Bridging marine ecosystem and biogeochemistry research: Lessons and recommendations from comparative studies

B. Salihoglu [a,*], S. Neuer [b], S. Painting [c], R. Murtugudde [d], E.E. Hofmann [e], J.H. Steele [f], R.R. Hood [g], L. Legendre [h], M.W. Lomas [i], J.D. Wiggert [j], S. Ito [k], Z. Lachkar [l], G.L. Hunt Jr. [m], K.F. Drinkwater [n], C.L. Sabine [o]

[a] Institute of Marine Sciences, Middle East Technical University, Erdemli, Turkey
[b] School of Life Sciences, Arizona State University, Tempe, AZ 85287–4501, USA
[c] The Centre for Environment, Fisheries and Aquaculture Science, Pakefield Rd., Lowestoft, Norfolk, NR33 0HT, UK
[d] ESSIC, University of Maryland, College Park, College Park, Maryland, USA
[e] Center for Coastal Physical Oceanography, Old Dominion University, Norfolk, VA 23529, USA
[f] Woods Hole Oceanographic Institution, 266 Woods Hole Rd., MS# 41, Woods Hole, MA 02543–1050, USA
[g] Horn Point Laboratory, University of Maryland Center for Environmental Science, P.O. Box 775, Cambridge, MD 21613, USA
[h] Laboratoire d'Oceanographie de Villefranche (LOV) B.P. 28, 06234 Villefranche-sur-Mer Cedex, France
[i] Bermuda Institute of Ocean Sciences, 17 Biological Lane, St. George, GE 01, Bermuda
[j] Univ. of Southern Mississippi Dept. of Marine Sciences, 1020 Balch Blvd. Stennis Space Center, MS 39529–9904, USA
[k] Fisheries Research Agency, Tohoku National Fisheries Research Institute, 3-27-5 Shinhama-cho, Shiogama, Miyagi 985–0001, Japan
[l] ETH Zürich Inst.f.Biogeochemie u.Schadstoffdynamik CHN E 23.1, Universitätstrasse 16 8092 Zürich, Switzerland
[m] School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle WA 98195, USA
[n] Institute of Marine Research and the Bjerknes Center for Climate Research Box 1870, Nordnes, N-5817 Bergen, Norway
[o] National Oceanic and Atmospheric Administration (NOAA) Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115, USA

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ABSTRACT

There is growing interest in linking marine biogeochemistry with marine ecosystems research in response to the increasing need to understand and predict the effect of global change on the marine ecosystem. Such a holistic approach combines oceanographic and biogeochemical processes and information on organisms, ranging from microbes to higher-trophic-levels. Comparative studies offer a means to improve understanding of critical mechanisms that influence marine systems by showing differences in ecosystem response to changing ocean conditions. Comparing similar biomes that differ in a particular set of physical or biological characteristics can provide insight into the susceptibility of the key features of a system to perturbation. Also, comparative studies based on long-term observations at fixed time-series stations enable the evaluation of long-term changes in the physical and biological environment, such as those driven by climate patterns. Moreover, the comparative approach provides a feasible alternative to costly and complex research programs designed to provide detailed end-to-end evaluations of marine systems. Planned and unplanned perturbations allow the investigation of the sensitivity of ecosystems and their biogeochemical processes to change at different time and space scales. In well-studied regions where sufficient data are available, models can provide comprehensive syntheses, mechanistic insights and even predictions. We present examples of successful comparative studies that incorporate both biogeochemical and ecosystems aspects. A framework for a basic approach for comparative studies is proposed that considers the interactions between biogeochemical cycles and ecosystems. This approach is based on constructing a minimalistic observational framework grounded within a conceptual model.

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1. Introduction

Marine ecosystems are undergoing rapid and observable changes as a result of both natural climate cycles (e.g., El Niño-Southern Oscillation, ENSO) and human-induced effects (e.g., harvesting resources and increased atmospheric CO_2). Predicting future responses to these changes requires an improved understanding of the complex interactions and linkages that define present day marine ecosystems. Studies that include characterizations of habitat, food web components, and biogeochemical cycles allow important processes to be defined and provide the basis for comparisons within and across marine ecosystems (Fig. 1). The understanding gained from these comparative studies allows development of modeling systems that then provide the framework for investigation of potential future states and the consequences of change for present day marine ecosystems.

A comparative marine ecosystem approach underpinned much of the research undertaken in the Global Ocean Ecosystem Dynamics

* Corresponding author.
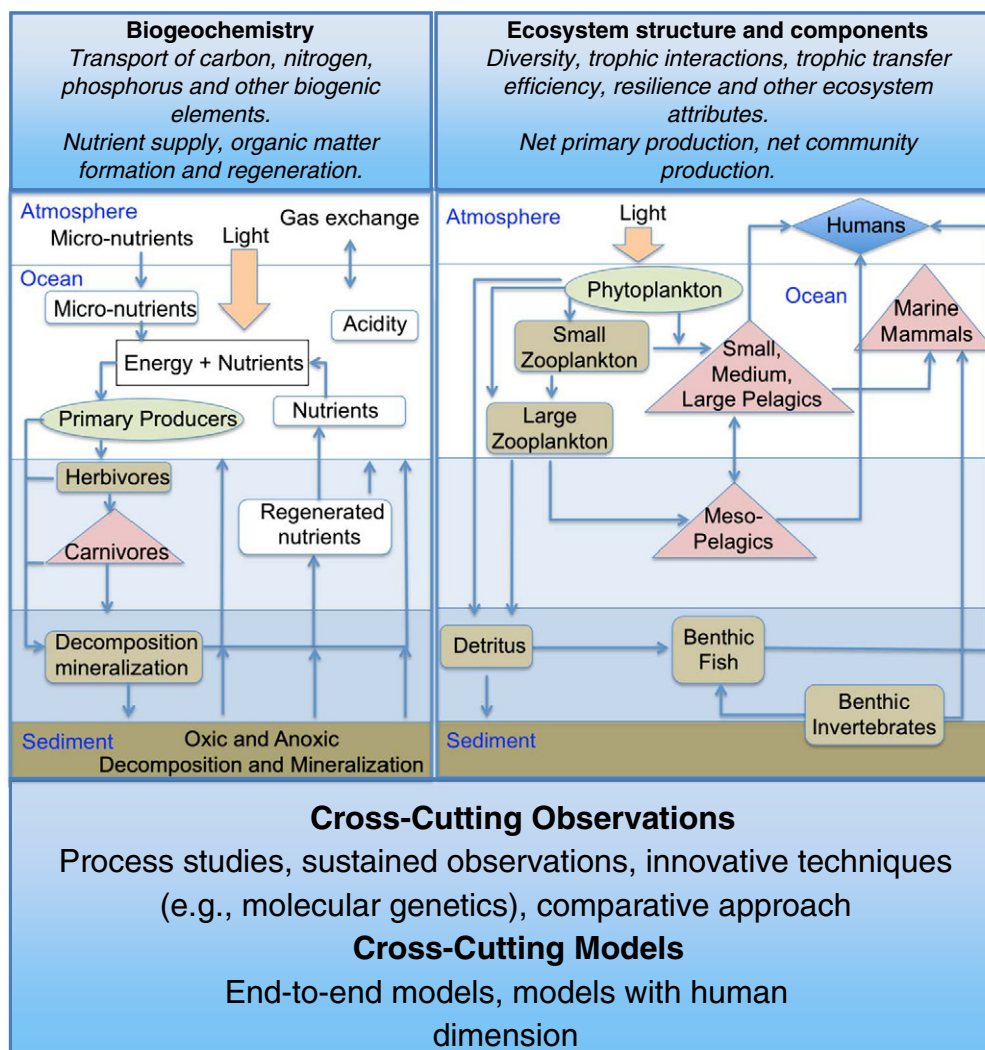E-mail address: baris@ims.metu.edu.tr (B. Salihoglu).

Fig. 1. Upper panels indicate the biogeochemistry and ecosystem processes that need to be integrated in comparative studies, middle panels show interactions of these processes, and the bottom panel provides an overview of cross-cutting tools for comparison.

(GLOBEC) Project, a 10-year international research program designed to understand marine population variability and responses to climate change (Barange et al., 2010). The GLOBEC studies used a target species approach to isolate effects of environmental processes and food web interactions of critical components of the life cycle, thereby allowing direct comparisons across several ecologically and commercially important species (Gifford et al., 2010; Moloney et al., 2010). The target species approach, implemented in regional research programs initiated through GLOBEC (Gifford et al., 2010) provided important insights into the structure and function of diverse ecosystems. Comparative studies among these regional programs were mostly undertaken during the GLOBEC synthesis and integration phase, which took place in the latter portion of the program (Barange and Werner, 2004). These comparative studies took different forms. Regional studies within given ecosystems have provided new insights about system functioning (e.g., Steele and Schumacher, 2000). Across-system or common process comparisons have provided the ability to extend what has been learned from local studies to more general concepts (Megrey et al., 2009; Moloney et al., 2010). An important lesson learned from the GLOBEC experience was that comparative studies allow emergence of new insights and understanding about the potential impacts of climate and human induced changes on marine ecosystems.

