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Comparative marine ecosystem analysis: Applications, opportunities, and lessons learned

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ABSTRACT

The papers in this special issue seek to evaluate how ecosystem structure and function interact to support fisheries production. We particularly elucidate which processes amplify or dampen spatial and temporal variation in that production within and between ecosystems. This paper attempts to assess the contribution of marine comparative ecosystem analysis to knowledge of the factors that affect the structure and function of marine ecosystems. We introduce the reader to the special volume, briefly highlighting the manuscripts in this special issue as organized by various thematic emphases. Papers in this volume are reviewed and briefly summarized with respect to current approaches, applications, opportunities, and lessons learned. Several approaches, applied to ecosystems over different spatial and temporal periods as well as the application of innovative statistical methods, facilitated comparisons and revealed basic underlying patterns that would not have been observable if only one ecosystem had been examined. Results imply that deeper eastern ocean boundary systems are more strongly influenced by bottom-up forcing; that shallower western ocean boundary systems, mainly continental shelves, are more strongly influenced by top-down forcing; and that synchronous events have taken place around the world's oceans. In many examples, it appears as if fisheries landings have shifted in emphasis from groundfish to invertebrates and that fish communities have shifted from a demersal to pelagic dominated groups. The benthos is an important, but understudied component of most ecosystems. We advocate database standardization at the onset of comparative studies as a mechanism to facilitate effective comparisons in future studies. Effective marine ecosystem comparisons require large, multi-national collaborations.

1. Background

The decision to pursue comparative ecosystem analysis was motivated by the urgent world-wide recognition that marine ecosystem management needs to move away from an exploited single species focus towards a more holistic, ecosystem-based management paradigm (Link, 2002a,b; Garcia et al., 2003; Browman et al., 2004; Murawski, 2007). There are few examples which demonstrate its practical implementation, despite the fact that the subject of the ecosystem approach to the management of the marine environment has received considerable world-wide attention.

The ecosystem approach to coastal and ocean management has been addressed by many over the past decade (Flaaten et al., 1998; Garcia et al., 2003; Browman et al., 2004; ICES, 2005). For example, the North Pacific Marine Science Organization (PICES) published a North Pacific Ecosystem Status Report (PICES, 2004). Similarly, the International Council for the Exploration of the Seas (ICES) is preparing a science plan (ICES, 2008) for how ICES could contribute to marine research and to the development of an Integrated Ecosystem Assessment for marine waters in the ICES area. Kenny et al. (this issue) report results directly from this effort. An integrated marine environment management plan for the Barents Sea and the Lofoten Islands area was also presented to the Norwegian Government in 2006 (Anon, 2006). As a final example, we note that the Joint Subcommittee on Ocean Science and Technology (JSOST) of the National Science and Technology Council of the White House Office of Science and Technology Policy, in recognition of the fact that the world's marine ecosystems are experiencing changes due a wide range of impacts, recommended a new course for the nation's ocean policy. Within this framework, JSOST identified a near-term need of undertaking comparative analyses of ecosystem structure and function to improve indices of ecosystem health and the stewardship of natural resources (JSOST, 2007).

Marine ecosystems the world over are experiencing stress from natural and anthropogenic sources that may cause substantial

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change to the structure and function of these ecosystems in the near future. These include impacts of climate change (Cury et al., 2008), exploitation (Pauly and Watson, 2003), coastal eutrophication (Cloern, 2001) and contamination (Jackson et al., 2001). Contextualizing ecosystem responses in a broader and more holistic manner has been suggested as an approach to better manage and minimize the impact of these stresses (e.g., Link, 2002a,b; Garcia et al., 2003; Murawski, 2007). But, adopting ecosystem approaches to the management of fishery ecosystems requires an understanding of the structure and function of these systems, their variability, how they respond to perturbations, and to what extent they are connected to (or reliant on) exchanges with other ecosystems. Importantly, marine ecosystems often demonstrate nonlinear or abrupt responses to perturbation (e.g., Hare and Mantua, 2000; Hunt et al., 2002, 2008; Scheffer and Carpenter, 2003; Steele, 2004). These nonlinearities result from the influence of multiple physical, environmental, anthropogenic and biotic drivers that operate and interact over multiple scales (deYoung et al., 2004). For example, marine ecosystems respond simultaneously at multiple spatial scales that may cascade from large basin-scale influences downwards or upwards from small-scale physical forcing. These in turn, interact with regional processes to affect overall control of local conditions. Similarly, marine ecosystems are impacted by multiple drivers that act on annual, interannual and multi-decadal time scales (e.g., storms, advective processes and large-scale atmospheric forcing). Trophodynamically, marine food webs are dynamic, often have open boundaries, and respond nonlinearly to climatic, anthropogenic and ecological influences (Hsieh et al., 2005). This inherent complexity and the large spatial scale of marine ecosystems suggests that progress towards an understanding of how the structure and function of marine ecosystems influence and regulate patterns of fisheries production will be aided by a comparative approach.

