COMPARATIVE ANALYSIS OF MARINE ECOSYSTEM ORGANIZATION

Science Plan

CAMEO Science Steering Committee

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Final report
PRELUDE

This document describes the goals and the science priorities of the Comparative Analysis of Marine Ecosystem Organization (CAMEO) research program that is designed to provide the information needed to better implement ecosystem-based management of marine ecosystems. The program supports fundamental research to understand complex dynamics controlling ecosystem structure, productivity, behavior, resilience, and population connectivity, as well as effects of climate variability and anthropogenic pressures on living marine resources and critical habitats. CAMEO encourages the development of multiple approaches, such as ecosystem models and comparative analyses of managed and unmanaged areas (e.g., marine protected areas) that can ultimately form a basis for forecasting and decision support. Central to the program is the emphasis on collaborations between academic and private researchers and federal agency scientists with mission responsibilities to inform ecosystem management activities. This research program, which was jointly funded by National Marine Fisheries Service and The National Science Foundation, has an emphasis on understanding the central role of climate and fishing in structuring marine ecosystems.

Funding for CAMEO began in 2009 and under two solicitations has supported 15 collaborative projects among 50 academic investigators at 25 different institutions and 21 NOAA investigators at 10 different NOAA laboratories. NOAA laboratories contributed nearly 50 work-months of labor from senior scientists. Numerous other collaborators were involved including one National Park Service and two United States Geological Survey investigators. The projects valued the broader impacts of scientific work and supported 19 post-doctoral positions, 17 graduate students, 5 technicians, and 6 summer internships. CAMEO supported two workshops as part of the long-running US-Canada-Norway Trilateral effort on fisheries and ecosystem modeling. The projects were widely distributed in the Pacific Ocean, Atlantic Ocean and Gulf of Mexico and included research on comparative dynamics of shelf and coastal current, estuaries and coral reef ecosystems and fisheries as well as two international workshops on modeling. These projects will continue through 2013.

Part way through the preparation of this document, changing federal budget conditions resulted in cancellation of the April 2011 CAMEO proposal review panel, which was to consider proposals submitted to the third solicitation under this program. This cancellation, plus the prospect of continued pressures on agency budgets, led to the conclusion that the existing mechanism for funding CAMEO-type research could not be continued. Despite this setback, the National Science Foundation and the National Oceanic and Atmospheric Administration remain committed to supporting collaborative research between federal and academic scientists to advance our understanding of marine ecosystems and their interactions with fisheries and other human activities. NOAA and NSF are discussing how to best support this kind of research going forward. Although the existing CAMEO program is suspended, we are publishing this report to provide a description of goals and science priorities that should be supported by a program of this nature directed at nationally important resources that are a part of our natural heritage.

Other key background documents and activities of the CAMEO Program are available at: http://cameo.noaa.gov/. Copies of this document may be obtained from:

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EXECUTIVE SUMMARY

The oceans are Earth’s greatest remaining wilderness and society’s last major source of wild-caught food. But food from wild fisheries and the myriad of other services oceans provide, depend on healthy intact marine ecosystems. Human activities are rapidly changing the Earth system, threatening the sustainability of ocean resources and altering the very fabric of marine ecosystems. Fishing, climate change, habitat destruction, and pollution are having increasing and cumulative impacts, sometimes pushing ecosystems “over the edge” into alternative states that fail to provide food and other services upon which we depend. In order to manage marine resources sustainably, we must learn to manage entire ecosystems, not just their individual components (e.g. fish populations).

Effective ecosystem management requires a clear understanding of ecosystem organization, function, and response to stressors, including those caused by human activities. Toward this goal, the CAMEO (Comparative Analysis of Marine Ecosystem Organization) research program seeks to:

Provide fundamental understanding of marine ecosystem structure, function and dynamics—with particular emphasis on climate and fishing as agents of change—to foster enhanced prediction and support for ecosystem-based management.
CAMEO will support research on four interrelated science themes (Figure on previous page, Box on this page), to address how coupled human-natural marine systems respond to drivers of change, with special emphasis on fishing and climate. This emphasis is due to widespread recognition that climate and fishing are the most pervasive and influential drivers of change in marine ecosystems. CAMEO is therefore intended to answer questions about how climate and fishing act individually and synergistically with other stressors to influence the abundance, productivity and resilience of marine populations and the ecosystems that support them.

Comparative analysis—drawing on contrasts within and among marine ecosystems—is a fundamental component of CAMEO. By drawing ecosystem-scale comparisons across environmental gradients and management regimes, we increase our understanding of the underlying principles that organize marine ecosystems and the roles of human actions therein. Additionally, predicting marine ecosystem responses to change is essential to developing ecosystem-based management strategies that will ensure the sustainability of marine resources and the livelihoods of those who depend on them.

Because of the imperative to unite basic science with management, the National Science Foundation and NOAA jointly developed and support CAMEO. Answering the broad interdisciplinary questions of CAMEO will require an effort much larger than any single research program and will require scientific efforts across a diverse array of disciplines. The interface between natural and social sciences will be especially important for understanding, predicting and managing interactions between human society and the world’s living marine resources. CAMEO will provide funding for federal and academic scientists to collaborate, share existing data sets, and develop and test new empirical studies, mathematical approaches and predictive models to inform ecosystem-based management.

**Science Themes**

1) **Connectivity** defines the fundamental structural and functional attributes of ecosystems and linkages among ecosystems.

2) **Response to Perturbations** examines the factors that control ecosystem responses to perturbations and stresses, including processes that can either enhance or diminish the tendency of ecosystem to shift into alternative states.

3) **Human Dimensions** examines the critical interactions between humans and marine ecosystem processes.

4) **Comparative Synthesis and Forecasting** explores novel approaches of integrating existing information on ocean ecosystems and human society to predict the response of marine ecosystems to climate and fishing.
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INTRODUCTION

The grand challenge of the 21st century is to understand the expanding influence of human dominance on the Earth’s system, and to manage that influence to promote the sustainable delivery of ecosystem services. Nowhere on the globe is this challenge more critical than in marine ecosystems because of the variety of ecosystem services they provide to society, including food from fisheries, shoreline buffering against storm impacts, biogeochemical cycling and recreational opportunities. Delivery of these services depends upon intact ecosystem processes and ecosystem productivity. However, marine ecosystems face increasing pressures from multiple interacting sources. Improved fishing technologies have enabled us to exploit—and significantly alter—the ocean’s fish and shellfish resources to meet society’s escalating food requirements. We now harvest the oceans’ resources farther from coasts, at more trophic levels, and in deeper waters with more precision and efficiency than in past centuries. Climate variability and change, including rising atmosphere and ocean temperatures, sea level rise, and increased intensity of weather disturbances, affect the physical, chemical and biological processes in marine ecosystems. These processes, in turn, determine the diversity, distribution and abundance of living marine resources.

The recent Executive Order (2010) endorsing the recommendations of the Interagency Ocean Policy Task Force called for ecosystem-based management as the guiding principle for managing our oceans and living marine resources. This approach requires that resources should be managed to take into account the relationships among all ecosystem components, including human and nonhuman components, and the environments in which they live. One particularly important application of ecosystem-based management is the application to living-marine resources, including fisheries and their associated habitats (NMFS 2009), but in order to apply the principal of ecosystem-based management we need to understand how these marine ecosystems function and respond to change.

The CAMEO research program will develop the fundamental scientific basis for ecosystem-based management of our ocean and coastal living marine resources and the services they provide. The overarching goal of CAMEO is to:

Provide fundamental understanding of marine ecosystem structure, function and dynamics—with particular emphasis on climate and fishing as agents of change—to foster enhanced prediction and support for ecosystem-based management.

As a partnership between the National Ocean and Atmosphere Administration (NOAA) through the National Marine Fisheries Service (NMFS) and the National Science Foundation (NSF), CAMEO will expand our fundamental understanding of ecosystem processes, and develop models to understand and forecast marine systems that can be used to inform and evaluate the effectiveness of local and regional ecosystem-based management efforts.
THE COMPARATIVE APPROACH

A central component of CAMEO is the use of comparative studies to improve our understanding of coupled human-marine ecosystems, how they respond to change induced by climatic and human drivers, and to improve forecasting of these responses (Megrey et al. 2009, Murawski et al. 2010). Spatial or temporal comparisons of ecosystems that are similar in most respects, but differ in specific ways or are under different management can provide information about how various factors influence the condition and dynamics of an ecosystem. This knowledge is critical to advance ecosystem-based management. Understanding the fundamental controls, and the contrast between systems, can provide the basis for better management of these systems.

The comparative approach also offers an alternative to the classic experimental method in cases where it is nearly impossible to impose experimental manipulations and controls. This is almost always the case when addressing ecosystem-level processes and responses at the large spatial scale characteristic of marine fisheries. Obvious components of the comparative approach are experiments, observational data, theoretical models, and ultimately sophisticated integrations of all three in empirical or modeling studies.

Comparative analysis may be effective when applied across ecosystems, within ecosystems over time or space, or across models of ecosystems. Comparative studies that use natural gradients in ecosystem features or contrasts in human activities, including management approaches, will help reveal how those features are manifest in ecosystem processes, organization and productivity. A spatial comparison of ecosystem function and structure within and outside management areas is one form of comparative analysis that may offer insights into how ecosystems respond to specific human activities. For example, comparison of ecosystem responses inside and outside of marine protected areas has illuminated the interactive effects of fishing and climate change on the resilience of kelp forest ecosystems (Ling et al. 2009). In addition, comparisons before and after large-scale climatic events (e.g., El Niño) or other perturbations that occur at large spatial scales, can illuminate the key factors that structure ecosystems.

Understanding ecosystem resilience is a unique challenge that may benefit from the comparative approach by providing an alternative to the normally very long time scales needed to assess resilience (Scheffer et al. 2009). Measuring resilience typically requires both a theoretical framework and a long data series (often decades), especially to infer thresholds or regime shifts. An understanding of state transitions by comparing ecological states under different environmental conditions or management approaches, whether in time (e.g., under changing climatic conditions) or space (e.g., inside and outside marine protected areas, or under different socio-political institutions) may provide insight on shorter time scales. Furthermore, comparing state transitions among different ecosystem types may illuminate general principles that apply across multiple marine ecosystems.

The spatial and temporal scale of comparative research should be appropriate to the ecosystem properties and management considerations being studied. CAMEO research is expected to provide a basis for interpreting and forecasting in the ‘years to decades’ time domain. Research can include intra-seasonal and interannual variability as it contributes to better understanding long-term trends. Longer time scales are particularly appropriate for predictive modeling and understanding the effects of management and feedbacks to human society. The spatial scale of comparative analyses can range from ocean basins to local oceanic
and coastal features (e.g., seamounts, shelves, bays and estuaries). In some cases, a regional focus may be most useful in understanding the ecosystem properties that are relevant to fished species, usually mobile organisms at the mid- to higher trophic levels.

**Fisheries and Climate as Key Drivers**

The CAMEO program emphasizes understanding the importance of fishing and climate as drivers and controllers of marine ecosystems. While many other important drivers influence specific marine ecosystems (e.g., eutrophication in coastal areas), CAMEO considers fishing and climate variability and change to be the most globally pervasive and important drivers of marine ecosystems. Additionally, these two drivers are likely to operate synergistically and interact with other stressors/drivers. Modern ecosystem management must understand and take into account the interactions between climate and fishing, rather than try to address each separately. These interactions are significant drivers of change in marine systems and have ramifications for ecosystems and those who depend on the services they provide.

**Fishing:** Arguably the most important direct driver of change in marine ecosystems over the last century has been fishing, which affects the structure, function, and biodiversity of the oceans (Jackson et al. 2001, Halpern et al. 2008). Fishing in the CAMEO context includes the direct extraction of target species and the process of fishing, including unintended bycatch of non-target species, effects on habitats, and indirect impacts on non-target species through ecological interactions. Fishing pressure is so strong in some marine systems that the biomass of fish (including both the target species and those caught incidentally) has been reduced to less than half of the levels prior to the onset of industrial fishing (Worm et al. 2009). These fishery-induced changes can restructure marine food webs and directly or indirectly alter the trophic pathways that previously supported fisheries and other managed species (Jackson et al. 2001, Steneck et al. 2004, Sandin et al. 2008). Promising signs of recovery in systems with effective management measures, point to the economic and ecological benefits of controlling fishing pressure (Worm et al. 2009).