The regional research programs (Table 1) underway as part of the Integrated Marine Biogeochemistry and Ecosystem Research (IMBER)

Project had, from the outset, a focus on comparative studies of marine food webs, including biogeochemical cycling. This focus provided the basis for the IMBIZO Workshop on comparative studies (see Preface, this volume) that brought together scientists involved in IMBER regional programs as well as scientists from the wider IMBER research community. The presentations and discussions from the workshop were intended to provide a basis for developing comparative studies of food web and biogeochemical processes across the IMBER regional programs.

The following Section 2 provides a discussion of the importance of comparative studies. This is followed in Section 3 by highlighting comparative case studies that show the importance of connections between environmental, ecological and biogeochemical processes in defining ecosystem structure and function. Section 4 provides a summary of approaches for comparative studies that combine food web and biogeochemical processes. The final section (Section 5) presents recommendations for the development of comparative studies and suggestions for implementation of these in future IMBER and other research programs.

2. Why are comparative studies important?

There is an increasingly urgent need to understand and predict the effect of global change on the marine ecosystems of the world. Warming temperatures, increasing acidification and fishing activities are ongoing

Table 1
Objectives, region of study, and related comparative study in this volume for IMBER regional programs.

Program	Objective	Region	Related comparative study
CLimate Impacts on Oceanic TOp Predators (CLIOTOP)	Identify impact of both climate variability and fishing on the structure and function of open ocean pelagic ecosystems and their top predators	Global	
Ecosystem Studies of Sub-Arctic Seas (ESSAS)	Understand the impact of global change on sub-Arctic seas and suggest innovative approaches to manage these regions	Atlantic and Pacific Sub-Arctic Seas	Hunt et al. (this volume)
Integrating Climate and Ecosystem Dynamics in the Southern Ocean (ICED)	Develop a coordinated circumpolar approach to better understand climate interactions in the Southern Ocean, their implications for ecosystem dynamics, the impacts on biogeochemical cycles and development of sustainable management	Southern Ocean	Murphy et al. (this issue)
Sustained Indian Ocean Biogeochemistry and Ecosystem Research (SIBER)	Improve understanding of the role of the Indian Ocean in global biogeochemical cycles and the interaction between these cycles and marine ecosystem dynamics	Indian Ocean	

challenges to marine systems that are affecting their productivity and structure. Accumulation of insights gained from process studies focussed on specific trophic levels with limited resolution in space and time are the usual way marine ecosystem science progresses. However, oceanic systems are integrated across space and time scales that span several orders of magnitude and include complex interactions among and within diverse communities with implications for biogeochemical cycling. Under these circumstances, comparative studies offer a means to improve our understanding by bringing attention to the critical processes that differentiate one system from another and result in differences in ecosystem response to a changing ocean system (Fig. 1). Once recognized, these critical mechanisms and their roles can be studied and modeled to predict responses to global change, which in turn affect ecosystem goods and services.

Ocean observation systems now span molecules to mammals (e.g., Bowler et al., 2009) facilitating enhanced genetic-level understanding without jeopardizing the ecosystem-level view. Simultaneously, the monitoring and understanding of climate change has also steadily improved and climate predictions and projections at global to regional scales are increasingly skillful and usable (IPCC, 2007). Comparative studies have been conducted for various environmental regimes such as upwelling ecosystems (e.g., Cury et al., 1998; Shannon et al., 2008), subtropical gyres (Neuer et al., 2002), subarctic seas (see Megrey et al., 2009 and references within), and the Southern Ocean (Murphy et al., this issue). These studies provide a comparative framework for the study of the environmental and ecosystem responses to anthropogenic stressors and the resulting top-down and bottom-up cascades, as well as the physical, biogeochemical, and ecosystem responses to these perturbations (IMBER, 2005). The multiple stressors inflicted on the environment by natural and anthropogenic activities directly and indirectly impact each level of a given food web (Stenseth et al., 2002). Bottom-up (e.g., increased nutrient inputs) and/or top-down (e.g., decoupling of phytoplankton and zooplankton cycles) effects have implications for the long-term productivity and biogeochemical cycling of marine ecosystems. Examples include increased extent of hypoxia and anoxia in response to eutrophication and increased abundance of gelatinous species as a result of over fishing, respectively. Global coverage afforded by space-based platforms also provides an excellent avenue for exploring some of these physical-biological interactions (Jochum et al., 2010; Kahru et al., 2011; Murtugudde et al., 2001; Wilson and Coles, 2005; Yoder et al., 2010).

Three general approaches provide structure for studies designed to increase understanding of ecosystem structure and function (Murawski et al., 2010): (1) controlled experimentation, (2) iterative programs of observation and modeling, and (3) comparative analysis. Controlled experiments using mesocosms and open ocean nutrient enrichment provide the only in situ approaches with any form of experimental control, but the former are limited in spatial extent and thus cannot capture the complexity of marine ecosystem dynamics (Vallino, 2000) whereas the latter so far only allow manipulation of iron and suffer from constraints imposed by sampling limitations (Buesseler et al., 2008). Synchronized

observational and modeling programs at local or ecosystem scales are valuable for the assessment of a specific process or mechanistic underpinning within an ecosystem, but do not lead to generally transferable products (Steele et al., 2013-this issue). Comparative ecosystem analyses complement the first two by inferring ecosystem processes and their biogeochemical implications based on comparisons of and differences in ecosystem responses to natural and human-induced perturbations. A hierarchical approach to possible comparisons provides focus on specific regional differences that can then be extended to more general results. Comparisons may focus on temporal changes within ecosystems ("before and after"), regional differences arising from spatial and temporal variability in physical and chemical features, as well as differences in climatic and/or fishery perturbations (e.g., between different coral reefs, Hughes et al., 2003). Also, comparisons between temperate continental shelves (Frank et al., 2007) or upwelling areas (Cury and Shannon, 2004; Lachkar and Gruber, 2011), or responses of specific species to such regional differences (e.g., Atlantic cod, *Gadus morhua*, Brander, 1994; Drinkwater, 2005; Planque and Frédou, 1999) provide an important platform for data syntheses and integration that enable even cross-system comparisons, e.g., coral reefs vs. boreal environments, polar vs. equatorial regions, or terrestrial vs. marine ecosystems (Steele, 1985). This hierarchical approach should lead to a better understanding of processes controlling biodiversity, productivity and resilience of marine ecosystems.

Comparative studies improve understanding of ecosystem structure and functioning by providing a basis for formulating hypotheses about control mechanisms and their impacts on systems (e. g., Hunt et al., this volume), and by allowing the emergence of a synthetic understanding through integration of results from multiple related individual studies. This, in turn can help determine what is fundamental and what might be unique within a particular system and what critical factors determine the functional characteristics of different systems (e.g., productivity, resilience, and complexity). The comparative approach is important for understanding resilience and for identifying thresholds for abrupt changes that may help to identify the tipping points in a particular system. These tipping points can be physical, physiological, behavioral, and can affect the structure of a system through re-arranging the functional relationships between components. Across-system comparisons also increase the sample size, which increases confidence in the understanding of a particular system. This is critical because the statistical significance of shifts in ecosystems has been quantified (e.g., Hare and Mantua, 2000) whereas the mechanistic understanding of climatic shifts remains largely elusive (e.g., Schneider and Cornuelle, 2005).

3. What have we learned from comparative studies?

Comparative studies are of value when comparing biogeographical regions that differ in a particular set of physical or biological characteristics because the results can provide insights into the importance of those factors as drivers of the system. These studies do not need to be restricted to regional comparisons. Indeed long-term observations at

fixed time-series sites enable one to determine the consequences of long-term changes in the physical, biogeochemical and biological environment driven by multi-year climate patterns. Some of the insights that can be gained from temporal comparative studies are illustrated by the following examples.

3.1. Long-term observations and climate forcing

The western subtropical Sargasso Sea is one of the best-studied open ocean regions because of the presence of ocean time-series extending over five decades. The long-term observations from this region have documented a slow warming and acidification (Bates, 2007). Over the last two decades at the Bermuda Atlantic Time-series Study (BATS, 31°50′ N, 64°10′ W), diatom abundances and biomass have decreased, whether it be assessed by changes in pigments (Lomas et al., 2010) or suspended biogenic silica (Krause et al., 2009), while the biomass (assessed by both pigments and direct cell counts) of the minute cyanobacterium *Synechococcus* spp. has increased (Casey et al., in review; Lomas et al., 2010). Furthermore this shift in functional groups has also led to an increase in total chlorophyll-a standing stock of ~60%, and similar increases in net primary production, shallow (150 m) carbon export production, and mesozooplankton biomass (>200 μm; Steinberg et al., 2012). These observations alone shake a fundamental paradigm in biological oceanography, namely that particle flux is driven by large, mineral ballasted cells grazed upon by mesozooplankton, and small picoplankton cells are 'recycled' in the euphotic zone by heavy microzooplankton grazing. Diatoms may be on the decline due simply to unfavorable N:Si ratios driven by differences in the vertical gradients of nitrate and silicate that result in the preferential input of nitrate (Krause et al., 2009), but it is clear that the increasing dominance of picocyanobacteria is neither a detriment to particle export nor to the sustenance of planktonic crustaceans. In fact, recent evidence suggests that even during winter mixing conditions, when one would expect a diatom dominance of carbon export, up to 30% of measured carbon export can be attributed to tiny cyanobacteria previously considered insignificant contributors to carbon flux (Lomas and Moran, 2011).