Obviously there have been prior marine ecosystem comparative studies (Baird et al., 1991; Baird and Ulanowicz, 1993; Ross et al., 1994; Blackford et al., 2004; Hunt and Megrey, 2005) and we note that the comparative approach has been used successfully in the study of marine fishery ecosystems (Hunt and Megrey, 2005; Moloney et al., 2005; Megrey and Aydin, 2009; Sakshaug and Walsh, 2000).

Yet we assert that this special volume is the first of its kind in that it provides a comprehensive, coordinated, and integrated view of a wide range of marine ecosystems by applying different approaches and efforts. This complements alternative approaches such as applying one model to multiple ecosystems (Aydin et al., 2007) or multiple models to one ecosystem.

The comparative approach has been at the core of several international, national and regional programs, including GLOBEC (Global Ocean Ecosystem Dynamics program), Euroceans IndiSeas, and CAMEO (Comparative Analysis of Marine Ecosystem Organization), among others. For example, the comparative method has been used successfully to gain insights into one particular species, cod, through the ICES/GLOBEC Cod and Climate program (e.g., Brander, 1994, 1995; Planque and Frédou, 1999; Dutil and Brander, 2003; Rätz and Lloret, 2003; Drinkwater, 2005). Synthesis of other regional GLOBEC programs such as Small Pelagics and Climate Change (SPACC – Checkley et al., 2009) and Ecosystem Studies of Sub-arctic Seas (ESSAS – Hunt and Drinkwater, 2005) has also occurred. These types of comparisons have also occurred in several upwelling ecosystems (e.g., Cury et al., 1998; Shannon et al., 2008).

The comparative approach is used widely in the newly emerging field of macoecology. Macroecology can be defined as the study of relationships between organisms and their environment, including patterns of abundance, distribution, and diversity of species at large spatial and temporal scales (Brown, 1995; Gaston and Blackburn, 2000; Blackburn and Gaston, 2003) or the study of broad, consistent patterns in the ecological characteristics of organisms and ecosystems (Cheung et al., 2008). Comparative macroecology permits the ability to draw generalizations, determining what is fundamental to ecosystems in general and what is unique to particular ecosystems. Such generalizations will be important for successful application of the ecosystem approach to fisheries and will help in determining the response of marine ecosystems to climate change.

We view the comparative approach as ideal for understanding marine ecosystems. Studying marine ecosystems is extremely challenging because these systems are spatially large, difficult and expensive to observe, biophysically complex, dynamic and nonlinear. As we have noted, comparisons among and between ecosystems, particularly via the use of statistical inference and dynamic models, is a powerful approach because it takes advantage of “natural experiments” that otherwise would not be feasible. Because of the size and complexity of marine ecosystems, it is essentially impossible to perform controlled *in situ* experiments. Comparative analysis provides the opportunity to perform “pseudo-controlled” experiments and clever contrasts can be instructive. We view differences in management regimes (e.g., time area closures, quotas, and moratoria) as examples of natural experiments that may be of particular utility in detecting the sources and patterns in variation of ecosystem structure and function.

The objectives of this introductory paper are threefold. First, to introduce the reader to the special volume, briefly highlighting the manuscripts in this special issue as organized by various thematic emphases. Second, to synthesize and summarize key lessons we have learned from the marine ecosystem comparisons presented in this special volume. Third, to highlight specific areas we feel will benefit other researchers attempting to perform similar ecosystem comparisons. That is, we want to assist with future comparative analysis research by posing a series of questions and topics meriting further elucidation, as informed by the works presented in this special volume.