**Climate variability and change:** The preeminent challenge in the next 50 years will be understanding, predicting and adapting to the changes in marine ecosystems induced by natural and anthropogenically-driven global climate variability and change. The sensitivity of marine ecosystems to natural climate variability at multiple temporal and spatial scales is well established (Lehodey et al. 2006), and the implications of climate change for fisheries have long been recognized (Cushing 1982, Glantz 1992, Everett 1995). Anthropogenically-driven climate change will impact marine ecosystems in numerous ways, including gradual ocean warming, changes in ocean currents and freshwater inputs from rivers, sea level rise, retreat of sea ice and glaciers, modifications to ocean chemistry (e.g. ocean acidification), and changes in the frequency and intensity of hurricanes and other extreme events (Scavia et al. 2002, Alheit et al. 2010). These changes are likely to have substantial impacts on all marine ecosystems. Poleward distributional shifts in some species have already been demonstrated in response to increased global temperatures (Cochrane et al. (eds.) 2009). Climate change is already altering the seasonality of biological processes and food webs, with currently unpredictable consequences for fisheries production (Cochrane et al. (eds.) 2009). Furthermore, natural cycles of climate variability, such as El Niño Southern Oscillation (ENSO), are likely to respond to climate change with significant impacts on global-scale ecosystems and fisheries. Changes in habitats, species distributions, and food web dynamics will require changes in the human communities that depend upon these ecosystems. Human communities will respond directly by altering their
behavior (e.g., where, when and what they fish for) and indirectly through new management, with both having repercussions across society.

**Interactions between Fishing, Climate and other stressors:** CAMEO recognizes that fisheries and climate change may act synergistically with each other and with other stressors to alter ecosystems in unexpected ways. For example, Fogarty *et al.* (2008) illustrated the synergistic effects of fishing and climate on Atlantic cod in the Gulf of Maine and the need to adjust harvesting strategies accordingly. More generally, Hsieh *et al.* (2008) and Perry *et al.* (2010) conclude that fished populations are generally less resilient to climate variability than unexploited species that have maintained a natural age structure and diversity of life history traits. Similarly, nutrient enrichment, which has long been an issue in coastal systems (Carpenter *et al.* 1998, Cloern 2001), and fishery-induced changes to food web structure, which is a widespread issue in marine ecosystems (Jackson *et al.* 2001, Worm *et al.* 2000, Micheli *et al.* 2005), have been shown have synergistic effects (Deegan 2002, Deegan *et al.* 2007, Vasas *et al.* 2007) and the potential to alter coastal ecosystem function. Thus, understanding and predicting how fisheries and climate interact with each other or other stressors to affect the sustainability of managed species and ecosystems is a critical challenge for CAMEO research.

**SCIENCE THEMES AND CHALLENGES**

Human activities and climate are rapidly changing the Earth System, altering the ocean’s vulnerability to change and impacting the sustainability of marine ecosystem services. Three interconnected elements of ecosystems are central to the CAMEO program: drivers, attributes, and responses. Drivers are the anthropogenic and environmental processes that shape ecosystems, including climate, fishing, ocean current dynamics, and nutrient loading. System attributes are the structural and functional elements of ecosystems, including species composition and spatial configuration and connectivity within and between ecosystems. Responses are the dynamics over time that follow from changes in drivers, and include the sensitivity, vulnerability and resilience of ecosystem attributes and processes (production, nutrient recycling, etc.) to perturbations.

Ecosystem productivity, the ecosystem process that results in the provision of goods and services in the form of fishery harvest, is one of the most important ways that marine ecosystems interact with human society. The basic property of productivity can be assessed for different levels or components of the ecosystem, and provides a common currency to describe changes in ecosystem status in response to drivers. Ecosystem dynamics, including the production of species at the middle and top of the food web, are often linked to nonlinear processes that control response to stressors. Effective management is predicated on understanding these interactions in order to predict the response of ecosystems to perturbation. CAMEO will provide information on issues such as:

- How the provision of goods and services by ecosystems with different characteristics respond to natural and anthropogenic pressures and drivers,
- Limits to ecosystem resilience, and identification of thresholds that, when crossed, lead to phase or regime shifts, as well as the nature of reversibility of such shifts,
• The relative performance of different management approaches (e.g. spatial versus non-spatial) by comparing the response of similar ecosystems, specific components, or fisheries subjected to different approaches.

• Relationships between the human dimension of ecosystems, drivers of change, and the triggers for management responses.

The CAMEO program will support work in four core research themes (Figure 1). For all themes, comparative studies are critical to advance our understanding of marine ecosystem responses to anthropogenic drivers, and enhancing our ability to predict ecosystem responses. These four themes are necessarily highly interconnected and many of the scientific challenges identified cut across multiple themes. For example, the fundamental ecological question of control by top-down versus bottom-up drivers of food web dynamics is both a question of connectivity (Theme 1) and ecosystem responsiveness (Theme 2). CAMEO research projects may focus on individual themes, or questions that span and integrate concepts across multiple themes. For example, predicting how human fishing behavior (Theme 3), will ultimately respond to and interact with changes in climate, requires knowledge of how ecosystem attributes (Theme 1) mediate an ecosystem’s response (Theme 2) to climatic events. Comparative synthesis and forecasting (Theme 4) will generate a deeper understanding of these relationships.

Figure 1. Schematic view of two major drivers (Climate and Fishing) and four science themes that define CAMEO research. See the text for a detailed description.
Theme 1: Connectivity of Marine Ecosystems focuses on understanding the connections within and across ecosystems and how these ecosystem attributes interact with climatic and human perturbations to determine the stability and resilience of an ecosystem. Here, connectivity is defined broadly, to include trophic connections and fluxes viewed from a food web perspective, as well as spatial and temporal connectivity of individual ecosystem components and how those linkages dictate structure and functioning of ecosystems.

Theme 2: Response to Perturbations focuses on understanding what controls ecosystem responses to drivers and how ecosystem attributes change in response to perturbations, including the emergent properties of stability, resilience and ecosystem state-transitions. This theme focuses on describing the nature and magnitude of ecosystem responses to perturbations, and identifying ecosystem attributes that enhance or diminish these responses. This theme also explicitly considers how these system responses might be predicted, including the identification of thresholds and tipping points, and understanding attributes that convey resilience.

Theme 3: Human Dimensions highlights potentially dramatic influence of humans as an integral part of marine ecosystems. Humans act not only as key elements of ecosystems, but also as fundamental drivers and responders, providing critical feedbacks, including management responses, between the causes and consequences of ecosystem change.

Theme 4: Modeling Synthesis and Forecasting recognizes the need to develop new modeling frameworks and analytical approaches that enable us to synthesize and forecast the dynamics of marine ecosystems, including the feedbacks between human society and marine ecosystems, as well as between humans, fishing and climate. These advances are essential to improve our ability to manage the ocean’s living resources, and to predict the effects of natural changes and management actions.

In the following sections we elaborate on these themes and identify critical gaps and potential research questions. The research questions are meant to provide guidance as to potential topics; they are neither complete nor prescriptive.

**THEME 1: CONNECTIVITY**

*How do patterns of connectivity within and among ecosystems, and human impacts on those patterns, influence the productivity and resilience of marine ecosystems?*

The structure and function of marine ecosystems and the ecosystem services they provide are strongly influenced by connectivity, both within and among ecosystems. Connectivity between components within an ecosystem includes the fluxes of energy and matter that support ecosystem structure. Connectivity among ecosystems, or spatial connectivity, includes the influx and export of organisms, energy, nutrients, and humans between ecosystems. Ecosystem connectivity is evidenced in the substantive and influential fluxes of organisms, nutrients, energy and matter between pelagic and benthic communities (e.g., Witman et al. 2003, Navarrete et al. 2005, Kirby et al. 2008), terrestrial, freshwater and coastal marine ecosystems (e.g., Diaz and Rosenberg 2008), nearshore and offshore ecosystems (e.g., Estes et al. 1998, Vetter and Dayton 1999) and among adjacent ecosystems defined by
discrete habitats (e.g., estuaries, salt marshes, seagrass, mangrove, coral and temperate reef ecosystems, Nagelkerken (ed.) 2009). Understanding and predicting how connectivity within and among ecosystems determines the productivity and resilience of marine systems is essential to inform ecosystem-based management decisions. Comparative approaches are necessary to reveal the ecosystem processes that underlie observed patterns of connectivity within and among ecosystems, and to rigorously test hypotheses across ecosystems with differing degrees of disturbance and human activity.

Management of marine living resources can be improved through better understanding of ecosystem connectivity, its sensitivity to fishing and climate, and how connectivity governs ecosystem resilience and stability. Clearly, improved knowledge of trophic connections within ecosystems can inform harvest policies by identifying key species and preserving those that play critical ecosystem roles. Moreover, by understanding how climate variability and climate change alters connectivity, policy makers can adapt fishing practices and levels to accommodate anticipated climate change and subsequent changes to ecosystems. Understanding connectivity within and between ecosystems will provide critical information for defining the appropriate spatial scale of management activities.

The following scientific challenges illustrate some of the ways that increased understanding of the roles of and threats to connectivity within and among ecosystems can support management of sustainable, productive and resilient ecosystems and the fisheries they support.

**Scientific Challenges**

**1.1: Resolving how the strength and patterns of interactions among ecosystem components act to regulate food webs, energy flow and responses to perturbations.**

Understanding linkages among food web components is needed to improve ecosystem-based management. This diverse field has a long history, beginning with Odum and Odum’s (1955) pioneering work on energy flux in coral reef ecosystems. Since that time, the field has developed multiple approaches to gauge connectivity in food webs (Post 2002), each of which reveals different information about the nature of interactions between ecosystem components.

Advancing our understanding of connectivity within ecosystems is critical to identify how anthropogenic and natural disturbances alter the fate and flow of energy in food webs. Energetic or mass-balance approaches describe the flux and fate of energy or material in food webs and can provide indirect measures of ecosystem state. This approach has a rich history in comparative marine ecology, revealing stark differences among ecosystems in the proportion of primary production that ultimately reaches upper trophic level organisms (Baird et al. 1991). Energetic approaches might be used to measure the fate of primary productivity, and the comparative framework can ask what key forcing variable or ecosystem component regulates this important ecosystem attribute. Ulanowicz (1996) developed a detailed theory of energetic characteristics of food webs that might be used to derive indicators of stressors (see Case Study 1: Defining metrics for cross-ecosystem comparison: the network analysis approach). Today, there are multiple stand-alone modeling frameworks that facilitate the development of energetic food web models (Polovina 1984, Christensen and Walters 2004).

A critical research objective is to identify the structural and functional properties of ecosystems that govern interaction strength and how the strength of these interactions can be predicted, including the conditions that facilitate strong interactions. Interaction strength
approaches describe the dependencies between the temporal dynamics of interacting species. This approach can be used to describe the stability of ecosystem structure and function as they relate to the pattern of weak and strong interactions (de Ruiter et al. 1995). Identifying strong interactions is also essential to improve predictive capacity and gauge ecosystem responses to targeted removal of ecosystem components (Bascompte et al. 2005). Interactions can be both “top-down” and “bottom-up”, and there is ample evidence of both of these in marine food webs (Baum and Worm 2009, Essington 2010). Measuring and predicting interaction strength is often hampered by limited data and the inability to conduct properly scaled experiments. Moreover, there is a need to identify how interaction strengths themselves change over time in response to physical forcing and climate change (Hunt et al. 2002, Essington 2010).

Topographical analyses can be used to describe the overall structure of connections within an ecosystem. Here, ecosystems are viewed as networks of connections, and the focus of analyses can be to describe the overall connectivity of a system (defined by the number of linkages, Link 2002a), or by several other indices that aim to define the potential importance of individual components that are revealed by their key position within networks (Jordan and Scheuring 2002). In a fisheries context, this might include identification of potentially key species that act as “hubs,” or connection points between many species in the food web (Gaichas and Francis 2008). This approach also underpins a large body of theoretical literature that relates food web patterns to ecosystem stability (e.g., Dunne et al. 2002a,b). Network analysis can reveal "nexus" species and identify how the ecosystem responsiveness is related to the degree and nature of connectivity. These may include the importance of biophysical forcing, biodiversity at multiple ecological levels, or depletion of ecosystem components through fishing.

1.2: Understanding how the rate and patterns of spatial connectivity (individuals, nutrients, energy, etc.) within and among ecosystems act to regulate productivity and response to perturbations.