These ecosystem changes have been linked to the phase of the North Atlantic Oscillation (NAO) which is hypothesized to alter the pattern of nutrient inputs into the euphotic zone. Increased frequency of deep mixing resulting in nutrient injections as well as dilution of phytoplankton biomass is analogous to a 'chemostat' growth mode for cultures, instead of a 'batch' mode when mixing is less frequent and the phytoplankton community is allowed to exhaust the ambient nutrient pool. Changes in the relative importance of ecosystem pathways of carbon export, such as aggregation and incorporation into fecal pellets of picoplankton, in response to climate drivers could reconcile these discrepancies between theory and observation (Lomas and Moran, 2011).

Observations at the Hawaii Ocean Time-series station (HOT, 22°45′N, 158°W) in the subtropical North Pacific also illustrate how the communities of primary and secondary producers respond to physical changes associated with variability in climate modes. Bidigare et al. (2009) showed that shifts of the PDO (Pacific Decadal Oscillation) and ENSO from positive to negative during the late 1990s caused a "cascade of events" by leading first to increased destratification and subsequent enhanced nutrient input. The increased nutrient availability resulted in a greater biomass of primary producers, as shown by increases in chlorophyll, eukaryotic nanophytoplankton pigments (fucoxanthin and derivatives) and cyanobacteria. This increase in growth and biomass of phytoplankton in turn increased the carrying capacity for higher trophic levels, as indicated by increases in mesozooplankton (Hannides et al., 2009), as well as an increase in particulate nitrogen export (Bidigare et al., 2009). This second example not only corroborates the importance of nutrient input and biology on particle export on multi-year time scales as seen in the North Atlantic, but also illustrates the importance of the trophic linkages in the biogeochemistry of these biomes.

At the higher trophic levels, fisheries statistics collected over centuries, accompanied by ocean climate and lower trophic level information have also provided insights into the marine ecosystem responses to climate variability. In the North Atlantic, there have been low frequency changes in surface temperature, which have been termed the Atlantic Multidecadal Oscillation (AMO, Kerr, 2000). This includes the general warming in the middle of the last century, followed by a cooler period, and then the recent warming that began in the late 1980s to early 1990s. Associated with the mid-20th century warming biologists observed significant changes in marine ecosystems that led to the first symposium on the impacts of climate change on the marine environment in 1948 (ICES, 1949). Benthic and fisheries communities were observed to shift northwards under the warming conditions, southern species that were rare or occasional visitors to northern regions appeared more frequently and in some cases took up residency. The growth rates of many species increased, recruitment improved, and abundance of several of the commercial species rose significantly (Beverton and Lee, 1965; Cushing, 1982; Cushing and Dickson, 1976; Drinkwater, 2006; ICES, 1949; Jensen, 1939). Suggested increases in phytoplankton and zooplankton production based on the few long-term plankton data time series led Drinkwater (2006) to conclude that bottom-up processes were likely to be the primary cause of these changes. During the following cool period the opposite occurred as species generally retreated southward, growth rates slowed, and fish abundances in the northern regions declined. Comparisons of the response of Atlantic cod in late-20th century to the mid-20th century conditions showed that while similar responses were observed in some areas including northward shifts in distribution, there has been on average lower cod production, which were attributed to the effects of fishing and ecosystem changes (Drinkwater, 2009).

3.2. Hypothesis testing

Comparison of the biogeochemical data sets from a time-series station in the eastern subtropical gyre (ESTOC, European Station for Time-series in the Ocean, Canary Islands) with those from the BATS site in the western subtropical gyre, led to the hypothesis that differences in the strength of the biological carbon pump across the subtropical North Atlantic gyre could be explained by differences in new nutrient supply (Neuer et al., 2002). Subsequent observation and model-derived nutrient budgets established that there was indeed a significant difference in the input of new nutrients at the two time-series sites (Cianca et al., 2007; Mouriño and Neuer, 2008). Mesoscale eddy activity accounted for much larger nutrient input at BATS relative to ESTOC, while winter convection was a more important nutrient supply process at ESTOC. Although overall new nutrient inputs were slightly higher at BATS, this was not sufficient to explain the differences in the magnitude of the biological carbon pump. A more extensive data analysis of the magnitude and composition of the sinking particulate matter suggested that there might be differences in the relative contributions of mineral-ballast and non-ballast phytoplankton to export (Helmke et al., 2010). Specifically, differences in the episodic nature of the late winter bloom at BATS, the importance of aggregation of non-ballasted picoplankton, and subsequent utilization by higher trophic levels in the mesopelagic realm which resulted in both higher export and remineralization rates of labile organic carbon at BATS were suggested as causes for the observed differences in the magnitude of the carbon pump (Helmke et al., 2010). This intra-basin comparison also showed that higher trophic levels potentially play an important role in biogeochemical studies, which is often overlooked.

3.3. Sensitivity to environmental change

The comparison of present day biogeochemistry and ecology of different biomes enables evaluation of their sensitivity to on-going and future perturbations such as those that accompany climate

change. Comparative studies in polar systems may provide a preview of potential impacts of global warming on marine ecosystems and biogeochemical cycles because these regions are warming rapidly and are very sensitive to change (Moline et al., 2004; Schofield et al., 2010; Wassmann et al., 2011).

The Arctic continues to be a natural laboratory for comparative analysis due to its regional niches for ecosystems situated in a semi-enclosed system that is responding to anthropogenic activities. Arctic sea ice provides an example of an important environmental feature that is potentially nearing a critical threshold, or tipping point. Reducing sea-ice cover exposes more open water which absorbs more heat, potentially leading to a state after which an irreversible loss of summer sea ice would occur due to reinforcement of the albedo feedback (Lenton et al., 2008). While the continuous decline of summer sea ice due to increasing green house gases is accepted, Tietsche et al. (2011) recently showed that recovery mechanisms exist and even an anomalously low summer sea-ice cover can rebound as a result of enhanced heat loss during fall and winter.

The Arctic and subarctic regions are expected to be among the most perturbed systems should summer sea ice disappear in the coming years, and may serve as a potential indicator for ecosystem response and biogeochemical processes under climate change. For example, abrupt discontinuities in the distribution of zooplankton, fish and seabird species along a gradient from the southeastern Bering Sea northward through the Chukchi and Beaufort Seas result from physical oceanographic features (fronts and circulation patterns), suggesting that these different ocean regions are likely to have complex and potentially quite different responses to global warming (Sigler et al., 2011).

Examination of long-term records of the timing of sea-ice retreat in the Bering Sea showed that a small shift in the timing of sea-ice retreat led to a large shift in the timing of the spring phytoplankton bloom, and the production of large crustacean zooplankton (the copepod *Calanus marshallae/glacialis* and the shelf euphausiid *Thysanoessa raschii*) (Hunt et al., 2011). This study showed that if the spring phytoplankton bloom occurred before significant retreat of the sea ice, then the large zooplankton thrived, and there was the possibility of a strong year class of the walleye pollock (*Theragra chalcogramma*), which is subject to the largest single-species fishery in the United States. However, if the ice retreated early in March, late winter storms delayed the onset of the spring bloom until the water column was stabilized by solar warming, and the resulting late spring phytoplankton bloom supported few large crustacean zooplankton (Hunt et al., 2011). Under these circumstances, pollock recruitment was low. Thus, a shift in the timing of sea-ice retreat of a few days or weeks, results in a major change in ecosystem structure and function in the southeastern Bering Sea.

Hunt et al. (this volume) show that in comparison to the Chuckchi Sea, the Barents Sea supports a much higher fish catch and bird and mammal populations, despite similar levels of primary productivity. They showed that the waters advected into the southwestern Barents Sea from the North Atlantic were warmer and richer in zooplankton than those advected from the northern Bering Sea into the Chukchi Sea. In the southern Barents Sea, these important differences led both to earlier sea-ice retreat and increased primary production, and an important supply of zooplankton to young fish. In the Chukchi Sea, a very short productive season and extremely cold, well-mixed water column in winter limited primary production and the overwintering of fish species from more temperate latitudes. Additionally, fish movements in the Barents Sea allowed the use of more abundant and more widely distributed food resources.

As part of the MENU (Marine Ecosystem comparisons between Norway and the US) project, Mueter et al. (2009) compared biological changes in response to recent warming in the Norwegian/Barents Seas, the Gulf of Maine/Georges Bank, the coastal Gulf of Alaska and the eastern Bering Sea. They observed more direct and larger changes in the higher latitude systems. Based on their comparative studies

they expounded upon possible future climate change scenarios but warned that inter-annual to decadal-scale variability is likely to remain high and that extrapolating observed relationships beyond historical ranges does not account for potential tipping points or other non-linearities. They did suggest some certain responses, including further shifts in spatial distribution and northward range extensions causing changes in the plankton and fish community structure and function but noted that it is impossible to predict which species will or will not do well. Overall productivity is likely to increase in the northernmost systems as the boundary between the Arctic and subarctic shifts northward and this will result in changes to fisheries and fishing communities.

These examples show that comparative regional studies of similar biomes, controlled by a different sets of physical and biological factors, can reveal the consequences of changes of both abiotic (such as advection of heat, sea-ice extent and duration, and variable nutrient supply), and biotic (such as the movement of zooplankton and fish populations) factors.

