influence of nutrient inputs and primary productivity on species variability should be assessed. If these aspects prove to be important they should be parameterized in a realistic fashion if the models are to provide accurate predictions. The modeling efforts must involve groups of species selected to represent the eastern boundary current ecosystem, since modeling of all species would be impossible. Further, the biological components of the biophysical models should focus on problems relevant to the U.S. GLOBEC CCS field program and should produce a portable model of general use to the community in the same spirit as the community ocean circulation models now available.

Rates of fundamental life history processes (i.e., birth, growth, consumption, mobility and mortality) will be required to complete the bio-physical models. In addition, some estimates of behavioral responses of organisms to physical and biological features are necessary. The importance of predator-prey relationships on species variability must be assessed and, if deemed important, should be incorporated at the appropriate time and space scales. Thus, much of the process-oriented field research will need to be devoted towards evaluating rates and behavioral responses of marine animals to bio-physical processes (Models A and B). Investigation of the sensitivities of the models to these rates and responses is essential. Studies that identify the most critical temporal or spatial periods of species life histories may reduce the effort in determining the critical rates.

Modeling efforts A and B will provide tools to address the short-term or local response of organisms to their environments. In particular, the impact of mesoscale physical features (fronts, eddies and jets) and wind and buoyancy forcing on planktonic populations and the recruitment of benthic organisms and fishes will be addressed. These modeling efforts may be aided by individual-based modeling studies and parameterizations obtained from research on how key rates and life history strategies depend on physical variables, such as turbulence intensity. Regional-scale and fine-resolution models should include continental shelf and slope regions to address mesoscale circulation over the shelf including cross-shelf transport processes, which may be critical in the life-cycle closure of species with nearshore adult life stages.

Modeling efforts A and B will contribute to the goals of both the Mesoscale and Large-Scale elements of the CCS GLOBEC program. Fine-resolution and regional-scale models may be used to evaluate mesoscale bio-physical processes within a single CCS region. Comparative model results from different regions will contribute to understanding the latitudinal differences in bio-physical processes. However, since circulation, and hence biological responses, within a single region are strongly dependent on linkages with adjacent regions, coupled biological-physical models of types A and B must be used to study the transition areas between the different regions. Understanding the inter-regional relationship will be an important prelude for accomplishing the more comprehensive large-scale modeling effort C.

Modeling effort C will investigate the link between regional-scale processes and larger scale forcing of EBC regions. This larger-scale physical forcing may be via oceanographic basin-scale circulation or large-scale atmospheric circulation. Given the large computational task associated with modeling effort C, it will be important to determine whether some of the important biological processes can be parameterized based on the results of the fine-scale and regional-scale biophysical models (efforts A and B). While each of the modeling tasks will contribute to assessing the effect of climate change on EBC populations, the coupling of regional models to a GCM will be particularly useful for investigating fundamental changes within latitudinal regions and shifts in their boundaries in response to changing climate. For instance, regional models could be forced and have boundary conditions derived from GCM simulations of the Pacific basin under various climate change scenarios, to provide an indication of how climate change may impact EBC ecosystems on the regional and mesoscale.

The biological components of the fine-scale biophysical models (Category A) would likely involve models describing the response of individual organisms or groups of individuals to physical forcing. To the extent possible, the biological components of modeling efforts B and C should synthesize and parameterize the information obtained from the biological components of the fine-scale biophysical models. Modeling effort D is concerned with the dynamics of metapopulations. Many harvested populations on the west coast are meroplanktonic metapopulations, i.e., they consist of a number of subpopulations of rather sedentary adults distributed along a coast, linked by dispersal of a planktonic larval stage. Metapopulation modeling can yield information about the expected amplitude and time scale of fluctuations in population abundances, the synchronicity of variability along the coast, and the conditions under which populations will persist. The physical environment affects metapopulation dynamics through its influence on the fraction of larvae that disperse and settle at various points along the coast. Models describing realistic physical transport should be merged with sophisticated biological metapopulation models. The biological interactions could be derived from an individual-based model that describes larval growth, motility (vertical migration, swimming), reproduction and mortality. The physical forcing will ideally be the output of realistic, verified ocean circulation models, but idealized physical transport and dispersal scenarios are a useful alternative. Understanding the dynamics of coastally distributed metapopulations in response to physically-induced variability in larval dispersal and recruitment will be useful for assessing the effects of climate change on some marine populations of the CCS.

Retrospective and Comparative Studies

The mesoscale and regional dynamics of ecosystems importance to U.S. GLOBEC are embedded within a hierarchy of scales in space and time (Haury et al. 1978; Ricklefs, 1990). The effective design and interpretation of the field studies undertaken on mesoscale and regional processes therefore require a realistic notion of the characteristic natural modes of temporal variability that distinguish the CCS and other EBCs.

Retrospective studies—including the event, seasonal, interannual, interdecadal and centennial time scales—provide this framework. Documenting and quantifying the properties of ecosystem change over this hierarchy of time scales requires a number of data sets with different characteristics and temporal resolutions to allow an examination of the coupling between the physical and biological systems. A rich collection of such data sets exist for the CCS, making it one of the few oceanographic regions where the data are sufficient to describe the natural modes of biological, as well as physical, variability. This must be done before it will be possible to separate anthropogenic from natural changes.

Comparative studies of different EBCs are useful for examining the important factors in physical forcing and biological response from the perspective of the entire ecosystem (Bakun and Parrish 1982; Parrish et al. 1983; Hutchings 1992). The value of such studies is their ability to reveal critical environmental factors controlling biological processes, with application to the potential impact of climatic changes on those factors. This approach seeks to distinguish these key factors, by comparing patterns of variability in similar processes in EBCs. Where patterns of human use vary between EBCs, comparative studies provide another tool for discriminating anthropogenic changes from natural changes.

The purpose of both comparative and retrospective studies is to provide a more robust description of EBC systems by increasing the number of cases with which we define the principal patterns of variability. Used in combination, the retrospective and comparative approaches provide a powerful means for determining the significance of trends and patterns in the large and complex ecosystem of the California Current.

Goals and Objectives

The overall scientific goal of retrospective and comparative studies is **the definition and understanding of the characteristic, natural modes of ecosystem variability over event to centennial time scales in EBC systems**. This goal will be achieved through the assembly, analysis and interpretation of retrospective time series for the CCS, as well as the analysis of contemporary data sets from other EBCs. Results from these studies will be incorporated into the development of field sampling strategies. They will be further integrated with the other major efforts comprising field-process studies, remote sensing, modelling, and long-term monitoring. These efforts will be organized around the following specific objectives:

- Document and quantify the properties of event-scale, seasonal, interannual and interdecadal variability in the CCS ecosystems through the analysis of existing historical physical and biological data sets and sample collections.
- Compare and contrast the nature of variability in process and pattern from event through interdecadal time scales in all major EBCs from the comparative analysis of existing historical data available for the Humboldt, Benguela, and Canary Systems.

- Document and quantify the interdecadal and centennial-scale variability in the pelagic ecosystems of the California, Humboldt and Benguela Current Systems through reconstruction of proxy variables from the paleosedimentary record.
- Determine the linkages of the mesoscale, seasonal, and interannual scales to the longer-term interdecadal scale through the integration of contemporaneous sediment trap studies with the field-process studies in the California Current and with the full set of retrospective analyses of both proxy paleoecological data and historical data sets.
- Using preserved samples that are archived (e.g., CalCOFI), examine the temporal and spatial genetic variability in target populations, especially as it relates to possible shifts in ecosystem state.

Relevance of Retrospective and Comparative Studies

This component of the U.S. GLOBEC EBC program directly addresses the nature of decadal and longer-term climate and ecosystem change. These are the time scales over which large and sustained changes in animal populations and in the structure and organization of the ecosystem occur. This element also is designed to identify and investigate the critical shorter-term processes whose dynamics are expected to vary with interannual through interdecadal scale change. This should be accomplished by examining forcing and responses within and between EBCs.

From the perspective of a human lifetime—and the traditional approaches taken by biological and physical oceanographers or by fisheries scientists—such decadal changes are often difficult and sometimes impossible to perceive as they occur. It is only when they lead to catastrophic effects on societies and economies that people take notice, as happened with the Pacific sardine and Peruvian anchoveta fisheries. Not only does success or failure in the exploitation of pelagic fish stocks occur on decadal time scales; this is also the scale over which we expect to observe climate change due to increasing concentrations of greenhouse gases. Examining the dominant modes of temporal variability in both climate and the ecosystem during periods of the past before anthropogenic activities, such as fishing mortality, significantly impacted the system is crucial to separating the impacts of anthropogenic forcing from those induced by natural variability in the climate system.

Questions and Hypotheses

The primary questions to be addressed using retrospective and comparative studies are:

- What are the characteristic modes of natural variability in physical and biological processes at the interannual and longer periods in the CCS and other EBCs?
- What are the most important processes affecting population distribution and abundance in EBCs and how do the varying strengths of these processes affect the response? Processes might include the intensity of upwelling, mixing, offshore and alongshore transport, stratification, temperature and the timing of seasonal transitions. Other factors may also be identified.
- What is the nature of the physical and biological transitions occurring at ca. 40-80 year time intervals in the CCS?
- Is there evidence for linkage between processes (both physical and biological) occurring at shorter (event-to-seasonal) and longer (interannual-to-interdecadal) time scales?

Methods

An integrated approach of retrospective and comparative studies will provide a broad context for interpreting the mesoscale and regional scale process research. Because ENSO is one of the best-documented and well-understood sources of interannual variability, and because of its immediate and observable impact on the structure and function of EBC pelagic ecosystems, particular attention will be paid to ENSO-associated variability (physical and biological variability on interannual time scales). However, long-term observations of the oceans and atmosphere also demonstrate that natural variability in both physical and biological systems at decadal and longer time scales is quite real and significant (see Section IX). Because the impacts of human activity are expected to influence global climate—and in turn ocean ecosystems—at time scales of several decades to centuries, U.S. GLOBEC must also address these temporal scales of variability.

A proper understanding of the hierarchy of time scales can be achieved through retrospective studies that provide the enhanced perspective and framework to describe the structure and dynamics of marine ecosystems. The strong ENSO signal is the basis for comparing linkages at larger and smaller time and space scales. Although ENSO is likely to be only an imperfect analog to longer term climate change, investigation of key relationships at ENSO time scales can still provide valuable insight into the biological response to physical forcing over longer periods. This will be carried out through retrospective analyses of the existing historical physical and biological data, and by reconstruction and calibration of high-resolution paleosedimentary data.

How animal populations will respond to climatologically altered forcing within the CCS can also be examined by comparing similar populations in different EBCs. EBC regions (California, Peru/Chile, NW and SW Africa) differ in the level of wind stress (upwelling and mixing), ambient temperature and stratification, and influences of the large-scale oceanic circulation. Since many of the climate change scenarios (Section IV) imply changes in these factors, the response (and biophysical strategies) of populations in present-day EBCs having different forcings will provide insights on potential future responses in the CCS. Comparative studies, using existing EBC data sets, should be

undertaken to identify and quantify these biophysical linkages. Ecosystem models which incorporate these mechanisms should attempt to reproduce present day differences among different regions of the CCS and differences among different EBC systems. It is important that the models be developed through an iterative process whereby testing of the model is done using mechanistic relations and data distinct from that used to develop the models (to avoid tuning the models to present day conditions in the CCS). Use of data and insights obtained from other EBCs will also give the ecosystem models the best chance of predicting responses of CCS populations to conditions which are outside the range of present conditions.

Many different types of data are available for retrospective studies of EBCs and the CCS in particular. The retrospective data can be organized by space and time scales into the five categories described below.

Repetitive observations from earth orbiting satellites. The longest data series available from satellite observations (ca. 15 years) is the sea surface temperature (SST) series from the Advanced Very High Resolution Radiometer (AVHRR) sensors. Their great value at present lies in the extensive spatial coverage and in the level of detail provided. The Coastal Zone Color Scanner (CZCS) data provides approximately seven years of global coverage with 4 km resolution and spotty temporal sampling. Both the AVHRR and CZCS data suffer from cloud contamination and neither the archived AVHRR nor the ocean color data can be used, at present, to examine interannual variability with confidence, due to contamination by volcanic aerosols and clouds. They can, however, be used to compare and contrast the responses of different EBCs to the present range in the magnitudes of the various forcing fields from the event scale through seasonal environmental variability. Altimeter data from the Geosat exact repeat mission cover about two years (November, 1986 through October 1988). Other altimeters will operate over the decade that started in 1992, with two sensors (ERS-1 and TOPEX/POSEIDON) operating at present and more planned. The SeaWiFS color sensor, with similar sampling characteristics but greater sensitivity than the CZCS will collect data for ca. 5 years after launch. Other color sensors may be launched on European and Japanese satellites.

Satellite-based studies will permit one to quantify the degree to which changes in the relative strengths of different forcing fields affect the structure of EBCs (in a comparative sense), the amount of mesoscale structure within each EBC, and the biological response to the mesoscale structure (using ocean color). The combination of ground-truth field measurements of circulation, temperature and pigment concentrations with altimeter, AVHRR and SeaWiFS satellite data will provide valuable information and aid in the interpretation of both future and past (reprocessed) satellite data. The combined data sets will be valuable to model development and validation, since the fields of satellite data are higher in spatial resolution and larger in spatial extent than can be sampled by conventional ship surveys.

Time series of point and gridded instrumental observations. In situ data at fixed points include sea level time series, measured winds from buoys or coastal sites, and shore-based SST and salinity data. Some of these data series extend back 100 years and often represent daily or even hourly observations. Another source of in situ data is the COADS data set from NOAA-NCAR. These data consist of surface ocean and atmosphere observations taken from ships and buoys, extending back more than 100 years. The MOODS data set, from the Naval Research Laboratory, consists of subsurface ship data from CTDs, BTs and XBTs, and extends back into 19th century. Gridded surface physical fields, such as the FNOC pressure and winds, NMC and European Winds, SST from NOAA, and others extend back in time 10 to 50 years. In addition, long time series

of climatic indices such as the Southern Oscillation, Aleutian Low, and coastal upwelling (Bakun) indices from surface pressure fields are available.

Ocean surveys of in-situ biophysical data. Complementary biophysical in situ survey data exist from large-scale sampling programs. The CalCOFI survey program has been the most ambitious and extensive effort in any EBC, spanning over 40 years with varying degrees of coverage and density in both space and time in the CCS (Hewitt, 1988). While physical data are immediately available from the CalCOFI surveys, much of the biological time series information, other than the abundance of fish larvae and plankton volumes, still remains in the archived collection jars. Although much younger, the Benguela Ecology program off South Africa is another effort producing valuable complementary biophysical data for use in comparative EBCs studies. Relatively long series of fish catch data in the EBCs, by species, are an available and underutilized data set.

Moreover, beyond descriptions of changing abundance and distribution patterns of organisms, archived biological samples may be useful for describing past changes in environmental or population characteristics. For example, it is now possible to examine genetic variability and genetic structure from preserved biological specimens. This means that a comprehensive data set, such as the CalCOFI collection, could be used to explore temporal and spatial aspects of the genetic structure of selected zooplankton or fish species. Also, retrospective analysis of radiocarbon in fish otoliths recently has been demonstrated to be an accurate proxy for past radiocarbon levels in temperate waters, and can provide valuable information on ocean circulation and carbon flux over decadal time scales (Kalish, 1993). When coupled with historical information on fish growth, which is estimated by measuring otolith growth in long-lived species, time series of radiocarbon can give us insight into the processes that influence fish growth and survival especially in areas of coastal upwelling. Appropriate collections of fish otoliths from long-lived species along the U.S. west coast are available for producing ocean radiocarbon time series extending back to the late 19th century. The CalCOFI data, in conjunction with other long series such as otolith records from long-lived fish and catch statistics for commercial fisheries, provide a unique and ongoing opportunity to quantify the dynamics of populations and communities over decades with complementary measurements of physical, chemical and biological parameters. Such consistent records of marine animal abundances are rare, particularly in the context of the biophysical associations. They provide not only histories of population sizes but estimates of growth and survival of early planktonic larvae of fishes and other living marine resources. This information is particularly valuable for the opportunities to link population variability with physical forcing at interannual time scales (i.e., ENSO variability) and enables us to compare and contrast this variability with that occurring over the interdecadal time scale.

The large number of diverse time series and survey data present a great opportunity to improve our understanding of the nature of EBC ecosystems before any additional field work begins. Many data sets have not been analyzed to any degree. Many biological collections remain largely unsorted by species or groups. Improved computer technology allows analysis of very large data sets that could not be readily manipulated in the past. Even those data that have been examined previously with traditional statistical techniques merit reanalysis with state-space statistical modeling and modern time series techniques.

Historical records of animal population changes. Fisheries data, and marine bird and mammal censuses provide extensive time series, some extending back more than 100 years. A special property of the long historical records of fish, mammal and bird abundances is that they may provide not only a history of variation in population size, but also may provide estimates of life table variables that control population growth.

Ultimately these population variables are the ones that must be linked to physical forcing variables to forecast the effects of climate change on marine animal populations. In this regard, time series of growth and survival of the early planktonic larvae of fishes and other living marine resources are a rare, and particularly valuable asset for U.S. GLOBEC because of the programs focus on planktonic stages. The CalCOFI program is by far the richest source of such information in the world, with its valuable store of sardine and anchovy data.

Time series reconstructed from paleoecological data of marine sediments. The annual to decadal chronological resolution desired for describing animal population fluctuations is preserved in anaerobic marine sediments along the continental margins of some EBC systems. Three known sites in the CCS are the Santa Barbara Basin off southern California, the Soledad Basin off southern Baja California, and Saanich Inlet of Vancouver Island, British Columbia. There are also several sites within the adjacent Gulf of California, Mexico. Descriptions of interdecadal variations of pelagic fish populations are being developed through the analysis of rates of fish scale accumulation (Baumgartner, et al., 1992; Holmgren and Baumgartner, 1993; Soutar and Isaacs, 1974). There is a potential site in Nootka Sound on the west coast of Vancouver Island, the site of an important sardine fishery during the 1930s. If this site contains a well-preserved record of fish scales, high-resolution records for the southern, central and northern populations of sardines and anchovies in the CCS can be reconstructed. The fish population data in these sediments are accompanied by other proxy information with ecological and climatic significance, such as the interannual and decadal scale variability in planktonic and benthic foraminifera abundance, and the carbon and oxygen isotopes in their shells.

There also are sites of high-resolution sediment records in the Humboldt and Benguela Current systems which have well preserved fish scales of the pelagic fishes, as well as more common microfossil remains. Development of proxy records from these sites will provide a network of high-resolution chronologies of fish populations and other ecological and climatic histories for EBC and regional comparative studies of interdecadal to centennial ecosystem variability.

Large-Scale Spatial Studies (Latitudinal Studies, Including ENSO Forcing)

The coastal ocean off western North American can be divided into at least four regions characterized by differences in wind stress, intensity of coastal upwelling, coastal morphology, freshwater inflow, and the influence of long-term and transient advection, turbulence, and buoyancy. These regions also differ somewhat in terms of the planktonic, benthic and fish assemblages present, the timing of plankton production cycles, feeding and reproductive activity in populations, and the presence or absence of specific life stages of key fish species. Critical mesoscale physical processes may be influenced by future changes in the global atmosphere and ocean, which in turn may impact populations. Regional differences in physical-biological linkages provide a natural laboratory for comparing potential changes in marine populations that may accompany different climate change scenarios.

The large-scale component of a U.S. GLOBEC CCS program will consist of field programs located at multiple sites that characterize and contrast the ecosystem's principal biophysical regions, but may also include large-scale drifter studies, satellite studies, regional numerical models nested in coarser basin-scale models, and the analysis of historical environmental data sets that will connect regions and areas of mesoscale studies. These will tie together comparative studies in the different regions and long-term monitoring. Although it is unrealistic to consider in situ measurements sufficient to

monitor the entire latitudinal extent of the CCS, other aspects of the large-scale system can be addressed by comparisons of detailed mesoscale studies in different regions across the large, latitudinal gradients in the system. These include: 1) regions with similar ecosystems but different environmental conditions; 2) the boundaries of distinct biological 'provinces' or physical regimes; and, 3) regions connecting the main body of the CCS to sites with long paleosediment records (the Southern California Bight). Investigations of the relation between the timing of life history stages and biological rates with respect to biophysical events are emphasized, as are investigations of genetic variability.

Although an ENSO cannot be guaranteed to occur during the field survey period, the program and monitoring will span the period of a typical El Niño/La Niña cycle. Thus much of the interannual variability observed may be related to that cycle and the field programs should be designed to make use of that variability, and address the following questions. Are El Niño and La Niña the extremes of the spectrum of interannual variability, or are these events unique in their physics and ecosystem impact? Can ecological conditions during ENSOs serve as useful proxies for the ecosystem alterations expected as a result of longer term climatic variability?