2. Ecosystems, major species, and processes

In this special issue of *Progress in Oceanography* the marine ecosystems compared are broad in their geographic scope (Fig. 1). All ecosystems are located in the northern hemisphere and are largely high-latitude ecosystems. This outcome is due mainly to the geographic emphasis of the MENU program and North Atlantic focus of the ICES contributions. No warm water oceanic or coral reefs ecosystems were included in the comparisons. System comparisons were made for various combinations of the eastern Bering Sea, Gulf of Alaska, Georges Bank, Gulf of Maine, Norwegian Sea, Barents Sea, the North and South Gulf of St. Lawrence, Scotian Shelf, Newfoundland Shelf, North Sea, Sørfjord Norway, Southern New England, Adriatic Sea, Gulf of Finland and Baltic Sea. All ecosystems examined have important commercially exploited species of fishes. Often the same species occurred in several ecosystems.

Papers in this issue describe ecosystems by emphasizing various aspects of these systems. These include: physical features such as thermal fronts (Belkin, this issue; Belkin et al., this issue), bathymetry, circulation, sea ice, and sea surface temperature (Drinkwater et al., this issue; Mueter et al., this issue); process description such as cross-ecosystem process comparisons (Mueter et al., this issue; Pranovi and Link, this issue), impacts on life history strategies (Suryan et al., this issue), basin-scale examination of spatial and temporal covariation in recruitment and life history (Megrey et al., this issue; Suryan et al., this issue), biophysical interactions (Mueter et al., this issue; Drinkwater et al., this issue); living marine resource-related biology such as biota (Link et al., this issue; Gaichas et al., this issue), fisheries (Link et al., this issue;

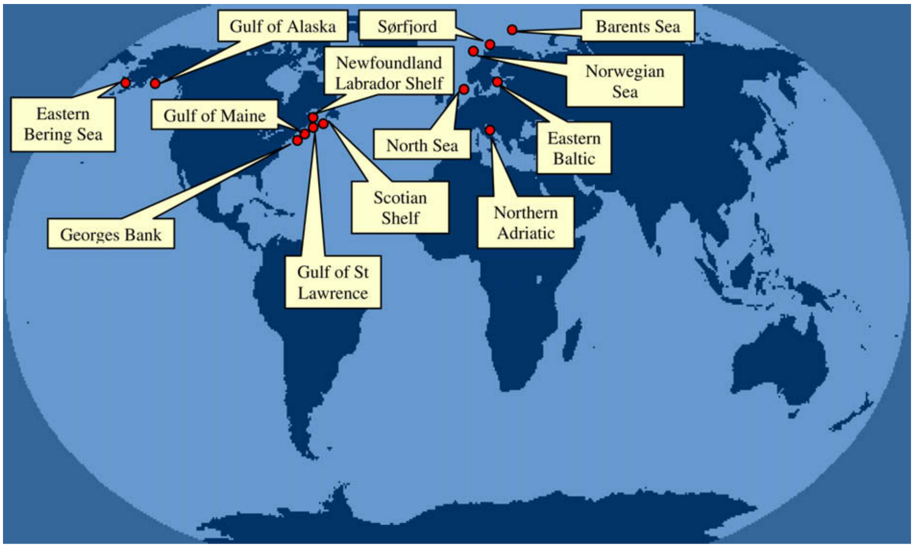

Fig. 1. Marine ecosystem examined in this issue.

Bundy et al., this issue), trophodynamics (Gaichas et al., this issue; Dolgov, this issue; Kenny et al., this issue; Tomczak et al., this issue), and food web organization (Gaichas et al., this issue; Pranovi and Link, this issue; Bundy et al., this issue; Morissette et al., this issue). The combination of comparisons and contrasts is as varied as the number of the systems examined, but provides a unique blend across a wide range of emphases.

3. Comparative methods – quantitative and qualitative

3.1. Quantitative approaches, models and analyses

The papers in this volume use a diverse set of qualitative and quantitative methods and models to facilitate ecosystem comparisons. Univariate statistics, regression and correlation play an important and central role (Megrey et al., this issue; Bundy et al., this issue; Mueter et al., this issue; Link et al., this issue).