The vast potential for movement of organisms, nutrients and energy in the marine environment is reflected in the great spatial connectivity of populations, communities and marine ecosystems (Steele 1985, 1991, Carr et al. 2003, Shurin et al. 2006). Understanding spatial connectivity, both connectivity between populations within an ecosystem and connectivity among ecosystems, is fundamental to effective ecosystem-based management. Population connectivity is the genetic and demographic consequence of movement of individuals from one local population to another (e.g., Kritzer and Sale 2006, Cowen et al. 2007, Cowen and Sponaugle 2009). Ecosystem connectivity is the movement of organisms, energy, nutrients, matter, and humans between ecosystems (e.g., Polis et al. 1997, 2004, Nagelkerken (ed) 2009). Together, these forms of spatial connectivity influence the structure, diversity, productivity, dynamics, and resilience of populations and marine ecosystems.

To advance our understanding of ecosystems it will be critical to identify the attributes of connectivity (e.g., magnitude, predictability, reciprocity), characteristics of species (e.g. longevity, fecundity) and features of ecosystems (e.g., spatial heterogeneity) that influence the structure, function and resiliency of populations to natural and anthropogenic perturbations. Population connectivity determines the genetic and demographic structure of marine populations. Correspondingly, the geographic distribution of fishing mortality can influence the genetic structure and diversity of populations (e.g., Kendall et al. 2009). The influence of biophysical processes, species traits, and patterns of habitat structure on dispersal, gene flow, and genetic structure remains poorly understood. Likewise, little is known about how genetic
structure influences the productivity and resiliency of populations. Given the particular importance of larval dispersal to the spatial structure and persistence of populations and the role of oceanographic processes in determining larval connectivity (e.g., Pineda et al. 2007, Cowen and Sponaugle 2009, Mitarai et al. 2009), it will be critical to understand how climate change will alter patterns of connectivity in order to forecast how fishery stocks will respond to climate change. For example, truncation in size structure and constricted geographic distribution from fishing may cause exploited populations to be more vulnerable to climate variability (Hsieh et al. 2008).

Another critical aspect of spatial connectivity is the relationship between heterogeneity (e.g., landscape scale habitat configuration, spatial variation in fishing mortality) and population connectivity. Understanding the spatial scales and geographic patterns of connectivity can inform spatially explicit approaches to ecosystem-based management. Many species move among habitats in regular migratory behaviors associated with seasonal shifts in resource availability and reproduction (Pittman and McAlpine 2003). Subsidies include the movement of organisms as parcels of nutrients and energy (e.g., Deegan 1993, Menge 2004) and the transport of materials by water movement (e.g., upwelling) among ecosystems. In turn, the spatial configuration of ecosystems across a landscape can strongly influence the structure of fish populations and assemblages associated with an ecosystem (e.g., Grober-Dunsmore et al. 2007, 2008). However, few studies have assessed how altering connectivity, through changes to nursery habitats, habitat fragmentation or fishing impacts, influence the spatial structure and persistence of adult populations and fishery production (e.g., Layman et al. 2004, Aburto-Oropeza et al. 2008, Lipcius et al. 2008).

1.3: Determining how spatial connectivity across ecosystem boundaries shapes the strength and patterns of interactions within ecosystems.

Understanding and predicting how changes in the spatial connectivity among populations and ecosystems influences the productivity and resiliency of marine ecosystems requires an understanding of how influxes of species, nutrients, and energy alter the structure, functions, and component connectivity of recipient ecosystems (Polis et al. 1997, 2004, Amaraesekare 2008). Although spatial connectivity models and ecosystem models are receiving growing attention, the lack of integration impairs advances in our understanding. Thus, another crucial research direction is the development of analytical approaches that integrate spatial and component connectivity to better predict region-wide and ecosystem-wide responses of species and ecosystems to human activities and management approaches (e.g., networks of marine protected areas). Comparisons of integrated modeling approaches within and among ecosystems can be particularly informative to this shortfall in the science of marine ecosystems. Advances in this direction will require the collaborative development and application of models involving at minimum oceanographers and ecologists, in partnership with social scientists and resource economists.

There is a critical need to quantify the temporal and spatial scales of marine food web interactions and to determine the data gaps and assumptions that contribute the greatest uncertainty in understanding and predicting ecosystem response. Nonlinear interactions or stochastic events may play a critical role in rapid and unpredictable shifts in ecosystem states. Although physical processes clearly control many marine food web interactions and energy transfers, some studies indicate that stochastic physical forcing can be amplified by biological processes to strongly influence ecological dynamics, potentially causing regime shifts (Scheffer
2009). Since different organisms have different generation times and spatial ambits, the spatial and temporal scales of interactions between external forcing and internal food web dynamics must be considered. Furthermore, short-term dynamics may be essential to the persistence of ecosystems as they can allow coexistence of predators, prey, and competitors (Hastings 2004).

Spatial heterogeneity within ecosystems may allow different systems to accommodate stressors in different ways and account for varying response thresholds (Hsieh et al. 2005). Separation of spawning and nursery areas, seasonal migrations, and connectivity between metapopulations may act to ameliorate small-scale perturbations. Similarly, fishing and other human activities may alter the spatial scale of ecosystem response. For example, larvae of exploited fish species were shown to have a greater geographical shift in distribution compared to unexploited species in response to environmental change (Hsieh et al. 2008). As a result, reduced spatial heterogeneity may cause exploited populations to be more vulnerable to climate variability. Marine protected areas and other spatial management strategies that increase the spatial heterogeneity of populations or human activities may provide opportunities to better understand the role that spatial heterogeneity plays in regulating ecosystem responses to change.

**THEME 2: RESPONSE TO PERTURBATIONS**

*How do different properties of ecological systems and coupled human-natural systems influence the responsiveness of marine ecosystems to perturbations?*

A fundamental goal is to identify, quantify, interpret, and predict responses of marine ecosystems to perturbations induced by climate change, fisheries and other drivers. Both external and internal drivers can induce shifts in ecosystem structure, which in turn alter ecosystem function, connectivity, and services. Humans are an integral and responsive component of marine ecosystems, and as such, ecosystem change may alter human behavior, potentially driving further change. To develop effective decision support tools for ecosystem-based management, it is critical to understand the processes and mechanisms that control how coupled human-ecological systems respond to change. An important part of CAMEO will be to develop comparative research that identifies the major drivers of ecosystem changes and aids in determining which of these drivers are likely to be most responsive to management.

Marine ecosystems may exhibit directional, progressive, or cyclical changes over a range of time-space scales. Responses can be complex, act over a variety of temporal and spatial scales, and be expressed as changes in productivity, diversity, or trophic structure. Ecosystem state transitions are an example of one type of ecosystem response to perturbations. If a system exhibits alternative stable states, then hysteresis can occur, whereby ecosystem restoration may be impaired by the reorganization of structuring processes (Scheffer et al. 2001). Understanding the likelihood of shifts between ecological states and the conditions required to reverse such shifts is critical for effective management of ecosystems and the services they provide.

Comparative approaches are proposed as an effective way to investigate and characterize marine ecosystem responses and susceptibility to change, not only to judge the
nature and magnitude of responses, but also the temporal and spatial scales over which responses occur.

**Scientific Challenges**

**2.1: Distinguishing the nature and extent of ecosystem responses to natural and human perturbations.**

Marine ecosystems are affected by a broad spectrum of natural and human stressors. Structural and functional features of individual systems can either moderate or exacerbate the effects of stressors. Understanding these features across different types of ecosystems will provide information needed for ecosystem-based management. Climate-induced impacts may exert effects at large spatio-temporal scales, potentially affecting virtually every aspect of ecosystem structure and function, from biogeochemical cycling to community composition at all trophic levels (Stenseth *et al.* 2002, Cury *et al.* 2008). Fundamental shifts in ecosystem productivity may occur in these systems under global climate change.

The human-induced impacts of fishing may have a variety of effects on marine ecosystems. In many cases, the direct effects of fishing through removal of target species biomass can be readily tracked and related to changes in the abundance and demographic structure of the target species. Although more challenging to measure, fishing may also have indirect effects by altering the abundance of target or bycatch species relative to interacting species, thus affecting trophodynamics and community structure in the ecosystem (see Case Study 2: State shifts in Caribbean coral reef systems). Other harvesting impacts, such as a reduction of structural complexity of benthic habitats by towed fishing gear, can potentially exert effects on the dynamics of ecosystem structure and productivity (Auster 1998, NRC 2002).

Stressors may act in a cumulative and synergistic fashion, controlling thresholds of ecosystem response and potentially leading to unpredictable ecosystem responses to traditional management strategies. For example, the potential interaction between changes in the environment and harvesting is critical because persistent shifts in population productivity require managers to be prepared to revise biological reference points that guide harvest policy decisions. It is clear that a dynamic concept of maximum sustainable yield and other reference points is required to account for the changing biological and physical conditions experienced by many marine populations.

Separation of natural and anthropogenic forcing is critical in any attempt to develop management interventions. By carefully selecting ecosystems and sites that are subject to differing levels of natural and anthropogenic impacts, it is also possible to address the issue of whether effects of these stressors are cumulative and synergistic.

**2.2: Identifying and developing metrics that will characterize ecosystems and their responsiveness to perturbations.**

Discerning and explaining how ecosystems respond to change in natural and human-induced stresses or forces is an important issue. While numerous metrics and indicators have been proposed to characterize the state of marine ecosystems, most fall short of describing an ecosystem with the specificity required for predicting ecosystem responses. New metrics that broadly define the responsiveness and susceptibility of different ecosystems to change, may ultimately find application as reference points and decision support tools in ecosystem-based
management (Murawski et al. 2010). It is particularly important to identify metrics that signal thresholds and tipping points in response to climate and fishing-related perturbations.

Numerous biotic and abiotic metrics and indicators of ecosystem state have been evaluated to categorize and compare the structure and productivity of ecosystems (Case Study 1: Defining metrics for cross-ecosystem comparison: the network analysis approach). Rice (2000) proposed four broad categories of response metrics to evaluate ecosystems: 1) diversity and similarity indices, 2) ordination methods, 3) aggregate community property metrics, and 4) emergent properties (derived from ecosystem modeling). Jennings (2005) identified pressure, state, and response indicators, the latter representing human responses, i.e., policy and management measures to relieve pressures and change or maintain the state of ecosystems. In a series of papers, Link (2002b, c, 2005) provided examples of indicators and metrics, arguing that many can serve as reference points for ecosystem-based management plans. A proposed hierarchical approach for indicator development, evaluation and utility presents a useful framework for future research (Rice and Rochet 2005). The power of comparative ecosystem analysis was demonstrated in two series of papers (Progress in Oceanography, Vol. 81, Journal of Marine Systems 79) in which indices were applied in comparisons of marine ecosystems across the globe (Megrey et al. 2009, Alheit et al. 2010). There is a foundation of research on metrics categorizing ecosystem structure, trophic relationships, and production potential, and a strong need for further research to identify and evaluate their performance.

In order to understand how ecosystems respond to stress, it is important to quantify and distinguish responses that represent shifts in ecosystem structure and function. Developing indicators or suites of indicators that 1) characterize responses, 2) are comparable across ecosystems, and 3) are based on time series to discern patterns and trends in ecosystem change will contribute to fundamental understanding of ecosystem behavior. Suites of indicators may include both static measures and dynamic metrics of ecosystem response; process-related indicators have special value. Indicators that compare and discern responses of ecosystems to natural and human-induced drivers (e.g., fishing, contaminants, habitat degradation) and can serve as management reference points will be important in development of marine ecosystem-based management plans.

2.3: Understanding how ecosystem properties regulate ecosystem response to changes at the top and bottom of the food web.

There is a critical need to advance our ability to predict how top-down and bottom-up responses will propagate through the trophic web and to quantify the magnitude of their impacts at each trophic level. Are there general rules based on aspects of the structure and function of marine ecosystems that allow us to predict ecosystem responses from the top-down, bottom-up, or combined forcing? Can we identify which types of ecosystem are responsive to either top-down or bottom-up forcing? Is there a minimum proportion of apex predators that should be maintained in an ecosystem to reduce adverse effects on the ecosystem of top-down forcing?

2.4: Understanding the temporal and spatial scales of ecosystem response to perturbations, and how they differ among ecosystems.

The state of an ecosystem is a result of a balance between a myriad of processes that occur over varying temporal and spatial scales. Marine research has tended to focus on specific time frames and regions (e.g., Georges Bank, California Current System, etc.) that do not
necessarily correspond with the scales of relevant processes. The variability of a regional ocean ecosystem is an integrated response to local- and basin-scale environmental changes that occur over both short- and climate-scale time frames. To measure an ecosystem response to external or internal forcing, or a change in ecosystem state, the spatial domain of the ecosystem and the frequency of observations must be defined relative to key physical, chemical, and biological processes that underlie ecosystem structure and function. For example, some processes, such as the timing of spring blooms or harmful algal blooms, are episodic, whereas other processes, such as ocean warming, occur slowly over decades. El Niño-Southern Oscillation events strongly impact ecosystems over time scales of one to two years, while other atmospheric-ocean oscillations (e.g., the Pacific Decadal Oscillation) operate over longer time scales and may lead to regime shifts (Hare and Mantua 2000, Mantua 2004).