Goals and Objectives

Although many of the key physical processes occur in all regions of the CCS, their relative importance, seasonal timing, and spatial extent and impact vary. Substantial biological differences also occur between regions, presumably due to these physical differences. The overall goal of the large-scale spatial studies is **to determine how regional differences in physical processes lead to the observed differences in the distribution, abundance and variability of marine organisms, and to relate these regional differences to the expected ecosystem response to climate change.** Other objectives include:

- Assess and quantify the relative impact of physical processes in different latitudinal regions on the distribution, abundance, vital rates and life history of key populations of marine animals.
- Understand the mechanisms behind these physical/biological linkages.
- Use interannual variability at given locations to further understand the mechanisms behind these physical/biological linkages.
- Identify variables and sites for monitoring, to document future ecosystem changes.
- Use the understanding of the mechanisms by which populations respond to present differences in forcing to formulate specific parameterizations for biophysical models, which will then project the responses of these populations to different climate change scenarios.
- Use the spatial and temporal variability determined by the large-scale study to develop a conceptual model for EBC ecosystem response to various climate change scenarios.

Relevance of Large-Scale Spatial Studies

Changes in large-scale atmospheric and oceanic forcing due to climate variations have a major impact on EBC mesoscale circulation which, in turn, affects the persistence of key

marine populations. This may result in shifts in physical and biological boundaries, as well as changes in the major physical processes within a region (e.g., changes in the intensity and timing of upwelling, seasonality and intensity of mesoscale jets and eddies, degree of vertical mixing, etc.). Understanding the mechanisms by which populations respond to present differences in forcing and circulation will allow us to predict how those same populations will respond to changes in climatic forcing.

The large-scale study tells us something about the entire California Current EBC system, and can be generalized to other EBCs. Interannual variability at the edges of species ranges and transition zones, where the strongest gradients in physical and biological constituents occur, is the best analogy for what might occur if the climate actually shifts. To some degree, the boundaries between physiographic regions correspond with zoogeographic and population boundaries. It is not known to what extent the movement of physical and biological transition regions in response to climate change will coincide. One specific response of the large-scale CCS to climatic changes in local and distant forcing may consist of simple shifts in the locations of the boundaries between the regions, with expansion and contraction of present ranges of species. Species ranges are delimited by either hydrographic/circulation (water mass) restrictions, topographic restrictions, or a combination of the two. Only species whose range is delimited by the first will likely change with changing climate. Species whose current center of population or range limits are determined, at least in part by unique interactions of coastal topography with physical forcing, may not be able to either exploit other habitats or persist in their present habitat with changing environmental conditions, and so will experience a collapse. Latitudinal shifts in these boundaries on interannual to interdecadal time scales provide one model of how climate change affects EBC ecosystems.

Some species (e.g., hake) must cope with processes in more than one CCS region. Although some species appear fixed to specific regions, others migrate along the coast, using different regions as the primary habitat for different life stages; others exist as distinct populations in several locations. An understanding of the linkages between the environment and a population's life cycle must consider significant processes occurring over a broad latitudinal range. Understanding why and how these organisms adapt to conditions in different regimes will provide a better indication of the consequences of climate change to the ecosystem.

Questions and Hypotheses

The primary questions of interest in latitudinal variability include:

- What is the spatial variability in physical forcing among the four regions?
- How do ecosystem structure and dynamics differ in the four regions and how might they respond to climate change?
- To what degree are biophysical boundaries geographically anchored (i.e., do boundaries shift proportionally to variations in forcing, or is there a "threshold" value of climate change necessary to move boundaries)?

In addition, the large-scale studies should address the following set of hypotheses:

- Variability in large-scale atmospheric and oceanic forcing in EBC systems plays a critical role in the recruitment and maintenance of key marine animal populations through its influence on advection, turbulence and productivity.

- The success of key populations in EBC systems is set by the interaction of their life-history strategies with the speed, direction and timing of physical transport and retention of planktonic stages of these species, their predators and their prey.
- Major regional differences in the amount of advection due to the mesoscale features exists, and is related to regional differences in the recruitment dynamics of benthic invertebrates.
- Strong latitudinal differences in the interaction between mesoscale oceanic features and the distribution, abundance, vital rates and life history of key populations can be used to understand and predict future ecosystem structure and dynamics under different climate change scenarios.
- The interannual variability that accompanies the El Niño/La Niña cycle, while not an exact analog of climate change, causes changes in local surface forcing and basin-scale currents, which perturb the biophysical interactions within the CCS and provide insight into the mechanisms that determine how the system responds to changes in forcing, such as will be caused by climate change.

Methods

A multi-year field program is suggested for several locations along the North American west coast to compare the relationship between large-scale atmospheric and ocean forcing mechanisms, the principal mesoscale circulation features, and the distribution, abundance, population dynamics and genetic composition of plankton, benthic organisms and fishes at each site. The focus of the field program is two-fold: (1) regional comparison of the effects of mesoscale circulation on the dynamics and life histories of marine populations—to understand the dynamics of similar ecosystems located in different physical environments; and (2) variability of transition regions in the flow field and faunal provinces—to understand the processes that cause and maintain these transition regions and to project the impact of future climate change scenarios on them. Field sampling should combine Eulerian "mapping" studies of physical and biological parameters at selected sites (in comparison with other locations) with Lagrangian "tracking" of water and organisms through and between regions. The surveys will employ the methods described in the Mesoscale Spatial Studies section (addressed next).

Comparative surveys should be conducted in the various physical/biological regions as well as near the transition zones between these regions; the location of these surveys must consider the range and life history of the key species being studied as well as the principal physical processes. For example, comparative studies could examine mesoscale features off central-northern Oregon (Region I), central-northern California (Region II), and the Southern California Bight (Region III). Collaborations with Mexico (Region IV) and Canada (north of Region I) should be established to further examine spatial variability on the largest scales. Transition studies should focus on the boundaries of the biological provinces and the physical regions, while realizing that not all species observe the same boundaries (which may provide useful information in itself). The study also should be part of a large international program whose focus is the comparison of EBC ecosystems.

Mesoscale Spatial Studies

Interactions between coastal topography, winds and a seasonally intensified CCS jet produce a complex system of along- and cross-shelf circulation along the west coast of North America that includes mesoscale (10-100s of km) features whose locations, in

some cases, may be predictable (e.g., regions of persistent offshore or onshore transport, creation of quasi-stable eddies, fronts). Although these features sometimes appear to be spatially predictable, the observed variability between seasons and years indicate that their exact location, intensity and vertical structure may be affected strongly by winds, buoyancy flux, and larger-scale currents. This dependence imposes temporal variability ranging from seasonal-to-interannual, which suggests that mesoscale features may be altered significantly by climate change. In Section IV the argument is presented that mesoscale activity may increase due to future greenhouse-gas mediated climate change. Among other properties, local temperature, current strength and stratification will depend on the nature and strength of these mesoscale features. Considerable population variability, and the evolution of life history strategies, is related to mesoscale physical features and processes (e.g., timing of spawning in relation to the timing of the spring transition). Therefore a suite of important biological properties and processes should be affected by and predictably linked to these wind-topography-current interactions. It is important to determine whether zooplankton (including ichthyo- and meroplankton) modify their behavior (e.g., vertical migration) in response to their location within the different types of mesoscale structure in ways that affect their transport and ultimate population persistence.

Mesoscale studies are important components of the large-scale comparisons described above. Given the U.S. GLOBEC focus on interactions between zooplankton and their environment, emphasis is placed on (1) processes involving transport, retention, aggregation, and vital rates as functions of location within mesoscale features, or at their boundaries; (2) timing of the appearance of life history stages with respect to seasonal mesoscale evolution; and (3) spatial variability in the distribution and abundance of species that settle or recruit in shallow water ("life cycle closure"). Spatial and temporal variability in fish recruitment and benthic organism settlement will be a key measurement in mesoscale studies. Mesoscale field studies are envisioned to include a broad spectrum of measurements and platforms, including moorings, fast surveys (electronic sensors on undulating vehicles), slower surveys (water-collecting CTDs and animal collections for abundance estimates and shipboard experiments), surface drifters and neutral floats, and land- and satellite-based remote sensing.

Goals and Objectives

The overall goal of the mesoscale spatial studies is **to understand the extent to which the present spatial and temporal variability in mesoscale circulation in the CCS impacts the abundances, species composition, growth, mortality, genetic composition, transport and recruitment of holoplankton, meroplankton and ichthyoplankton, and to relate this present variability to differences in mesoscale circulation expected as a result of climate change.**

Many specific relationships between planktonic organisms or populations and mesoscale features must be determined, including but not limited to:

- The degree to which the amplitude, position and timing of mesoscale features may be altered by climate change.
- The role of various mesoscale features in determining cross-shelf and along-shore transport of meroplankton, holoplankton and ichthyoplankton.
- The role of mesoscale features in driving active or passive aggregations and maintaining the spatial and temporal coherence or fidelity of populations.

- The role of frontal dynamics in producing or maintaining gradients in vital rates, and the exchange between or genetic isolation of populations.
- The role of mesoscale features in determining the links between plankton dynamics and the ultimate spatial and temporal variability in recruitment of fish and benthic organisms.
- The extent to which zooplankton within mesoscale features use behavior to mediate their net transport.
- Links between life histories of target species and the timing of seasonal changes in atmospheric forcing and mesoscale circulation features.

Relevance of Mesoscale Spatial Studies

The life histories of key marine populations are affected by mesoscale circulation, which, in turn, is controlled by processes that are highly susceptible to changes in large-scale forcing due to climate change. This may result in shifts in physical and biological boundaries, as well as changes in the major physical processes within a region (e.g., changes in the intensity and timing of upwelling, seasonality and intensity of mesoscale jets and eddies, degree of vertical mixing, etc.). Changes in mesoscale processes lead to changes in mesoscale features, resulting in changes in ecosystem dynamics. Understanding the mechanisms by which populations respond to present differences in forcing and circulation will allow us to predict how those same populations will respond to climatic changes in forcing.

Mesoscale circulation features may be altered strongly by interannual variations in winds, buoyancy flux and basin-scale circulation, especially during strong ENSO events, and should be affected significantly over longer time scales by climate change. Recent evidence (Huyer et al. 1991; Washburn et al. 1993) suggests that much of the advection within Region II of the CCS occurs in mesoscale features, which also may affect the local intensities of upwelling, downwelling, mixing and primary productivity. This evidence suggests that mesoscale features may be important to plankton dynamics, but this link has not been rigorously evaluated. The intensity and location of mesoscale circulation features should strongly impact the degree of cross-shelf transport as well. Consequently, these features should be important in the retention or loss of regional populations of zooplankton, fishes and benthic animals, and may play a significant role in determining their spatial and temporal variability, and therefore the maintenance of populations may be sensitive to changes in mesoscale circulation associated with a changing climate.

Questions and Hypotheses

Many of the issues raised in Section V will be addressed in the mesoscale studies. Specifically, the following general hypotheses are formulated:

- Spatial and temporal variability in mesoscale circulation is determined by local wind forcing and basin-scale currents, both of which will be affected by climate change.
- Mesoscale features significantly affect zooplankton biomass and production, and their retention or loss from coastal regions.
- Variability of mesoscale dynamics in the CCS plays a critical role in the "life-cycle closure" of juvenile fish and larvae of benthic invertebrates, both by determining their survival at sea and the intensity of their recruitment.

Methods

Mesoscale studies at selected sites in the CCS will take place over several years and may include the following:

- Collection of meteorological, physical and biological data by satellite and shore-based remote sensors, drifters and fixed moorings.
- Repeated at-sea sampling of plankton, fishes, hydrographic and nutrient data. Both Eulerian-frame (fixed grid and feature oriented) sampling and Lagrangian-frame (following water parcels and/or individual populations) sampling will be employed.
- Onshore and nearshore sampling to document the ultimate recruitment of benthic organisms and fish.
- Interaction with the modeling activities to parameterize the rates and behaviors in a manner which allows their inclusion in models; comparisons of model-predicted and measured responses to variations in forcing.

Because of the striking differences among the various regions of the CCS in the patterns of wind (seasonality, direction and strength), coastal orography and nearshore bathymetry, it would be especially illuminating to carry out mesoscale studies in two or more regions simultaneously and contrast their results (e.g., Latitudinal Studies). Biological and physical oceanographic field measurements should be closely coordinated with modeling programs that address CCS circulation and biological responses to physical forcings and climatic fluctuations. Coordination will ensure that key parameters are identified, targeted for in situ study and measured with adequate spatial and temporal resolution.

Mesoscale spatial physical and biological oceanographic measurements are needed within two broad time frames. High horizontal and temporal resolution measurements will be made over several-week periods that define time scales of many mesoscale features. These measurements will permit resolution of important, shorter period events as well, such as diurnal migrations of plankton. This time frame also will ensure that significant progression of developmental stages of planktonic populations has been followed. These high resolution programs should be carried out two or more times during a season to encompass the staggered reproductive periods of the key fauna in the CCS. For example, planktonic stages of Dungeness crab (*Cancer magister*) and the red urchin (*Strongylocentrotus franciscanus*) typically occur during winter and early spring in the CCS, whereas development of many key zooplankton species, as well as certain fish and benthic invertebrates, are more closely tied to the onset of spring blooms. High resolution programs should occur in several consecutive years so that interannual variability in biological responses to key physical processes can be evaluated.

Superimposed upon these high-resolution measurement programs will be a series of coarser-resolution, fixed-point measurements (moored, shore-based, and monitoring cruise measurements) that will extend continuously over longer periods of time (multiple years). Winter and summer conditions may demand different fixed mooring locations or measurement technologies/strategies. These measurements are necessary to evaluate seasonal as well as interannual variability in key physical forcings in the CCS, as well as some basic biological responses on this scale of variability.

High-resolution measurements of biological oceanographic variables and processes should be coordinated closely with near real-time measurements of mesoscale features. Satellite data, including AVHRR and color images, or data acquired from aircraft fly-overs, could identify locations of particular mesoscale features and be used to track a feature's location and strength through time. These data will be used to guide the field sampling program that includes acquisition of diverse physical and biological oceanographic data. Ultimately, satellite or aircraft images should be related to measured fields of surface currents and wind fields obtained at high resolution in regions extending 10-20 km offshore, using shore-based Doppler radar and Lidar.

High-resolution field studies of biological responses to mesoscale features could include both fixed mooring and ship-based sampling. Moorings also might be an important component of the longer-term, continuous measurement program. Moorings located within predictable mesoscale features (e.g., regions of persistent offshore transport near headlands) could provide good temporal resolution measurements of (1) cross-shore variability in transport, and (2) key physical and biological variables. Measurements obtained from moorings should include temperature, salinity, ADCP currents, and bio-optical data (PAR, pigments). Vertical arrays of settling plates placed on separate moorings (so that they can be easily exchanged) could be used to measure short-term settlement patterns of some benthic invertebrates relative to other variables measured using moorings. Moored sediment traps can provide information on the temporal and spatial variability in the rate and composition of sinking material.

A key aspect of the ship-based mesoscale program is pairwise sampling of zooplankton populations within and outside of specific mesoscale features. This should be augmented by a more sophisticated sampling program wherein populations inside and outside of features are followed over time. To accomplish this, sampling should occur over time in the vicinity of drifters that are released inside and outside of specific features. This would permit documentation of the time rate of change of demographic and physiological properties of zooplankton populations as driven by sub-mesoscale features.

The use of Lagrangian drifters that can follow water at specified densities could provide a unique and important data set. In addition to tracing water movement, the drifters could be equipped with GPS receivers and internal data storage so that temperature and velocity measurements over short time scales can be acquired continuously within individual mesoscale features. Such Lagrangian-frame data can be especially useful in documenting the importance of various frontal and mesoscale features to the retention or loss of populations of plankton.

Biomass in mesoscale features can be mapped rapidly using acoustics or optics. In particular, spatial surveys of biomass could settle some of the important questions about the ecological importance of mesoscale features. Collection of these data will be driven by satellite and aircraft-derived images of the location of mesoscale features. Biomass determinations are by themselves insufficient to evaluate the importance of mesoscale features to the population biology of zooplankton. Detailed measurements of species and stage abundances, mortality rates, genetic composition and population vital rates also must be determined relative to specific mesoscale features. Practical constraints demand that these measurements must be limited in time and spatial coverage; thus they should be focused on especially important locations and times of interest.

The high resolution, ship-based sampling program will provide data linking the dynamics of planktonic organisms and populations to mesoscale variability in circulation within the CCS. To complete the analysis of life-cycle closure these measurements should be augmented with a sampling program that will document spatial and temporal variability

in the ultimate recruitment of key benthic organisms and fish, relative to plankton dynamics. These studies should aim to resolve early recruitment (of fish) or settlement (of benthic organisms) soon after the planktonic stage ends, so that the impact of post-recruitment events (e.g., fishing, predation) on populations is minimized—this will provide the best opportunity to link biological and physical influences on planktonic stages to recruitment.

Monitoring

Over the course of a 5-7 year period, much of the interannual variability within the CCS may be related to the ENSO cycle. Examining the biological response to ENSO-related physical variability provides an approach for identifying and quantifying biophysical interactions within the CCS. The intensive field studies will provide detailed "snapshots" of the biophysical interactions, but unless they are extremely fortuitously timed, the field studies will not resolve the full evolution of biological responses to an ENSO cycle. While some features of the biological responses and physical causes are relatively well known, the study of the biophysical linkages has been piecemeal in the past, relying on observation systems existing for other purposes. Present monitoring of the conditions of the CCS consist mostly of surface or coastal measurements and are primarily of physical parameters only. Existing monitoring may be sufficient to provide the rough physical context of the ENSO cycle, but it is clearly not adequate for monitoring the biophysical interactions that occur. The CalCOFI surveys in Region III off Southern California provide an important exception. To place the process studies within the context of the interannually varying biophysical interactions, occurring over the 5-7 year period, it will be necessary to augment monitoring of both biological and physical measurements, especially in regions other than the Southern California Bight.

As in most coastal ocean locations, a number of physical parameters are measured on a regular basis along the west coast of the U.S., providing a good basis for designing an augmented monitoring system. These include sea level at various tide gauge stations, surface meteorology (met) over coastal land stations and at buoys 10-20 km offshore (over the shelf), SST and wave statistics at other nearshore buoys, coastal SST and salinity at selected locations, and surface met and SST from merchant vessels. Subsurface temperature has been measured from a small number of merchant vessels along a few ship tracks in the past, but this activity has decreased in the last decade. Under cloud-free conditions, NOAA satellites measure SST four times each day and the SeaWiFS color sensor will provide an estimate of surface pigment concentrations every two days. At present sea surface height is measured by altimeters along tracks separated by 100-300 km, which can be used to estimate the large-scale surface circulation patterns starting 50 km offshore, with one realization every 10-35 days. Satellite scatterometers provide estimates of wind stress fields starting 50 km offshore, with resolution of 50-100 km every 1-4 weeks. Existing weather forecast models provide estimates of surface wind stress and heat fluxes over the ocean every 6-12 hours, with horizontal grid spacings of 100-500 km. The value of these measurements to U.S. GLOBEC EBC is limited, because they are: (1) almost entirely physical; (2) made predominantly at the surface; and (3) either shore-based or provide only very coarse resolution off-shore.

The suggested biological-physical interaction monitoring should augment existing monitoring programs. Most of the augmentation will deal with specific biological responses to physical variability at daily to interannual time scales and mesoscale phenomena at the coast and at the core of the California Current.

Goals and Objectives

The overall goal is **to build a new augmented set of measurements in support of the U.S. GLOBEC EBC program at the mesoscale, seasonal and interannual time scales through regular monitoring**. To interpret the latitudinal gradients and interannual scales, measurements in each of the four regions should begin as soon as possible. Standardized methods should be used to permit comparison now among regions and through time. Several approaches to implement better monitoring of the CCS are being considered:

- Increase the number of parameters measured from meteorological buoys over the shelf to include subsurface measurements (e.g., temperature, conductivity, ADCP water velocity, acoustically derived plankton patchiness and biomass, chlorophyll, nutrients).
- Establish a network of nearshore biological sampling with uniform methods (such as settlement plates) to estimate rates of retention, advection and recruitment of benthic invertebrates.
- Establish several buoys similar to those over the shelf but located offshore of a few selected shelf buoys to independently describe shelf and deep water forcing and dynamics and to estimate cross-shore gradients of wind stress (the most important component of the curl during spring and summer) and zooplankton biomass and patchiness (using acoustics).
- The CalCOFI program and the Canadian La Perouse Bank Study provide seasonal subsurface biophysical data in Region III and at the northern end of Region I, respectively. Augment this monitoring with a small number of offshore transects in Regions I and II, while encouraging a similar effort off Baja California, Mexico (Region IV). Measure key physical (e.g., T, S, water velocity) and biological (e.g., size-specific phytoplankton production, chlorophyll, zooplankton species abundance and production, and fish egg production) parameters over the upper several hundred meters, extending several hundred kilometers offshore, with seasonal coverage. Use chartered vessels or research vessels-of-opportunity for more frequent biological sampling on the inner portion of the transects.
- Establish a program of seasonally-released drifters to build up Lagrangian statistics on the circulation of the CCS within which annual migrations and recruitment of marine populations take place.
- Establish a network of moored sediment traps to maintain a long time series of selected variables of the biological response to climate change, and to calibrate the long-term sediment record in time and space.
- Intensify the merchant ship XBT program along a few representative lines.