Although numerous whole system or end-to-end ecosystem models are available, such as ATLANTIS (Fulton et al., 2003a,b, 2004; Fulton, 2004; Fulton and Smith 2004), SEAPODYM (Lehodey et al., 2003) and APECOSM (Maury et al., 2007a,b), the papers in this volume (Gaichas et al., this issue; Tomczak et al., this issue; Bundy et al., this issue; Pravoni and Link, this issue; Morissette et al., this issue) mainly relied on the ECOPATH/ECOSYSTEM (EwE, Christensen and Pauly, 1992; Christensen and Walters, 2004) approach. However difficulties with comparisons can arise when different levels of trophic aggregation exist. Often choices on how best to aggregate whole system models are subjectively made by the analyst and can create problems when making comparisons (Megrey and Aydin, 2009). It is easier to go from a highly disaggregated model to a more aggregated model. Gaichas et al. (this issue), Tomczak et al. (this issue) and Pranovi and Link (this issue) paid careful attention to creating equivalent aggregated functional groups among the ECOPATH models they examined. Trophic Network Analysis, available as part of the ECOPATH software, contributed an additional perspective on ecosystem properties. These model outputs have proved useful for calculating macrodescriptor system level metrics (Gaichas et al., this issue; Tomczak et al., this issue; Bundy et al., this issue; Morissette et al., this issue; Pranovi and Link, this issue).

Analysis of anomalies and calculating coefficients of variation were commonly used methods. These data manipulation techniques facilitated comparison by putting variables on the same scale, minimizing differences due to absolute magnitude of a time series, or by calculating a relative measure of variation (Megrey et al., this issue; Mueter et al., this issue; Kenny et al., this issue; Link et al., this issue). Smoothing filters, used to remove high frequency variation, made long-term patterns more apparent (Megrey et al., this issue; Mueter et al., this issue; Kenny et al., this issue).

The use of ecosystem indicators was a common metric for comparing ecosystem production. Metrics such as: fisheries landings; total finfish biomass; planktivore, demersal, benthivores, and flatfish biomass; mean individual fish length; mean individual fish weight; indicator species or keystone species; mean trophic level of the landings; commercial invertebrate biomass; the pelagic-to-demersal biomass ratio; and the commercial invertebrate-to-demersal biomass ratio (Pranovi and Link, this issue; Bundy et al., this issue; Gaichas et al., this issue) were all commonly applied.

Mutivariate methods, ordination methods, and time series analysis methods also play a major role to reconcile disparate data in comparative analyses. Methods such as Dynamic Factors Analysis (Zuur et al., 2003) were applied by Link et al. (this issue) and Megrey et al. (this issue), spectral and time series analysis to identify multivariate cross-correlations (i.e. coherence in time between ecosystems; Kenny et al., this issue) the more common Principal Correlation Analysis (PCA) and Empirical Orthogonal Functions (EOF) demonstrated by Kenny et al. (this issue), Megrey et al. (this issue) and Bundy et al. (this issue), as well as time series methods to statistically identify regime shifts (i.e. STARS, Rodionov, 2004; Rodionov and Overland, 2005). Kenny et al. (this issue), Link et al. (this issue) and Megrey et al. (this issue)) applied this new technique to their time series data.

Although by no means exhaustive, there are a wide range of analytical methods showcased in this special issue that should serve as useful methodological examples for future ecosystem comparisons.

3.2. Strategies for ecosystem comparisons

Ecosystem comparison strategies varied and several approaches were attempted given the data with which to perform comparisons. There is value to each approach, and we highlight three general strategies here as they have been employed by the papers in this special issue.

3.2.1. Within ecosystem comparisons

In this approach, often more than one model is applied to the same ecosystem and is assessed at different points in time (Townsend et al., 2008; Plagányi, 2007). If more than one model is applied, then this comparison removes the "location/species group" as a confounding variable. It is possible to examine patterns between major energetic pathways (i.e. pelagic vs. benthic) (Frank et al., 2007), explore dynamic changes in biological community composition and trophic connections (Gaichas et al., this issue; Link et al., this issue; Mueter et al., this issue), investigate interactions between fishing effects (i.e. truncation of the age distribution, predatory release, large biomass removals), and climate (Mueter et al., this issue).