4. Comparative studies of marine ecosystems—approaches and guidance

Marine food web and marine biogeochemistry research have developed historically as two different disciplines. The first focuses on relations among marine organisms and between them and their environment. The second deals with the cycling of elements among natural reservoirs (e.g., living, particulate, dissolved organic and dissolved inorganic) as influenced by marine organisms. The two disciplines have finally met, and sometimes partly merged, in the last decades in response to the need to understand how global change will impact marine ecosystems, biogeochemical cycles and their interactions (Fig. 1), which now underpins IMBER science.

Methods and approaches for carrying out large-scale regional comparisons of fishery impacts exist (Shin et al., 2010 and references within) and those for assessing ecosystem effects on the biogeochemical cycling of carbon are being developed (Legendre and Niquil, 2013-this issue). Comparative studies can be done using a within-ecosystem regional focus (Steele and Gifford, 2010) or using across-systems or common process comparisons (Megrey et al., 2009). End-to-end comparative studies also have relevance to management, especially in terms of the impacts of nutrient enrichment and climate change on higher trophic levels. For example, several studies indicate that the combination of climate change and fishing pressure can have compounding effects and that these can manifest differently in different regions, making attribution of the dominant driver difficult if not impossible (Perry et al., 2010; Planque et al., 2010; Stenseth et al., 2002). Below we present a variety of approaches and ways to conduct comparative studies that combine aspects of research focused on both ecosystem and biogeochemistry.

4.1. Observational approaches

In general it is too costly and complicated to carry out detailed end-to-end evaluations of systems for the purposes of comparisons except, perhaps, with models developed for a few well-studied regions where sufficient data and resources are available. However, this is not the norm for most marine ecosystem studies. An alternative approach is to construct an observational framework that includes key processes and variables (cf. Section 5) and is grounded within a conceptual model. An example of this approach might be the comparison of fish yield/productivity of different systems that is carried out in the context of classical theory on how physical control of nutrient loading impacts the complexities of the marine food web and trophic transfer efficiency (Pauly and Christensen, 1995). Through comparisons one can determine if theoretical considerations of the interactions between the environment, phytoplankton species assemblage composition,

and nutrient supply/recycling are consistent with observed differences in fish yield/productivity in different regions. Based upon the outcomes, the observational framework can then be expanded in the most efficient manner for the system under study. Although this approach is not new, it provides one simple, classic example of how a comparative study can be carried out using existing observations and theory that considers the link between biogeochemical cycles and ecosystem dynamics.

In general, there is a need to synthesize existing large databases, theories and models so that end-to-end comparative studies can be carried out. Towards this end, existing knowledge can be used to build on the typology matrix framework of Legendre and Niquil (2013-this issue) and to identify the type of information that can be obtained from the comparative approach. These databases also need to be mined and combined into new comparative studies. Hunt et al. (this volume) and Murphy et al. (this issue) provide examples of this data mining-based approach that brings together a variety of different data sets collected over many years that include physical processes, biogeochemical data and higher trophic level studies to understand differences in fisheries productivity in different Arctic ecosystems and food web structure in regions of the Southern Ocean, respectively.

It is also important to take advantage of opportunities that enable regional comparisons in large national and international programs, e.g., the GLOBEC Small Pelagics and Climate Change (SPACC) project made datasets from existing projects and time-series available to the broader research community, thus enabling regional comparative studies. Observational studies done through multidisciplinary research programs such as GLOBEC, the Joint Global Ocean Flux Study (JGOFS), and the Bering Ecosystem Study-Bering Sea Integrated Ecosystem Research Program (BEST-BSIERP) required a huge investment of resources. Planning and funding that allows within-program or post-program comparative and synthetic studies are crucial.

4.1.1. The choice of the study region

A range of considerations may influence the selection of ecosystems that can be targeted for comparison. Ecosystems or regions can be selected to provide the opportunity to study impacts of environmental change on biogeochemical cycles (and impacts of biogeochemical change on ecosystem dynamics), and their susceptibility to climate change and other anthropogenic impacts. Comparing regions may also be useful for understanding the internal variability and predictability of ecosystems and for assessing the portability and skill of models (for an example of the latter, see Friedrichs et al., 2007). In addition to the polar systems (cf. Section 3.3), the rapid warming of the Indian Ocean (Alory and Meyers, 2009; Alory et al., 2007) might afford opportunities for conducting comparative studies of tropical and subtropical ecological and biogeochemical responses. Dust source regions distributed around its northern boundaries (Leon and Legrand, 2003; Prospero et al., 2002) result in pronounced basin wide dust deposition gradients and a diversity of natural iron fertilization regimes. Further, the Indian Ocean should be a particularly good place to study the contrasting impacts of upwelling intensification associated with amplified monsoonal forcing (e.g., during the southwest monsoon in the Arabian Sea, Goes et al., 2005), enhanced stratification derived from increased riverine flow (e.g., in the Bay of Bengal), and expected changes in nutrient supply, and primary production, hypoxic water volume and higher trophic level impacts that are anticipated under global warming, projected population increases and modernized agricultural practices.

The designation of relatively large areas of the coastal ocean as Large Marine Ecosystems (LMEs, Hempel and Sherman, 2003) provides defined regions that can be used as the basis for comparative studies. The LME regions share the characteristic of enhanced primary production that supports important fisheries production and designation of these regions is based on similar ecological (productivity, trophic relationships) and habitat (bathymetry, hydrology) criteria. Moreover, the research strategy that is applied to the current sixty-four LME regions is designed to provide similar and consistent metrics from each LME that in turn will facilitate across system comparisons (Duda and Sherman, 2002; Sherman et al., 2005, 2011).

4.1.2. Responses to perturbations

Planned changes to human activity and unplanned perturbations to marine ecosystems can provide information on how controls on biogeochemical and ecosystem variability evolve. Planned changes, such as the designation of marine protected areas, allow systematic studies of responses to the addition or removal of a particular forcing or process (e.g., Murawski et al., 2000). Similarly, unplanned perturbations, such as the introduction of alien species, can be useful in identifying how various ecosystems components respond to human activities and/or climate change (e.g., Oguz and Gilbert, 2007).

The Black Sea provides a case study of the usefulness of an unplanned perturbation in understanding marine ecosystem response; a ctenophore was unintentionally introduced by ballast water from its quite restricted home region, the New England coast. A shift in the food web dominance from an anchovy (fish) to *Mnemiopsis* (invasive ctenophore) occurred as a result of combination of direct and density-dependent effects of overfishing, anthropogenic nutrient enrichment, climate-induced over-enrichment (enhanced vertical mixing and stronger upwelling associated with intensification of the cyclonic basinwide circulation system), and temperature-controlled *Mnemiopsis* spring production (Bilio and Niermann, 2004; Kideys, 2002; Oguz and Gilbert, 2007; Oguz and Velikova, 2010; Zaitsev, 1992). Nutrient enrichment made the Black Sea system vulnerable to further enrichment due to a severe winter regime during 1985–1987. As *Mnemiopsis* was acclimating to a colder environment, increasing nitrate flux into the euphotic layer further enhanced the carrying capacity of the system but a *Mnemiopsis* biomass increase was delayed until spring temperature conditions returned to normal in 1989–1990. Then the enhanced carrying capacity provided a competitive advantage to *Mnemiopsis* through increased food availability, and warm spring temperature conditions promoted much higher spring-summer production of the ctenophore that allowed for very rapid biomass accumulation. Relative to the high stock regime of the early-1980s, increasing fishing pressure prior to the *Mnemiopsis* population outbreak caused two-thirds of the total anchovy stock loss. The loss of the remainder of the fishery occurred during the *Mnemiopsis* outbreak period due to the sum of continued high fishing pressure and increasing role of *Mnemiopsis* as a competitor for food resources within the food web. The shift event, however, did not alter the system to a permanent *Mnemiopsis*-dominated quasi-stable regime. Rather, the anchovy populations started recovering when the subsequent strong 1991–1993 cooling regime limited *Mnemiopsis* population growth once again. These variations provide useful insight into the controls on ecosystem structure that can be used to predict how the system might respond to future perturbations.

4.1.3. Appropriate scales of time and space

Different time and space scales of variability within regions need to be considered in comparative studies, i.e., the relevant scales for characterising systems need to be defined. Differences in scales for open versus closed systems, life histories (e.g., of fish), biogeochemical cycling, and ecological responses must be considered. It is also important to recognize that variability can be induced in both time and space through physical, chemical and biological forcing factors. For example, Feely et al. (2008) showed how coastal upwelling events in the California Current System (CCS) can transport subsurface waters with high levels of CO_2 and low pH values onto the continental shelf. These acidified waters can be undersaturated with respect to aragonite, providing a significant stress for benthic calcifying organisms. However, further analysis by Fassbender et al. (2011), showed that the level of undersaturation is strongly dependant on the timing of the upwelling and the time scale of biological response. Productivity from upwelled nutrients can, within a matter of days, reduce the

surface water CO_2 levels from more than three times atmospheric levels to below atmospheric, making the waters again supersaturated with respect to aragonite. That productivity also has consequences for the entire CCS ecosystem structure.