Several planned activities within NOAA may help accomplish these objectives. The addition of downward looking ADCP and/or subsurface temperature sensors to existing National Data Buoy Center (NDBC) buoys has been discussed at NDBC. Prototypes of these buoys should be deployed in the regions chosen for long-term monitoring and intensive process studies (which should coincide) in the U.S. GLOBEC CCS study. The connection between the California Current System and the tropical Pacific should be explored using measurements collected by the Tropical Ocean Global Atmosphere

(TOGA) program and its successor, Global Ocean Atmosphere Land System (GOALS) program. It would be ideal if more observational elements (tide gauges, ATLAS moorings, etc.) could be located along the eastern margin of the Pacific to explore the oceanic connection between the tropics and the Pacific EBCs, especially the CCS. This would provide a data set with which to validate the interplay between the nested regional models and the basin-scale GCM.

Questions and Hypotheses

The monitoring component addresses the questions of local and distant forcing directly, in addition to these general questions:

- What are the natural modes of biological and physical variability at interannual and longer time scales?
- Where do the spatial surveys and other process study measurements collected as part of the mesoscale and large-scale studies during the U.S. GLOBEC 5-7 year EBC project fit into the basin-scale ENSO cycle and longer period modes of variability in the CCS?
- Can we distinguish anthropogenic impacts from natural variability at some point in the data record?

These questions assume, and we recommend, that the monitoring continue beyond the end of the 5-7 year U.S. GLOBEC study, in order to define the longer term variability, to provide the data needed to drive and validate the ecosystem models, and to provide the system for detecting climatic changes.

Methods

Monitoring the biological response to climate change. Regular biological and hydrographic surveys in Regions I (La Perouse Bank) and III (CalCOFI) must be augmented in Regions I, II and possibly IV. Pelagic and demersal fish and target invertebrates should be surveyed seasonally to accompany the offshore drifter and buoy data. Biological data should be collected on along- and cross-shelf transects. Standard concurrent CTD sampling includes bottle sampling at a number of depths. Towed, undulating vehicle surveys may only include chlorophyll fluorescence with depth, but surface "flow-through" sampling may be possible that will still contribute biological information. Eventually, acoustic and optical instruments, and chemical sensors will be available to measure biological variables in an automated fashion. Small NOAA or chartered vessels should be used to provide more frequent biological sampling over the shelf. An inexpensive network of shore monitoring stations associated with government or academic institutions should be established and funded long-term to collect both physical and biological data. A shore station with meteorological, tide gauge, SST, salinity and biological measurements should be maintained at the inshore end of each transect and within any region routinely surveyed for abundance of larvae and adults of key species. Methods at all stations should be standardized to assure intercomparability. Because of the dynamic nature of Region II, there should be several new monitoring sections established to complement the seasonal surveys now done in Regions I, III and northern part of IV. Ideally such sites would be located where historical data, especially subsurface data, are available. To the extent possible, the different types of measurements should be co-located. For instance, the shelf and offshore meteorological buoys with subsurface measurements should lie along one of the offshore transects and the offshore buoy should lie under an altimeter track or cross-over point. If this could

coincide with a merchant ship XBT line, the benefit would be increased. Efforts should be made to encourage similar and coordinated Canadian and Mexican monitoring programs.

Sediment trap data. To fully exploit the potential of the high-resolution sediment records to study climate change and its impact on marine biota, it is important to monitor the processes that create the sediment record. This is done using sediment trap moorings near the sites of deposition. Sediment trap studies provide information on how the seasonally varying input of biogenic and terrigenous material relates to changing environmental conditions, and what proxies of biological and physical processes are preserved in the sediments. Time series sediment trapping, combined with hydrographic measurements and remotely sensed observations of surface ocean conditions provide an ideal means to investigate these questions and should be an integral part of the monitoring efforts of the U.S. GLOBEC EBC program so that we may link the mesoscale and regional process studies to the seasonal, interannual, and interdecadal changes preserved in the sediment records. A spatial array of traps moored near and distant from sediment records could give an indication of the spatial variability of sedimentation, thus the degree to which the sediment time series represents historical variability on larger space scales.

Physical forcing and processes of importance to marine populations.

Inflow/Outflow at the boundaries—Altimeter alongtrack heights allow the calculation of cross-track geostrophic surface velocity along tracks that are more than 20-50 km from the coast. By defining a volume inshore of a system of tracks, one can calculate geostrophic inflow/outflow at the surface. An altimeter does not sense wind-driven Ekman drift, which may be calculated from wind stress—most likely from model winds, since the scatterometer may alias storms. Thus, with data already available from satellites and/or surface buoys, surface currents can be calculated (except within 20-50 km of the coast). To examine currents over the shelf (nearshore) and vertical current shear, either CTD data or ADCP current data (at buoys) are needed. Augmenting the offshore meteorological buoys with downward looking ADCPs would be extremely valuable, especially if located under altimeter tracks or crossover points, for verifying the winds and the baroclinic shear in the upper ocean that the altimeter is missing.

Wind stress, surface mixing, wind stress curl, timing of seasonal events—The present system of meteorological buoys located 10-20 km from the coast, along with model winds, probably provide everything needed except the wind stress curl. The model winds underestimate the curl and smooth it over large distances due to their coarse spatial resolution. The cross-shelf component of the curl in spring and summer could probably be measured by placing a met buoy farther offshore (approximately 100 km) and another located only 1 km from the shore, but a denser (in the along-shore direction) array of buoys would be needed to capture the curl in winter.

Water temperature and stratification—AVHRR images, met buoys and merchant vessels all provide SST. To document subsurface temperature changes, including stratification, we need to add subsurface temperature measurements at met buoys, strengthen the XBT program and make periodic vertical slices (transects), either cross-shelf at a few locations and alongshelf at physical boundaries.

Transport—The altimeter does not sample well within 50 km of the coast and is presently unusable within 100-200 km of the coast off Oregon and Washington because of incorrect tidal corrections. Offshore CTD transects will measure the mean geostrophic transport relative to some depth and ADCP measurements will improve the calculations.

Cross-shelf transects will reveal jets or eddies crossed along the way, if sampling is sufficient. Towed, undulating vehicles with CTD sensors provide the best coverage. Complete small-scale 3-D surveys are needed to define the eddy field (scales of 10-200 km), which are prohibitive for a monitoring component. Drifters provide information on the eddy field statistics and typical velocities. Presently available winds are probably adequate to describe the surface Ekman transport. Rough estimates of upwelling and vertical transport made from geostrophic wind fields are probably adequate.

Movement of regional physical boundaries—When clouds are absent, the surface signature of these boundaries sometimes may be monitored from satellite SST and color images. However, some of the regional boundaries do not have surface expressions. To describe these boundaries, an alongshelf transect (CTD, ADCP) will be most effective.

Vertical structure—Buoys may provide continuous profiles of temperature structure and velocity at a point, providing information on the forcing of internal mixing. Merchant vessel XBTs provide stratification periodically along regular routes. Regular transects can provide information about the vertical structure of chlorophyll and nutrients. The depths of the thermocline and nutricline are of particular interest, since they may change in some climate change scenarios.

SECTION VII—RECOMMENDATIONS FOR INITIAL ACTIVITIES

This Science Plan has emphasized the broad questions which need to be answered in order to increase our understanding of how the distribution and abundance of animal populations in the California Current System (CCS) may be affected by global climate change. As stated in the Introduction to this document, the text before you is a Science Plan, not an Implementation Plan. As such, it will form the basis for Announcements of Opportunities (AO) for research on relationships between climate variability and ecosystem dynamics in the California Current. **The recommended initial AO will focus on three activities: retrospective data analysis, modeling and monitoring.** Later AOs will be recommended to focus on technical development and regional field process studies.

It should be clear that one cannot sample the entire large, four dimensional California Current, with its many habitats and species, with sufficient resolution to determine its internal response to external forcing at very many points in time and space. The challenge is to design and implement a research program that takes advantage of existing temporal and spatial variability to isolate mechanisms that determine how populations in the CCS respond to climate variability. To facilitate the efficient implementation of this plan, we will follow one of two courses: each AO should contain a detailed statement of research topics for which research proposals are sought. Alternatively, U.S. GLOBEC will release under separate cover an Implementation Plan for each proposal solicitation. We recommend the first AO be released as soon as September/October 1994.

We also note that the Coastal Ocean Processes (CoOP) Program is planning a study of wind-driven transport processes on the U.S. west coast before the end of the decade. The central motivating question of their study is: "What processes control the cross-margin transport of biological, chemical and geological materials in a strongly wind-driven system?" They plan to support modeling studies and 1-2 years of interdisciplinary process-oriented field research. Specifics of the program have not been fully defined—but there are ongoing efforts within the steering committees of CoOP and U.S. GLOBEC to ensure that the two programs complement each other in the most complete manner possible. The general questions identified by CoOP as important in this region are: (1) How do ocean-atmosphere feedbacks act to structure the system? (2) How and where do chemical species enter and leave the euphotic zone from the interior and near-bottom regions? (3) How are plankton distribution patterns over the continental margin maintained? and (4) How do exchange processes between the active sediment layer and the water affect the distribution and fate of biologically, chemically and geologically important materials? Although it does not identify specific sites where field work would be done, the CoOP Science Plan (in its Draft form) suggests that much could be learned from a comparison between a wind-driven flow over a strongly frontal region (with a front over the shelf, as off central Oregon) and less-frontal region (where a front may be found much farther offshore, as off northern/central California). These two areas lie within the regions defined by U.S. GLOBEC as Regions I and II. Thus, the two programs have mutual interests in similar scientific questions (especially processes that affect the transport of benthic invertebrate larvae and maintain planktonic populations nearshore) and in the regions where field work could be designed to answer these questions (Regions I and II, in the U.S. GLOBEC plan). In addition, CoOP is very interested in nutrient and phytoplankton dynamics, which would be a valuable addition to the information collected by U.S. GLOBEC.

U.S. GLOBEC recommends that the activities discussed below be considered as part of an initial Announcement of Opportunity:

(1) Compilation and analysis of a physical oceanography-plankton-fisheries database of historical measurements in the CCS, as a function of latitude. This will serve to define better the regional differences in forcing and response within the CCS, and the extent to which long term changes are regionally focused or coherent throughout the CCS. Existing satellite data archives also need further analysis, including comparisons of the CCS to other EBCs, in order to extend the observed range of forcing and response.

Examples of data that need further analysis include existing coastal meteorology, sea surface temperature, salinity and sea-level, merchant ship records, paleoecological data from sediments in anoxic basins, the CalCOFI data, fisheries landings data, and data in hydrographic and current meter archives. Most of the data are not widely available to the academic or government scientists, and few of the data sets have been cross-indexed and examined in a multidisciplinary, hypothesis-testing mode. Relatively little effort has been given to examining them in the context of climate variability, or in terms of regional or among EBC comparisons. Moreover, numerous biological samples remain uncounted in jars in various archives at oceanographic centers along the U.S. West coast. We believe a first step in a U.S. GLOBEC CCS program should be an examination of data sets and samples that have been collected to date from the CCS. These will ultimately be of immense value in attempting to describe changes, whether they be long-term and gradual or abrupt, in the CCS ecosystem. Satellite data, available over a relatively shorter time scale (2-14 years), should also be analyzed to determine regional differences in mesoscale features and movement of transition zones. This analysis will be useful in prescribing field sampling locations and strategy. Comparative studies of other EBCs could also provide useful information as to experimental design, by providing hypotheses on the direction that certain changes might take either due to ENSO or climate change variability.

(2) Modeling studies should be started now to develop and validate the biophysical models, and to explore the sensitivity of coupled physical-biological models to flow fields and to biological processes of growth, fecundity and mortality. The modeling component of the program should determine likely environmental conditions under different climate change scenarios and attempt to link GCM and regional-scale models, and couple physical and biological parameters in regional models. Model studies of biological rates and responses to physical conditions should begin as soon as possible. Output from these models will be useful in establishing sampling sites along the coast, and in suggesting how present latitudinal differences may be applied toward forecasting the consequences of climate change.

(3) Augmentation of existing monitoring programs, or the initiation of new monitoring programs, at different locations in the CCS should begin as soon as possible. This activity will provide a measure of interannual variability, especially as related to ENSO. Ongoing monitoring allows one to place intensive field process experiments in a temporal context. Concurrent coordinated monitoring programs at different localities should utilize comparable measurement methods. To the extent possible, this monitoring should include real-time reporting of the data, allowing a fast response to ENSO or other unusual events.

SECTION VIII—OCEANOGRAPHIC BACKGROUND

This section provides a detailed exposition of physical and biological aspects of the California Current ecosystem, building on information provided in Section III. Topics treated include seasonal variations in physical processes, zoogeographic boundaries, biophysical interactions, long-term variability as gleaned from paleoceanographic records, and a brief comparison of processes and species interactions in other eastern boundary current systems.

Seasonal Changes in Physical Processes in Regions I-IV

Wind speed and direction, water circulation, and transport in the California Current vary within the four regions, on seasonal to decadal time scales. Processes ranging from basin scale to local scale control seasonal variations. In this section we present details about the seasonal evolution of large scale structure in the CCS, for each of the four regions identified in Figure 1 (page 13).

Region I

In Region I, coastal wind stress is relatively strong, and wind direction reverses seasonally, although the annual mean wind stress is northward, due to strong and frequent winter storms. These cause intense mixing and alongshore northward advection (Huyer et al. 1978, Thomson 1981, Hickey 1989, Thomson et al. 1989). The region has a straight coastline and a narrow shelf. Significant freshwater input occurs throughout most of the year from the Strait of Juan de Fuca and the Columbia River (Figure 1). Large estuaries are common in Region I providing nursery areas for many species.

Hickey (1979, 1989) and Huyer (1983) describe the flow field in Region I. After the onset of southward winds in the spring, upwelling raises isopycnals next to the coast, creating a density front and an equatorward jet over the shelf. The front and jet move farther offshore in response to stronger southward winds, and return onshore when the wind relaxes or reverses. A subsurface, poleward undercurrent is usually found over the shelf break. During summer, the southward jet moves farther offshore (up to 100 km), and poleward nearshore counter currents are often found. Storms begin in fall and the flow field becomes less organized. Eddies are found offshore in winter and the poleward Davidson Current develops over the shelf and slope.

Region II

The flow field in Region II has been the subject of intense study in the 1980s and 1990s, with the most effort concentrated in the region between 37°N-41°N. Although wind stress varies seasonally, the annual mean is equatorward (Bakun and Nelson, 1991). The transition between winter storms, with strongly fluctuating alongshore winds, to persistently southward winds can occur rapidly. In spring and summer, there are relaxations of several days in these winds, with periods of 1-3 weeks. After the onset of southward winds, measurements over the shelf suggest that a nearshore equatorward jet develops and quickly moves offshore. A poleward undercurrent is found over the shelf break and slope. During relaxations of the southward winds, currents over the shelf are often poleward, even when winds are still equatorward. Poleward flow is often found next to the coast in late summer. In the late fall and winter, after storms with strong northward winds begin, the northward Davidson Current develops (see numerous papers in *J. Geophys. Res.*, vol 92, C2).

Coastal promontories in Region II cause changes in the local coastline orientation and topography which strongly affect the direction and intensity of coastal wind (Zemba and Friehe, 1987). Enhanced upwelling has been seen at Cape Mendocino (Largier et al. 1993), Point Arena (Kelly 1985), Point Ano Nuevo (Rosenfeld et al., in press) and Point Sur (Traganza et al. 1981).

Suppressed upwelling has been observed both upwind of capes (e.g., north of Cape Mendocino, Largier et al. 1993) and downwind of capes (e.g., south of Point Ano Nuevo, in Northern Monterey Bay, Graham and Largier, submitted; Rosenfeld et al., in press.). Further, if there is a substantial area of weak winds downstream of a cape (i.e., in the lee of a cape), an upwelling shadow can be found (Graham et al. 1992). Moreover, in the lee of some capes, circulation patterns occur that are retentive. Energetic coastal jets and large offshore meanders also appear to be associated with some of these promontories, although it is not yet known whether the behavior of these mesoscale features is relatively more affected by changes in wind forcing, coastal geometry or bottom topography (Mooers and Robinson, 1984, Davis 1985, Kosro and Huyer 1986, Huyer and Kosro 1987, Brink and Cowles, 1991, and other papers in the same volume). Cape Blanco (43°N) is the most northern of these capes and the boundary between Region I and Region II. It has been hypothesized to be the location where the southward 'upwelling jet', found over the shelf or shelf break farther north, first separates from the shelf and begins its meandering path through Region II (Smith, 1992). In some locations (e.g. Pt. Arena) upwelled water advects up to 300-500 km offshore (Figures 2 and 3 show one such example) at high velocities ($>50 \text{ cm s}^{-1}$) in jets usually 20-50 km wide and 100-200 m deep (Brink and Cowles, 1991). Eddies are found in association with the surface jet, often cyclonic inshore and anticyclonic offshore of the jet, although eddies of both sign have been found on either side of the jet (Figure 4). Upwelling at the coast and within the eddies and meandering surface jet create the filaments seen in the satellite images of SST (Figure 2) and color (Figure 3).

When long-term averages are formed from the CalCOFI data, the core of the California Current off Region II lies about 100-200 km from the coast, with maximum equatorward velocities of less than $5\text{-}10 \text{ cm s}^{-1}$ (Chelton, 1984). The offshore portion of southward flow is seen up to 1000 km offshore and extends deeper than 500 m, but the inshore section of the Current is limited to the upper 200 m over the continental slope (Hickey, 1979). It has been suggested that this average core is actually the temporally and spatially smoothed expression of the more intense, meandering alongshore jet that moves offshore between spring and fall (Huyer et al., 1991; Kosro et al., 1991; Strub et al., 1991; Smith, 1992).

Region III

Region III has been heavily sampled by the CalCOFI surveys. Whereas seasonal upwelling dominates coastal regions off Regions I, II and IV, the eastward reorientation of the coastline that forms the northern border of the Southern California Bight results in weaker winds with an onshore component, which produce very modest coastal upwelling and weak wind- and wave-induced mixing. Seasonal changes in the wind field are also relatively weak. Freshwater input is insignificant in this region and interleaving of different water masses occurs (Hickey, 1979, Lynn and Simpson 1987, 1990, Tsuchiya 1980). Region III is particularly sensitive to ENSO events because it is closer to the equator than more northern regions and because storm tracks bring energy from the tropics to the mid-latitudes within Regions III and IV more frequently than they impact more northern regions.

The presence of a bathymetric ridge and islands causes considerable recirculation in the current pattern (Lynn and Simpson 1987). During most seasons, the mean current makes a sharp shoreward turn near the U.S. Mexican border (32°N), where it splits—one part turns poleward into the Bight while the other turns equatorward to flow into Region IV. During fall and winter months, the poleward branch joins the countercurrent and in summer months, it feeds a cyclonic gyre, circulating around the entire Bight, called the Southern California Eddy, which is centered over the ridge and islands. For a period in spring, the alongshore winds overpower these recirculation features and result in overall equatorward flow through the southern half of the Bight and along Baja California (Figure 4). The sharp shoreward turn in the California Current jet at times is accompanied by a modest offshore flow, producing a feature termed the Ensenada

Front (Pelaez and McGowan, 1986; Thomas and Strub, 1990). This zonal feature acts as a biophysical division, which forms a faunal boundary (Brinton, 1967; Haury, 1984).

Plumes, jets and filaments that develop off northern and central California, feed into the California Current jet, which in turn enriches offshore regions off southern California. Pockets of upwelled water occur around the islands and within the Southern California Eddy. Although the above description of the flow patterns would imply mean flow out of the Santa Barbara Basin toward the west and into the main core of the California Current, a recent analysis of current meter data suggests there is some mean flow from the core of the California Current into the Santa Barbara basin just north of the islands (Aquad, 1992). The amount of connection between the Santa Barbara basin and the main California Current is important, since there is a long paleo-sediment record in the Santa Barbara basin, raising the question of whether it represents the rest of the California Current or only very local conditions.