Understanding the spatial and temporal scales of ecosystem responses, how they differ across ecosystems, and identifying relationships between ecosystem type (e.g., upwelling, coral reef, offshore banks) and the spatial scale of the response is needed if managers are to develop appropriate support tools and regulations that protect marine resources.

2.5: Determining the role of diversity in ecosystem state transitions and testing theory against real systems.

The associations between diversity, productivity and resilience of ecosystems are important considerations for conserving, harvesting, and managing marine resources (see Case Study 2: State shifts in Caribbean coral reef systems). These links are two-way: productivity, an ecosystem function, as well as resilience, a description of ecosystem response to perturbation, both depend on and drive changes in the diversity of the system. Various approaches to conservation, such as effort limitation or protected areas, have the potential to produce different patterns of diversity, different stock levels available for harvest, and different responses to other perturbations, such as climatic changes and eutrophication. At the center of these interactions is the question: what is the role of diversity at different ecological levels (population, community, ecosystem) in determining resilience and ecosystem structure?

A critical management concern is “restoration” of individual species, yet there is emerging evidence that, for some ecosystems, resilience may be a property expressed at the community rather than individual species or population level. For example, even if diversity returns to previous levels, the original species composition might not return, leading to “resilience without restoration” (Gifford et al. 2009). At the community level within or across taxa, the system may be considered resilient, but at the population level it may appear to have crossed some threshold or tipping point. Therefore, studies that investigate state shifts at ecological scales are critical to our understanding of resilience. In particular, we need to understand how state transitions at the population level fit into changes at the community and ecosystem level. For example, if total production remains the same, a transition in dominance between fish species may signal resilience at the level of the fish community or trophic level, but not at the population level. Furthermore, we need to determine the consequences of resilience at these different levels for a range of management priorities. Community resilience may be an appropriate measure for some aspects of conservation, whereas persistence of populations of particular species can be considered essential for fisheries.

Using comparative analyses to understand what controls patterns of biodiversity and testing the effects of biodiversity on the stability and resilience of an ecosystem in response to disturbance, is a priority research area. Knowing whether societal choices in target fisheries can
be changed to improve diversity, productivity and, especially, the resilience of the managed system is critical to ecosystem-based management.

A major challenge to understanding the applicability of state transition theory is connecting the theory to data from real ecosystems. The applicability of our current model-based understanding of state transitions, stability and resilience to actual ecosystems is controversial (Holling 1973, Petraitis and Dudgeon 2004) and limited by the long temporal scale necessary for data-driven confirmation of theory (Scheffer at al. 2009). Understanding the sustainability and resilience of marine ecosystems to the long-term effects of human activities, and identifying appropriate approaches to ecosystem restoration, are critical for effective ecosystem management. Key questions include: When do alternate stable states and hysteresis apply to managed marine systems? How do we determine whether an ecosystem is in an alternate stable state, or recovering slowly from a state transition caused by environmental conditions? (see Case study 3: Multiple independent stresses, not alternative stable states in the Black Sea ecosystem).

In addition to the recovery of a previous state, a scientific understanding of state transitions could also inform the potential for management to avoid state shifts. Is it possible to anticipate shifts between states, and if so, how? Recent simulation studies suggest that increases in variance and autocorrelation may serve as indicators of incipient regime shifts (Scheffer et al. 2009; Biggs et al. 2009). However, both the ability to anticipate shifts to detect shifts once they have occurred, rely on the ability to distinguish state shifts from background noise. Are there signatures of a state shift that distinguish it from stochastic processes? In other words, we need improved theoretical and observational methods to assess the probability of state transitions occurring. At present we can see such shifts only a relatively long time after the event, and only for relatively simple switches. Management requires earlier prognoses for more complex situations. Developing practical methodology for detecting the proximity of an ecosystem to a threshold or regime shift, is a potentially important area for future research.

THEME 3: HUMAN DIMENSIONS

*What is the nature and extent of the feedbacks and interactions between humans and marine ecosystems?*

Because human activities can strongly influence marine ecosystem dynamics and because human actions can be managed, understanding the coupled human-marine ecosystem is central to CAMEO’s mandate of supporting research that contributes to ecosystem-based management. CAMEO supported research, including the human dimension, should lead to a better understanding of the multiple ways in which human interactions with the oceans affect marine ecosystem structure and function, and provide insight into effective management strategies. Disciplines that explicitly make links between changes in human and natural systems, such as marine governance and the resultant impacts on marine ecosystems, are currently a priority for the CAMEO program. In the longer term, CAMEO is intended to address two-way interactions between the services provided by natural ecosystems and the impacts on multiple dimensions of human society.
The Northwest Atlantic codfish collapse (see Case Study 5: Coupled human-resource transitions in cod-dominated ecosystems in Canada) provides an example of how the dual drivers of fishing and climate altered a marine ecosystem, and how this altered the human society that depended upon it. The depletion of cod stocks due to fishing and climate influences, lead to a shift to higher value shrimp and crab fisheries, which resulted in major differences in who participated in the fishery. This not only changed the distribution of wealth but set up economic incentives that currently inhibit attempts to restore cod populations. Better understanding of the links between fishing, the effects on living marine resources and the implications of these changes for fishing communities might have resulted in a more equitable and sustainable fishery.

Managing the influence of human dominance on marine ecosystems requires an understanding of the interactions and feedbacks among human decisions and natural system responses. Key concepts are the coupled social-ecological system, (e.g., the ecosystem, fishery and fishing community) and the effects of different management approaches on ecological and social outcomes (e.g., biomass, landings, biodiversity, fishing efficiency, equity, and accountability) (Ostrom 2009). The features of governance systems (e.g., property rights systems, operational rules), user groups (e.g., social heterogeneity, leadership), and resource units (e.g., economic value, behavior of lobster) that give rise to different ecological and social outcomes can be quantitatively or qualitatively assessed using well-developed methodologies (Ostrom 2009). Improved understanding of coupled social-ecological systems (Ostrom 2009) is heavily dependent on comparative analyses (Liu et al. 2007a). One important element is to understand whether human-natural couplings are direct and local or indirect and global – this distinction can be key in influencing human responses (Ostrom 2009).

The associations between human interventions (e.g., conserving, harvesting, and regulation) and diversity, productivity, and resilience are a special focus of CAMEO. Marine ecosystem resilience, for example, can be a function of human behavior, which is in turn affected by governance institutions such as government, science, business, family, and community. More generally, research integrating the biophysical and social sciences at an academic level with agency mandates is essential to the development of ecosystem-based approaches to management of marine resources.

**Scientific Challenges**

3.1: Understanding the relative importance of anthropogenic and natural controls on the transition dynamics and determinants of resilience in coupled human-natural systems.

A goal of marine ecosystem-based management is often to implement “ecologically sustainable fishing,” a management approach that allows the persistence of a particular ecological state and the sustainable delivery of the ecosystem services associated with that state (Zabel et al. 2003). Defining and understanding the resilience and persistence of a system depends on careful consideration of appropriate spatial and temporal scales. The spatial scale can extend from a small coral reef, through a marine protected area (MPA) to a large marine ecosystem (LME), while the governance scale can span local, national, and international jurisdiction. Understanding the relevant spatial scales of both the marine system and the human system is necessary to compare the attributes and mechanisms that determine resilience. Finally, determination of whether a state shift has occurred, as opposed to delayed but eventual recovery from a perturbation, requires implementing a study at a time scale that is appropriate to the ecological system and the scale of perturbation.
The framework of complex adaptive systems may be useful for defining resilience in the context of state shifts. This framework can be used to understand the dynamics of state transitions in marine ecosystems, but also to inform ecosystem-based management when considering the coupled human-natural system as a complex adaptive system (Levin and Lubchenco 2008).

Increasing the organizational scale from natural ecological systems to dynamically coupled human-natural systems raises a unique set of questions. Given the variety of anthropogenic and natural influences on the state of ecosystems, changes in one forcing function can substantially influence the resilience of another, with state shifts being more likely given multiple perturbations (see Case Study 3: Multiple independent stresses, not alternative stable states, in the Black Sea ecosystem). A fundamental question is: what is the interaction between multiple anthropogenic and natural forcing functions in determining possible ecosystem states and resilience?

When considering the dynamics of coupled human and natural systems, the management approach can influence the resilience within and across both human and ecological sides of the system (see Case Study 5: Coupled human-resource transitions in cod-dominated ecosystems in Canada). For example, some management approaches [e.g., spatial planning in the form of a marine protected areas, (MPA)] might enhance the resilience of the ecological system to natural perturbations, and management approaches that allow tight feedback between ecological changes and management adjustments might reduce the chance of anthropogenically-driven state shifts.

We need to understand the effects of alternate management strategies on resilience at the population and community levels, in both marine and human systems. For example, it is likely that marine protected areas, gear restrictions, catch limits and catch shares will have different consequences for resilience of marine populations and communities. Similarly, different governance structures will affect the resilience of the coupled human-natural system in different ways. An important question is: How is the likelihood of achieving “ecologically sustainable fishing” influenced by the relationship between the spatial and temporal scales of management and those of the coupled human-natural system that characterizes a fishery?”

3.2: Determining how human activities alter the benefits humans receive from marine ecosystems (i.e., value of ecosystem goods and services).

Understanding the linkages between changes in marine ecosystem functions and changes in ecosystem services—values humans get from ecosystems—is critical to understanding the ability of marine systems to support multiple human needs (Barbier et al. 2008, Aburto-Oropeza et al. 2008, Palumbi et al. 2009, Lester et al. 2010). Ecosystem services from marine systems include provisioning of food from wild-caught fisheries or aquaculture, protection offered by biogenic habitats from coastal erosion or inundation, energy generation, recreational activities such as surfing, SCUBA, and beach-going, and supporting services such as water purification, carbon storage and sequestration, and biogeochemical cycling (Peterson and Lubchenco 1997). Few studies have quantified how changes in marine ecosystem processes give rise to changes in the value of services provided (e.g., Sanchirico and Murumby 2009). For example, quantifying how human activities change marine habitats and food webs—which in turn changes fishery landings, wildlife viewing opportunities, and shoreline buffering from storms—can improve our understanding of what benefits ecosystems are capable of producing under different states. Comparing changes in ecosystem services due to climate or human
activities across multiple ecosystems will improve our mechanistic understanding of the linkages among such drivers.

Valuation methods are relatively well developed for goods traded in markets (e.g., fisheries), but methodologies are in their infancy for valuing other marine ecosystem services humans care about, such as recreational activities in different locations or aesthetic and cultural values (NRC 2005, Wilson and Liu 2008, Wainger and Boyd 2009). Developing methodologies for non-market ecosystems service would provide managers with a way to evaluate the tradeoffs inherent in ecosystem management.

3.3: Understanding how humans respond to changes in marine ecosystems and how their responses affect ecosystem structure and function.

Comparing governance systems, their effects on human use patterns, and the resulting effects on ecosystem attributes (e.g., productivity, biodiversity) can shed light on whether governance reform will contribute to ecosystem recovery and sustainability. Governance refers to “the formal and informal arrangements, institutions, and mores which determine how resources or an environment are utilized, how problems and opportunities are evaluated and analyzed, what behavior is deemed acceptable or forbidden, and what rules and sanctions are applied to affect the pattern of resource and environmental use” (Juda 1999). Similarly, analyses of regulatory systems and the resulting human use patterns can illuminate similarities and differences in ecosystem response and organization (Murawski et al. 2010, Table 1). For example, it is not well understood how particular approaches to fisheries management, such as marine protected areas or catch-share programs, will work in marine ecosystems with different properties. Conversely, determining how different approaches to fisheries management function in marine ecosystems with similar properties can highlight promising fishery management options. Comparing place-based systems, such as short-distance fisheries or spatial regulations (protected areas, area licenses), with highly mobile, large scale fishery systems in similar marine ecosystems or in different areas of the same marine ecosystem can illuminate whether couplings between human and natural components of a marine ecosystem are direct and local or indirect and global. The scale of such relationships can be a key factor influencing how humans respond to signs of change in the ecosystem.