4.2. The application of modeling studies

4.2.1. General considerations

The use of models to carry out ecosystem comparisons includes the application of a specific model to different ecosystems as well as the application of different models to a particular ecosystem (e.g., Friedrichs et al., 2007). Because no model is perfect for all purposes, a number of different models and modeling approaches are needed (see Murphy et al., 2012). Each comparison should be formulated around a question so that each model is defined, in part, by its use in testing a specific hypothesis. The types of models could include general circulation models (GCM) coupled to nutrient–phytoplankton–zooplankton–detritus (NPZD) models, mass-balance food-web models, size-based models, and dynamic multispecies and aggregate stock production models (Murphy et al., 2012). In addition, there are socio-economic and management models that can be effectively evaluated within a comparative framework (e.g., Ecopath with Ecosim, Table 2). The open nature of marine ecosystems and exchange across boundaries is a fundamental challenge to undertake comparative analysis, but substantial differences between ecosystem dynamics and biogeochemical cycles in different oceanic regimes can be readily identified and modeled. Applications of models also provide invaluable opportunities to understand the connections within and between ecosystems.

Numerical models that allow consideration of the impacts of climate change and anthropogenic effects on biogeochemical cycles and ecosystem dynamics are needed to advance our understanding and the predictive capacities to resolve marine ecosystem responses to global change. Sensitivity studies can be used to assess the separate effects of drivers on the ecosystem (e.g., Keller and Hood, this issue) and the comparative approach can facilitate the separation of the effects of climate from those of anthropogenic drivers such as fishing. Different processes and mechanisms that invoke differences in production, and structure and function of ecosystems can be assessed. Efforts that focus on specific concepts such as resilience or thresholds are needed.

One of the main differences between the available biogeochemical and ecosystem models that can be used for comparative analyses is the extent of the representation of the ecosystem components. Some models focus only on a subset of the ecosystem (cf. Fig. 2), either the plankton (e.g., NPZD-type models, see overviews in Hood et al., 2006) and fish community components (cf. Fig. 2), or a selection of trophic levels (Hermann et al., 2001; Sourisseau, 2002). Other models represent the larger ecosystem, considering large functional groups from the plankton community to top-predators. The range of trophic levels represented depends on the objectives addressed when developing the model, with fundamental differentiation imposed by whether assessment of export flux (i.e., carbon burial) or apex predator distribution/abundance, for example, is of interest.

The end-to-end modeling approach requires full coverage of ecosystem components, the integration of physical and biological processes at different scales and two-way interaction between ecosystem components (e.g., Fulton et al., 2005, 2007). End-to-end models attempt to include all major relevant processes in the system (Fig. 2). Including the dominant processes that are needed to dynamically represent the entire ecosystem is a major challenge in itself and has been the focus of ongoing research efforts (cf. review by Fulton, 2010; Travers et al., 2007).

The usefulness of comparing regional models depends on the skill of the models (Murphy et al., 2012). A challenge is to define the optimal degree of process simplification that is appropriate. Models focused on predator–prey interactions at the plankton level and on primary production often include relative little 'biology'. Modeling

Table 2
Examples of models combining (green-shaded) lower (light blue, top) and higher (light blue, bottom) trophic levels suitable for comparative studies.

Model	Description	References
NPZD (Nutrients, Phytoplankton, Zooplankton and Detritus)-type models	Represent lower trophic levels and biogeochemical cycles in marine ecosystems as Eulerian state variables with mathematically specified flows between each compartment.	For reviews see Hood and Christian (2008), Hood et al., (2006)
Ecosim with Ecopath (EwE)	Defines the food web in the form of functional groups representing species and/or groups of species linked by trophic interactions.	Christensen and Pauly (1992), Christensen and Walters (2004)
ERSEM and ERSEM II	Among the first examples of end-to-end models, fish and seabirds were inclusions in the original models.	Baretta-Bekker et al., (1995), Baretta-Bekker et al., (1997)
NEMURO.FISH	Formed by addition of a fish model to the detailed NPZD (nutrient, phytoplankton, zooplankton, detritus) model NEMURO.	Ito et al., (2004), Megrey et al., (2007)
SEAPODYM	A complex example of the coupled approach, which includes a biogeochemical model, vertically structured mesopelagic fish and an age-structured fish population model that can also include fishing pressure.	Lehodey et al., (2003) Lehodey et al., (2008)
APECOSM	Uses size spectra to represent forage layers in models focusing on top predators.	Maury et al. ,(2007)
ATLANTIS	Involves the explicit inclusion of physical and biogeochemical system components to higher trophic levels and incorporates the potential to consider human dynamics in some detail.	Fulton et al., (2005), (2007)
OSMOSE	A multispecies and Individual-based model (IBM) which focuses on fish species.	Shin and Cury (2001), (2004)
Multispecies Virtual Population Analysis (MSVPA) model	A trophic dynamics model focusing on interactions between fish species within exploited communities	Magnusson (1995)

[1] Christensen and Pauly 1992, Christensen and Walters, 2004, Baretta-Bekker et al., 1995, Baretta-Bekker et al., 1997, Ito et al., (2004), Megrey et al., 2007, Lehodey et al., 2003, Lehodey et al., 2008, Maury et al., 2007, Fulton et al., 2005, 2007.
[2] Hood and Christian, 2008, Hood et al., 2006.
[3] Shin and Cury, 2001, 2004.
[4] Magnusson, 1995.

approaches that use structurally fixed plankton functional type (PFT, Hood et al., 2006) models need to be complimented by those that allow adaptation in response to environmental conditions (Follows et al., 2007), a combination that will explicitly address the fluidity of ecosystem structure (Hood et al., 2007). Despite their limitations, simple NPZD models coupled to an ocean or an ocean–atmosphere model are effective tools for exploring the impact of dynamic–thermodynamic coupling (e.g., circulation and temperature gradients) on ecosystem-biogeochemical responses under climate variability and change. The differences in the coupling between the dynamics and thermodynamics of various regions of the world ocean serve as excellent starting points for comparative studies of ecosystems and biogeochemistry.

Comparative models also need to consider regional specificities in physics, key species (e.g., Antarctic krill in the Southern Ocean), important functional groups (e.g., nitrogen fixers in tropical oceans), and physical–biological feedbacks. These regional specificities can be critical for the global warming response of these systems and can thus provide alternative foundations for comparative studies.

It is also important to learn from the unexpected in ecosystem responses, which have been termed "loopholes" (Bakun and Broad, 2003) or "black swans" (Murawski et al., 2010). The term "loophole" refers to interactions between strategies and environmental conditions producing gaps in the biological control that result in a significant mortality reduction of early stage species (especially fish). The "black swan" events
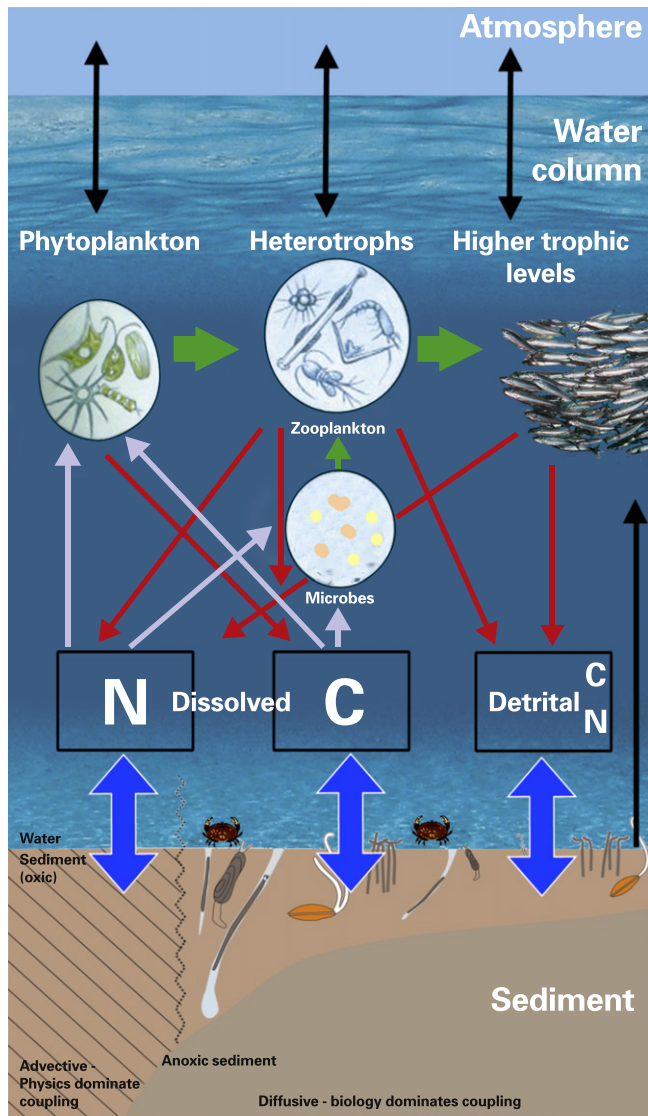
Fig. 2. Conceptual diagram illustrating the main carbon (C) and nitrogen (N) flows between pelagic and benthic food webs. Main feeding (trophic) pathways are from phytoplankton to heterotrophs (e.g., zooplankton) to higher trophic levels (e.g., fish), and from benthic fauna to fish. Nutrients which drive the system are available from dissolved and detrital pools, and atmospheric inputs. Sediment communities include microbes, meio-fauna (<1 mm) and macro-fauna (>1 mm). These are influenced by sediment types (coarse through muddy) and the depth of the oxic layer; with biogeochemical fluxes dominated by physics in coarse (advective) sediments and by biological processes in more diffusive (muddy) sediments (from Painting et al., 2012).