At most times of the year, an undercurrent flows poleward along the continental slope at levels between 75 and 250 meters. Part flows through the narrow opening into the Santa Barbara Channel and part passes along the northern islands and through openings in the bathymetric ridge. Evidence suggests that dynamic instabilities of the undercurrent are instrumental in generating mesoscale eddies which migrate offshore (Lynn and Simpson, 1990). An anticyclonic eddy is commonly found on the western edge of the California jet, near 33°N (Simpson et al., 1984).

Region IV

The circulation in Region IV is similar to that in other upwelling regions of Eastern Boundary Currents (e.g., like that found in Regions I and II further north), but differs slightly in the season when upwelling is greatest. Winds are upwelling favorable on average during the entire year, but maximum upwelling occurs in March-May, earlier than it occurs in Regions I and II. Wind speed is greater than in Region III but less than Region II. Monthly maximum offshore Ekman transport is approximately 60% that of May-July of Region II but twice that found in Region I (Parrish et al., 1983). Parrish et al. (1981) refer to the region between 28°N-30°N as the central Baja upwelling maximum, although CZCS surface pigment concentrations are maximum in May-June slightly further south, between 24°N to 28°N (Thomas et al., 1994). Off Baja California, Punta Eugenia (28°N) is the dominant cape most likely to affect the alongshore flow and upwelling dynamics.

CalCOFI has coarsely sampled the region off Baja California for many years. Monthly maps of surface and 200 db (200 m) dynamic height, relative to 500 db, have been published by several authors. Lynn and Simpson's (1987) maps for January, April, July and October indicate the strongest and most continuous equatorward surface flow next to the coast along Baja California in spring (see Figure 4; page 17). Flow is still fairly strongly equatorward but more convoluted in summer. It becomes weaker and even more convoluted in fall and winter, although still equatorward. This pattern is also shown by monthly maps of mean flow (Roesler and Chelton 1987). All of the analyses agree on the strongly coherent equatorward flow in spring, coincident with the maximum upwelling favorable winds. They also show the meander around Punta Eugenia for much of the year, as depicted in Figure 4. The less smoothed maps of Hickey (1979) and the individual surveys of Wyllie (1966) indicate a strong degree of mesoscale activity in Region IV, which has been confirmed from drifter releases in the northern part of the region (Poulain and Niiler, 1989). At approximately 200 m, a poleward undercurrent is found in the region within 100 km of the coast for much of the year, except in spring when the strong equatorward flow extends to this depth.

Using CalCOFI data, Huyer (1983) shows the mean SST fields for January and May. The May SST field shows strong cross-shelf gradients indicative of upwelling wherever the coast is parallel to the southward winds, i.e., everywhere from 25°N-32°N, except for the region just north of Punta Eugenia (28°-29°N). In contrast, SSTs in January show little evidence of upwelling, except perhaps weak upwelling between 30°N-32°N.

Studies off northern Baja California suggest that conditions are highly variable due to onshore movement of offshore eddies and wind-forced equatorward surface currents (Badan-Dangon et al. 1989)—e.g., responses similar to that observed over the shelf off northern California (Huyer and Kosro 1987). Farther south, at 27°N, Walsh et al. (1977) found that the oceanic response to variability in wind forcing is similar to the classic picture of upwelling off Oregon (Huyer 1983)—winds were upwelling favorable, isopycnals sloped upwards toward the coast, surface currents were to the south and offshore, flow at depth was onshore, and a poleward undercurrent.

Biological Provinces

Many species exhibit distinct distributional boundaries that coincide with changes in the regional oceanographic conditions described previously. These boundaries are indicators of responses of marine organisms to key physical factors and may provide clues to the principal processes underlying production in the CCS. A brief description of these provinces follows.

Phytoplankton Provinces

Much of the work examining phytoplankton phylogeography in the CCS has been nearshore and on small regional spatial scales. Allen's twenty-year program (1920-1939), sampling daily or weekly from the Scripps Pier (Allen, 1936, 1941; Tont, 1986), is the longest and most comprehensive data set. Bolin and Abbott (1963) analyzed weekly samples collected from six stations over a seven-year period (1954-1960) in Monterey Bay. Smaller programs, consisting of one to several cruises (e.g. Abbott et al. 1990; Balech 1960; Briand 1976; Cullen et al. 1982; Hood et al. 1990, 1991; Matrai 1984; Reid et al. 1978; Venrick 1992) have contributed to our understanding of species assemblages and associations in and around the CCS. A good summary of the phytoplankton of the Southern California Bight can be found in Eppley (1986).

Local oceanographic conditions appear to influence the distribution of phytoplankton. Tont (1976, 1981) showed diatom abundances to be associated with coastal upwelling, with several blooms of 5-6 weeks duration during summer. Hood et al. (1990, 1991) and Abbott et al. (1990) showed *Chaetoceros* and *Skeletonema costatum* to be the dominant diatoms in several chlorophyll maxima in the CTZ region. Their distribution, however, was patchy, with *Rhizosolenia alata*, *Thalassiosira* spp. and *Nitzschia* spp. dominating in a tongue of cold water extending seaward from Cape Mendocino.

Shifts in phytoplankton species dominance occur over alongshore distances of less than 100 km and time periods of days. Abbott et al. (1990) found that species composition along a drifter track changed over time scales of 2-3 days. This change was ascribed to in situ growth of large centric diatoms (probably *Actinocyclus* or *Thalassiosira*) in newly upwelled water. Concentrations of nitrate+nitrite dropped from 10 micromolar to zero during this time, while chlorophyll decreased and cell volume increased.

Zooplankton Provinces

For the oceanic zooplankton, the CCS is a region where the Subarctic Pacific, Transition Zone, Central, and Equatorial faunas overlap, along with some Warm Water Cosmopolites (see Table

1.2 in McGowan 1971). The Subarctic fauna (e.g., copepods *Neocalanus plumchrus*, *Eucalanus bungii*, *Calanus marshallae*; euphausiids *Thysanoessa longipes*, *Tessarabrachion oculatus*; chaetognath *S. elegans*) generally extend south to Cape Blanco or Cape Mendocino, and thus may be considered Region I species. There are no Region II endemics among oceanic taxa. Point Conception, the approximate boundary between Regions II and III, can be a significant boundary between cool water taxa occurring in Region II (e.g., *T. spinifera*, Figure 5) and warm water taxa occurring in Regions III and IV (e.g., *Nyctiphanes simplex*, Figure 5). The Region II/III boundary is better defined for coastal and neritic taxa, including these two euphausiid species and coastal copepods (see Newman 1979), while open ocean taxa often show broader latitudinal distributions.

The Transition Zone fauna (e.g., copepods *Eucalanus californicus*, *Pleuromamma borealis*; euphausiids *Nematoscelis difficilis*, *Thysanoessa gregaria*; chaetognath *Sagitta scrippsae*) can extend from British Columbia to the tip of Baja California, thus spanning Regions I-IV. Notable among the euphausiids is *Euphausia pacifica* which inhabits both the Subarctic and the Transition Zone, with centers of abundance in both the Gulf of Alaska and off central and southern California (Brinton 1962).

The population dynamics and phenology of some zooplankton species which span Regions I-III have been examined and found to differ between regions, perhaps due to adaptations to local environmental conditions. For example, although seasonal variations in wind stress, upwelling indices, and particulate organic matter are detectable in Region III (Brinton 1976, Mullin 1986) seasonal variations in primary production rates are relatively damped and sometimes greatly exceeded by interannual variations (Mullin 1986). The seasonal cycle of zooplankton biomass, measured as displacement volume, has a lower amplitude in Region III than in regions of the CCS further to the north (Roesler and Chelton 1987). The life history characteristics and reproductive responses of zooplankton in Region III are correspondingly less seasonal. The copepod *Calanus pacificus* has been found to reproduce year-round in Region III (Mullin 1991), while egg production stops in winter in Puget Sound within Region I (Runge 1985). Similarly there is some year-round recruitment of older copepodid stages of *C. pacificus* in Region III (Mullin and Brooks 1967), while population growth is quite seasonal in higher latitudes with overwintering accumulations of copepodid stages IV and V.

Within individual species of zooplankton, the population genetic structure may correspond to different water types or portions of coastal and upwelling hydrodynamic features (Bucklin 1991). *C. pacificus sensu lato* is widely distributed and abundant in Regions I-III of the CCS, but appears to have subspecies that are associated with either the Subarctic Pacific in Region I (*C. pacificus oceanicus* Brodsky) or with Regions II and III (*C. pacificus californicus* Brodsky). Recent preliminary mitochondrial DNA studies (Bucklin and Kann 1991) have found genetic differentiation between northern and southern populations of *C. pacificus*, confirming that regional differentiation of closely related species has occurred within the CCS.

There is no defined faunistic boundary for zooplankton between Regions III and IV; some Transition Zone and other cool water zooplankton species occur in the upwelling zone off Punta Eugenia at 27°N. The Equatorial and Eastern Tropical Pacific zooplankton faunas can extend northward from lower latitudes along the coast of Baja California into Region IV.

Recurrent patterns of cross-shelf zonation are known for copepods off Washington and central Oregon (Peterson et al. 1979; Peterson, 1980): several species are almost completely restricted to the nearshore zone, out to water depths not exceeding 50 m (*Acartia hudsonica*, *Centropages abdominalis* and the cladocerans *Evadne nordmanni* and *Podon leukartii*), other species are found predominantly in mid-shelf and slope waters (*A. longiremis* and *Calanus marshallae*) and one ranges across the entire domain (*Pseudocalanus mimus*). Behavioral mechanisms which lead to cross-shelf zonation and retention in the Oregon upwelling zone are discussed in Peterson

et al. (1979) for five copepod species, and Peterson (1980). Attempts to model retention mechanisms proposed by Peterson et al. (1979) using a physical transport model were only partially successful (Wroblewski 1980, Wroblewski 1982) and should be revisited.

Cross-shelf zonation does not seem to be observed off central or southern California. Coastal/shelf species such as *C. pacificus*, *Pseudocalanus mimus*, *Paracalanus parvus*, *Acartia tonsa* and *A. longiremis* are common hundreds of kilometers seaward of the shelf. Total zooplankton biomass is high out to several hundred kilometers from shore as well (Bernal and McGowan 1981). The apparent lack of zonation off California as compared to Oregon may reflect the fact that upwelling off Oregon is restricted to the shelf whereas off California the area affected by upwelling is far more broad and includes Ekman upwelling nearshore, Ekman pumping offshore and offshore transport of upwelled water via filaments, jets and eddies.

Invertebrate Benthos Provinces

Two major faunal provinces have been defined for the nearshore marine benthos inhabiting the CCS. These are the Oregonian province in the north and the Californian province in the south, with a faunal boundary between them located approximately at Pt. Conception. This faunal boundary constitutes a local maximum in number of species for a variety of nearshore organisms (including molluscs and barnacles as well as coastal and neritic copepods; see Newman 1979). The local maximum arises from the mixture of the faunas of both the Oregonian and Californian provinces in the vicinity of Pt. Conception. Since most of the benthic invertebrates have planktonic larval stages, it is likely that this faunal boundary is determined by processes occurring in the pelagic habitat (i.e., larval stages).

Marine Fish Provinces

The CCS supports a diverse group of fish that exhibit a variety of strategies to adapt to local ocean conditions. Over fifty rockfish species, seventeen flatfish species, six salmonids (including steelhead and Pacific salmon), and three clupeoids (northern anchovy, Pacific herring and Pacific sardine) are found in the CCS (Tables 2-5).

The CCS contains fish common to several zoogeographic provinces. Allen and Smith (1988) defined zoogeographic provinces for the marine fish common to the North Pacific. Allen and Smith (1988) also defined life zones to describe the principal location in the water column that adult fish occupy (Table 6). Based on these definitions it appears that Region II may represent a transition zone between subtropical and subarctic fish species (Tables 2-5). Further south, Parrish et al. (1981) noted that Magdalena Bay (25°N) is the average location of a front that forms the boundary between tropical and subtropical fauna.

In general, rockfish, flatfish, and groundfish all exhibit regional distributions that appeared to have either northern or southern boundaries in Region II (Tables 2-5), reflecting two major provinces--a northern subarctic and a southern subtropical. Out of all of the species considered, only ten species inhabit all four regions. These ten species all exhibited pelagic or mesopelagic behaviors (Table 3). Of these, the northern anchovy and Pacific sardine include separate spawning stocks in the north, central and southern portions of the CCS (Parrish et al 1989, Methot 1989).

Table 2. Maximum length, maximum depth, location, life zone, primary region inhabited in CCS, and species range of the common rockfish species found in region I or II of the CCS.

Species	Common name	Adult		Primary Life Zone Inhabited	Region	CCS Range
		Maximum Length	Depth			
<i>Sebastes aleutianus</i>	Rougeye rockfish	97cm	100-300m	Mid-shelf - meso-benthal	I	EBP
<i>S. alutus</i>	Pacific ocean perch	51	100-300	Outer shelf - meso-benthal	I	K-A
<i>S. aurora</i>	Aurora rockfish	39	300-500	Outer shelf - mesobenthical	I	O-SD
<i>S. babcocki</i>	Redbanded rockfish	64	150-350	Outer shelf - mesobenthical	I	EBP
<i>S. borealis</i>	Shorttraker rockfish	105	250-450	Mid-shelf - bathybenthical	I	EBP
<i>S. brevispinus</i>	Silvergrey rockfish	71	100-300	Outer shelf - mesobenthical	I	EBP
<i>S. caurinus</i>	Copper rockfish	55	10-50	Inner shelf	I-II	O
<i>S. ciliatus</i>	Dusky rockfish	41	100-300	Outer shelf - mesobenthical	I	A
<i>S. crameri</i>	Darkblotched rockfish	57	100-200	Mid-shelf - mesobenthical	I	EBP
<i>S. diplaproa</i>	Splitnose rockfish	46	200-400	Outer shelf - mesobenthical	I-II	ETP
<i>S. elongatus</i>	Greenstriped rockfish	38	150-250	Mid-shelf - mesobenthical	I	EBP
<i>S. emphaeus</i>	Puget sound rockfish	18	0-100	Inner shelf	I	O
<i>S. entomelas</i>	Widow rockfish	60	100-250	Mid-shelf - mesobenthical	I	O-EBP
<i>S. flavidus</i>	Yellowtail rockfish	66	100-200	Mid-shelf - mesobenthical	I	EBP
<i>S. helvomaculatus</i>	Rosehorn rockfish	41	150-300	Outer shelf - mesobenthical	I	EBP
<i>S. maliger</i>	Quillback rockfish	61	10-100	Inner shelf	I-II	O-EPB
<i>S. melanops</i>	Black rockfish	60	10-100	Inner shelf	I	EPB
<i>S. nebulosus</i>	China rockfish	43	10-75	Inner shelf	I	O
<i>S. nigrociuctus</i>	Tiger rockfish	61	75-200	Mid-shelf	I-II	O
<i>S. paucispinis</i>	Bocaccio	91	100-250	Mid-shelf - mesobenthical	I-II	O-SD
<i>S. pinniger</i>	Canary rockfish	76	100-200	Mid shelf - mesobenthical	I	EBP
<i>S. polyspinus</i>	Northern rockfish	40	50-200	Mid shelf - mesobenthical	I	A
<i>S. proriger</i>	Redstripe rockfish	51	100-250	Outer shelf - mesobenthical	I	EBP
<i>S. reedi</i>	Yellowmouth rockfish	54	150-375	Outer shelf - mesobenthical	I	EBP
<i>S. ruberrimus</i>	Yelloweye rockfish	91	100-250	Mid-shelf - mesobenthical	I	O-EBP
<i>S. varigatus</i>	Harlequin rockfish	32	150-250	Mid-shelf - mesobenthical	I	A
<i>S. wilsoni</i>	Pygmy rockfish	21	50-150	Inner shelf	I-II	O
<i>S. zacentrus</i>	Sharpchin rockfish	33	150-250	Outer shelf - mesobenthical	I	EBP

Provinces: A — Aleutian; EBP — Eastern Boreal Pacific; ETP — Eastern Tropical Pacific; K — Kurile Islands; O — Oregonian; SD — San Diegan

Table 3. Maximum length, maximum depth, location, life zone, primary region inhabited in CCS, and species range of the common rockfish species found in regions II, III or IV of the CCS.

Species	Common name	Adult		Primary Life Zone Inhabited	Region	CCS Range
		Maximum Length	Depth			
<i>Sebastes atrovirens</i>	Kelp rockfish	42cm	10-20m	Inner shelf	III	O-SD
<i>S. auriculatus</i>	Brown rockfish	55	20-80	Inner shelf	I-III	O-SD
<i>S. carnatus</i>	Gopher rockfish	39	15-40	Inner shelf	II	O-SD
<i>S. chlorostictus</i>	Greenspotted rockfish	50	90-179	Mid-shelf	II	O-SD
<i>S. chrysomelas</i>	Black & Yellow rkf.	39	1-15	Inner shelf	II	O-SD
<i>S. constellatus</i>	Starry rockfish	46	90-149	Inner shelf	III	O-SD
<i>S. dalli</i>	Calico rockfish	25	60-89	Inner shelf	III	SD
<i>S. ensifer</i>	Swordspine rockfish	30	180-239+	Mid shelf - mesobenthical	III	SD
<i>S. eos</i>	Pink rockfish	56	100-300	Mid shelf - mesobenthical	III	O-SD
<i>S. gilli</i>	Bronze spotted rkf.	91	75-375	Mid-shelf - mesobenthical	III	O-SD
<i>S. goodei</i>	Chillipepper	56	100-250	Mid shelf - mesobenthical	II-III	O-SD
<i>S. hopkinsi</i>	Squarespot rockfish	29	60-119	Mid shelf	III	O-SD
<i>S. jordani</i>	Shortbelly rockfish	32	100-250	Mid shelf - mesobenthical	II	O-SD
<i>S. levis</i>	Cowcod	94	180-239+	Mid-shelf - mesobenthical	III	O-SD
<i>S. macdonaldi</i>	Mexican rockfish	66	100-200	Mid-shelf	IV	SD
<i>S. melanostomus</i>	Blackgill rockfish	61	300-500	Outer shelf - mesobenthical	II-III	O-SD
<i>S. miniatus</i>	Vermillion rockfish	76	150-239+	Mid-shelf - mesobenthical	II-III	O-SD
<i>S. mystinus</i>	Blue rockfish	53	10-100	Inner shelf - outer shelf	II	O-SD
<i>S. ovalis</i>	Speckled rockfish	56	90-149	Mid-shelf	III	O-SD
<i>S. rastrelliger</i>	Grass rockfish	56	0-15	Inner shelf	II-III	O-SD
<i>S. roxaceus</i>	Rosy rockfish	36	60-119	Inner shelf	II-III	O-SD
<i>S. rosenblatti</i>	Greenblotched rkf.	48	100-200	Mid-shelf	II-III	O-SD
<i>S. rubrivinctus</i>	Flag rockfish	51	150-250	Mid-shelf - mesobenthical	II	O-SD
<i>S. rufus</i>	Bank rockfish	51	210-239+	Mesobenthical	II-III	O-SD
<i>S. saxicola</i>	Stripetail rockfish	34	150-250	Inner shelf - mesobenthical	II	O-SD
<i>S. semicinctus</i>	Halfbanded rockfish	25	120-149	Mid-shelf	II-III	O-SD
<i>S. serranoides</i>	Olive rockfish	61	20-100	Inner shelf	II-III	O-SD
<i>S. serriceps</i>	Treefish	41	5-90	Inner shelf	III	SD
<i>S. umbrosus</i>	Honeycomb rockfish	27	30-90	Inner shelf	III	SD

Provinces: A—Aleutian; EBP—Eastern Boreal Pacific; ETP—Eastern Tropical Pacific; K—Kurile Islands; O—Oregonian; SD—San Diegan

Table 4. Maximum length, maximum depth, location, life zone, primary region inhabited in CCS, and species range of common sharks, skates, groundfish and pelagic fish species found in the CCS.