How human activities, such as fishing, respond to ecological changes is poorly understood. However, the economic implications of spatial-dynamic processes at various scales have been developed in theory, showing how connectivity and related processes such as dispersal rates affect the fishing sector under different conditions of access and control (Smith et al. 2009, Sanchirico and Wilen 2007). Economics and institutional arrangements in turn feed back into the ecological system through the redistribution of harvesting effort in space and time, but very little comparative work on these dynamics in different ecosystems has been done. Human movement among ecosystems can take place very rapidly, outpacing regulatory efforts, and with significant ecological consequences, as shown in the history of sea urchin exploitation around the globe (Berkes et al. 2006). Accordingly, studies of marine ecosystems that incorporate coupled human-natural phenomena and account for the connectivity implications of regional and global movements of people, material, and information, will greatly improve our ability to predict the outcomes of coupled human-natural systems.

Recognition of biophysical transitions such as regime shifts in marine ecosystems (see Theme 2: Responsiveness to Perturbations) has highlighted the importance of exploring how fishing effort and climate may contribute not only to ecological impacts, but also social and
economic consequences of regime shifts. For example, such comparative analyses can be used to generate system-level indicators of “regime shift risk” to combined climate and fishing pressures (Kenny et al. 2009).

Examining the environmental, economic, informational, and governance conditions which lead to “adaptive” responses by fishing fleets, industries, and/or management systems can provide insight into the obstacles to resilience in complex adaptive systems. For example, comparing “data-poor” marine ecosystems with those where data are better or perceived as more trustworthy will highlight the types of information and knowledge most critical for marine ecosystem-based management. Comparisons among ecosystems where marine resource-dependent communities are poor, as in much of the developing world, versus those where they have more resources, including alternative livelihoods, will elucidate the degree to which economic status affects the ways that human communities respond to environmental change and hence the adaptive capacity of the coupled system. For instance, systems with strong El Niño effects and frequent experience with them may have more socio-economic and governance capacity for adaptive response than systems that are experiencing incremental and novel effects of climate change.

Comparative studies of marine ecosystems can be furthered by analyses of the coherence between key bio-physical features and the governance structures. This includes political jurisdictions (i.e., whether international boundaries or state-federal distinctions exist and are appropriately dealt with), legislative mandates (i.e., whether appropriate laws exist, the gaps and overlaps that occur, Ekstrom et al. 2009), and how institutions structure the incentives for behavior (including the large topic of property rights, Sutinen ed.) 2000). Particular approaches to marine ecosystem management, such as ocean zoning, marine protected areas or limited access and catch share programs can be analyzed as governance components of marine ecosystems. Various approaches to conservation, such as effort limitation and protected areas, have the potential to produce different patterns of diversity, different stock levels available for harvest, and different responses to other perturbations, such as climatic changes or eutrophication. Our understanding, derived from both empirical and modeled results, of regulatory systems and their effects on human use patterns and ecological systems, includes significant gaps that need to be filled. Theory is well developed for the extremes of open access and full private property, but the real world and policies involve complex variations between those extremes.

### THEME 4: COMPARATIVE SYNTHESIS AND FORECASTING

**How can new analytical approaches improve synthesis and forecasting in marine ecosystems?**

The goals and characteristics of the CAMERO program will require the development of novel analytic methods. These include advances in quantitative modeling and statistical analysis that foster the comparative approach in its application to ecosystem-based management. The broad scope of CAMERO’s ecosystem-based approach implies a need to expand the types of analytical methods and quantitative models that have traditionally been used to provide strategic and practical advice.
The expansion from the traditional single populations of fisheries science to include the ecosystem, and also to include adaptive human interactions (see Theme 3: *Human Dimensions*) has two broad implications. The first is that advances in modeling approaches will be needed, such as fully integrated or "multi-models" (Gross and DeAngelis 2002) that link radically different kinds of models, including models downscaling of climate change predictions, models of ocean currents, chemistry, and temperatures, and models of trophic interactions, individual fish populations, and human actions. Multi-modeling is still in its infancy, and the mix of mathematics, statistics and computational methods still needs to be developed. *Therefore, CAMEO is expecting to support work that develops and tests complex multi-component models that span different levels of ecological processes (e.g. biogeochemistry, physical oceanography, predator-prey, fisheries and economics).*

The second implication is that such an expansion to large models, or multi-models, can add complexity in an almost open-ended way, which can lead to a dramatic rise in the uncertainty of predictions (Yodzis 1988), particularly when model parameterizations are not constrained by formal statistical fitting or even "tuning" to past dynamics. Moreover, Punt and Butterworth (1995) demonstrated that the predicted impact of a management action (the culling of seals) was highly sensitive to aggregation of model components, indicating either positive or negative effects on the intended policy goal (fishing yields), depending on how components were aggregated. This poses a fundamental problem for generating ecological forecasts for marine ecosystems. Because of the uncertainties in predictions of complex systems, CAMEO is interested in the development of effective approaches that contribute to reducing these uncertainties. These approaches may come, for example, from methodologies of ecosystem comparison, advances in mechanistic modeling, or advances in statistical techniques for both estimating parameters and extracting other relevant information from data.

The ongoing advancement of statistical methods – fostered in part by improvements in computing power – provides an opportunity to identify, develop, and apply novel statistical methods to the comparative analysis of marine ecosystems. How to develop standardized, powerful and unbiased procedures that can best identify the contribution of individual human activities to ecosystem responses in a comparative framework is an important area of work. The challenge lies in separating true effects from confounding effects that result from uncontrolled comparisons across temporal and spatial scales. Integration of statistical and machine learning methods with modeling may benefit from a greater standardization and uniformity in the way fundamental biological processes are modeled.

Many models of marine ecosystems exist, but it has been pointed out that there is a general “lack of a common set of parameterizations of fundamental biological processes” in these models and this “hinders progress in simulation skill, reliability, and predictability” (Tian 2006). For example, a fundamental feature of food web models is the functional response, which relates feeding rates of predators to prey and predator densities, yet Jeschke *et al.* (2002) identify over 40 forms of this relationship that have very different implications for the dynamics of populations of predators and prey.

The comparative synthesis and forecasting approach also relies on developing and using key indicators, both biological and physical, that track the marine ecosystem state when direct observations of a specific ecosystem component of interest are impossible or difficult to attain. The development of new ecosystem indicators relies heavily on understanding the dynamics underlying the statistical links between the indicators and the ecosystem variables of interest.
**Scientific Challenges**

4.1: Developing new ecosystem modeling strategies that increase our ability to synthesize and predict marine ecosystems states.

The current state of ecosystem modeling suggests a tension between the need to include essential process realism and the ability to forecast change in marine ecosystems. Past experience in food web modeling (e.g., Yodzis 1988) suggests great difficulty in predicting even the directional effects of change in a driver (e.g., temperature increase, fishing pressure decrease) on a particular species through simulation modeling involving a large number of components. This creates a dilemma. On the one hand, ecological realism demands that some level of complexity be included in a model of an ecosystem (e.g., Logan 1994). In addition, it may be essential to include spatial extent and heterogeneity, to model physical conditions such as currents, or to couple ecological models with economic or social models that have key feedbacks on marine ecosystems, to capture crucial mechanisms that ultimately determine the ecosystem response. Without them, phenomena of key concern, such as regime change or resilience to change, propagation of top-down and bottom-up effects, or the effects of spatial heterogeneity and connectivity, may be missed. On the other hand, models that are highly complex may create a false sense of realism (May 2004). The inclusion of greater complexity also leads to greater uncertainty (e.g., Yodzis 1988, Fulton et al. 2003).

This dilemma occurs not only in the modeling of marine ecosystems, but is a universal problem in the modeling of ecological and biological systems. For this reason, a great deal of attention has been given to finding ways to avoid both the perils of oversimplicity and overcomplexity. Modelers in all fields of biology and ecology are seeking to find an intermediate zone of model complexity, called the ‘Medawar zone’ in honor of the biologist Peter Medawar, who called attention to the problem of finding the right level of model mechanistic complexity (Grimm et al. 2005). Predictability is a balance between a highly detailed description and a simple description. There is a tradeoff between realism of mechanisms and multiplication of uncertainty.

As the above considerations indicate, avoiding the uncertainty associated with attempting to model all relevant aspects of ecosystem dynamics, requires compromises and simplifications. Detailed structures of biological populations are idealized by considering only key species, or by grouping species when their functional and behavioral traits appear similar. The challenge is to take those aspects that are (approximately) known, and to build a formulation that still enables the extraction of new results and understanding. Numerous approaches to the aggregation of individual species into trophic levels or functional groups (i.e., a group of several species with common prey and predators) have been used, but improvements in the methodology are still needed. Given the centrality of multispecies trophic models and current modeling approaches to ecosystem-based management, comparisons of different approaches to modeling marine food webs, including aggregative techniques, are important (Hollowed et al. 2000, Whipple et al. 2000). Appropriate methods of aggregation should facilitate application of common models across different ecosystems (Link et al. 2010).

4.2: Developing statistical and analytic methods that can extract information from existing observations and which lead to better estimates and forecasts of marine ecosystems states.

Observations of ecosystem variables are often unable to constrain the state and functions of a given marine ecosystem. Combining existing observations with modeling
techniques is necessary to improve the models and to estimate the ecosystem state. Estimating the state of a marine ecosystem is critical to initialize the ecosystem forecast models. Due to the high degree of non-linearity in the ecosystem dynamics, common data assimilation methods that combine observations with “linearized” versions of the ecosystem dynamics may have limited success in estimating ecosystem functions and states, and in initializing the forecast models. Novel approaches, however, are being developed in ecology and related fields that have potential to deal with complex, non-linear systems.

An important aspect of modeling marine ecosystems involves advances in statistical and empirical modeling. New statistical methods are continually being developed to make more effective use of available data, such as drawing inferences from comparative studies or making better estimates of model parameters. For example, Bayesian approaches have been applied to estimate model parameters (e.g., van Oijen et al. 2005) and relationships, such as functional responses (Bailey et al. 2010). Bayesian calibration is especially useful, as it applies to models of any type or size. It provides not only parameter estimates, but also measures of uncertainty and correlation among the parameters. The predictive uncertainty of the model can be quantified by running it with different parameter settings, sampled from the posterior distribution. One can also evaluate the posterior probability of the model itself (rather than that of the parameters) and compare that against the probability of other models, to aid in model selection or improvement. Bayesian approaches are being used in large-scale modeling in ecology and related sciences, and further advances in the approach are likely, e.g., Bayesian belief networks as applied to the analysis of large complex ecosystems (Hosack et al. 2008).

Statistical advances are also needed in the analysis of time series data, which can help identify causal connections. Sugihara and May (1990) developed pioneering methods of nonlinear time series analysis involving a flexible nonparametric structure (see also Sugihara 1994). These methods underlie the approach used by Hseih et al. (2005) described earlier. Hierarchical state-space models (Cressie et al. 2009) offer promise in revealing underlying processes that dictate the dynamic behavior of ecological systems. One of the key uses of statistics, in combination with mathematical or computer models, will be to reveal the proximity of possible major regime shifts in ecosystems (see Theme 2). Mathematical and computer simulation models may indicate that certain temporal patterns in the ecosystem may signal an impending shift. However, picking out such signals from noise will require sophisticated methods of pattern recognition. Machine learning techniques (e.g., Recknagel 2003, Welk et al. 2008) are likely among the methodologies that will advance prediction in complex ecosystems.

Modeling approaches that address the response of ecosystems to climate and fishing induced changes in populations, ecosystem organization and ecosystem processes are a priority. Theoretical models in ecology have dealt with resistance to changes in the sizes of populations within food webs in the face of perturbations (e.g., Harrison and Fekete 1980 and many subsequent papers), and resilience, or the ability to resist regime shifts (e.g., Borrvall et al. 2000). As another example, structurally dynamic models (SDMs), which account for the changes in the model parameters due to the adaptation or the shift in species composition resulting from current changes in the forcing functions, will also be applicable in this general context (Jorgensen 2009). Studies on the effects of climatic change and fishing on marine ecosystems might ideally be tied to testing current theory or advancing theory in these areas (see both State Transitions and Stability and Responsiveness to Perturbations).
4.3: Developing modeling strategies that incorporate ecosystem and human feedbacks on the drivers, and that are applicable across ecosystems.

Ecosystems differ in spatial scale, physical conditions, trophic structure, human impacts, and in the dynamics of species of interest, posing significant challenges to developing general models that apply across ecosystems. A full representation of differing ecosystems may involve linking a variety of different models. Difficulties can arise due to the different spatial and temporal scales that are relevant to various disciplines, differences in degrees of uncertainty of data and models, and communication problems between disciplines.