3.2.2. Cross-ecosystem comparisons

In this method, attributes of several ecosystems are compared, usually via a time series metric between ecosystems on similar temporal and spatial scales. The objective of this approach is to elucidate larger spatial and temporal patterns of behavior. This approach removes the "metric" and "model" as a confounding variable, and has the advantage of applying one equivalent model to different ecosystems or functional groups (e.g. EwE). This approach also has the advantage of using more than one model in one ecosystem/functional group to calculate an ensemble result, like IPCC climate change scenarios (IPCC, 2007).

Examples of potential comparisons include ecosystems that cover large latitudinal gradients, those that are open, deep basin vs. shallow shelf vs. more enclosed coastal ecosystems, are influenced by inflow of warm water vs. those dominated by cold water, are connected by large-scale atmospheric, low frequency teleconnected forcing (i.e. impacts and associations between ecosystems affected by the North Atlantic Oscillation vs. the Pacific Decadal Oscillation); as well as ecological differences such as different dominant functional groups and feeding guilds within and between ecosystems (i.e. pelagic vs. benthic-feeding fishes). Some of these particular contrasts are examined in the works contained in this special volume, but we recognize that many more could also be done.

3.2.3. Common process comparisons

Isolating a common process removes the "location/species group" as a confounding variable. The idea is to take one theme (i.e. temperature vs. recruitment) and apply the metrics thereof to one species over wide geographic scale and across ecosystem. This approach removes the "mechanistic process" as a confounding variable. Large spatial contrasts (Belkin, this issue; Belkin et al., this issue; Suryan et al., this issue; Mueter et al., this issue) should make differences more apparent.

4. Lessons learned

4.1. Basin-scale comparisons, the big picture

In the study of large marine ecosystems, the comparative approach provides a means of putting these already large systems into the bigger picture of the global ocean and associated forcing agents that operate at very large scales (see Belkin, this issue; Belkin et al., this issue). To accomplish this objective, it is necessary to develop time series of comparable system metrics for each region. These comparisons can reveal within and between basin patterns that demonstrate the role of large-scale atmospheric forcing and the importance of bottom-up processes both within and between ecosystems in one ocean basin as well as in cross-basin comparisons.

For example, Megrey et al. (this issue) show that there were large-scale negative correlations in fish recruitment between the Pacific and Atlantic ocean basins, though, as might be expected, within-basin relationships were positive and often stronger. Megrey et al. (this issue) suggest that these synchronies in periodicities may reflect the role of regime-like influences from large-scale atmospheric teleconnections (see also Megrey et al., 2007). These results from groundfish are similar to the synchronies found in small pelagic fish in many areas of the World Ocean (e.g., Kawasaki, 1983; Schwartzlose et al., 1999; Lehodey et al., 2006; Tourre et al., 2007), and may be the first recognition that a regime shift took place in the North Atlantic in the mid-1970s (Megrey et al., this issue).

In contrast, Link et al. (this issue) show that cod are decreasing over all systems reviewed, whereas stocks of pelagic fish are generally increasing, resulting in a large-scale shift from demersal to pelagic species. Despite this shift, the ratios of demersal to pelagic biomass differs widely among the subject ecosystems (Gaichas et al., this issue). The cause(s) behind these ratios and this shift are not understood, though they may include both heavy fishing pressure on demersal species (e.g., northwest Atlantic cod stocks, Murawski et al., 1997; Myers et al., 1997), or shifts in energy pathways driven by climate (eastern Bering Sea, Hunt et al., 2002, 2008; Mueter et al., 2006). Bundy et al. (this issue) also address the decline of cod in a different set of ecosystem comparisons and Dolgov (this issue) notes changes in food habits data for the same species in a set of different ecosystems. Megrey et al. (this issue) suggest that pelagic stocks are more sensitive to bottom-up forcing than demersal stocks, perhaps because pelagic species are generally short-lived and their recruitment is believed to be linked more strongly to lower trophic level production (Beaugrand et al., 2003). Interestingly, Link et al. (this issue), Pranovi and Link (this issue), Bundy et al. (this issue) and Tomczak et al. (this issue) find little change in the overall biomass in the systems studied, suggesting resilience to perturbation at the level of the ecosystem. This may be a conservative property of shelf ecosystems.