<u>Species</u>	<u>Common name</u>	Maximum Length	Adult Depth	<u>Primary Life Zone</u>	<u>Region</u>	<u>CCS Range</u>
<i>Galeorhinus zyopterus</i>	Southern shark	198cm		Neritic - epipelagic	All	SD - O
<i>Squalus acanthias</i>	Spiny dogfish	158	50-250	Inner shelf - mesobenthical	I - III	ATT
<i>Traikis semifasciata</i>	Leopard shark	198	0-90	Neritic - epipelagic	II-IV	SD - O
<i>Raja binoculata</i>	Big skate	244	50-200	Inner shelf - mesobenthical	I	EBP
<i>R. inornata</i>	California skate	76		Inner shelf - mesobenthical	III	SD
<i>R. rhina</i>	Longnose skate	137	50-300	Inner shelf - mesobenthical	I	EBP
<i>Hydrolagus collicii</i>	Spotted ratfish	97	50-250	Mid-shelf - mesobenthical	II-III	O-C
<i>Anoplopoma fimbria</i>	Sablefish	102	100-400	Inner shelf - bathybenthical	I	EBP
<i>Gadus macrocephalus</i>	Pacific cod	114	50-200	Inner shelf - mesobenthical	I	CBP
<i>Hexagrammos decagrammus</i>	Kelp greenling	53		Inner shelf - bathybenthical	I	EBP
<i>Ophiodon elongatus</i>	Lingcod	114	50-200	Estuarine - mesobenthical	I	EBP
<i>Scorpaenichthys marmoratus</i>	Cabezon	99	0-200	Estuarine	I	O
<i>Clupea pallasii</i>	Pacific herring		0-150	Estuarine - epipelagic	All	ACP
<i>Colobis saira</i>	Pacific saury	36	0-200	Epipelagic - mesopelagic	All	TNP
<i>Engraulis mordax</i>	Northern anchovy	23	0-250	Neritic	All	SD - O
<i>Merluccius productus</i>	Pacific whiting (hake)	91	50-300	Neritic - mesopelagic	All	ETP
<i>Oncorhynchus gorbuscha</i>	Pink salmon	76	0-250	Fluvial - epipelagic	I	AO&NEBP
<i>O. keta</i>	Chum salmon	102	0-250	Fluvial - epipelagic	I-II	AO&NEBP
<i>O. kisutch</i>	Coho salmon	98	0-250	Fluvial - epipelagic	I	AO&NEPB
<i>O. nerka</i>	Sockeye salmon	84	0-250	Fluvial - epipelagic	I	AO&NEPB
<i>O. tshawytscha</i>	Chinook salmon	147	50-250	Fluvial - epipelagic	I - II	AO&NEPB
<i>Salmo gairdneri</i>	Steelhead trout	114	0-250	Fluvial - epipelagic	I - II	AO&NEPB
<i>Sarda chiliensis</i>	Pacific bonito	102	0-100	Neritic - epipelagic	All	ETP
<i>Sardinops sagax caerulea</i>	Pacific sardine	41	0-100	Neritic	All	ATT
<i>Scomber japonicus</i>	Pacific mackerel	64	0-300	Neritic	All	ATT
<i>Thunus alalunga</i>	Albacore tuna	125	0-100	Epipelagic	All	ATT
<i>Thunus thynnus</i>	Bluefin tuna	430	0-100	Epipelagic	III - IV	ATT
<i>Trachurus symmetricus</i>	Jack mackerel	81	0-400	Epipelagic	All	ATT

Provinces: A—Aleutian; ACP—Arctic-circumboreal Pacific; AO—Arctic Oceanic; ATT—Antitropical-temperate; C—California; EBP—Eastern Boreal Pacific; ETP—Eastern Temperate Pacific; K—Kurile Islands; NEBP—Northeastern Boreal Pacific; O—Oregonian; SC—San Diegoan; TNP—Temperate North Pacific

Table 5. Maximum length, maximum depth, location, life zone, primary region inhabited in CCS, and species range of common flatfish species found in the CCS.

Species	Common name	Maximum		Primary Life Zone Inhabited	Region	Range
		Length	Depth			
<i>Atheresthes stomias</i>	Arrowtooth flounder	84cm	50-250m	Inner shelf - mesobenthhal	I	EBP
<i>Citharichthys sordidus</i>	Pacific sanddab	41	50-150	Inner shelf - mesobenthhal	II	O-SD
<i>C. xanhostigma</i>	Longfin sanddab	25	0-135	Inner shelf - mid-shelf	III-IV	SD
<i>Eopsetta jordani</i>	Petrale sole	70	50-250	Inner shelf - mesobenthhal	I	EBP
<i>Errex zachirus</i>	Rex sole	59	50-300	Mid-shelf - mesobenthhal	I	EBP
<i>Hippoglossoides elassodon</i>	Flathead sole	46	50-200	Inner shelf - mesobenthhal	I	K-A
<i>H. stenolepis</i>	Pacific halibut	267	0-200	Inner shelf - mesobenthhal	I	ANEBP
<i>Microstomus pacificus</i>	Dover sole	76	50-300+	Mid-shelf - bathybenthhal	I-II	EBP-SD
<i>Paralichthys californicus</i>	California halibut	150	0-100	Inner shelf - mesobenthhal	II-IV	SD
<i>Platichthys stellatus</i>	Starry flounder	91	0-100	Estuarine - sublittoral	I	ACB
<i>Pleuronectes bilineatus</i>	Rock sole	57	0-150	Inner shelf - outer shelf	I	NEBP
<i>P. isolepis</i>	Butter sole	55	0-100	Inner shelf - outer shelf	I	EBP
<i>P. vetulus</i>	English sole	57	0-150	Inner shelf - outer shelf	I	EBP-SD
<i>Pleuronichthys decurrens</i>	Curfin sole	36	18-350	Inner shelf - mesobenthhal	II-IV	O-SD
<i>P. verticalis</i>	Hornyhead sole	36	10-180	Inner shelf - outer shelf	III-IV	SD
<i>P. ritteri</i>	Spotted sole	30	0-50	Inner shelf	III-IV	SD
<i>Psettichthys melanosticus</i>	Sand sole	53	0-50	Inner shelf	I	EBP

Provinces: A—Aleutian; ACP—Arctic-circumboreal Pacific; AO—Arctic Oceanic; ATT—Antitropical-temperate; C—Californian; EBP—Eastern Boreal Pacific; ETP—Eastern Temperate Pacific; K—Kurile Islands; NEBP—Northeastern Boreal Pacific; O—Oregonian; SC—San Diegoan; TNP—Temperate North Pacific

Table 6. Definition of life zone classifications (from Allen and Smith 1988).

- I Peripheral environments:
 - Fluvial (riverine)
 - Estuarine
 - Intertidal
- II. Pelagic environments:
 - Neritic (0-200m)
 - Oceanic
 - Epipelagic (0-200)
 - Mesopelagic (200-1000m)
 - Bathypelagic (1000m -4000m)
- III. Benthic environments:
 - Sublittoral
 - Inner-shelf (0-50m)
 - Mid-shelf (50-100m)
 - Outer-shelf (100-200m)
 - Bathyal
 - Mesobenthal (200-500m)
 - Bathybenthal (500-2500m)

The zoogeographic boundary of many marine fish stocks may be located in Region II because ocean conditions there may not be favorable to spawning success. As noted by Parrish et al. (1981), few fish species spawn in the surface waters of Region II. Those species that do reproduce there tend to employ life history traits (e.g., live-bearing, spawning in estuaries, anadromous spawning) that minimize the risk of offshore transport in open ocean waters. Hence Region III, and to some extent Region I, are major centers of fish reproduction and of potential fish-zooplankton interactions in the CCS. Region III is the preferred spawning site for over 90% of the epipelagic fish biomass (hake, sardine, anchovy) in the southern part of the CCS. Pacific hake (*Merluccius productus*) are particularly notable because they undertake a migration of approximately 2,000 km from Vancouver Island to spawn in the offshore waters of Region III (Bailey et al. 1982). At the top of the trophic pyramid, the white shark *Carcharodon carcharias* displays a similar seasonal and migratory cycle: breeding and pupping in Region III, then moving north to Regions I and II.

Bird Provinces

Characteristic of this and other eastern boundary current systems, a high degree of endemism is evident within the marine avifauna of the CCS; confined to this region, for example, are the Ashy Storm-Petrel *Oceanodroma homochroa*, Brandt's Cormorant *Phalacrocorax penicillatus*, Western Gull *Larus occidentalis* and Xantus' Murrelet *Synthliboramphus hypoleuca*. A number of avian species behave like some of the fish, breeding in Region III but spreading north into Regions I and II during the remainder of the year: e.g., Black-vented Shearwater *Puffinus nativitatus*, Brown Pelican *Pelecanus occidentalis* and Heermann's Gull *L. heermanni*. By far the greatest avian biomass is confined to Regions I and II, and is dominated by the Common Murre *Uria aalge* (a subarctic species having a non-migratory subpopulation in the CCS), Sooty Shearwater *P. griseus* (which breeds in the SW Pacific), Cassin's Auklet *Ptychoramphus aleuticus*, Western Gull and Brandt's Cormorant. Several other subarctic species are also abundant in Regions I and II, many moving to CCS waters during the winter.

Circumstantial evidence suggests that the distribution of some marine birds may be determined by key prey items in the diet. For example, *Thysanoessa spinifera* is a critical prey item in the diet of Cassin's Auklet. Vermeer (1981) suggests that the geographic distribution of this euphausiid in the eastern North Pacific determines that of the auklet—both *T. spinifera* and Cassin's Auklet extend from southeast Alaska to northern Baja California, Mexico.

El Niño Effects on Zoogeographic Boundaries

El Niño conditions may influence the distribution of marine life in the CCS. A major shift in phytoplankton species composition was recorded during the 1957-1958 El Niño. Bolin and Abbott (1963) and Balech (1960) found unusually high concentrations of the dinoflagellate genus *Ceratium* from La Jolla to Monterey Bay. Balech notes that many of the species present during the winter of 1957 and summer of 1958 were warm-water and tropical species, and suggests that they were advected northward during the unusual physical conditions.

Geographic domains typically inhabited by faunal assemblages may shift northward during extreme ENSO events (Fulton and LeBrasseur 1985, cf. Ware and McFarlane 1989). During the 1983 El Niño, inshore waters off Oregon were dominated by southern copepods, *Paracalanus parvus* and *Acartia tonsa*, and there were many occurrences of all life stages of the euphausiid *Nyctiphanes simplex*—previously recorded only as far north as central California (Fig. 5; Miller et al. 1985). Brinton (1967) noted that the southern euphausiid (*Euphausia eximia*) extended its range north in coastal waters during warm periods. The zoogeographic boundary of some fish species is altered during El Niño events (Percy and Schoener 1987, Arntz et al. 1991). Bailey and Incze (1985) noted that El Niño effects appear to favor stocks at the northern end of their range with opposite effects on stocks at the southern end of their range. They also predict that

the impact of ocean warming will have the greatest influence on sedentary species and species that exhibit homing or slow migrations. Increased mortality rates for key prey species may be observed when pelagic fish predators shift their distributions. If a prolonged change in ocean conditions occurred, local species assemblages may change due to competition for space and resources, resulting in shifts in species dominance. Moreover, range extensions can have significant impacts on trophic relations, as evidenced by Pearcy et al.'s (1985) observation that *Nyctiphanes simplex* was the most common euphausiid prey of juvenile coho salmon off Oregon and Washington in 1983. Understanding the potential response of marine stocks to climate change would help to predict future community structures in the CCS.

Biophysical Interactions

Overview of Biophysical Interactions

Physical factors may influence biological systems directly or indirectly. Direct physical influences include changes in transport pathways in both the horizontal and vertical planes, alterations in physiological rates and shifts in the spatial boundaries of acceptable habitat. Indirect pathways include secondary responses of production to influences on nutrient concentrations, food availability, the distribution of predators, growth rates, and reproductive capabilities.

In the CCS the underlying importance of large scale physical forcing on marine organisms is evidenced in several comparative studies. Hollowed et al. (1987) noted that extreme year classes of several marine fish tend to occur synchronously even when species are separated by large geographical distances. Synchronicity over large geographic areas would not be expected if the principal processes influencing survival were linked to local ocean conditions. These synchronous extreme year classes tend to occur during periods of unusual environmental conditions (Hollowed and Wooster 1992, Beamish 1993). Further evidence of the importance of large scale physical forcing on marine organisms is found in numerous single species studies that demonstrate an apparent relationship between survival and physical forcing (Tables 7-8). Many of these studies show apparent linkages between biological response variables and temperature, wind driven transport or ENSO. Long-term trends in the abundance of marine fish stocks also show coherent patterns of association with large scale physical forcing. Francis and Sibley (1991) and Beamish and Boullion (1993) found coherent long term population trends in many stocks of Pacific salmon, with the southern (CCS) and northern (Canadian and Alaskan) stocks being out of phase. On an even broader scale, time series of Pacific sardine catch from populations in the southeast, northeast, and northwest Pacific all show remarkably similar trends (Kawasaki 1992). These comparative studies suggest that production of marine fish stocks is linked to large scale (but unknown) ocean processes.

A notable feature of time series of physical and biological measurements in the eastern boundary currents are that they both exhibit abrupt changes in state. The most recent shift occurred in the mid 1970s when coastal sea surface temperatures abruptly became warmer than average in the California Current (Hollowed and Wooster 1992, Trenberth 1990, Royer 1993, Figure 8). This shift was accompanied by a drop in zooplankton abundance, recovery of the depleted Pacific sardine population in the Southern California, and reduced size of many salmon runs in Oregon and Washington. Evidence of similar shifts at earlier times are found in the paleoclimatic records (Baumgartner et al. 1992). Together the paleoclimate and historic records suggest that the CCS response to gradually increasing concentrations of greenhouse gasses may be abrupt changes in qualitative states of the physical and biological system, rather than gradual change.

A principal goal of the U.S. GLOBEC CCS project is to identify the processes linking physical change to observed biological responses at the population level. Quantifying the impact of environmental change on survival rates of marine organisms may be difficult because the

Table 7. Summary of potential influences of physical change on major fish populations of the California Current System.

<u>Species</u>	<u>Author</u>	<u>Process Influenced</u>	<u>Physical Co-Variate</u>	<u>Response Variable</u>
Dover sole	Hayman and Tyler 1980	Prey availability, transport	Vertical velocity, wind	Recruitment
English sole	Kruse and Tyler 1989	Larval advection, prey availability	Temperature	Recruitment
	Kruse and Tyler 1983	Spawn period, gonadal development	Temperature	Spawn time
	Hayman and Tyler 1980	Delayed spawning, egg condition, larval transport	Storm frequency, wind speed, sea level, temperature	Recruitment
	Botsford et al. 1989 Forrester 1977 Ketchen 1956	Prey availability Egg viability Growth & larval transport	Productivity Temperature	Recruit., distrib. Hatch success Recruitment
Flathead sole	Alderice and Forrester 1974 Ketchen and Forrester 1966	Egg distribution and survival Larval transport	Temperature Temperature	Egg condition Recruitment
	Parker 1989	Larval transport	Wind	Recruitment
Petrale sole	Alderice and Forrester 1971 Forrester 1977	Incubation, hatching success Growth, settling time, prey conc.	Temperature and salinity Temperature	Egg condition Egg cond., size
Rock sole	Fargo and McKinnell 1989 Forrester 1977	No proposed mechanism Incubation, larval retention	Temperature Temperature, transport	Recruitment Recruitment
	Tyler & Westrheim 1986 Tyler and Crawford 1991	Larval transport Larval transport	Transport and temperature Transport	Recruitment Recruitment
Sablefish	McFarlane & Beamish 1986 McFarlane & Beamish 1992	Prey concentrations Prey concentrations	Transport and temperature Aleutian low, circulation	Recruitment Recruitment, weight
	Norton 1987	Larval transport	Advection, circulation, Aleutian low	Recruitment
Salmon-coho	Nickelson 1986 Pearcy 1992	Growth rate, predation Prey availability, predation	Upwelling, temperature Upwelling, Aleutian low	Smolt survival Survival, catch
	Pearcy et al. 1985 Kope and Botsford 1990 Johnson 1988	Predation None Prey availability	Upwelling, temperature ENSO, upwelling, temperature ENSO	Survival index Catch Adult weight
Salmon-sockeye	Mysak 1986 Thomson et al. 1992 Xie and Hsieh 1989 Beamish and Bouillon (1993)	Migratory pathway Migratory pathway Migratory pathway Prey availability	ENSO Wind driven current Temperature, river discharge Aleutian low, circulation	Migratory path Migratory path Migratory path Catch

Table 7 (cont.) Summary of potential influences of physical change on major fish populations of the California Current System.

<u>Species</u>	<u>Author</u>	<u>Possible Process</u>	<u>Physical Co-Variate</u>	<u>Response Variable</u>
Jack mackerel	Zwiefel and Lasker 1976	Incubation period, growth	Temperature	Egg condition
	Theilacker 1986	Starvation, predation	Productivity	Larval condition
	Hewitt et al. 1985	Starvation, predation	Productivity	Larval condition
Northern anchovy	Lasker 1975, 1981	Prey concentration	Turbulence	Feeding success
	Peterman & Bradford 1987	Prey concentration	Turbulence	Recruitment
	Husby and Nelson 1982	Transport & Prey concentrations	Turbulence, upwelling, thermocline	Distribution
	Power 1986	Larval transport	Upwelling	Distribution
	Fiedler 1984	Spawning range	ENSO	Distribution
	Zwiefel and Lasker 1976	Incubation period, growth	Temperature	Egg condition
	Methot 1986	Maturity schedule	Temperature	Percent mature
Pacific hake	Bailey 1981	Larval transport	Upwelling, temperature	Distr. & recruit.
	Zwiefel and Lasker 1976	Incubation period, growth	Temperature	Egg condition
	Bailey and Francis 1985	Transport, growth, spawn, location	Upwelling, temperature	Recruitment
	Hollowed and Bailey 1989	Transport, growth, prey conc.	Upwelling, spg. transition	Recruitment
Pacific herring	Pearcy 1983	Prey concentration	Storms, freshets, ENSO	Recruitment
	Alderice & Hourston 1985	Embryonic respir., salinity tolerance	Temperature, salinity	Egg & larval cond.
	Stocker et. al. 1985	Physiology, prey concentration	Temperature, river discharge	Recruitment
	Schweigert & Noakes 1991	Larval transport	Ekman transport, upwelling	Recruitment
	Tanasichuk & Ware 1987	Change in spawning potential	Temperature	Fecundity
	Reilly 1988	Growth	ENSO	Size
	Ware 1992	Growth, food supply, predation	Upwelling, temperature	Catch, Survival rate
Pacific mackerel	Sinclair et. al. 1985	Larval transport	ENSO, temperature	Recruitment
	Parrish and MacCall 1978	Prey conc., predation, distribution	Temperature, upwelling, wind stress	Spawning success
	Prager and MacCall 1993	Spawning success	Upwelling, sea level, temp., rainfall	Egg condition
Pacific sardine	Zwiefel and Lasker 1976	Change in duration of incubation	Temperature	Recruitment
	Bakun and Parrish 1980	Prey concentration	Upwelling, wind stress curl	Distribution
	Lluch-Belda et al. 1991	Spawning distribution, abundance	Upwelling, temperature	Recruitment
	Ware and Thompson 1991	Prey availability	Upwelling	Catch
Bluefin tuna	Mysak 1986	Migratory pathway	ENSO	Distribution

Table 8. Summary of potential physical influence on major invertebrate populations.