Nevertheless, linked-modeling approaches have been advocated in aquatic-ecosystem modeling (DeAngelis and Cushman 1990, Crockett 1994), in part because a major advantage of linked modeling is that well-accepted models for specific processes can be used. For example, Saito et al. (2001) and Hanna et al. (1999) linked a two-dimensional hydrodynamic model (CEQUAL-W2) with a bioenergetics model and a food web-energy transfer model to investigate effects of revised dam operations on the upstream reservoir ecosystem of Shasta Lake, California. Different model types have also been linked in marine ecosystems, including hydrodynamic and food web models (Lynch et al. 2009). Numerous models include some human component (see the Human Dimension), e.g., Duarte et al. (2003). Human components of models may need to be expanded to whole submodels, in which humans react adaptively to changes in the marine system.

Hybrid modeling methods are approaches that can be useful in linking models. These approaches are being used where, for example, individual-based modeling (IBM) is employed for higher trophic levels, while a state variable model is employed from other components. That is, fish populations of interest, are modeled using IBMs, but are coupled to traditional state variable nutrient-phytoplankton-zooplankton-detritus (NPZD) models that provide the prey fields. Hybrid approaches in the marine environment to date have focused on larval fish (e.g., Hermann et al. 2001).

Other concepts from theoretical ecology, such as macroecological relationships, can be combined with food web approaches. Progress in the theoretical area of macroecology is providing ways to simplify marine ecosystem models, while still simulating the key processes, especially energy flow. The main idea is to predict the energy flow to the higher trophic level consumers. This can be done using a minimal level of knowledge on temperature, size spectra of organisms, and primary production. The size spectrum of organisms allows one to determine the trophic structure, and theory from macroecology provides relationship between body size, temperature, and metabolism. From this information, energy reaching top consumers can be estimated. This approach does not provide precise information for a given marine ecosystem, but can provide estimates of global patterns of production of higher trophic levels (e.g., Jennings et al. 2008).

Spatial upscaling of models can be used to extend local measurements to spatially extended models. One of the most fundamental issues of modeling at the level of whole ecosystems is how to scale up from measurements at small spatial scales to the much larger scales that are often of interest. Simple scaling can lead to errors in estimates of such quantities as primary production and carrying capacities (Duarte et al. 2003). Progress in upscaling is being made in many areas of ecology (e.g., Bugmann et al. 2000, Wirtz 2001), and further innovative approaches will be needed to improve our ability to compare across ecosystems.
SUMMARY

The CAMEO program has emerged from the past several decades of coordinated marine ecosystem research programs that have increased our ability to describe processes and model aspects of marine ecosystems. For example, GLOBEC was initiated to understand how global change affects the abundance, diversity and productivity of marine populations comprising a major component of oceanic ecosystems. GLOBEC has provided an important focus on phytoplankton to zooplankton production dynamics. CAMEO research will build on work started under programs like GLOBEC to include higher trophic levels and more connections the food web with a specific focus on climate and fishing as drivers of ecosystem change. CAMEO, by employing a comparative and synthetic approach, will build on the work of previous and other current programs to extend our understanding of the structural and functional attributes of marine ecosystems that support their diversity and resiliency.

Collaboration and coordination with other existing programs is an important aspect of the CAMEO program. To achieve the goal of CAMEO will require multifaceted research and resources beyond this single program. In recognition of the other existing programs with related elements at NSF and NOAA, CAMEO will encourage connections but will not duplicate existing programs. At NSF these existing programs include but are not restricted to: ocean acidification, harmful algal blooms, ecology of infectious disease, coupled human and natural science and ocean ecology associated with biogeochemical cycles. Additionally, CAMEO will not explicitly request development or assessment of Decision Support Tools for management because other NOAA programs (Integrated Ecosystem Assessment, Fisheries and the Environment) have this role. But it is entirely appropriate for CAMEO to facilitate transfer of fundamental scientific information generated research to managers and to consider effective means to do so.

The CAMEO program supports research in which similarities and divergences among and within ecosystems are evaluated to provide insights into marine ecosystems relevant for management and policy. CAMEO research will focus on the science that underpins ecosystem-based management of marine species, habitats and ecosystems, and will likely involve multiple trophic levels. The program has an explicit emphasis on exploited ecosystems and species, and addresses processes affecting higher trophic levels (e.g., beyond zooplankton) and/or multi-species interactions. Moreover, the CAMEO program will strengthen our understanding of marine ecosystems and their intersection with human society at temporal and spatial scales that are relevant to management of ecosystems. The CAMEO program will lead to greater understanding of marine ecosystems and thereby improve our ability to predict ecosystem responses to climate and human-related perturbations.

Central to the program is an emphasis on collaborative partnerships between academic research communities conducting basic science and federal agency scientists with mission responsibilities to inform ecosystem management activities. NSF and NOAA will jointly provide funding for federal and academic scientists to collaborate, share existing data sets, and develop new empirical studies and mathematical approaches which will inform model development and evaluate their predictive capability.
SCIENCE STEERING COMMITTEE

The Science Steering Committee has been assembled to provide guidance to the agencies in identifying, prioritizing, and focusing scientific challenges for the CAMEO program. Active scientists will have the best perspective on which are cutting edge research areas and where gaps in knowledge or research tools exist.

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CASE STUDY 1: DEFINING METRICS FOR CROSS-Ecosystem COMPARISON: THE NETWORK ANALYSIS APPROACH.

Relevance to CAMEO: This case study illustrates the importance of developing ecosystem metrics to provide a basis for comparison across ecosystems comprised of different species.

All ecosystems have unique species assemblages and biophysical forcing processes that dictate their dynamics and organization. This distinctiveness poses challenges to developing standardized metrics for comparison across ecosystems, and thus, quantitative cross-ecosystem comparison has historically been limited. A crucial component of cross-ecosystem analysis is the identification of relevant metrics that speak to important structural or functional attributes of ecosystems and while being comparable across ecosystems. Network analysis of ecosystem models provides one salient example of how ecosystem organization can be compared across ecosystems using quantitative metrics. Here we describe the application of this particular tool to illustrate usefulness of developing comparable ecosystem metrics.

Baird and Ulanowicz (1993) applied an analysis of network models of four estuarine ecosystems to evaluate their hypothesis that more highly disturbed systems would exhibit properties that were indicative of stress. Unlike their earlier work (Baird et al. 1991), these comparisons were drawn among similar ecosystem types (estuaries) so that differences among systems could more easily be attributed to the physical attributes or degree of anthropogenic disturbance (nutrient and other pollution and altered freshwater flows) in each estuary. The ecosystems used in this comparison were: the Ems estuary, a relatively undisturbed ecosystem exhibiting little evidence of eutrophication, the Swartkops and Ythan estuaries, which were considered impacted by pollution from sewage, industrial and agricultural activities, and the Kromme estuary which had been altered through diversion of freshwater inputs.

Baird and Ulanowicz (1993) used data on standing biomass and rates of energy flow within and exported from the estuaries to parameterize network models for each ecosystem. By using a common model framework, they could compare multiple network metrics that described the patterns of energy flow in ecosystems. These comparisons revealed relationships between structural and functional attributes of the ecosystems and the relative extent of human impact. These metrics included trophic efficiency (how much energy contained in one trophic level is transferred to the next highest level), average path length (the average number of transfers a unit of carbon will undergo until it leaves the ecosystem), energy retention, plus several measures of “global ecosystem organization” that account for the rates and organization of flows within each ecosystem.

This analysis revealed relatively similar structures among the four ecosystems, but very different patterns and pathways of energy cycling (Table CS 2.1). They concluded that:

1. The efficiency of energy transfer – especially among mid and upper trophic levels – was markedly different among the ecosystems.
2. Relative importance of phytoplankton vs. macroalgae was variable and was likely a consequence of differences in water depth among ecosystems.
(3) The Ems estuary was characterized by the greatest number of cycles and the highest overall trophic transfer efficiency.

(4) The Swartkops estuary exhibited network properties that were most consistent with predicted patterns of a disturbed or stressed estuary.

One limitation of this comparative analysis is that results are correlative in nature and more than one set of hypotheses might explain the observed differences among ecosystems. The four study estuaries provided contrasts not only in the relative degree of anthropogenic disturbance, but also differed in latitude, and other physical attributes. Still, this type of comparison suggested several hypotheses to explain differences in ecosystem structure between study estuaries and provided a theoretical underpinning for future empirical studies aimed at understanding ecosystem-level impacts of human activities. CAMEO projects will undoubtedly develop other metrics or indices that can foster comparative analysis of marine ecosystems.

**Table CS 1.1. Comparison of network attributes across estuarine ecosystems.**

<table>
<thead>
<tr>
<th>Network Attribute</th>
<th>Ythan</th>
<th>Swartkops</th>
<th>Kromme</th>
<th>Ems</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Total ecosystem flow in cycle of 1 path length</td>
<td>163.9</td>
<td>80</td>
<td>61.9</td>
<td>61.8</td>
</tr>
<tr>
<td>Mean cycles / nexus</td>
<td>1.4</td>
<td>1</td>
<td>1.11</td>
<td>15.3</td>
</tr>
<tr>
<td>Average path length</td>
<td>2.86</td>
<td>3.95</td>
<td>2.38</td>
<td>3.42</td>
</tr>
<tr>
<td>Number of cycles</td>
<td>15.1</td>
<td>14.6</td>
<td>19</td>
<td>26</td>
</tr>
<tr>
<td>Trophic efficiency (geometric mean, %)</td>
<td>6.64</td>
<td>4.02</td>
<td>6.02</td>
<td>12.49</td>
</tr>
<tr>
<td>Relative ascendancy (%)</td>
<td>34.4</td>
<td>28</td>
<td>33.7</td>
<td>38.3</td>
</tr>
<tr>
<td>Total cycled flow (mg C m⁻² d⁻¹)</td>
<td>2389</td>
<td>7679</td>
<td>4378</td>
<td>390</td>
</tr>
<tr>
<td>Total system throughput (mg C m⁻² d⁻¹)</td>
<td>9350</td>
<td>17541</td>
<td>16879</td>
<td>1298</td>
</tr>
</tbody>
</table>
**CASE STUDY 2: STATE SHIFTS IN CARIBBEAN CORAL REEF SYSTEMS**

*Relevance to CAMEO:* This case study illustrates the importance of comparisons in time and across systems to understand the potential for state transitions in ecological systems, ecosystem responses to perturbations, and the role of food web connectivity in structuring ecological systems.

Transitions between coral-dominated states and macroalgae-dominated states in tropical reefs are driven by a series of factors and occur over intrinsic time scales. For example, in Jamaica, a series of events caused a shift from the historical coral-dominated state to a macro-algae dominated state (Hughes 1994). First, harvesting reduced the diversity of herbivores from a heterogeneous complex of fish and invertebrates to one primary herbivore, the sea urchin *Diadema antillarum*. Second, a disease outbreak substantially reduced *D. antillarum* densities. Third, hurricanes reduced coral densities. At that point, low herbivore density allowed unchecked growth of macroalgae. The resultant macroalgae-dominated reef has the potential to inhibit future coral recovery by reducing coral recruitment.

This classic example illustrates a number of key properties of state transitions, including the role of diversity (in this case, herbivore species richness) in determining the resilience of an ecosystem to catastrophic events (disease and storm events) as well as the interaction between multiple natural and anthropogenic impacts (fisheries, disease, storms) in causing state shifts. In this example, a comparison across time (pre- and post-hurricane disturbance) was necessary to understand the potential for alternative ecosystem states as well as the interaction between top-down (herbivore grazing) and bottom-up (storm-dependent coral mortality) processes in structuring the ecological system and driving the overall response.

A more recent analysis by Bruno et al. (2009) that compares tropical reef systems globally, allows exploration of the extent to which results from Jamaica are applicable to other coral reef ecosystems. Their comparison of the macroalgae cover and “phase shift index” across five tropical reef systems spanning multiple ocean basins indicates that Jamaica is unique in its persistent distinct states (Figure CS 3.1), suggesting a lower likelihood of long-lasting transitions to macroalgae dominated states than previously assumed. However, the effects of transient dynamics and the potential role of algal guilds not captured under the descriptor of macroalgae
(such as turf algae) may make it difficult to distinguish phase shifts based on macroalgae cover alone. The ongoing debate over whether coral- and macroalgae-dominated states are alternative stable states demonstrates the challenge of connecting state transition theory to data.

Our understanding of tropical reef systems and the dynamics that determine coral or macroalgal dominance in these systems has benefited greatly from the spatial and temporal comparative analysis presented in this case study. However the consequences of state transitions for reef-dependent fisheries and how island fishing communities respond has yet to be studied.