(Taleb, 2007) refer to a prevalent theme in ecosystem studies that is the occurrence of abrupt ecosystem change or "tipping points" (Collie et al., 2004), which can often reveal basic properties of ecosystems and second-order interactions not interpretable from small perturbations from status quo. After the event these can be simulated as regime shifts (van Nes and Scheffer, 2005) but they may be practically impossible to predict.

Fully exploiting the understanding achieved in comparative studies and translating this into model improvements is a major challenge (e.g., Fulton, 2010; Travers et al., 2007). It is possible that previous comparative studies such as the one discussed in Hunt et al. (this volume) could be reanalyzed with the aid of models to further explore aspects of the Barents Sea and Chukchi Sea ecosystems. They may then be used to plan future comparative studies that consider, for example, environmental variability as an integral part of the comparative understanding. In the Bering Sea, the period of five warm years followed by five cold years provides a potential opportunity to glimpse how the marine ecosystem of

the southeastern Bering Sea might change with longer-term warming (Coyle et al., 2011; Hunt et al., 2011; Mueter et al., 2011). In general, the goal should be to extract organizing principles in each region (e.g., for productivity, resilience, and complexity) and synthesize them to see if any universal rules exist across all or most domains. This is especially possible in the context of mathematical modeling to seek holistic principles in ecosystem functioning such as overall stability (Gross et al., 2009; Hood et al., 2007). Terrestrial ecosystem comparisons may also yield useful insights into marine ecosystem functioning in terms of the stability of any given ecosystem to symmetric and asymmetric dependencies between predators and prey.

4.2.2. Examples of model-based comparative studies

An example of cross-ecosystem comparison approach is given by Lachkar and Gruber (this volume) who used a physical–biogeochemical coupled model to explore how productivity and air–sea CO_2 fluxes might respond to enhanced upwelling in the CCS and the Canary Current System. Using simple assumptions and identical model settings, upwelling favorable wind intensification was shown to lead to contrasting biological responses in the two eastern boundary current upwelling systems, with major implications for the biological pump and the carbon cycling. Bottom-up limitation factors, such as light and temperature as well as factors controlling the nearshore–offshore exchange timescales such as the shelf topography and the level of eddy activity were also shown to substantially modulate the biological response to enhanced upwelling in both systems.

Similarly, Van der Molen et al. (2012) used a coupled physical–biogeochemical model to describe important ecosystem interactions and flows of carbon and nutrients at three hydrodynamically distinct sites in the southern and central North Sea. Differences in ecosystem structure and functioning were shown to affect carbon (and nitrogen) budgets at each site, and sensitivity to the impacts of environmental change due to trawling and climate change. Model results showed that a large proportion of the primary production is recycled in the water column, with relatively small fractions of the primary production being available to the benthic food web. Also, climate warming is likely to increase rates of carbon cycling in the pelagic system (by up to 20% by 2098), making less carbon available to the benthic system, resulting in reduced biomass of benthic organisms, and shifting the balance towards a more pelagic-oriented system than at present. Implications include a reduced biomass of benthic organisms which are important prey items in the diet of commercially important fish stocks (particularly plaice, and juvenile cod and haddock), and changes in the storage of particulate carbon in sediments, the magnitude of which could not be assessed with site-specific models.

Another example is a comparison of bottom up processes related to herring growth in several regions in the North Pacific using the model NEMURO.FISH (Rose et al., 2007). The same climate forcing, plankton production model and fish growth model were used to investigate geographical differences of the herring responses to climate forcing. Despite having the same forcing and species, the modeled ecosystem responses depended on regional oceanographic conditions. In the southern region, the fish decreased their growth when the temperature increased since higher temperature enhanced stratification and the primary production was reduced. In contrast, in the northern region, the fish increased their growth, as the prey abundance was high enough to maintain the fish growth. The comparison using the mechanistic model improved the comprehensive understanding of regional differences in ecosystem response to climate forcing.

The choice of the models and their level of complexity depend on the question under consideration. For example, in Lachkar and Gruber (this volume) the focus is clearly on identifying the key physical processes that control the response of productivity and air-sea CO_2 fluxes to increasing winds in coastal upwelling ecosystems. To address this question, a realistic eddy-resolving circulation model coupled to an NPZD type ecosystem model can be sufficient to give a first indication

of how complex physics can shape the sensitivity of these ecosystems to upwelling intensification potentially induced by climate change. The comparative modeling approach provides an important tool to integrate knowledge and it enables quantitative analysis. However, the variety of models and model complexity is also important. Results of a complex model can be counterintuitive and difficult to understand whereas the results from simple models, such as an NPZD model, are usually easier to understand and in some cases they can even be more robust. Yet it has been shown that more complex ecosystem models are more portable from one region to another and can provide better predictive skill than simple models as long as there are sufficient data to constrain them (Friedrichs et al., 2007). Additionally, model-to-model comparisons can reveal weaknesses, adaptability and even the resilience of models (Friedrichs et al., 2006, 2007; Travers et al., 2007).

4.2.3. Future directions

Past food web studies have tended to treat the upper and lower trophic levels separately. In general, the use of detailed simulations of physical dynamics requires some limitation on biology. This led de Young et al. (2004) to propose that "rather than model the entire ecosystem we should focus on key target species and develop *species-centric* models", which is the antithesis of the ecosystem based management approach. For studies emphasizing the benthos and the upper trophic levels, the focus is often on predatory interactions based on fish diet data (Garrison and Link, 2000; Heath, 2005). Linear, steady-state, food-web models have been used to represent these complex interactions (Christensen and Pauly, 1993). This *trophic-centric* approach does not include the dynamics of individual species and neglects the physical processes. Steele and Gifford (2010) argue that there are no contradictions between the two sets of simplifying assumptions. They are complementary and answer different questions about the dynamics of individual populations and the productivity of ecosystems. An important issue is the extent to which these methods, jointly, can illuminate the concept of ecosystem-based management; and how they can be combined to answer questions about short- and long-term conservation of marine resources.

Recently, in response to the desire for ecosystem-based management, end-to-end models combining bottom-up and top-down components have been developed (Rose et al., 2010). These very large, complex models are intended for "strategic management evaluations" (Fulton et al., 2004) of particular ecosystems, rather than comparisons across several systems (Steele et al., this volume). An alternative is to combine aggregated versions of existing food web models of the upper trophic levels, with NPZD formulations of the microbial web, and with simplified representations of the main physical forcing (Aydin et al., 2005: Steele et al., 2007; Steele and Ruzicka, 2011). The critical issue is whether the use of functionally defined groups or guilds, rather than species, as variables, can achieve portability while retaining adequate realism.

Cross-ecosystem, multi-model comparisons are difficult to conduct. They often require substantial computational power and intense scientific effort. However, to evaluate the robustness of the ecosystem responses to climate change and/or anthropogenic forcing, this approach is essential. To conduct these kinds of studies, support by international programs such as IMBER is needed. Additionally, to reduce the uncertainty of the ecosystem response, accurate representation of the physical conditions is essential. One approach is to use climatologies developed in a consistent manner with agreed upon approaches (e.g., GODAE, Brasseur et al., 2009) to provide a common physical field for the ecosystem model. This will reduce the uncertainty of the ecosystem model simulation and facilitate the investigation of uncertainty caused by using different ecosystem models (see also, for example, Friedrichs et al., 2006, 2007).

4.3. Application of remote sensing observations

4.3.1. Remote sensing contribution to comparative studies

Within the context of comparative studies, remote sensing observations have a clear role in provision of information to supplement field programs where broader spatial perspective affords critical additional interpretive framework. Further, the ongoing accumulation of remote sensing observations contributes to obtaining the basis needed to characterize the current ecological and biogeochemical state of local and regional domains. Such a basis can also contribute to efforts that rely solely, or principally, on remote sensing data to carry out comparative studies that focus on identifying how marine ecosystems within a given domain respond to anthropogenic influences or climate modes. Remote sensing data are also well suited for conducting interregional comparative studies (e.g., Sherman et al., 2011).

The spatial perspective and the regular temporal coverage provided by remote sensing platforms makes the data they provide a natural complement to field-based comparative studies. An illustrative example of this synergy is the analysis by Platt et al. (2003) of larval fish recruitment on the continental shelf off Nova Scotia. This study explored the hypothesis that the relative timing of fish spawning and the peak of the phytoplankton spring bloom were the key deterministic factors for the abundance of the resulting year-class (i.e., the Hjort-Cushing hypothesis, Cushing, 1990). In this study, Coastal Zone Color Scanner (CZCS) data were included since determining the timing of the bloom only requires comprehensive spatial coverage for the period on which temporal derivatives were performed. With data from the observational periods of both CZCS and Sea-viewing Wide Field-of-view Sensor (SeaWiFS), Platt et al. (2003) found that bloom timing explained 89% of the variance of the annual haddock survival index calculated from a thirty-year stock assessment record.