4.2. The comparative approach provides a "natural experiment" for investigating mechanisms

Large marine ecosystems are not amenable to experimental manipulation, and thus testing hypotheses concerning mechanisms of ecosystem control is challenging. For mechanisms held in common, one approach is to use a comparison of different ecosystems as a means of increasing the "sample size" (Drinkwater et al., this issue; Megrey et al., this issue; Mueter et al., this issue; Suryan et al., this issue). When mechanisms operate similarly across ecosystems, it provides a degree of assurance that the mechanism may be of "universal" significance, whereas other mechanisms may prove unique to a given system (Drinkwater et al., this issue). For instance, although several systems investigated were dependent on advection of water masses for much of their heat, those in the Pacific basin, were somewhat more influenced by atmospheric heating than those in the Atlantic (Drinkwater et al., this issue), with Pacific systems possibly more sensitive to short-term climate variability. Likewise, the relative importance of mechanisms such as tidal stirring vs. wind mixing, or whether the source of freshwater for a region is primarily river inflows or advection from afar, may influence the vulnerability of a region to climate impacts (Drinkwater et al., this issue; Belkin et al., this issue). The relative importance of heat vs. freshwater in stabilizing the water column of a region may also have implications for local responses to changes in climate (Carmack, 2007; Drinkwater et al., this issue; Belkin et al., this issue). Differences in the dominant underlying mechanisms between systems provide the impetus for the development of new explanatory hypotheses.

Comparative studies also reveal the relative importance of bottom-up and top-down mechanisms in the control of zooplankton in the study systems. Nutrient supply rates and concentrations vary greatly among the study regions, which may affect primary production and bottom-up control of zooplankton (Gaichas et al., this issue; Mueter et al., this issue; Tomczak et al., this issue; Bundy et al., this issue; Morissette et al., this issue; Pranovi and Link, this issue). For example, in the Georges Bank–Gulf of Maine region, zooplankton is controlled by bottom-up processes and, in turn, may control the biomass of pelagic fish (Mueter et al., this issue; *sensu* Link et al., this issue). Net primary production is anomalously high there, and Mueter et al. (this issue) suggest that this high level of production is supported by year-around re-supply of nutrients coupled with sufficient light and stratification for primary production to occur during winter. In contrast, in both the Barents and Norwegian Seas, both bottom-up and top-down controls of zooplankton were detected. In the Norwegian Sea, zooplankton is closely coupled to phytoplankton, and their grazing prevents the formation of a strong spring bloom, a situation analogous to that in the North Pacific Sub-arctic gyre (Miller, 1993). In the Barents Sea, zooplankton biomass is positively related to sea surface temperature, which is possibly an index of advection in warm Atlantic water, and negatively related to capelin biomass (Mueter et al., this issue; Dolgov, this issue).

Presumably, when zooplankton is controlled by fish predation, the removal of fish will leave surplus zooplankton to support recruitment and growth of the remaining fish taxa. However, when climate affects the production of zooplankton, as recently shown in the Bering Sea (Hunt et al., 2002, 2008; Baier and Napp, 2003), the advection of zooplankton, as in the Barents Sea (Skjoldal et al., 1992; Ottersen and Stenseth, 2001) or the Gulf of Maine (Greene and Pershing, 2007), allows competitors to move into or recover from within the system, then climate may indirectly limit the recovery of depleted fish stocks through limitation of prey abundance to the preferred species.

4.3. The comparative approach may facilitate the separation of the effects of climate from those of fishing

Given the expected long-term warming trend in our global oceans (IPCC, 2007), there is a need to predict how marine ecosystems will respond to climate change, and whether ecosystems will be able to sustain fisheries removals under future scenarios. In building these predictions, it will be critical to separate out the relative importance of climate working through bottom-up processes, changes in distribution or behavior in response to changing water temperatures and the results of fishing pressures. Mueter et al. (this issue) suggest that high-latitude marine ecosystems may be more sensitive to climate change than those at lower latitudes because components of the study systems, from primary production to fish recruitment and distributions, respond to changes in water temperature. Primary production, both within and among regions, is positively related to sea surface temperatures. However, stocks of pollock and cod in the eastern Bering Sea have been negatively related to temperature increases since the 1977 regime shift, and recruitment of other species in the eastern Bering have been positively correlated with increasing temperatures (Mueter et al., this issue). In the case of Atlantic cod, comparison of the responses of individual stocks to warming was critical for understanding the different responses of southern and northern stocks to increasing water temperatures (Brander, 1994; Drinkwater, 2005; Planque and Frédou, 1999). With warming sea temperatures, southern stocks showed decreases in growth and recruitment, whereas northern stocks appeared to benefit. Additionally, there is some evidence that the sensitivity of species to climate variability may vary with the type of habitat occupied. For example, Rose (2005) has hypothesized that species spawning in shallow, low salinity shelf waters may be more sensitive to climate variability than species that live in deeper, more hydrographically stable, waters, a hypothesis that can be tested using the comparative approach. Thus, pelagic fish may be one of the groups most vulnerable to the effects of climate change on the upper water column. Gaichas et al. (this issue) note that each system has a unique ratio of pelagic-to-demersal fish biomass, and that those fisheries that directly or indirectly are dependent on the biomass of pelagic fish may be the most affected by climate change.