Species	Author	Proposed mechanism	Physical co-variate	Response variable
Dungeness crab	Johnson et al. 1986	Transport, settlement	Wind stress	Catch
	Wild 1980	Egg devel. & hatching success	Temperature	Catch, hatch succ.
	McConnaughey et al. 1992	Larval transport & Settlement	Geostrophic transport	Settlement & catch
	Hobbs et al. 1992	Larval transport	Ekman transport	Larval Dist.&abun.
Pandalid Shrimp	Love and Westphal 1981	None	Sun spots	Catch
	Wing et. al. (in press)	Alongshore transport	Wind, temperature, sea level	Settlement rate
Sea urchin	Hannah 1993	Transport to nursery grounds	Spring transition, upwelling, sea level, temperature	Recruitment
	Ebert and Russell 1988	Settlement success	Turbulence, upwelling, transport	Settlement
Common barnacle	Wing et al. (in press)	Larval transport	Wind, temperature, sea level	Settlement rate
	Gaines et al. 1985	Settlement success	Upwelling, transport	Recruitment
	Roughgarden et al. 1988	Settlement success	Upwelling, transport	Distribution
	Roughgarden et al. 1991	Settlement success	Upwelling, transport	Recruitment
	Farrell et al. 1991		Turbulence, upwelling, transport, fronts	Settlement

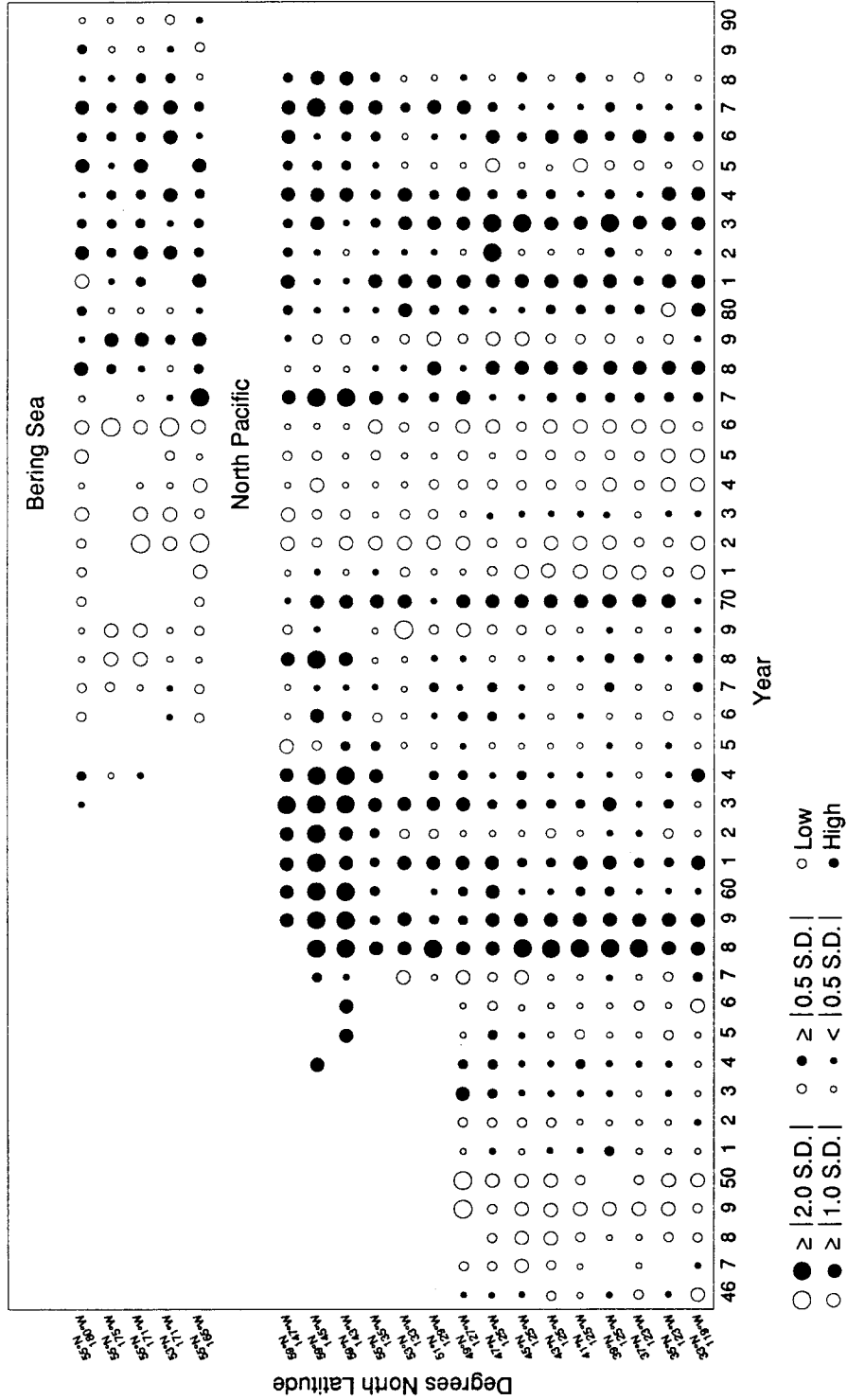


Figure 8. Eastern North Pacific winter (January-March) SST anomalies (from a 1970-81 base) in two-degree rectangles between 32° and 60°N, 1946-1990. Values in upper panel are from the Bering Sea. (From Wooster and Hollowed, in press).

responses are often non-linear and may involve a sequence of events rather than a single factor. Detailed studies of the processes underlying survival have been conducted for only a few fish/shellfish species (English sole, northern anchovy, salmon, Dungeness crab, sea urchins, shortbelly and widow rockfish (underway)), the common barnacle, the copepod *Calanus marshallae*, and a euphausiid (*Euphausia pacifica*) in the CCS. These studies have illustrated the importance of environmental processes that occur on the scale of days, weeks and seasons. Sources of short term variability on the scale of days to weeks include upwelling-relaxation events, changes in turbulent mixing of the upper ocean and variability in upwelling jets and California Current meanders and eddies. Variations on seasonal scales include changes in storm tracks and frequency, frequency and intensity of upwelling, turbulent mixing, poleward flow (Davidson Current), California Current position and strength, air-sea heat exchange and freshwater runoff.

This overview illustrates that while there appears to be coherence in time series of abundance on the long time and large space scale, there is also considerable variability on the short time and small space scales. Predicting the consequences of climate change ultimately rests on accounting for the processes that generate variation in population processes at all time and space scales.

The following section summarizes our current understanding of the major biophysical interactions in each region. This background may assist in the development of research initiatives designed to enhance our understanding of processes influencing production of our nations marine resources in the CCS.

Biophysical Interactions Involving Phytoplankton

Studies of the response of phytoplankton to physical forcing have been conducted in all four regions. In Regions I and II upwelling is the dominant control of primary production, supplies "new" nutrients to euphotic zone, leads to high primary production rates and high phytoplankton standing stocks (Small and Menzies 1981; Dugdale and Wilkerson 1989). These regions experience strong seasonal changes in rates of primary production due to seasonal shifts in the intensity of prevailing winds. The predominant equatorward wind stress in Regions I and II results in high rates of coastal upwelling during spring and summer and subsequent high levels of primary production. The positive wind curl leads to Ekman pumping and increased primary production in areas of surface divergence (Chelton et al. 1982; Strub et al. 1991), and an offshore maximum in zooplankton biomass (Chelton et al. 1982). Variations in the wind field are believed to play a major role in determining the distribution of phytoplankton and zooplankton (Abbott and Barksdale 1991).

There appears to be a close link between mesoscale features (eddies, jets) and the distribution of marine organisms in Region II. Satellite imagery suggests high concentrations of chlorophyll are associated with jets, eddies and other mesoscale features that occur as a result of coastal upwelling and the advection of this water (Flament et al. 1985). Chavez et al. (1991) found that high-nutrient and phytoplankton regions occur south and inshore of the Pt. Arena upwelling jet. Two distinct phytoplankton communities (coastal diatom and oceanic single-cell) are found in Region II and occur as separate populations on either side of upwelling fronts or divided by jets (Chavez et al. 1991).

In Region III, dense dinoflagellate blooms, often with very restricted vertical and horizontal distributions, are common features of the Southern California Bight during the summer (reviewed in Beers, 1986). Many of these dinoflagellates are important prey for larval anchovies (e.g. Lasker et al., 1970). Lasker (1981) noted differences in the abundance and nutritional content of dinoflagellates and diatoms in Region III as related to the food requirements of first feeding northern anchovy. Lasker's work demonstrated the importance of identifying not only the amount of production, but the type of production that occurs in a given year.

Biophysical Interactions Involving Zooplankton

Large scale circulation may influence CCS species through its influence on zooplankton production. The biomass and abundance of zooplankton has a distinct seasonal cycle, with a two- to five-fold difference between winter and summer. Seasonality is most pronounced in inshore waters, less so offshore. Cycles are similar from Oregon to Baja California, Mexico, with high abundance and biomass in spring-summer, and low in autumn-winter (Brinton 1976; Peterson and Miller 1977; Chelton et al. 1982; McGowan 1989). These patterns are thought to be related to the monsoonal pattern of coastal upwelling (off Oregon) and to seasonal variations in southward transport of the California Current (central to Baja California). Species that depend on zooplankton for prey may have adapted to the timing of seasonal changes (Cushing's (1972; 1990) match-mismatch hypothesis). If the timing of key seasonal changes is altered these may influence subsequent survival of organisms at higher trophic levels.

Within a season, several studies indicate climate change could influence zooplankton by influencing the location and persistence of mesoscale features such as semipermanent eddies, or upwelling jets. In Region I, consistent maintenance of some copepod species within a nearshore band has been explained on the basis of two-celled upwelling (Peterson, et al. 1979) and intermittent upwelling (Wroblewski 1980).

Zooplankton in Region II appear to be influenced by mesoscale features. Smith and Lane (1991) hypothesize that upwelling jets or eddies may transport the copepod, *Eucalanus californicus*, to the surface and onshore where egg laying occurs. Mackas et al. (1991) summarized the distribution of zooplankton near a jet in Region II. This study showed zooplankton species composition can change dramatically in response to fronts, resulting in distinct coastal and oceanic zooplankton communities. More recently, Laurs, Lynn and Peterson (unpublished) conducted a CTD, chlorophyll and zooplankton survey of a portion of the California Current jet and two associated eddies (34°-37°N, 123°-126°W, several hundred kilometers off Monterey and Point Sur) in July 1991. The Mackas survey and the Laurs et al. survey demonstrated that the California Current was enriched in zooplankton hundreds of kilometers seaward of the coast, in contrast to Washington and Oregon where zooplankton biomass is far higher on the shelf than over the slope. The zone of enrichment is separated from the warm offshore water by the meandering California Current "jet", a narrow (50 km wide) zone of low salinity water (32.7-32.9 ppt) that winds its way southward from the Oregon shelf to as far as southern California.

Numerous studies have been conducted on biophysical interactions of zooplankton in Region III. The distributions of many zooplankton taxa in Region III are influenced by a recurrent, deep offshore eddy southwest of Point Conception. The distributions of euphausiids, both those species with cool water, more northerly affinities and those with warm, more southerly affinities have been shown to be markedly affected by this offshore eddy (Haury et al. 1986), as have several other zooplankton species (Haury 1984).

Spatial variations in primary production and microplankton food influence different taxa in different ways. For example, in Region III, Checkley (1980) found that the copepod *Paracalanus parvus* became increasingly more food limited with distance from shore (to 50 km), while *Calanus pacificus* and *Rhincalanus nasutus* were found to have higher lipid contents and presumably better nutritional conditions in offshore waters of the CCS (Hakanson 1984). On smaller spatial scales, multi-species patches of copepods occur (Star and Mullin 1979), suggesting some common patterns of response to patch-generating processes.

Biophysical Interactions Involving Benthic Invertebrates

Research on the influence of water column physical processes on benthic invertebrate recruitment has been conducted in Region II. These studies suggest that recruitment in some benthic invertebrates is influenced by mesoscale transport processes. Roughgarden et al. (1988) noted that both the landward edge of the distribution of larvae of a pelagic barnacle and the seaward edge of the distribution of larvae of a coastal barnacle moved further from shore during upwelling. From observations near Monterey that coastal barnacles settled during relaxation events (Farrell, et al. 1991), Roughgarden, et al. (1991) postulated that larvae were entrained in the upwelling front and settled only when it moved closer to shore during relaxation in upwelling. Based on settlement data, Wing et al. (in press) showed that crab larvae are transported northward during upwelling relaxation events. Sea urchin settlement in northern California is episodic on both annual and intra-annual scales (Pearse and Hines 1987, Wing, et al. in press; Ebert et al., in press; CDF&G). Shifts in the frequency and intensity of short term storm events may be important to plankton. Recruitment of meroplanktonic larvae to the intertidal zone may also be influenced by internal tidal bores (Pineda 1991).

Biophysical Interactions Involving Marine Fish and Shellfish

Many studies of biophysical interactions involving marine fish and shellfish populations have been conducted in the CCS (Tables 7-8). Most of these studies demonstrated significant relationships between key biological processes and variations in temperature, upwelling and ENSO. These physical factors relate to large-scale circulation processes, the type of process that would be strongly influenced by large scale climate change (see Section IV).

Earlier (Section IV) we developed hypothetical climate change scenarios based on our current understanding of the processes linking climate and oceanography. Sixteen key physical changes were identified (Table 1). In this section we extend our hypotheses to include potential direct impacts of these changes to major fish and shellfish communities. This exercise is not intended to suggest that we are certain of the biological responses. The importance of the exercise is to identify the most important biophysical interactions and to point out areas where we lack knowledge about specific biological responses to physical changes.

Based on the background information found in Tables 7-8 and the predicted influence of climate change (Table 1) we identified the expected biophysical responses of marine fish and shellfish (Tables 9-11). An important outcome of this exercise was that it revealed areas where the expected biological responses were unknown. Very few studies have been conducted to identify the impact of changes in turbulent mixing (variable 9), transport in eddies and meanders (variable 10), changes in the depth of the thermocline (variable 13), or changes in the intensity or frequency of storms (variables 14 and 15).

Many species exhibited mixed responses to the climate change scenario. The most common case of mixed responses was the expected biological response to upwelling and temperature. This mixed response may be a product of our hypothesized physical scenario, where both upwelling-favorable winds (based on the Bakun hypothesis) and temperatures increase (based on general warming in GCMs). Increased upwelling may still produce cooler temperatures at the coast than farther offshore, but the mean temperature will be everywhere warmer than at present. If the hypothesized increase in stratification is strong enough or if the thermocline is deeper, the upwelled water may come from above the thermocline and nutricline and decrease both the cooling and fertilizing effect of upwelling, as in the warm phase of ENSO events off South America. Since most of the biophysical studies were conducted under present ocean conditions, an inverse correlation between upwelling and temperature is built into our present thinking. The presence of mixed responses to upwelling and surface temperatures illustrates the need for an

understanding of the process underlying the biological responses, particularly when the relationship between physical variables is expected to change. Use of comparative studies between latitudinal regions, between several EBCs, and measurements during unusual periods (such as warm ENSO events) will help broaden our experience and understanding.

The predicted response of marine fish and shellfish to our hypothetical climate change scenario is consistent with the ideas of Bailey and Incze (1985) who expected that species at the northern (southern) end of their range would increase (decrease) in response to El Niño like ocean conditions. The majority of the species that spawn in Region III showed positive responses to our global warming scenario (Table 11). The notable exception to this trend is the northern anchovy stock that is expected to decline (Table 11). Predicting the response of species that spawn in Region I is more difficult because of the large number of unknown responses (Table 9-10). However, the tables suggest that coho and chinook salmon, Pacific herring and dungeness crab stocks will all decline.

The importance of developing an understanding of processes underlying production of marine fish and shellfish has been recognized and process oriented research has been initiated for a few key species. In Region I, process oriented research has focused on larval transport mechanisms. In Region I, direct observations of spatial distribution of some planktonic organisms, and the temporal course of settlement give some indication of potential transport mechanisms. In observations of the cross-shore distribution off the Oregon coast, pelagic larvae (primarily fish) could be separated into 3 zones: coastal (<30 km), transitional (approximately 30 km), and offshore (> 30 km) (Richardson and Percy 1977, Richardson, et al. 1980). These were thought to be due to the distance from shore of spawning locations and the fact that currents were primarily alongshore. Some crabs and fish which migrate into the neuston were exceptions, being spawned nearshore but appearing offshore. During the 1982-83 ENSO, most of the ichthyoplankton found nearshore were "offshore" species (Brodeur et al. 1985). Hobbs et al. (1992) showed that the cross shelf distribution of Dungeness crab megalopae over the California to Washington coast matched that expected on the basis of a wind driven transport mechanism.

In Region II strong offshore flows (jets) may lead to short nearshore residence times. Species that rely on advection to return to nearshore locales may not survive in this environment. Eggs and larvae will be carried offshore in regions where the coastal jet first separates from the coast (flowing from shelf to deep ocean) or meanders back onto or near the shelf and then offshore again. At present, species that successfully spawn in Region II brood their eggs and larvae or extrude live larvae (e.g., rockfishes), or use protected embayments as spawning and nursery grounds (e.g., Pacific herring) to reduce the probability of offshore transport of pelagic larval stages (Parrish et al. 1981). Wing et al. (in press) examined event scale processes and found that crab larvae (primarily *Cancer* sp.) settled reliably in response to upwelling relaxation. Concentration of larvae in upwelling shadows south of promontories, then subsequent northward transport may provide a retention mechanism in the face of strong southward currents during upwelling. Offshore transport also may affect larvae by the removal of their prey.

Region III is the main spawning ground for the major pelagic species of the CCS (Pacific sardine, northern anchovy, Pacific hake, Jack mackerel and Pacific mackerel). While process oriented studies have been conducted on many species in Region III, the most complete study has been conducted on the northern anchovy. NOAA's SWFC conducted process oriented research on the northern anchovy for the last twenty five years. These studies include analysis of the spatial distribution of spawning (MacCall 1984), temperature effects on adult maturation (Fiedler et al. 1986), estimates of the rates of egg production (Stauffer and Picquelle 1981), larval retention through transport or eddies (Power 1986, Hewitt 1981, Fiedler 1986), egg dispersal and incubation rates (Smith and Hewitt 1985, Zwiefel and Lasker 1981), larval condition (O'Connell 1980, Theilacker 1986, Theilacker and Watanabe 1989), larval daily growth and mortality rates (Methot 1983, Butler 1989, Lo 1986), predator distributions (Hunter and Kimbrell 1980, Webb

Table 9. Expected responses of marine fish and shellfish from Region I to hypothetical changes in 16 physical processes of the CCS. + = Favorable response; - = Unfavorable response; NC = No Change; ± = Dome shaped response

Species	Physical Process Number from Table 1*															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Dover sole	U	U	NC	NC	+	U	U	NC	U	U	NC	NC	U	NC	NC	U
Egg	U	U	+	-	+	U	U	NC	U	U	-	-	U	NC	NC	U
Larval hatch	U	U	NC	NC	NC	U	U	NC	U	U	NC	NC	U	NC	NC	U
Larval Drift	U	U	+	+	NC	U	U	NC	U	U	NC	NC	U	NC	NC	U
Settlement	U	U	+	+	NC	U	U	NC	U	U	NC	NC	U	+	+	U
English sole																
Egg	U	U	U	NC	NC	U	U	NC	U	U	+	+	U	U	U	U
Larval hatch	U	U	U	NC	NC	U	U	NC	U	U	NC	NC	U	U	U	U
Pelagic stage	U	U	U	NC	NC	U	U	NC	U	U	NC	NC	U	+	U	U
Settlement	U	U	U	+	-	U	U	NC	U	U	+	+	U	+	+	U
Flathead sole	U	U	U	U	-	U	U	U	U	U	U	U	U	U	U	U
Petrale sole	U	U	U	U	+	U	U	U	U	U	U	U	U	-	U	U
Rock sole	U	U	U	U	±	U	U	U	-	U	U	U	U	U	U	U
Pacific cod	U	U	U	U	-	U	U	-	U	U	U	U	U	U	U	U
Sablefish	+	+	U	U	+	U	U	U	U	U	U	U	U	U	U	U
Widow rockfish	+	+	U	U	+	U	+	U	U	U	-	-	U	U	U	U
Chilipepper rockfish	-	-	U	U	-	U	-	U	U	U	+	+	U	U	U	U

(*) Physical Processes: 1—Intensity of west wind drift; 2—location of west wind drift; 3—Freshwater input; 4—Coastal wind stress; 5—Mean sea surface temperature; 6—Stratification; 7—Mean transport of CCS; 8—Alongshore transport in upwelling jets; 9—Turbulent mixing; 10—Transport in eddies and meanders; 11—Offshore transport; 12—Vertical transport (upwelling); 13—Mixed layer depth; 14—Winter storm frequency; 15—Winter storm intensity; 16—Timing of spring transition.

Table 10. Expected responses of marine fish and shellfish from Region I to hypothetical changes in 16 physical processes of the CCS. + = Favorable response; - = Unfavorable response; NC = No Change; ± = Dome shaped response

Species	Physical Process Number from Table 1*															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Coho salmon	-	-	+	U	U	U	-	U	U	U	+	+	U	-	U	U
Chinook salmon	-	-	+	U	U	U	-	U	U	U	+	+	U	-	U	U
Pacific herring	U	U	+	U	+	U	U	U	+	U	U	U	U	U	U	U
Egg	U	U	U	U	-	U	U	U	U	U	-	-	U	U	U	U
Larvae	U	U	U	U	-	U	U	U	U	U	-	-	U	U	U	U
Juvenile	U	U	U	U	-	U	U	U	U	U	-	-	U	U	U	U
Dungeness crab	U	U	-	±	±	U	+	-	-	U	-	-	U	+	+	U
Pandalid shrimp	U	U	-	+	-	U	-	+	U	+	+	+	U	+	+	+

(*) Physical Processes: 1—Intensity of west wind drift; 2—location of west wind drift; 3—Freshwater input; 4—Coastal wind stress; 5—Mean sea surface temperature; 6—Stratification; 7—Mean transport of CCS; 8—Alongshore transport in upwelling jets; 9—Turbulent mixing; 10—Transport in eddies and meanders; 11—Offshore transport; 12—Vertical transport (upwelling); 13—Mixed layer depth; 14—Winter storm frequency; 15—Winter storm intensity; 16—Timing of spring transition.