A similar use of temporal derivatives, applied to the SeaWiFS ocean color climatology, was used to characterize phytoplankton bloom dynamics over the Indian Ocean basin (Lévy et al., 2007). With the monsoonal cycle fundamentally influencing the basin's biological variability northward of 10°S, this represents a challenging undertaking since much of that area is subject to semi-annual bloom peaks. Through application of a systematic methodology, Lévy et al. (2007) generated distributions of summer and winter (Boreal) bloom onset over the basin and regionally partitioned summer and winter blooms with consistent characteristics (e.g., biomass accumulation and bloom initiation). In a follow-up effort that applied the same methods to output from a basin scale coupled physical-biogeochemical model, the distribution of winter and summer bloom onset, as well as the regionally parsed blooms, were nicely captured (Koné et al., 2009). This certainly represents a more critical means of assessing a free-running biogeochemical model's capabilities than has typically been applied; however, the original analysis of Lévy et al. (2007) also provided an invaluable spatial framework of autotrophic variability that could (and should) be applied toward comparative analyses of higher level trophic interactions in the monsoon-impacted Indian Ocean. Further, Lévy et al. (2007) succeeded in demonstrating a technique that leverages the ocean color data in a way that exhibits clear potential for application to other regions of interest.

To explore how two recent occurrences of the Indian Ocean Dipole (IOD, 1997/1998 and 2006/2007) differentially affected sub-regions of the Indian Ocean, anomalies of sea surface temperature (SST), winds, sea surface height (SSH), subsurface temperature (via Argo), chlorophyll and net primary production (NPP) were analyzed (Wiggert et al., 2009). The signature feature of the IOD is the phytoplankton bloom along Indonesia that extends westward in southern tropical waters and along the equator (Murtugudde et al., 1999). During both the 1997/1998 and 2006/2007 IODs the production estimates indicate regional increases/decreases of up to 50% in the east/west, with local monthly means in waters offshore of Indonesia exhibiting positive anomalies exceeding 900 mg C $m^{-2}d^{-1}$ (Wiggert et al., 2009). While

an essentially zero-sum basin wide impact on NPP during both IODs is estimated by Wiggert et al. (2009) the geographical rearrangement of carbon uptake, as estimated by the Behrenfeld et al. (2005) NPP algorithm, is profound and has clear implications for substantially altered biogeochemical flux distributions to accompany the spatial shifts in apex predator abundance that have been identified (cf., Menard et al., 2007).

4.3.2. Future directions

Oceanic remote sensing has matured considerably since the cohort of proof of concept missions launched in 1978 (i.e., TIROS-N, Seasat and CZCS). Taken in concert the core variables (i.e., SST, winds, SSH and ocean color), whose measurement was first successfully demonstrated at that time, make for a reasonably comprehensive environmental characterization that can provide significant insight into the mechanisms underlying the physical-biological interaction signatures that manifest in the remote sensing record. The one environmental measure that has only recently become available is salinity (Lagerloef et al., 2010), which bodes well for future interdisciplinary studies, in particular any efforts undertaken in regions dominated by large-magnitude river systems. Surprisingly, it is rather uncommon for more than a couple of remote sensing data fields to be included as part of any given analysis. This may relate to the presence of disciplinary "silos" that require some effort, be it conceptual or methodological, in order for an interdisciplinary remote sensing approach to be successfully achieved.

Satellite ocean color radiometry provides data products that are most closely related to marine ecosystem and biogeochemical processes; with further in situ or remote sensing observations to provide characterization of environmental conditions, the value of ocean color measurements increases significantly. A remarkable aspect of the field of ocean color remote sensing is that the capabilities of supporting applications continue to expand and evolve at a rapid pace. One promising recent advancement exploits the two bands for measuring phytoplankton fluorescence (667 nm and 678 nm), first available on the MODIS-Aqua sensor, to develop global distributions of phytoplankton physiological state (Behrenfeld et al., 2009). The split observational bands enabled determination of fluorescence line height, which was used to infer patterns of nutrient stress and iron limitation; these patterns showed remarkable agreement with micronutrient distributions in the Pacific and Indian Oceans obtained by biogeochemical models (Moore et al., 2006; Wiggert et al., 2006).

In combination with the improvements in identifying PFTs (e.g., Alvain et al., 2005, 2008; Hirata et al., 2011; Subramaniam and Carpenter, 1994; Westberry et al., 2005) and phytoplankton community composition and size classes (Aiken et al., 2007; Mouw and Yoder, 2010; Uitz et al., 2010), these new ocean color-derived advances suggest an excellent potential for significantly improving the capabilities of coupled physical-biogeochemical models that rely on NPZD-based ecosystem models, which increasingly strive to include size classes, functional types and micronutrient influences in their configuration (Hood et al., 2006). It is critical for this advancement in ocean color techniques and applications to be accompanied by rigorous in situ validation. Global coverage of phytoplankton speciation and function types, and the associated biogeochemical distributions and rates, that these methods could provide would maintain the ongoing sea change in our understanding of the oceanic ecosystem functioning that global views of upper ocean physical environment and phytoplankton biomass distributions have afforded; however this potential will only be realized if the obtained information is thoroughly ground-truthed.

5. Conclusions: general guidelines for comparative studies

The focus of the IMBER program on interactions and feedbacks between food webs and biogeochemical cycling brings together two areas of marine science that have typically proceeded in parallel, with little cross integration. As a result, attributing cause and mechanisms to observed changes in marine ecosystems has been difficult and incomplete. The observational and modeling programs now underway through IMBER (Table 1) have a focus on end-to-end ecosystem studies, which is already influencing the structure of models (cf. Table 2) and types of observations. Within the IMBER regional programs, comparative studies are underway which are providing synthesis and integration of historical and diverse data sets, the results of which provide a basis for across-region comparative studies. The IMBER focus on comparative studies from the outset will potentially ensure that the data sets and models are adequate and appropriate to undertake these studies.

One challenge to the science community is to extend the comparative studies of the natural system to include human, social, economic and cultural effects.

The general guidelines for comparative studies emerging from the IMBIZO workshop discussions are intended to support planning and implementation of new programs, and to improve existing programs. First and foremost, integrated studies of marine ecosystems (food web and biogeochemistry) should be underpinned by one or more conceptual models of key ecosystem processes relevant to the study, and identification of the key high level (e.g., policy or societal) and scientific questions to be addressed. Together these can be used to inform what field measurements are required (cf. Table 3) and the appropriate selection of models and other investigative tools. The proposed guidelines indicate key ecosystem components, which should be considered, including magnitude and fate of primary production, habitat characteristics, nutrient and carbon cycling, biological community structures and population dynamics. Key issues to be taken into account include forcing factors (e.g., atmospheric warming, NAO), human pressures (e.g., nutrient enrichment, fishing), the ecosystems or biomes (e.g., coastal or offshore, polar or equatorial), spatial scales (e.g., regional versus intra/inter-basin comparisons), temporal scales (e.g., daily to multi-decadal), physical oceanographic or habitat features, trophic levels of detailed interest (e.g., primary and secondary production vs. cod recruitment), species or functional groups of interest, rates and/or fluxes relevant to the species or functional group or trophic level of interest, and bottom-up and top-down effects on ecosystem functioning.

Most studies that integrate food web and biogeochemistry research focus on structure and functions of the present day ecosystem. A key question is what the limitations of even long-term (~50 year) time-series of data are in improving the understanding of present day biogeochemical processes, and how these have evolved over longer time periods. Extension of studies of present day systems to include an evolutionary time-frame is needed to enable assessments of the impacts of future climate change. However, differentiating changes that occur on an evolutionary timescale (i.e. adaptation) versus those associated with ecosystem shifts (i.e. acclimation) is difficult. Projections of ecosystem-biogeochemistry interactions that may occur over century time scales (e.g., 2100) can represent acclimation or adaptation, depending upon the organisms under consideration, i.e. microbes can evolve on this timescale whereas larger organisms like fish cannot. Thus, the impacts of climate change are difficult to address from a comparative ecosystem perspective. Inherently, comparative ecosystem analysis is a present or a present versus past activity, not a future one. The emphasis should therefore be on heuristic forecasting and should be based on the best available understanding.

The global vision for clean, safe, productive and biologically diverse oceans and seas is the basis for managing sustainable human utilization of the goods and services provided by the seas. The challenge for science is to provide an understanding of the state and function of the marine environment and thus put future forcing such as climate change or changes in human activities into that context. This requires the development of methods/metrics to describe the

Table 3

(a) Key ecosystem processes to be considered in research programs focused on lower trophic levels, which could form the basis for comparative studies. These processes are formulated here as key questions. Each process may be influenced by a number of factors, which have implications for ecosystem structure and function. Those in italics indicate minimum fieldwork requirements. Phytoplankton are used here as primary producers, but macrophytes and angiosperms can be included. (b) Examples of more detailed requirements for data on environmental/habitat characteristics, nutrient cycling, biological community structures, population dynamics, and carbon cycling. (c) Examples of requirements for comparative ecosystem studies focused on higher trophic levels.