**Case Study 3: Multiple Independent Stresses, Not Alternative Stable States, in the Black Sea Ecosystem**

*Relevance to CAMEO:* This case study illustrates the importance of understanding multiple drivers and the time scale of ecosystem responses to perturbations.

The iconic example of a regime shift includes changes in a single driver and the response of a single ecosystem metric. But large marine systems are often subjected to multiple drivers, both natural and anthropogenic. Identifying the consequences of each driver, such as climate change, nutrient input or fishing, whether their actions are additive or synergistic, is critical to inform management decisions. Moreover, myopic focus on a single driver can be highly misleading and may give the appearance of breakpoints, thresholds and alternative stable states that do not exist.

The Black Sea ecosystem has been subjected to a number of changes in external forces: decadal changes in sea temperature and in nutrient input, invasions of an alien jelly fish predator on zooplankton, and increased harvest of anchovies (Oguz et al., 2008). The changes in average concentration of phytoplankton biomass provide a metric that integrates the physical, chemical and biological responses of the ecosystem to these forces.

One hypothesis is that the ecosystem has undergone a state transition in response to increased nutrient loading. Indeed, when one plots phytoplankton biomass against nutrient load (Fig. CS 4.1a), the ecosystem dynamics seem to imply the presence alternate stable states. Namely, productivity is low with low nutrient inputs, high for high nutrient inputs, and is alternatively high or low for intermediate nutrient inputs. This pattern fits the classic expectation of multiple stable states caused by changes in a single driver variable. However, by

Figure CS 3.1. A) Comparison of nutrient load with phytoplankton biomass for the years 1969-2000 indicating possible alternative states of the ecosystem, B) Representation of the changes in phytoplankton biomass in relation to changes in 2 drivers, temperature and nutrient loading (adapted from Oguz and Gilbert, 2007)
examining the response of phytoplankton biomass to the combined effects of both nutrient and temperature (Figure CS 4.1b), it becomes apparent that the perceived alternative states as a function of nutrient load are simply a response to an additional driver—water temperature.

This lesson is critical for the evaluation of dynamic marine ecosystems driven by multiple forcing functions. Exploration of ecosystem response in general, and identification of state transitions in particular, needs to rely on developing tools that can integrate and consider all plausible environmental drivers. This type of consideration is critical for bridging the gap between expectations derived from theoretical mathematical models and dynamics of real marine ecosystems.

**CASE STUDY 4: COUPLED HUMAN-RESOURCE TRANSITIONS IN COD-DOMINATED ECOSYSTEMS IN CANADA**

**Relevance to CAMEO:** This case study provides an example of the impacts of the dual drivers of fishing and climate, and the interrelationships between change in the marine ecosystem and the human society that depended on the productivity of this system.

The past few decades in Atlantic Canadian waters have shown major transitions linked to the human removal of top predators, including Atlantic cod. Canadian stocks of Atlantic cod declined precipitously from the 1980s to the recent past (Figure CS 5.1) leading to closure of most fisheries and a recent recommendation by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) that cod be listed as “endangered” on the legal list of species at risk (http://dalnews.dal.ca/2010/05/06/cod.html). Investigations demonstrated regional differences in the ecological process and consequences—in some regions seals have become top predators and in all regions forage fish have increased—but with similar net results. All systems have shifted to alternative states producing hysteresis in system behavior that is retarding recovery of depleted stocks (Bundy et al. 2010).

Collapse of groundfish populations, particularly cod, followed by closures or sharp reductions in allowable catches, had major repercussions for businesses, families, communities, and government (Shrank 2005). In Atlantic Canada the closure of the cod fisheries in 1992 was called “the greatest industrial disaster” in Canadian history. It led to lay-offs of harvesters and

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Figure CS 4.1. Time series of spawner abundance data for nine Canadian stocks of Atlantic cod (*Gadus morhua*; from Hutchings and Reynolds 2004, Figure 4, p. 304).
processing employees, large and costly government subsidies and retraining programs, and eventually the depopulation of fishery-dependent coastal communities (Shrank 2005). A concomitant increase in invertebrate fisheries off Newfoundland and Labrador and pelagic fisheries off Nova Scotia has been observed (Frank et al. 2005). It is has been hypothesized that these shifts are related to reduced predation pressure on the invertebrate and pelagic fish communities as cod and other predatory species have declined.

Because of their higher market value, catches of snow crab and northern shrimp have risen to a comparable or greater in value than the former cod fishery in Newfoundland and Labrador. Changes in landings by species type in one part of Newfoundland, the Avalon Peninsula, document the replacement of cod by crab and shrimp as major components of total fisheries value from the mid 1980s to 2000 (Figure CS 5.2). (It should be noted that by 2000 the “groundfish” in the catches were almost entirely turbot, or Greenland halibut, rather than cod. The pattern is similar today, 2010, although a small fishery for cod has resumed). The cod-to-crustacean shift eased the economics of the transition. However, income from the alternative fisheries is distributed differently among the people and places engaged in fisheries (Hamilton and Butler 2001). Crab and shrimp fishing take place further offshore, requiring more costly investments in boats and gear. The results are major regional, inter-community, and intra-community differences in human participation in fisheries (Hamilton and Butler 2001), with far fewer people benefiting. The social costs of this transition have been extremely high. Economic incentives, scientific uncertainties, and politics played major roles in the overexploitation of cod (Hutchings and Myers 1994, Haedrich and Hamilton 2000). The ability of fish harvesters and industries to shift to other and more valuable populations (crab, shrimp, and lobster) has reduced political pressure for actions that would facilitate restoration of groundfish particularly given that adult cod eat crustaceans. It has also proved difficult to assign responsibility for depletion and restoration given multiple stressors (for example, temperature changes and seal predation), and continued scientific uncertainty about groundfish in marine ecosystems.
APPENDIX I: NSF/NOAA FUNDED CAMEO PROJECTS

1) BUILDING THE FOUNDATION IN N. CALIFORNIA CURRENT SHELF-SLOPE-OCEANIC ECOSYSTEMS. **Investigators: Hongsheng Bi (OSU) and William Peterson (NOAA)**

Researchers will develop qualitative and quantitative ecological indicators to forecast the survival of salmon, hake, sardine, and sablefish populations off the coasts of Washington and Oregon. A broad suite of data streams including satellite altimetry, winds, SST, and color and in situ data from cruises (hydrography and plankton) and moorings will be used to improve upon our existing forecasting capability. Researchers will also compare zonal and latitudinal gradients in ecosystem structure, connectivity, and resilience.

2) ROLE OF PREDATOR-PREY INTERACTIONS IN MARINE ECOSYSTEM ORGANIZATION: DEVELOPMENT OF A NEW TOOLBOX AND A COMPARISON OF KEY INTERACTIONS IN THE BERING SEA AND GULF OF ALASKA ECOSYSTEMS. **Investigators: Lorenzo Ciannelli (OSU), Kung-Sik Chan (UI), Kevin Bailey, (NOAA), Kerim Aydin (NOAA)**

Researchers will investigate key trophic interactions in the Bering Sea and Gulf of Alaska, regions at similar latitudes with greatly contrasting landscapes. In particular, the project will focus on the characterization of predator-prey functional and numerical responses across scales. Results from this study are expected to have direct and immediate application in fisheries management. For example, it is expected that the predatory impact of arrowtooth flounder and adult pollock on juvenile pollock under different scenarios of climate and fishing regimes will be predicted.

3) MECHANISMS FOR LOW-FREQUENCY VARIABILITY OF FORAGE FISH: A COMPARATIVE ANALYSIS OF NORTH PACIFIC SARDINE SYSTEMS. **Investigators: Enrique Curchitser (Rutgers), David Checkley (SIO/UCSD), Christopher Edwards (UCSC), Jerome Fiechter (UCSC), Kenneth Rose (LSU), Francisco Werner (Rutgers), Bernard Megrey (NOAA), Alec MacCall (NOAA)**

The aim of this project is to understand how the physics, biogeochemistry, and biology combine to result in the various patterns of synchronous variability across widely separated sardine and anchovy systems. The main tool for this work is a model that simultaneously integrates the climate system with the lower trophic level biology, an individual-based, full life cycle model for the target fish species and a model of a fishing fleet that will represent the top predator of the system. With this model researchers will be able to evaluate the relative effects of climate variability and fishing pressure on the variability of the sardine and anchovy populations.

4) NEW STATISTICAL TOOLS FOR ANALYZING COMMUNITY DYNAMICS WITH APPLICATIONS TO MARINE ZOOPLANKTON. **Investigators: Elizabeth Holmes (NOAA), Mark Scheuerell (NOAA), Stephanie Hampton (NCEAS/UCSB), Steve Katz (NOAA), Eric Ward (NOAA), Brice Semmens (NOAA)**

Statistical modeling of long-term plankton time series has revealed important features about the dynamics and environmental drivers of plankton - the foundation of aquatic productivity. Joint research by researchers at the Northwest Fisheries Science Center (NWFSC), the National Center for Ecological Analysis and Synthesis (NCEAS) and the Channel Islands
National Marine Sanctuary (CINMS) will extend these modeling approaches to oceanic plankton datasets. This work seeks to tease out the primary environmental determinants of oceanic plankton variability and to understand how oceanic and freshwater plankton dynamics differ.

5) AN INTEGRATIVE APPROACH TO MANAGING THE DEWATERING OF ESTUARIES.

Landsapes and the water cycle are being altered by changing climate and human systems. One large manifestation of these changes is dewatering of estuaries caused by diverting freshwater flows from the coastal zone. This project will integrate social and natural sciences to create decision support tools needed to enhance managing environmental flows to estuaries. There is probably no better place on Earth to compare effects caused by altered inflow than the Texas coast, because the major estuarine systems lie in a climatic gradient where runoff decreases 56 fold resulting in a gradient where the inflow balance in estuaries ranges from strongly positive, moderately positive, neutral, to negative. We will use existing long-term observational data to predict how changes in water diversion and climatic variability influence the structure and function, and ecosystem services, of estuaries.

6) COMPARATIVE DYNAMICS OF ECOSYSTEM COMPONENTS FROM THE NORTH EAST ATLANTIC SHELF AND PACIFIC COAST: NEW APPROACHES TO FORECASTING AND UNDERSTANDING VARIABILITY AND STRUCTURE IN MARINE ECOSYSTEMS. Investigators: A. A. Rosenberg (UNH), George Sugihara (SIO), M. J. Fogarty (NOAA), Les Kaufman (BU), Chi-Hao Hsieh (National Taiwan University)

Ecosystems can be investigated by reducing the dimensionality of their complex webs to a subset of interacting variables. In this hypothetical example, three species (anchovy, squid, and copepods) appear to be uncorrelated in time even though they are functionally coupled. However, by combining their time series (each as an axis to reconstruct an attractor) their dynamic functional relationship (attractor) is revealed. Such state space (attractor) reconstruction can be exploited for short-term predictability which, coupled with medium-term scenario exploration models, can feedback into forecasting the future states of marine ecosystems.

7) CAMEO: BUILDING THE FOUNDATION: AN END-TO-END MODELING WORKSHOP.
Investigators: John Steele (WHOI), Dian Gifford (URI), Eileen Hofmann (ODU), Kerim Aydin (NOAA)

This is a schematic of possible steps relating input of drivers and data for a range of different ecosystems, to processes relevant to Decision Support Tools (DST’s). Each system can have as input different models such as NPZ (nutrient; phytoplankton; zooplankton), ECOPATH and IBM (individual based models). These are integrated to give end-to-end representations of a range of individual food webs. Researchers expect the output from a meta-analysis of these systems to be a range of metrics such as diversity indices, productivity estimates, and measures or resilience and connectivity. These should be configured so that they can support the decision making process for environmental issues.
8) A COMPARATIVE ANALYSIS OF STABILITY IN FOOD WEBS OF THE CALIFORNIA CURRENT ECOSYSTEM. Postdoctoral Fellow: Tessa Francis (NOAA NWFSC)

Successful ecosystem models of large marine ecosystems rely on an understanding of fundamental, underlying dynamics such as species interactions. Using multivariate autoregressive (MAR) time series models, I will investigate the relative importance of management actions (i.e. fishing pressure, Marine Protected Areas) versus climate drivers (e.g. Pacific Decadal Oscillation, El Niño-Southern Oscillation) on food web interactions and stability in the California Current, for example on groundfish interactions as depicted in this image.