5. Discussion

Ultimately, the papers in this special issue seek to evaluate how ecosystem structure and function interact to support fisheries production, and what processes amplify or dampen spatial and temporal variation in that production across and between ecosystems. Multiple hypotheses have been put forward to explain the wide variation in fisheries production among ecosystems. Hypotheses have invoked: patterns in total primary production (Nixon, 1982; Ware and Thomson, 2005); the timing and retention of primary production pulses (Friedland et al., 2008); seasonal predictability of oceanographic forcing (Cushing, 1995); production and growth of larvae scaled to appropriate environmental signals (Mueter et al., 2007); connectivity among neighboring ecosystems (Frisk et al., 2008); and the efficiency of food webs at moving production from lower to higher levels (Baird et al., 1991). These hypotheses invoke different mechanisms and processes as sources of production variability. Each source may induce different patterns of response in marine ecosystems that reflect different production characteristics and ultimately have different management consequences with regard to limits to sustainable exploitation. Thus, identifying the sources, patterns, and consequences of variability in the structure and function of marine ecosystems as it impacts fisheries production is key towards building sustainable ecosystem-based management plans.

From these hypotheses, we posit some questions that merit being addressed in the context of ecosystem-based management of living marine resources, as facilitated via ecosystem comparisons (Table 1). Here we have emphasized a comparative approach to identify driving and controlling processes in large marine ecosystems across a wide range of biophysical and trophodynamic features. Despite the multiple hypotheses put forth to explain variable fisheries production, we assert that the works in this special issue can and have identified common, unique, and fundamental

Table 1
Key questions to evaluate the efficacy of comparative marine ecosystem studies and to prioritize among the multiple, competing hypotheses attempting to explain variability in fisheries production.

- Is there an indication that such comparative studies bring better understanding of the structures and drivers in the systems?
- Are there any indications of a regime shift?
- How can we tell if there have been concurrent and/or contiguous regime shifts?
- Do community organizational rules change with regime shifts?
- Both top-down and bottom-up processes impact all marine ecosystems. How can we tease apart their relative importance?
- Do fisheries and climate interact to influence an ecosystem and vice versa?
- If yes, how? And what is the relative proportion of explainable variance attributed to each?
- Do fisheries and climate interact to influence change in landings? and why?
- Have there been synchronous events around the World's Oceans?
- Are there indicators that can be developed across ecosystems?
- Ultimately, what is the value, if there is value, in marine ecosystem comparisons? That is, how can or have the results of such studies influence living marine resource management?

features of ecosystem structure and function, as well as important drivers for many of these marine ecosystem. At the very least these works have highlighted the approaches that can lead to better understanding of these marine ecosystems. Two such instances merit highlighting.

We suggest that the open nature of marine ecosystems and the frequent movement of biological components of the ecosystem across their boundaries is one of the most fundamental challenges to undertaking a comparative analysis of marine ecosystems. This is particularly true for regional ecosystems, where a substantial number of the fishes undertake extensive seasonal movements for feeding and/or reproduction. Efforts to understand the dynamics of individual stocks within an ecosystem have primarily been at a regional scale due to political, spatial and sampling constraints. Yet, the existence of widespread movements by fishes within an ecosystem has meant that each regional assessment has had to account for the substantial fluxes of biomass across its boundaries. Although a regional approach yields stock dynamics which are balanced with respect to biomass, we assert that these stocks may have dynamics driven by processes occurring outside of the region, and by extension outside of the domain of these regional models. Therefore, we believe it is of critical importance to understand the impact of the spatial scale at which population-level analyses are conducted on inferences regarding management actions if ecosystem approaches to management are to be successful.