Table 11. Expected responses of marine fish from Region III to hypothetical changes in 16 physical processes of the CCS. + = Favorable response; - = Unfavorable response; NC = No Change; ± = Dome shaped response

Species	Physical Process Number from Table 1*															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Northern Anchovy	-	-	U	U	-	+	-	+	-	U	-	-	-	U	U	U
Pacific sardine	+	+	U	-	+	+	-	-	-	U	-	-	-	U	U	+
Pacific hake	+	+	U	+	+	U	+	+	U	U	-	-	U	U	U	+
Jack mackerel	-	+	U	-	+	U	+	+	U	U	-	+	+	U	U	U
Pacific mackerel	+	+	U	-	+	+	+	-	U	U	-	+	-	U	U	+
Bonito	+	+	U	U	+	U	+	+	U	U	U	+	U	U	U	U
Skipjack tuna	+	+	U	U	+	U	+	+	U	U	U	U	U	U	U	U
Yellowfin tuna	+	+	U	U	+	U	+	+	U	U	U	U	U	U	U	U
Bluefin tuna	+	+	U	U	+	U	+	+	U	U	U	U	U	U	U	U

(*) Physical Processes: 1—Intensity of west wind drift; 2—location of west wind drift; 3—Freshwater input; 4—Coastal wind stress; 5—Mean sea surface temperature; 6—Stratification; 7—Mean transport of CCS; 8—Alongshore transport in upwelling jets; 9—Turbulent mixing; 10—Transport in eddies and meanders; 11—Offshore transport; 12—Vertical transport (upwelling); 13—Mixed layer depth; 14—Winter storm frequency; 15—Winter storm intensity; 16—Timing of spring transition.

1981, Alvarino 1980), the influence of turbulence on prey type and availability (Scura and Jerde 1977, Lasker 1975, 1978, Wroblewski 1984) and regional differences in survival (Owen et al. 1989). These studies demonstrate that factors determining year class strength of pelagic spawning marine fish are complicated and can involve several different physical events (or processes).

Biophysical Interactions Involving Bird Populations

Marine birds have proved to be sensitive to perturbations in marine climate, food-web structure and prey availability (e.g. Crawford and Shelton 1978, Glantz and Thompson 1982, Barber and Chavez 1986, Ainley and Boekelheide 1990, Ribic et al. 1990, Cairns 1992). Seabirds, in fact, have proven useful as indicator species of oceanographic conditions owing to their great mobility (quick response), large numbers and easy visibility (e.g. Schreiber and Schreiber 1989) and sensitivity to variations in food supply.

The most extensive research linking oceanographic processes to production and survival of marine birds has been conducted in Region II. In this region a unique 22-year time series of data has been collected on the reproductive phenology, demography, diet and at-sea occurrence patterns of several species including the Cassin's Auklet, a planktivorous seabird. This time series shows the auklet to be a sensitive indicator of the effects of coastal upwelling on zooplankton abundance and species composition, especially the euphausiids, *Thysanoessa spinifera* (a coastal species) and *Euphausia pacifica* (an oceanic species). The auklets near the Farallon Islands breed successfully in years when *T. spinifera* is available in great quantity near the surface and poorly or not at all when the euphausiid is not available, as during ENSO warming events (Tables 12 and 13; Ainley and Boekelheide 1990). Egg laying closely follows the "spring transition" to upwelling conditions (Huyer et al. 1979), which often leads rapidly to the offshore spread of cold, upwelled water and surface swarms of *T. spinifera*. During late summer, when *T. spinifera* is no longer available as prey (as demonstrated by its disappearance and the appearance of *Euphausia pacifica* in the auklet diet), breeding ceases and remaining chicks are abandoned.

The importance of the auklet lies both in their use as zooplankton samplers (through diet analysis) and as analogs for other top trophic level species. They are especially useful because their favored prey, *T. spinifera*, is also important in the diet of other species including targets of major fisheries (hake, rockfish and salmon), other sea birds and baleen whales. For instance, analysis of stomach contents of salmon show that they, like the auklet, switch in spring from their winter diet of cephalopods and other prey to gorge on *T. spinifera* in the outer waters of Region II (Adams et al., ms).

Summary of Biophysical Interactions—Hypothesis Formulation

The wide variations of physical and biological conditions observed in the CCS facilitate the formulation and testing of hypotheses. Existing biophysical hypotheses for fish and shellfish populations include the 'match-mismatch' (Cushing 1972), 'stable ocean' (Lasker 1975, 1978), 'basin' (MacCall 1984), and 'habitat retention' (Isles and Sinclair 1982, Sinclair 1988) models. The 'match-mismatch' hypothesis involves the physical and biological coupling at the seasonal or shorter scale of production or bloom phenomena and the reproductive cycle of marine species. The 'stable ocean' hypothesis suggests that periods of low physical mixing which initiates and maintains vertical stability necessary for growth and aggregation of phytoplankton are necessary for organisms that rely on phytoplankton for food. The 'basin' hypothesis links population expansion at the periphery to population density at the core during the portion of the life cycle which is dominated by density-dependent phenomena. The 'habitat retention' model proposes that population structure of resource populations is determined by physical forcing which maintains the dispersive phase of the population in the appropriate range of sites which constitute

a population home base. Knowledge of the geographic and seasonal distribution of upwelling, transport, mixing, transitions, productivity and life cycles of key marine species is necessary to test these hypotheses.

Historical Variability in the CCS

The long series of observations for the CCS show that major qualitative changes in both physical and biological characteristics have occurred over the past 60 to 70 years. Abrupt changes in the physical background and ecosystem structure were first clearly recognized in 1958 with the occurrence of widespread "anomalous" conditions which could be quantified and compared to the previous ten years of CalCOFI survey data and with temperature and pressure data stretching back to the early decades of the twentieth century (Reid, 1960). These changes are now well understood as a regional manifestation of the Pacific-wide variability associated with the El Niño-Southern Oscillation phenomenon. The physical response of the CCS to the interannual climate variability of ocean-atmosphere coupling of ENSO has now been documented (e.g., from CalCOFI data).

We have been much slower to recognize the nature and significance of changes in EBCs which occur over longer time scales. This is not surprising since our understanding of a dynamical system is constrained by the dimensions of space and time encompassed by our observations. Instrumentation and fisheries time series records are not sufficiently long to permit a comprehensive description of the variability in the physical environment and the biological response at longer scales, at which very large and fundamental changes occur.

The Last 100 Years

With nearly 100 years of combined physical and biological observations, we are able to qualitatively patch together an outline of one major oscillation in the physical and biological structure of the pelagic ecosystem of the California Current. One of the long, continuous time series of measurements available is the SST from Scripps Pier in La Jolla (Figure 9, bottom curve) which begins in 1917. The patterns and trends seen in the Scripps Pier SST time series are reflected to varying extent at other sites along the west coast of North America, as well as in the large-scale Pacific and even global SST records (e.g., the blended SST anomalies for the Northern Hemisphere in Folland et al., 1990.)

The spatial coherence of correlations of winter temperature anomalies in the CCS to Scripps Pier SST (Fig. 10, Mooers et al. 1986) indicates that Scripps Pier SST is a useful proxy for temperature fluctuations over a large area of the CCS. The Scripps Pier temperature series shows three distinct periods: 1) a period (ending around 1945) of relatively warm temperatures; 2) a period (from 1945-1976) of generally cooler temperature, interrupted briefly by the warm temperatures of the 1957-1958 El Niño; and, 3) a warm period from 1977 to present. Transitions between these periods were abrupt, occurring within 1-2 years.

Although the Scripps (SIO) Pier SST time series reflects the general patterns of SST along the west coast, an examination of available multi-decadal time series (of many parameters, not just SST) along the west coast of North and South America shows that superimposed on the generally coherent patterns and trends of the basin-scale indices are substantial regional differences in wind forcing (Mendelssohn 1994), sea level (Schwing 1994b), SST and salinity (Schwing 1994a,b). Regional variability includes differences in the long-term rate of change, response to interannual differences (e.g. ENSO events), and changes in seasonal patterns. Figure 10 illustrates the decorrelation between SIO SST and U.S. west coast SST during summer. Within regions, whose spatial extent approximates the four regions defined earlier, these signals appear to be more coherent, suggesting that fundamental differences in the atmospheric and oceanic

Table 12. Mean annual dates for first-clutch eggs of Cassin's Auklet, 1970-90, at the Farallon Islands. Means are ranked earliest to latest; lines connect similar means (Student-Neuman-Keuls test, $p < 0.05$).

Date	3/24	3/28	3/30	3/31	4/4	4/5	4/7	4/8	4/9	4/12	4/16	4/18	4/19	4/24	5/29
Year	71	74	76	79	75	81	90	73	87	72	77	70	80	78	83
		88			85			82		84		86			
		89													

Table 13. Percent numerical contribution of euphausiids to auklet diets and auklet breeding productivity at the Farallon Islands, 1971-1990.

Category \ Year	1971*	1977	1979	1980	1981	1985	1986	1987	1988	1989	1990
Percent Euphausiids	22	99	66	46	82	92	95	96	97	98	94
Percent <i>T. spinifera</i>	major	85	68	6	55	22	27	43	37	37	22
Percent <i>E. pacifica</i>	—	15	32	75	40	70	62	53	60	61	58
Auklet chicks produced/pair	0.8	0.9	1.1	0.6	0.7	0.7	0.7	0.7	1.1	0.6	0.4
Anomaly of mean chick weights, percent	+5	+1	0	-3	+2	-3	-3	+10	-4	0	+5

* Data for 1971 from Manual (1974), who presented data on the proportion of euphausiids in the diet and stated that *T. spinifera* was the "major" euphausiid species. No data on diet for 1972-76 and 1982-84; see Ainley and Boekelheide (1990) for auklet productivity in those years.

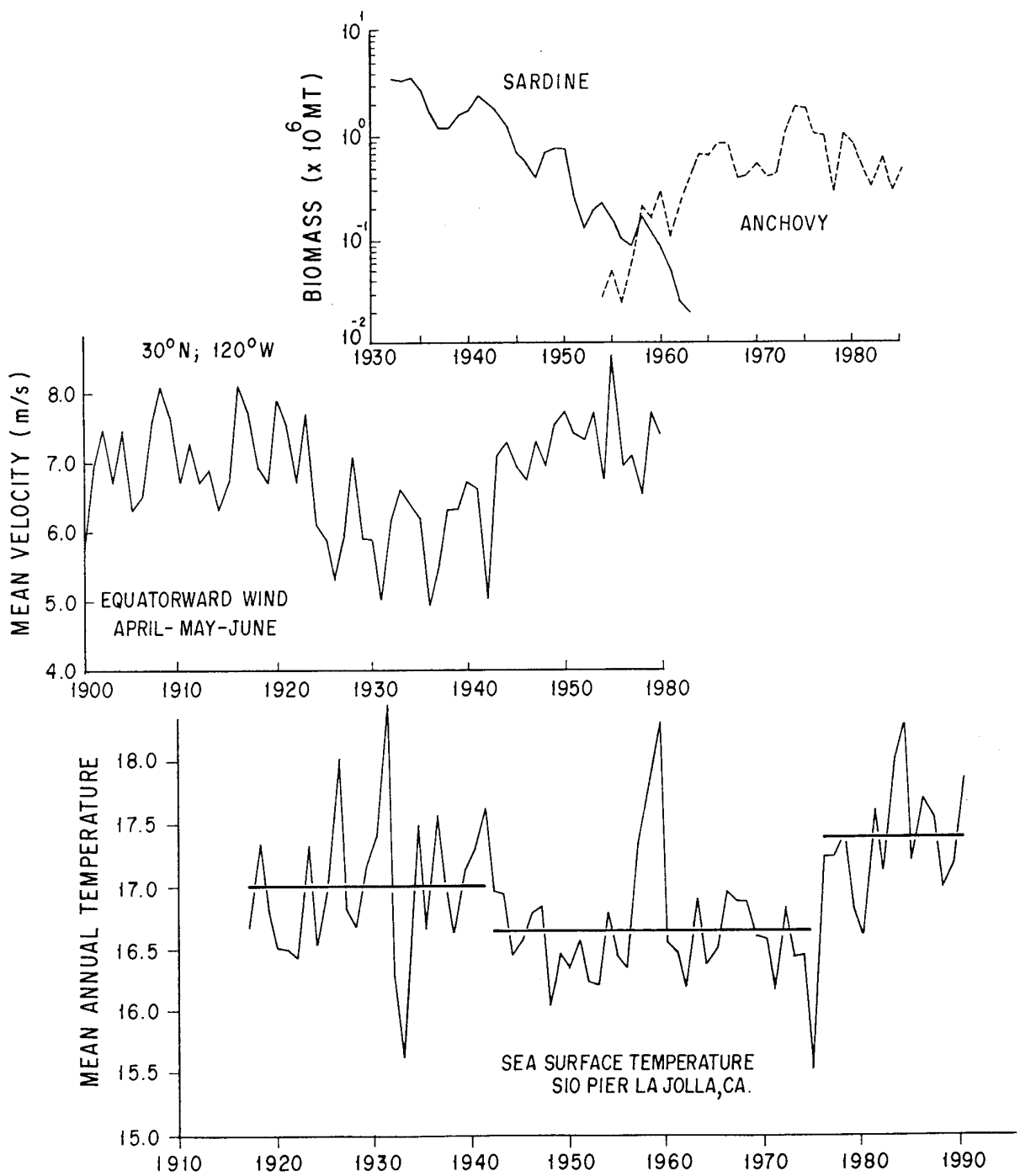


Figure 9. California Current sardine and anchovy biomass time series (from MacCall, 1986) aligned with time series of wind field (from Ware and Thomson, 1991) and the annual SST at the SIO pier.

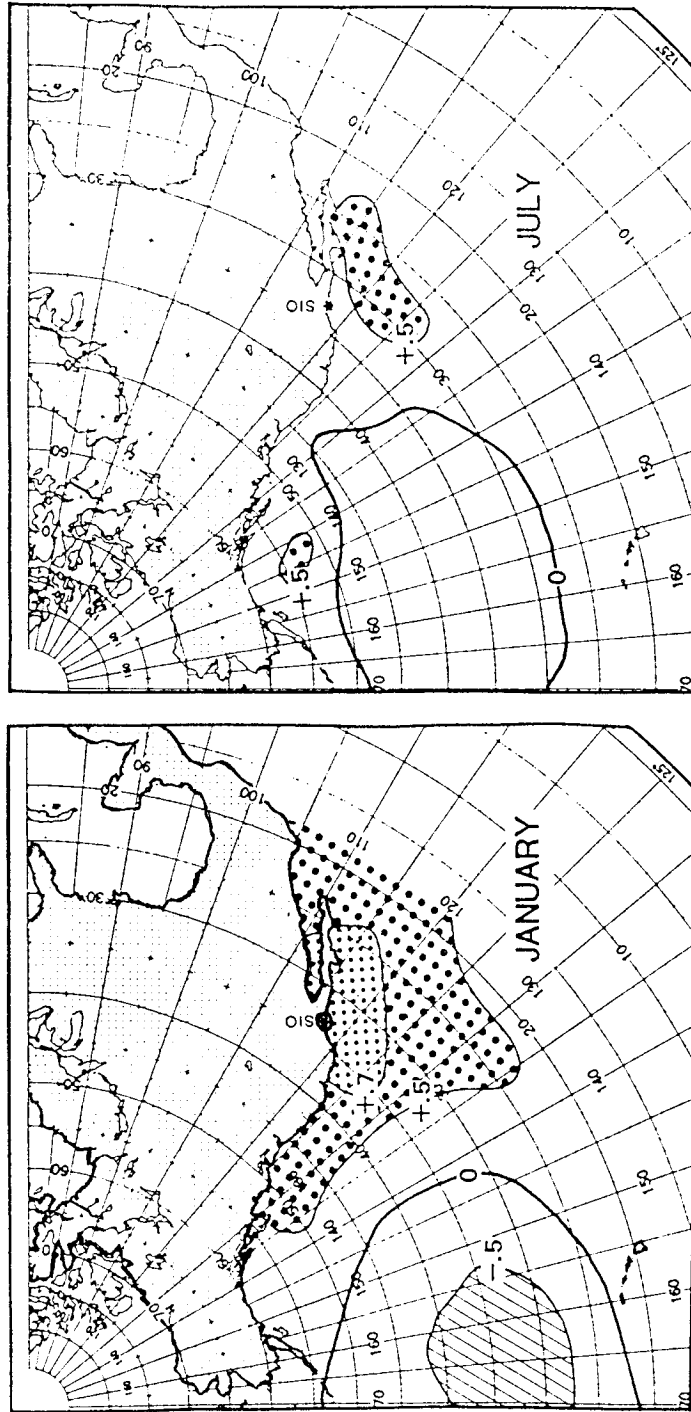


Figure 10. Correlation between Scripps Institution of Oceanography pier sea surface temperature (indicated by star and the initials SIO) versus North Pacific Ocean average 5° grid SSTs (ship observed) based on 1947-1985 data. A negative correlation greater than 0.5 is denoted by hatching; a positive correlation greater than 0.5 is denoted by dot shading. (From Mooers et al. 1986)

processes that dominate in each region may impact the environmental response to climate change on those space scales.

Plotted above the time series of Scripps Pier SST in Figure 9 is the equatorward component of the mean geostrophic wind during spring (April-June) at 30°N between 110° and 130°W (from Ware and Thomson (1991) and estimates of sardine and anchovy biomasses for the central region of the CCS. Wind speed and ocean temperature show a striking inverse relationship during the period when the time series overlap (1917-1960). Periods of cooler temperatures in the 1950s and 1960s are associated with higher wind speeds. Elevated temperatures from 1925 through 1945 occurred in a period of diminished northerly winds.

The time series of sardine and anchovy biomass estimates for the central region of the California Current (Figure 9, upper plot) indicates an intriguing coincidence between a major shift in species dominance in the schooling pelagic fish of the ecosystem and the transition from a period of lighter wind conditions and warmer SSTs to cooler SSTs with stronger northerly winds. The recovery of the sardine population (and decline of the anchovy population) beginning in the late 1970s or early 1980s (data not shown) also suggests a link to the ocean environment which is forced by regional climate change. Although the decline of the sardine population after the 1940s has long been thought to be a result of intensive fishing, some fisheries scientists are now suggesting that fishing may have exacerbated what would have been a natural and much less serious shrinking of the population. The heavy fishing mortality resulted in the near-complete collapse of the population, and may also be responsible for the sluggish recovery after 1977 (Jacobsen and MacCall, in press).

Physical and biological measurements from the CCS and the central North Pacific indicate that the interdecadal variability appears to be part of basin-wide processes of ocean-atmosphere coupling. Associated with the shift to warmer temperatures in 1977 and the subsequent sputtering recovery of the Pacific sardine in the CCS, is a notable decrease in zooplankton biomass in Region III of the CCS (Roemmich and McGowan, 1994). Concurrently, the ocean interior of the central North Pacific has cooled and a significant increase in deep phytoplankton biomass has been measured there between 1968 and 1985 (Venrick et al. 1987). At slightly longer time scales, MacCall and Praeger (1988) suggest that the large changes in fish populations sampled by CalCOFI ichthyoplankton surveys since 1951 reflect an ecological response to a shift between distinct physical regimes.

These multi-decadal changes in physical and biological conditions of the CCS may represent abrupt shifts between climate states or "regimes" in the ocean/atmosphere system (e.g. Trenberth, 1990). It is now believed that the ocean-atmosphere circulation changed dramatically after 1976 (Trenberth, 1990; Graham, 1994; Miller et al., 1994a, 1994b; Trenberth and Hurrell, 1994). This occurred by an eastward shift in the position of the Aleutian Low pressure system and intensification of the atmospheric low leading to (1) cooler SSTs in the interior North Pacific and (2) warming along the coast. Between 1945 and 1976 the Aleutian Low pressure system was further westward and weak compared to more recent times (Trenberth and Hurrell, 1994).

The Last 1500 Years

By the early 1960s the CalCOFI program had recognized the importance of climate-scale changes in the CCS and began to develop strategies to describe these longer-term changes in fish populations and other components of the pelagic ecosystem (CalCOFI Committee, 1965). This led to historical-retrospective studies focusing on the use of annually layered (varved), anaerobic sediments to examine past sizes (biomasses) of fish populations (from the abundance of scales in the sediments; Soutar and Isaacs 1969; Soutar and Isaacs 1974). Bottom regions having high deposition rates and poor ventilation (and thus are anoxic and experience no bioturbation) can have annually layered sediments suitable for dating and examining interannual

variability in ocean conditions. Although these conditions are not common, several such coastal sites have been identified on the U.S. west coast. One of these, the Santa Barbara Basin, lying near the center of the spawning habitat of the sardines and anchovies off southern California has provided the longest and best preserved record of sardine and anchovy abundance so far (Figure 11; Baumgartner et al. 1992).. The time series extends from AD 300 to 1970 and permits description of the fundamental time scales of variability in the population sizes of major coastal pelagic fishes. Using such data it is possible to begin to discriminate sources of population variability, including distinguishing between the effects of industrial fishing by man and natural fluctuations.