9) TOWARD LONG-TERM ECOSYSTEM MANAGEMENT OF THE NORTHEAST ATLANTIC SHELF. Postdoctoral Fellow: Hui Liu (NOAA NEFSC)

The specification of time and space scales as well as management units is central to the development of ecosystem based management. In this project, I will conduct spatial pattern and multivariate time series analyses to identify management units referred to as functionally coupled units or groups of species that exhibit inter-related dynamics for further ecosystem modeling in the larger spatially explicit Multi-scale Integrated Models of Ecosystem Services framework.

10) COMPARATIVE APPROACHES TO PREDICTING THE CONSEQUENCES OF AN IMPENDING RE-INVASION: TOP PREDATOR EFFECTS ON CALIFORNIAN NEARSHORE FISHERIES. Investigators: Mark Carr (UCSC), Jim Estes (USGS), Tim Tinker (USGS), Phil Levin (NOAA), and Jennifer Caselle (UCSB)

The establishment of Marine Protected Areas and the impending re-establishment of sea otter populations across large portions of the California Coast create the potential for dramatic changes to kelp forest ecosystem dynamics, and fisheries yields. Researchers will employ empirical data and comparative analysis of three ecosystem modeling approaches to generate predictions of ecosystem response under the interacting effects of MPAs and otter predation. Insights gained from this study will potentially inform management decisions and help balance the conflicting objectives of protecting both sea otters and nearshore fisheries.

11) MULTISCALE MODELS OF HAWAII’S CORAL REEF COMMUNITIES. Principal Investigators: Megan Donohue (U. Hawaii) and Paul Jokiel (U. Hawaii) Eric Brown (National Park Service), Ku’ulei Rodgers (U. Hawaii), Greg Piniak (NOAA), Erik Franklin (U. Hawaii)

A key challenge in the effective management of marine ecosystems is translating from small scale studies of distribution and dynamics to the regional scale of management action. In this study, we will synthesize the available data from coral reef surveys (>1500 records from >6 entities) to generate predictive maps of coral distribution for the Hawaiian Archipelago using ecological niche modeling. Based on this distribution of coral and environmental drivers, we will use several modeling approaches to investigate the spatial dynamics of coral communities. The maps and models of coral communities will guide ecosystem based management of the Hawaiian Archipelago, resulting in significant impacts beyond the research community.
12) FISH PRODUCTIVITY AND FISHING IMPACTS COMPARED ACROSS A RANGE OF MARINE ECOSYSTEMS. Investigators: Ray Hilborn (UW), Julia Baum (SIO/UCSD), Elizabeth Clarke (NOAA), Jeremy Collie (URI), Mike Fogarty (NOAA), Anne Hallowed (NOAA), Olaf Jenson (Rutgers), Trevor Branch (UW)

This project compares the impacts of fishing across a range of marine ecosystems using a data base we have assembled of catch, stock assessment and research survey data. Key questions include (1) the response of the ecosystems to fishing pressure, (2) how to minimize depletion of unproductive fish stocks while sustainably harvesting productive ones, and (3) determining rate of stock rebuilding and factors leading to rebuilding.

13) PATTERNS OF CONNECTIVITY IN NORTHWEST ATLANTIC ECOSYSTEMS. Investigators: Thomas Miller (Maryland), Jason Link (NOAA), Jeremy Collie (URI), Michael Frisk (Stony Brook), Robert Latour (VIMS), Howard Townshend (NOAA), Michael Wilberg (Maryland)

The overall goal of our research is to understand the patterns and consequences of spatial and temporal connectivity on ecosystem structure, function and resilience. We will approach this goal by focusing our work on analyzing the properties of 10 different ecosystems that present a nested hierarchy of organization. For example are the ecosystem properties of the Chesapeake Bay similar to those of the coastal mid-Atlantic region, and are these both similar to the combined estuarine/coastal ocean ecosystem. These analyses will lead to insights about the consequences of adopting different spatial scales for ecosystem approaches to management.

14) USING INTERDECADAL COMPARISONS TO UNDERSTAND TRADE-OFFS BETWEEN ABUNDANCE AND CONDITION IN FISHERY ECOSYSTEMS. Investigators: Andrew Pershing (U. Maine), Jonathan Deroba (NOAA), Walter Golet (UNH), Jon Hare (NOAA), Molly Lutcavage (UNH), David Richardson (NOAA), Jeffrey Runge (U. Maine), Graham Sherwood (GMRI), Jason Stockwell (GMRI), Rebecca Tien (Ohio State)

Our project will investigate how changes in physical conditions such as temperature, primary productivity, and fishing affect the abundance (rounded rectangles) and condition (weight of an individual, represented by ovals) of key species in the Gulf of Maine. We will use data from the 1980s (low herring, low stratification) with the 1990s (high herring, high stratification) and 2000s (moderate herring, intermediate stratification) to fit models with and without the condition variables. By comparing the models for each period, we will evaluate the role of bottom up processes (changes in physical conditions and productivity) relative to top down forces (e.g. fishing) in shaping large-scale ecosystem changes. Our work has immediate relevance to the management of ecosystems dominated by a few small pelagic fish (i.e. herring or anchovies) and will help use predict how the Gulf of Maine will respond to climate change.
15) A NOVEL TOOL FOR VALIDATING TROPHIC POSITION ESTIMATES IN ECOSYSTEM-BASED FISHERIES MODELS. Investigators: Brian Popp (U. Hawaii), Jeffrey Drazen (U. Hawaii), Michael Landry (SIO/UCSD), Carolyn Hall (Oceanic Institute), Robert Olson (Inter-American Trop. Tuna Comm.)

Recent management efforts guided by ecosystem-based models have shown promise for reestablishing natural marine ecosystems and restoring fisheries. These mass-balance models represent trophic linkages among biomass pools based on diet however there has been no reliable independent method to validate the depiction of trophic structure in these models. We will test and apply a new stable isotopic approach, amino acid compound specific nitrogen isotope analyses, that can provide efficient, time-integrated and unbiased assessments of the trophic status of organisms across marine ecosystems.

16) DEVELOPING LINKED WATERSHED-MARINE ECOSYSTEM SERVICE MODELS TO EVALUATE COASTAL MANAGEMENT. Investigators: Mary Ruckelshaus (NOAA), Phil Levin (NOAA), Mark Plummer (NOAA), Howard Townsend (NOAA), Gretchen Daily (Stanford), Katie Arkema (Stanford), Jodie Taft (Stanford), CK Kim (Stanford), Tom Minello (NOAA)

Human activities on land affect transport of materials between watersheds and nearshore and marine systems. In most cases, management strategies aimed at providing ecosystem services such as food from fisheries and aquaculture, recreation, coastal protection from erosion and inundation, or energy generation, do not account for condition of uplands draining into coastal environments. This project will integrate watershed and nearshore/marine ecosystem process models to explore the consequences of accounting for land- and water-use management in managing for marine services.

17) Cameo: Comparatives analyses of Natural and Human Influences on Coral Reef Community Structure, Diversity, and Resilience. Investigators: Stuart Sandin (SIO/UCSD), Russell Brainard (NOAA) Jennifer Smith (SIO/UCSD), Ivor Williams (NOAA), Stewart Allen (NOAA), Stephanie Hampton (NCEAS/UCSB)

Coral reefs provide important services to people living near the coasts across the tropics, but in turn, human activities change the structure and the functioning of the reefs upon which coastal populations depend. The Coral Reef Ecosystem Division of NOAA (PIFSC) has been monitoring the coral reefs of the U.S. Pacific for the past decade, quantifying key aspects of the biology, chemistry, and physics of over 40 islands and atolls of the tropical Pacific. Our aim is to synthesize these monitoring data to gain fundamental insights into the ecology of Pacific coral reefs, with specific reference to the roles played by human stressors at the local (e.g., fishing, pollution) and global (e.g., climate change) scale. This project will couple a comprehensive set of ecosystem data with sophisticated statistical analyses to test and validate reliable indicators of coral reef health, thereby establishing clear metrics for management of this imperiled ecosystem.
APPENDIX II: DEVELOPMENT OF THE SCIENCE PLAN

The Scientific Steering Committee developed this Science Plan with input from other members of the research community. The initial concepts were developed in a workshop held at Woods Hole, MA (2009) and refined in a second workshop held in San Francisco, CA (2010). The draft plan was reviewed in a two-tiered process, with detailed review by US and international scientists nominated by the Scientific Steering Committee and further review by the open scientific community via a web-based comment solicitation process. These reviews are available from the Program Office.

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CAMEO Annual Report

Activities
1 August, 2009 – 1 January 2010

Members of the CAMEO Science Steering Committee met 24-26 August, 2009, at the Marine Biological Laboratory, Woods Hole, Massachusetts, for the first CAMEO in-person workshop meeting. The workshop was organized by the CAMEO Science Program Office, located at the Marine Biological Laboratory, Woods Hole, Massachusetts. Dr. Linda Deegan is the Director of the Program Office. Mary Ann Seifert, the CAMEO Administrative Assistant, was responsible for making meeting arrangements (travel, lodging, meeting space, reimbursement requests, etc.) as well as arranging conference calls, taking minutes at SSC meetings and distributing minutes to committee members and posting to the CAMEO Google page.

Participants in the CAMEO Workshop were: Marissa Baskett, University of California, Davis; Mark Carr, University of California, Santa Cruz; Lora Clarke, NOAA representative; Kendra Daly, University of South Florida; Don DeAngelis, USGS, University of Miami; Linda Deegan (Director, CAMEO Science Program Office and Committee Chair), Marine Biological Laboratory; Emanuele Di Lorenzo, Georgia Institute of Technology; Tim Essington, University of Washington; Mike Ford, NOAA representative; Mike Fogarty, NOAA, NMFS, Woods Hole, MA; Dave Garrison, NSF representative; Ed Houde, University of Maryland; Bonnie McCay, Rutgers University; Jeff Polovina, NOAA Fisheries, Honolulu, HI; Mary Ruckelshaus, NOAA Fisheries, Seattle, WA; John Steele, Woods Hole Oceanographic Institution; Cynthia Suchman, NSF representative.

Several topics were discussed including CAMEO’s identity, goals, project expectations, public outreach as well as the development of a CAMEO Science Plan.

The Program Office set up Google documents and calendar pages for information sharing by committee and continuously uploaded new information. Minutes of the meetings and phone calls, drafts of sections of the Science plan and background documents were added. The Program Office scheduled monthly conference calls (18 Sept., 6 Oct., 24 Nov., 22 Dec.) to discuss the issues from the August meeting, including the development and writing assignments of the CAMEO Science Plan.

The CAMEO Science Planning Office was involved in several activities from January to June, 2010. Dr. Deegan led, and the Program office coordinated, the semi-annual Science Steering Committee Meeting, which was held in-person in San Francisco. This meeting was attended by all 16 members of the Science Steering Committee and representatives from NSF (Cynthia Suchman, David Garrison) and NOAA (Mike Ford, Lora Clarke). During this meeting the first draft of the CAMEO Science Plan was written based on the outline developed over the fall. In February, Dr. Deegan attended the Ocean Sciences Meeting in Portland, Oregon. The CAMEO program held a Town Meeting session (Wednesday.) at this event, in which Dr. Deegan presented the conceptual components of the draft Science Plan and answered questions about the program. Representatives from NOAA and NSF also made remarks.

Work on the draft Science Plan continued throughout the spring by the Program Office and by an executive writing group of members of the Science Steering Committee. Monthly conference calls (21 March, 21 April, 19 May, 30 June) were coordinated and led by the program office. These calls were used to discuss the draft sections of the Science Plan and to consider issues of focus and membership for the Steering Committee. Agenda’s, and minutes were posted to the CAMEO SSC google.doc page.


The second semi-annual in-person Science Steering Committee was held 25-27 July in Woods Hole. This meeting was attended by 13 members of the SSC and representatives from NSF (Cynthia Suchman) and NOAA (Mike Ford, Lora Clarke). At this meeting the SSC approved the existing draft Science Plan, with some proposed revisions. During August, Dr. Deegan worked on revising the draft Science Plan, developing a survey for soliciting public comments on the Science Plan and letters for solicited comments on the draft Science Plan.

A major milestone was the development of a CAMEO web page and publishing the Draft Science Plan for public comment on 1 September with a link to the survey. In September, members of the Science Steering Committee solicited comments from specific scientists with a request for comments by 15 October. Email requests for public comments were distributed in September and October through the CAMEO list serve and several organizational listserves (ASLO, ESA, CERF, etc.), with the public comment period closing on 30 November.

The Program Office scheduled monthly conference calls (16 Sept., 7 Oct., 18 Nov., 9 Dec.) to discuss the issues from the July meeting, including progress in the development of the CAMEO Science Plan.