While application of quantitative models provides invaluable opportunities, we also realize that "All models are wrong, but some are useful" (Box, 1979), and what stands out is that "no model is perfect for all purposes" (Prager, 2003). As Prager (2003) points out, when multiple models are considered, each model provides, from its particular perspective, an imperfect view of reality. The more perspectives one gains, the better. The approach taken by multiple authors in this collection of papers is that the analyst does not presume to know which model provides the most accurate view of reality, so multiple approaches and analyses are taken in the hope that consistent results are obtained, thus facilitating a broad perspective.

6. Conclusions

The objective of comparative analysis is an integration of the results of individual studies into a more generally synthetic understanding. As we have noted, comparisons allow one the opportunity to take a broad perspective and permit the ability to draw generalizations. Here we raise issues that result from our observations and results presented in this special issue. We pose these as observations followed by questions to help determine what is fundamental to ecosystems in general and what is unique to particular ecosystems. We also provide such questions to stimulate consideration in future comparative studies. Not only are such generalizations important for successful application of the ecosystem approach to fisheries, but generalizations address macroecological questions that will benefit associated scientific disciplines as a whole.

The physical system provides the basic "seascape" within which biological dynamics take place. Details such as bathymetry, latitudinal/longitudinal boundaries, duration of light, variations in SST and advection, all affect local trophodynamics. We acknowledge that both fishing and the environment influence the structure and function of marine communities. Recognizing that the local physical system as well as fishing and climate change are major structuring forces, how can we best delineate the relative importance between "top-down" and "bottom-up" forcing factors in marine ecosystems? That is, how can we tease apart their relative importance of these and related processes?

From the papers contained in this special volume, it appears as though eastern ocean boundary systems (deeper) are more strongly influenced by bottom-up forcing. It also appears as though western ocean boundary systems, mainly shallower continental shelves, are more strongly influenced by top-down forcing. Is this observation based on the limited number of ecosystems considered here, or is it generally true for the World's Oceans?

In many examples, it appears as if fisheries landings have shifted in emphasis from groundfish to invertebrates. In many examples, it appears as if the fish community has shifted from a demersal to pelagic dominated group. In many systems, the benthos is an important, but understudied component of the ecosystem. Are these observations and potentially generic shifts true of all marine ecosystems undergoing (excessive) exploitation? In particular, more resources need to be devoted to the study and understanding of processes controlling the benthic realm of marine ecosystems.

We recognize that data for comparisons will never be perfect, and that it is often collected for other purposes. Are there particular quality control or quality assurance concerns or methodologies that need be included as part of future comparative process? We advocate database standardization at the onset of comparative studies as an approach to facilitate effective comparison of future studies. To be comparable, data need to be put on the same time scale, space scale, and in comparable units (e.g., g C/m^2/yr vs. t/km^2). Additionally, many data need to be normalized to minimize scaling effects. Are there other normalizing and standardizing methods we should consider in the comparative process?

Effective marine ecosystem comparisons require large, multinational collaborations. Local experts are needed to supply data, interpret results, and provide perspective for a given ecosystem. Opportunities to gather local experts to compare data and perspectives require substantial financial support outside of local laboratories. We strongly endorse and encourage such programs.

From the works in this special issue, it appears as if there have been synchronous events around the World's Oceans. Even acknowledging this, it begs some questions: what are the main driving forces for such events and how do they vary among ecosystems? Are there "teleconnections" across marine ecosystems, and are they particular to different ocean basins? How can we tell if there have been concurrent and/or contiguous regime shifts? Do similar species in different ecosystems 'respond' in similar ways, or do the local ecosystem dynamics override signals from global forcing factors?

Ultimately we need to ask "What is the value in marine ecosystem comparisons"? Will things we learn help us to improve how we implement an ecosystem approach to management? Certainly those questions are worth posing, but we trust that the examples provided in this issue begin to affirm the value of such comparisons, shed insight into how marine ecosystems function, provide an enhanced knowledge base for ecosystem-based management of living marine resources the world over, and stimulate additional explorations into this most intriguing subject of marine ecosystem ecology. We wait for the next wave of exploration with high anticipation.

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