Spectral analyses of the sardine and anchovy population abundance estimates of Figure 11 indicate strong peaks at ca 60 year periods. During the ca. 1500 year long record there were 22 cycles of alternation in species (sardine vs. anchovy) dominance (Fig. 12). Average length of these cycles is ca. 65 years--similar to the length (55 years) of one ocean-atmosphere cycle observed in SST this century (from ca. 1922-1977; Fig. 9). The relationship between the two small pelagic species is consistent with the observation (Fig. 9) that sardines dominate during warm coastal ocean phases and diminished northerly winds while anchovies dominate during the opposite ocean-atmospheric phase (regime). Similar alternating dominance of sardines and anchovies (or anchovetas) have been observed in other boundary current systems during the twentieth century (Daan, 1980; Lluch-Belda et al. 1989).

From these observations it is reasonable to formulate a hypothesis that interdecadal fluctuations in ocean climate over the North Pacific of the kind modeled by Miller et al. (1994b) create changes in habitat which tend to alternately favor sardines or anchovies for intervals of roughly 30 years. The sardine-anchovy relationship in Figure 12 would thus imply that the process of reorganization of the ocean-atmosphere coupling has gone on for at least the past 1500 years with a characteristic period averaging around 65 years in length.

Global Eastern Boundary Currents

Parrish et al. (1983), review the four major global eastern boundary currents in terms of physical characteristics and factors influencing reproductive success in sardines and anchovies, species of which are present in all EBCs. The California, Peru-Chile, Canary and Benguela Current Systems feature similar environmental dynamics, characterized by narrow continental shelves, equatorward wind stress, coastal upwelling, meandering equatorward surface flows, subsurface poleward undercurrents and cool, highly productive coastal waters. Despite the fact that these are large systems, usually with more than one region of maximum upwelling, separated by regions of lower upwelling, often due to coastline variations (the Southern California Bight, the change in coastal orientation off southern Peru, the region between southern Portugal and Northwest Africa), Parrish et al. (1983) were able to make a number of statements which generalize EBC systems.

Collectively, EBC systems account for approximately 35% of the total marine fish catch (FAO Yearbook of Fishery Statistics, 1990). The dominant fisheries are listed in the table below, from Parrish, et al. (1983). The primary analogous stocks that are discussed in the literature are the clupeoids (sardines, anchovies, i.e., *Sardinops*, *Sardina* and *Engraulis*), although there are also similarities between the *Merluccius* (hake), *Trachurus* (jack mackerel), *Scomber* (mackerel) and *Sarda* (bonito). The last two groups are not as numerous. In contrast, there is little similarity between demersal fish species in eastern boundary currents, except for the *Merluccius*.

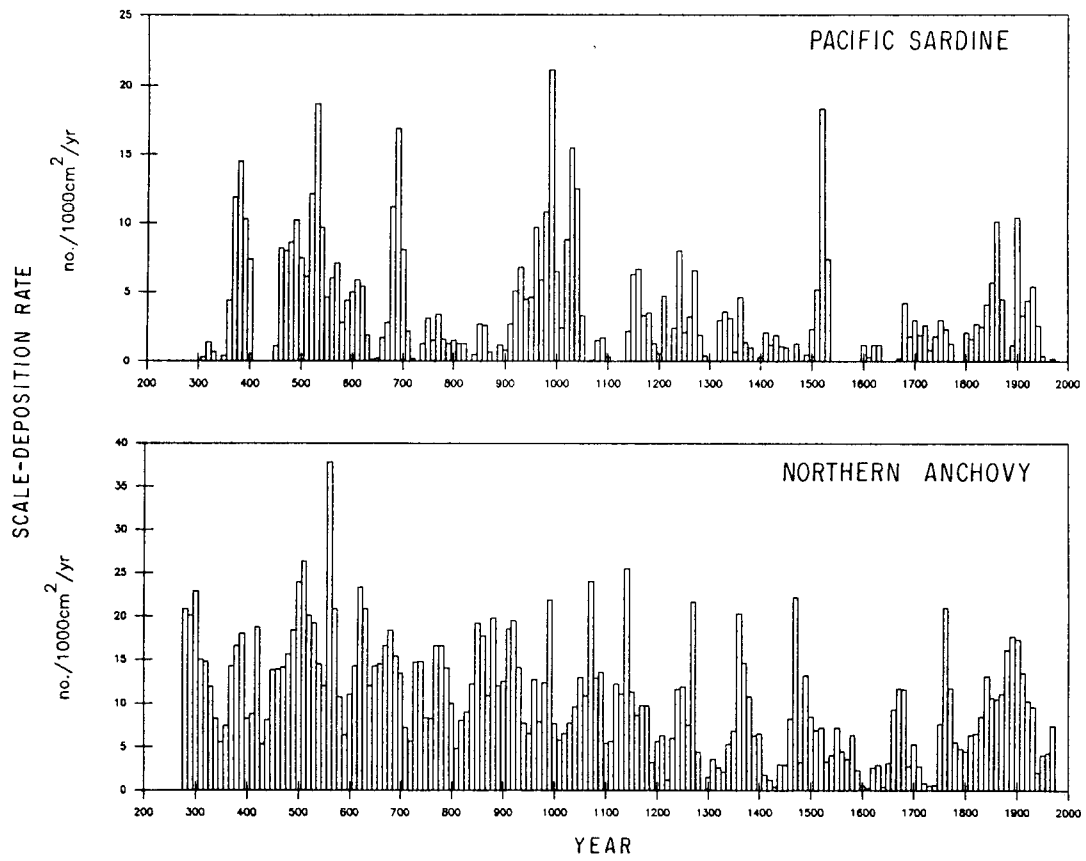


Figure 11. Time series of sardine and anchovy scale deposition rates. (from Baumgartner et al. 1992)

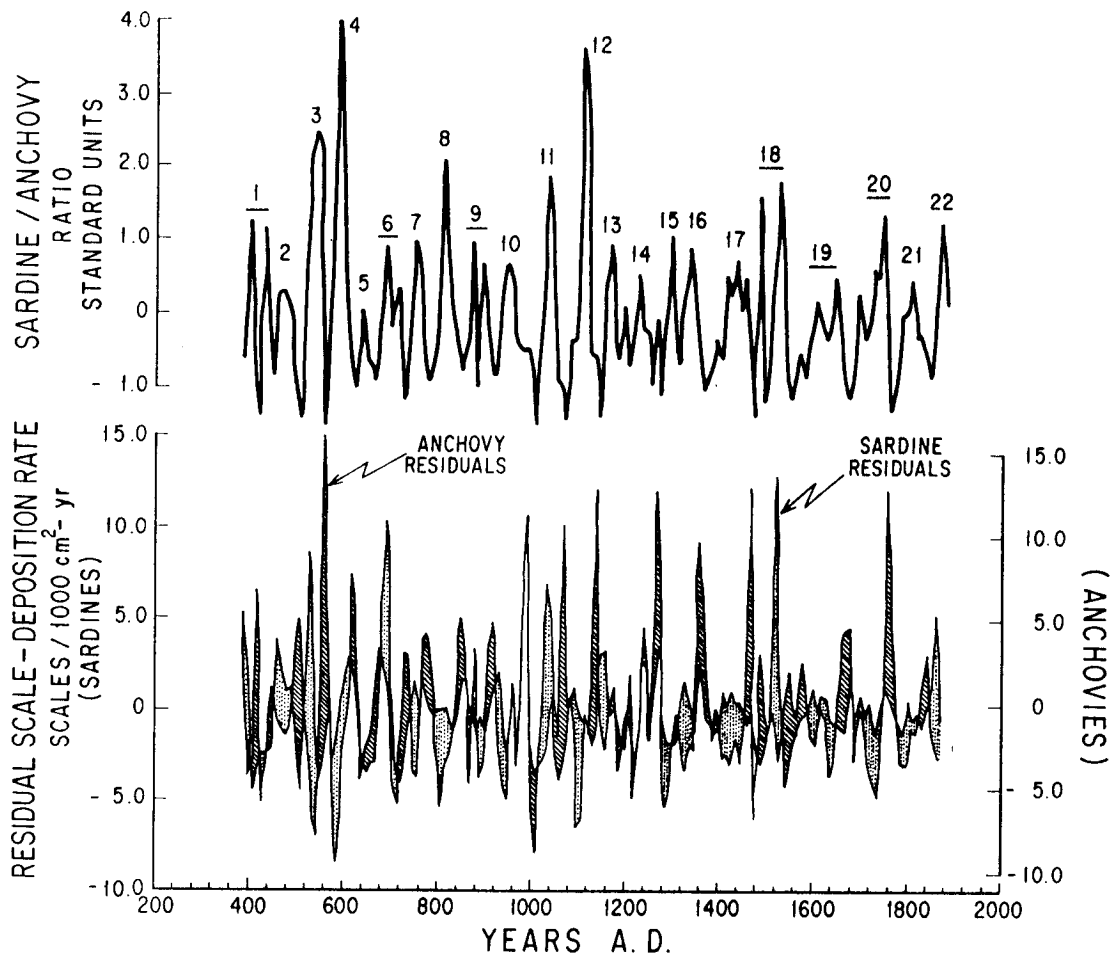


Figure 12. Comparison of the high-frequency components of the variability (periods <150 years of length) in the sardine and anchovy scale-deposition rates (SDRs) of the original series of Figure 11. These high frequency residuals were calculated by subtracting the deviations from a smoothed curve for which periods less than 150 years have been removed by low pass filtering. The lower plot shows the superposition of the two time series of the high-frequency residuals of the sardines and anchovies. This combined plot exhibits a general pattern of alternation between sardines and anchovy dominance by dots (sardine SDR > anchovy SDR) and diagonal hatching (anchovy SDR > sardine SDR). The upper plot is a time series formed by the ratios of the sardine residuals to the anchovy residuals. The positive peaks are formed by periods in which sardine SDRs are greater than the anchovy SDRs. The minimums in the upper curve are intervals with anchovy SDRs > sardine SDRs. Note that there are 22 cycles of alternation between the two species. Each cycle greater than 40 years length is numbered in sequence. Bars under some numbers indicate that the cycle includes more than a single peak. (From Baumgartner, Soutar and Ferreira, in preparation).

Dominant anchovy (*Engraulis*), pilchard (*Sardinops/Sardina*), horse mackerel (*Trachurus*), hake (*Merluccius*), mackerel (*Scomber*) and bonito (*Sarda*) in the four EBC ecosystems (after Bakun and Parrish, 1980)

<u>CALIFORNIA CURRENT</u>	<u>PERU CURRENT</u>	<u>CANARY CURRENT</u>	<u>BENGUELA CURRENT</u>
<i>Engraulis mordax</i>	<i>E. ringens</i>	<i>E. encrasicolus</i>	<i>E. capensis</i>
<i>Sardinops sagax</i>	<i>Sardinops sagax</i>	<i>Sardina pilchardus</i>	<i>Sardinops ocellatus</i>
<i>Trachurus symmetricus</i>	<i>T. symmetricus</i>	<i>T. trachurus</i>	<i>T. trachurus</i>
<i>Merluccius productus</i>	<i>M. gayi</i>	<i>M. merluccius</i>	<i>M. capensis</i>
<i>Scomber japonicus</i>	<i>S. japonicus</i>	<i>S. japonicus</i>	<i>S. japonicus</i>
<i>Sarda chiliensis</i>	<i>S. chiliensis</i>	<i>S. sarda</i>	<i>S. sarda</i>

Similar to the fish assemblage, the copepod assemblage of eastern boundary current ecosystems is often dominated by two or three small and one or two large calanoid species. Small species are: *Pseudocalanus mimus*, *Acartia hudsonica* and *A. longiremis* (Oregon); *Paracalanus parvus* and *A. tonsa* (southern California); *P. parvus* and *A. tonsa* Peru/Chile; *P. parvus*, *P. crassirostris* and *Ctenocalanus vanus* (Benguela). The large calanoid in each system is a *Calanus* species: *Calanus marshallae* (Oregon), *C. pacificus* (California), *C. chilensis* (Peru, Chile), and *C. australis* (Benguela, Agulhas Bank). Conspicuous in all systems is the cyclopoid, *Oithona similis* s.l., and often an *Oncaea* spp.. In addition, an intermediately sized "omnivorous" genus, *Centropages*, is abundant off Oregon (*C. abdominalis*), Peru, Chile and South Africa (*C. brachiatus*), Northwest Africa (*C. chierchiaie*), but is missing off California. Sometimes in the CCS, other large calanoids (e.g., *Metridia* or *Eucalanus* spp.) can be locally abundant. The South American and African systems each contain an additional dominant genus, *Calanoides*—*C. patagoniensis* (Chile) and *C. carinatus* (Northwest Africa, West Africa, Benguela, Brazil?, Arabian Sea).

Parrish et al. (1981) argue that the fisheries of the CCS are not limited by the system's carrying capacity, but by environmental fluctuations. Lluch-Belda et al. (1989) have shown that the long-term temporal variability of the sardine catch during the 20th century is similar for the California and Peru-Chile systems, as well as for the Japanese system, with some similarity to the mean ocean temperature, as well. The Pacific sardine catches do not covary with the North Atlantic sardine catch, however. Increases in the yield of Chilean sardines in the early 1980s are attributed to increases in primary and secondary productivity associated with water mass shifts in the Humboldt Current (Sherman, 1992). As described above, a decline in Pacific sardines in the California Current and a subsequent increase in anchovy abundance are believed due to natural environmental variability rather than species competition. Likewise, abundance shifts in horse mackerel and sardines in the Iberian Coastal Ecosystem, and horse mackerel and pilchard in the Benguela Ecosystem, are attributed to natural environmental fluctuations associated with changes in horizontal circulation and upwelling. Thus, for the most part, the abundances of major fish populations in EBCs are determined by large-scale environmental factors, not density-dependent factors.

Eastern boundary currents are forced by both large-scale 'local' wind systems and by basin-scale circulation patterns. Where the forcing is dominated by the atmospheric surface forcing, these ecosystems may reflect climate changes that develop in the atmosphere (e.g., wind forcing, coastal cloud and fog formation, air-sea heat exchange) long before direct changes occur in the ocean (e.g., large-scale changes in stratification due to global warming (Bernal 1993), changes in basin-scale circulation, etc.). Although the CCS appears to be more strongly driven by the winds over it, this may not be true of all subregions of all EBCs. Thomas et al. (1994) use satellite color imagery to compare surface pigment concentrations in the Peru-Chile Current System and the California Current System. The strong upwelling region off Peru shows high values when upwelling winds are strong (winter), as expected, while off Chile at 40°S, there are low surface pigments in summer when winds are most upwelling favorable (but weaker than off North America), and higher values off Chile in winter. In the Benguela System, high pigment values are more closely in phase with the winds, as they are off Northwest Africa. They are out of phase, however, off Portugal, where winds are upwelling favorable, but again are weak in summer, like off Chile.

In the Peru-Chile Current System, there is a poleward countercurrent (often called the undercurrent, though it often extends to the surface) off southern Peru and northern Chile (Fonseca, 1989; Huyer et al. 1991), that lies offshore of the narrow, equatorward current next to the coast. Fonseca (1989) comments that this countercurrent is often the dominant feature off northern Chile. Off Peru at 10°S, Huyer finds only a very shallow equatorward current, inshore of both an undercurrent and a countercurrent. Lukas (1986) has shown both the undercurrent and countercurrent off Peru at 6°S to be connected to the equatorial undercurrent. Thus, the region off Chile may be more strongly forced by basin scale currents than by local winds, which are weak (compared to Peru and North America). Since climatic changes such as global warming or the natural oscillations already discussed may change both basin-scale currents and local winds, comparisons between present global EBCs may be an efficient way to examine the responses of EBC ecosystems to different levels of these two types of forcing.

Bakun and Parrish (1982), Parrish et al. (1983) and Hutchings (1992) make the case for comparative studies in EBCs from an ecosystem standpoint. Comparative studies may reveal the environmental factors controlling reproductive success of these fisheries and the potential impact of climate change. They consider the dominant physical factors for reproductive success in sardines and anchovies to be transport, turbulence and temperature (seasonal or upwelling). There are also biological factors, such as food, predation and population density that may be important for some species, but are argued, above, to be less important for sardines and anchovies. This allows Parrish et al. (1983) to use a comparative analysis approach that seeks to differentiate between these few factors, by looking at common patterns of variability in eastern boundary currents. The use of more than one system increases the significance of trends and patterns over the "noise" level of individual ecosystems, giving more robust results (more degrees of freedom). An example is their attempt to differentiate between turbulence and offshore wind-driven Ekman transport effects on fish populations. In most cases, winds are equatorward in these systems, so high winds lead to both high offshore transport and increased turbulence, making it difficult to distinguish their effects. They are able to find instances, however, where the sardines choose to spawn in regions of increased turbulence—in those cases the transport is directed onshore, suggesting that turbulence is less detrimental than offshore transport. This demonstrates the power of comparative studies to provide enough instances to differentiate between factors.

SECTION IX—RELATION TO OTHER U.S. AND INTERNATIONAL PROGRAMS

Linkages To Other West Coast Programs

Numerous field programs, mostly sponsored by NOAA, NSF, ONR, and MMS, have obtained large volumes of multidisciplinary data from the CCS. It is expected that other studies (e.g., CoOP) will be occurring at the time of a U.S. GLOBEC CCS study. This is in addition to regular, long-term sampling programs conducted by CalCOFI, NMFS, state agencies, power plants, municipal sewage outfalls and numerous regional research and academic institutions. An example is the annual larval and juvenile rockfish survey conducted (every June; often Feb-March also) by the Tiburon NMFS laboratory in Region II of Northern California. However, most of these programs focus on a limited area, not the larger-scale and none are climate-oriented. The U.S. GLOBEC west coast regional program offers an opportunity to link other programs via regional comparison. A focused study sponsored by CoOP is in the planning stage and could be coordinated with a subset of the U.S. GLOBEC modeling activities and mesoscale studies. The U.S. GLOBEC Science Plan committee is maintaining contact with the CoOP SSC and will continue to explore mutual interests as planning proceeds.

The NMFS FORAGE study proposed to the NOAA Coastal Ocean Program, which targets ground fish along the U.S. west coast would naturally fit within the framework of a U.S. GLOBEC study. It would provide valuable data on the distribution and abundance of ground fish larvae with several distinct life history strategies. The NMFS RACE program conducts triennial summertime acoustic surveys extending along the west coast from the Queen Charlotte Islands to Point Conception; they are currently scheduled for 1995, 1998 and 2001. NOAA initiatives such as the Global Ocean Observation System (GOOS) and Coastal Forecast System (CFS) could provide resources for collecting important environmental data, and conducting long-term regional monitoring. Analysis of historical data within the retrospective component of the west coast U.S. GLOBEC program will help define the requirements for these programs. The NDBC program is planning to add further ocean instrumentation to the present buoys (workshop report in preparation), which would be especially useful for monitoring if one or more of their prototypes could be located at sites chosen in collaboration with the U.S. GLOBEC study off the west coast.

Linkages To International Programs

Mexico and Canada conduct frequent and regular physical and biological surveys off their west coasts. An example is the La Perouse Bank program off of Vancouver Island, British Columbia. Both countries are developing national GLOBEC programs. International collaboration with these programs would greatly facilitate the regional comparison of mesoscale features and the study of transition zones along the west coast. NOAA, ORSTOM, and ICLARM support the CEOS program, which focuses on comparative studies of EBCs primarily as retrospective data analysis and modeling of multi-decadal and climate change. The examination of the CCS in comparison to other EBC's gives the U.S. GLOBEC program a natural link to these studies, as well as to other developing national GLOBEC programs off South America, northwest, equatorial, and southwest Africa, and the Iberian Peninsula. The U.S. GLOBEC program could serve as a model for other EBC programs. The IOC and FAO have sponsored fishery recruitment studies, and would be logical partners for U.S. GLOBEC in a comparative EBC study. PICES is interested in supporting multi-national cooperative research on climatic variability and species changes in the North Pacific. U.S. GLOBEC's west coast studies

could be a key component of this program. The Inter-American Institute for Global Change Research (IAI) is in the process of developing a program in "Comparative Studies of Oceanic, Coastal and Estuarine Processes in Temperate Zones" and in "ENSO and Interannual Variability", which should include comparative studies off the west coasts of North and South America. GOALS is an extension of work begun during TOGA, and the TOGA-TAO observational network in the central equatorial Pacific will provide important information concerning the basin-scale climate variability during the U.S. GLOBEC study of the CCS. If possible, observations along the eastern Pacific margin, linking the two systems along the coastal wave guide, should be established during the observational period in the CCS and afterward, to complement the monitoring and prediction activities. Finally, GLOBEC International has endorsed a new recent working group on Small Pelagic Fish and Climate Change (SPACC) which will focus on living marine resources in coastal upwelling regions, emphasizing especially Eastern Boundary Current Regions (workshop report in preparation)—a natural link for U.S. GLOBEC's planned CCS study.

SECTION X—REFERENCES

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