(a) Key questions	Influencing factors	Ecosystem/Biogeochemistry implications
What is the magnitude of primary production (PP) in the ecosystem?	1. *Phytoplankton community structure*. 2. *Phytoplankton growth rates* 3. Phytoplankton growth timescales vs. advective timescales (e.g., water renewal rates) 4. *Seasonal* (temporal) *and oceanographic / environmental* (spatial – both horizontally and vertically) variability. 5. Variability due to human impacts 6. Variability due to climate change (regime shifts) and known climate modes (e.g., NAO).	1. Environmental variability (e.g., seasonality) drives shifts in plankton species composition, food web structure and function (i.e., total PP and fate of PP) 2. Influenced by environmental factors such as nutrients (absolute and ratios), light availability, etc. 3. Impacts the efficiency of biological assimilation of nutrient/carbon 4. More robust estimates of total PP may increase (or decrease) estimates of primary production at regional scales, and impact estimates of carrying capacity for higher trophic levels such as fish. 5. The magnitude of PP may be influenced by, for example, nutrient enrichment and sediment re-suspension (e.g., by beam trawls and aggregate extraction). 6. Changes in oceanography (e.g., surface warming, and increased duration and intensity of stratification) will impact phytoplankton blooms, e.g. onset, duration, and magnitude and fate of primary production.
What is the fate of primary production (PP) in the water column?	1. Conversion into larger organic carbon particles (through *grazing* and growth of zooplankton and other heterotrophs). as well as aggregate formation). 2. Recycling in the water column, by the microbial food web (including viruses), with high carbon losses due to respiration. 3. *Sedimentation* to the seabed. For conversion to particulate organic carbon (benthic biomass), burial, or nutrient recycling. 4. Variability in function due to human impacts (e.g., fishing) and climate change.	1. More robust estimates of secondary production in the water column may increase estimates of overall productivity and carrying capacity for higher trophic levels such as fish, and help constrain the partitioning between 'exported' vs. 'recycled' carbon. 2. Remineralisation in the water column sustains primary production, enhanced remineralization decreases drawdown of atmospheric CO_2 due to increased respiration of CO_2 and decreases flux of particulate material to seabed. Viral lysis may short-circuit fluxes through the food web leading to further enhanced microbial loop. 3. Magnitude of sedimentation to the seabed constrains benthic biomass, impacts drawdown of atmospheric CO_2. Provides organic input to other sectors, for consumption and/or recycling. 4. Shifts in plankton species composition impacts food web structure and function (e.g., sedimentation).
How much particulate primary production (PP) reaches the seabed?	1. Magnitude of PP 2. Pelagic fate of PP 3. Structure of planktonic food web (role of micro-zooplankton and hyperbenthos) 4. Across or off-shelf advection 5. Extent of permeable coarse sediments and advective flows induced by tides and waves	1. Increased primary production during the spring bloom (e.g., due to human impacts or climate change) may increase the flux of PP to the seabed. Particularly where there are delays in grazing by the planktonic food web, and nitrate depletion is followed by bloom senescence 2. As above 3. The presence of active microbial food webs in the water column will *reduce* the flux of particulate PP to the seabed. However, hyperbenthic species may *increase* the availability of dissolved and detrital nutrients (e.g., as faeces) to benthic communities. 4. Large areas of the coastal seas (e.g., North Sea, Chukchi Sea and Bering Sea) are strongly advective. As a result, much of the PP may not be available to benthic communities in shallow shelf systems but rather advected off the continental shelf. 5. Coarse sediments may cycle carbon faster, but observations may be more difficult to make reliably. Provides information on spatial patchiness of benthic remineralization.
What is the fate of primary production (PP) that reaches the seabed?	1. Conversion to particulate biomass, through feeding and growth of *benthic communities* 2. Burial of particulate organic material, through activities of burrowers/ bioturbators. 3. Aggregation in dynamic "fluff layers" in the benthic boundary region 4. Remineralisation of macro and micronutrients 5. *Sediment type* 6. Influence of human impacts, especially trawling	1. As above, and improved understanding of impacts of functional differences in biodiversity on carbon and nutrient cycling in the benthos 2. Changes in burial rates will impact geological timescale drawdown of atmospheric CO_2 3. Aggregates of particulate material may form a food source for detritivores, contributing directly to secondary production. Or they may be sites of active microbial activity, enhanced rates of nutrient recycling, and further decreasing the efficiency of the biological pump due to respiratory losses and reduced drawdown of CO_2 4. Changes to functional groups (climate, human activities) may affect the rate of remineralisation of detritus and will impact the significance of benthic-pelagic coupling in terms of sustaining primary production in the water. 5. Sediment grain size influences advective flows through the seabed, and hence the absolute and relative rates of burial, denitrification and recycling 6. Trawling may have a direct influence on benthic–pelagic coupling (e.g., re-suspension) or an indirect affect by altering the structure of the benthic community

(continued on next page)

Table 3 (continued)

(b) Basic data required	Examples
Environmental or habitat characteristics	Bathymetry, sediment types, circulation, water masses, atmospheric forcing/meteorology
Nutrient cycling	Macronutrients, micro-nutrients
Biological community structures	Species assemblages, invasive species
Population dynamics	Growth and mortality rates
Carbon cycling.	Biomass of all trophic levels, grazing and consumption rates, transport (vertical and horizontal) of carbon

(c) HTL models	Examples
Environmental or habitat characteristics	Bathymetry, circulation, water masses, atmospheric forcing/meteorology
Biological community structures	Species assemblages, invasive species
Population dynamics	Physiological preferences, growth and mortality rates, stock sizes, recruitment
Carbon cycling	Magnitude and fate of primary production, dietary preferences, prey abundances,

state of an ecosystem and mechanisms to minimize the impacts of human activities to avoid undesirable disturbances and tipping points. We need to go further and attempt to quantify key functions, which characterize ecosystems and predict the impact of such functions of natural variability and human activities. Ecosystem studies typically focus on key linkages between hydrography, pelagic food webs, benthic food webs and higher trophic levels such as fish (Fig. 3). Approaches include field measurements, ecosystem models and other tools (cf. Section 4). For comparative studies, key issues include establishing general requirements, particularly in terms of field measurements, and resolving the level of detail required. In terms of the latter, the benefits of complex (detailed) versus simple approaches need to be clarified. Simple approaches with clear assumptions may be more powerful (e.g., Lachkar and Gruber, this volume), but species-based approaches are also needed.

Integrated studies of biogeochemistry and food webs need to be underpinned by one or more conceptual models of key ecosystem processes relevant to the study, and identification of the key high level (e.g., policy or societal) and scientific questions to be addressed. Together these can be used to inform field measurements required and the appropriate selection of models and other investigative
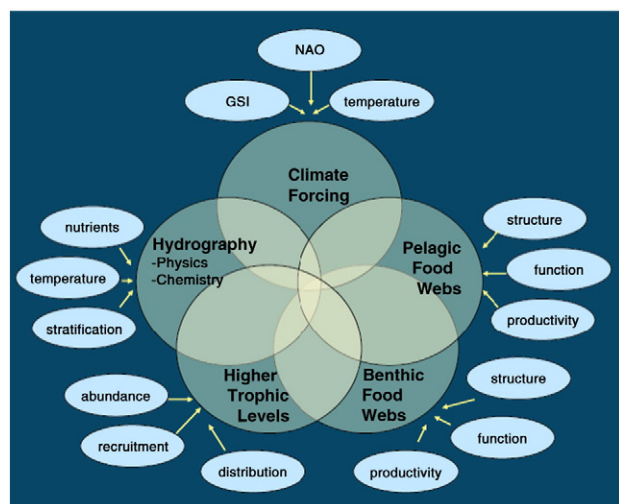

Fig. 3. Key linkages driving ecosystem dynamics and biogeochemical cycles. Climate is influenced by factors such as the North Atlantic Oscillation (NAO), the variations in difference of normalized pressures in winter between Lisbon, Portugal and Stykkisholmur, Iceland (Hurrel, 1995), the Gulf Stream Index (GSI), a measure of the position of the northern boundary of the Gulf Stream where it diverges from the American coast (Taylor, 1995), and temperature (Reid et al., 2009), and affects the physical and chemical oceanography (hydrography). Both impact upon benthic and pelagic food webs (in terms of structure, function and productivity) and higher trophic levels (e.g., abundance, distribution and recruitment of fish), as well as cycling of elements.

tools. As an example, Table 3 shows proposed guidelines for comparative studies, focussed on key scientific questions which integrate biogeochemical and food web studies through improved understanding of the sources and sinks of primary production. The important variables that influence the key questions form the basis for the field measurements, that, without being overly prescriptive, should facilitating future comparative ecosystem activities. These requirements provide guidance for new programs, ensuring that the results obtained will be relevant for comparative work. Existing programs, which do not have all the measurements, could perhaps add them over time. Studies could therefore range from those based on simple measures or indices of ecosystem structure (e.g., chlorophyll a) to those based on complex, species level data. Intermediate level studies, investigating functional groups, could also be included. Such studies include, for example, N_2-fixing organisms, diatoms, and large and small planktonic eukaryotes. While it is not possible to establish species lists for every part of the global ocean, we could, at least for microbes and phytoplankton, include trophic and taxonomic attributes derived from a combination of tools available to date, such as high-performance liquid chromatography (HPLC), flow cytometry and epifluorescence microscopy and DNA-based molecular tools. Shifts in community structure, such as a shift in diatom dominance from *Skeletonema* to *Thalassiosira*, or a decline of diatoms and increased abundance of cyanobacteria (with no change in total chlorophyll) may provide valuable indicators of changes in ecosystem structure and functioning.

Responses of marine ecosystems to global warming are expected to differ among biogeochemical provinces (Sarmiento et al., 2004). Understanding and defining what these responses might be is critical to the development of mitigation strategies and management policies. Well-designed comparative analyses, based on observations, models or both can be applied within and across ecosystems. As such, they provide an approach for identifying key processes and constraining the range of potential ecosystem responses. As illustrated by the discussions and presentations at the IMBIZO workshop and the contributions in this special issue, many successes have been achieved. But much still remains to be done in terms of developing the datasets, models and expertise to be able to undertake comparative studies that bridge biogeochemistry and ecosystem research in marine systems.

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