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Meeting report

Comparative analysis of marine ecosystems: international production modelling workshopJason S. Link^{1,*}, Bernard A. Megrey², Thomas J. Miller³, Tim Essington⁴, Jennifer Boldt⁵, Alida Bundy⁶, Erlend Moksness⁷, Ken F. Drinkwater⁸ and R. Ian Perry⁵¹National Atmospheric and Oceanic Administration, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA 02543, USA²National Atmospheric and Oceanic Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, WA 98115, USA³Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD 20688, USA⁴School of Fisheries and Aquatic Sciences, University of Washington, Seattle, WA 98195, USA⁵Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, Canada, V9T 6N7⁶Department of Fisheries and Oceans, Bedford Institute of Oceanography, Halifax, Nova Scotia, Canada, B2Y 1A2⁷Institute of Marine Research, Flødevigen Marine Research Station, His 4817, Norway⁸Institute of Marine Research and Bjerknes Centre for Climate Research, Bergen 5817, Norway*Author for correspondence (jason.link@noaa.gov).

Understanding the drivers that dictate the productivity of marine ecosystems continues to be a globally important issue. A vast literature identifies three main processes that regulate the production dynamics of such ecosystems: biophysical, exploitative and trophodynamic. Exploring the prominence among this ‘triad’ of drivers, through a synthetic analysis, is critical for understanding how marine ecosystems function and subsequently produce fisheries resources of interest to humans. To explore this topic further, an international workshop was held on 10–14 May 2010, at the National Academy of Science’s Jonsson Center in Woods Hole, MA, USA. The workshop compiled the data required to develop production models at different hierarchical levels (e.g. species, guild, ecosystem) for many of the major Northern Hemisphere marine ecosystems that have supported notable fisheries. Analyses focused on comparable total system biomass production, functionally equivalent species production, or simulation studies for 11 different marine fishery ecosystems. Workshop activities also led to new analytical tools. Preliminary results suggested common patterns driving overall fisheries production in these ecosystems, but also highlighted variation in the relative importance of each among ecosystems.

Keywords: production modelling; triad of drivers; ecosystem comparisons; trophodynamics; biophysical forcing; fisheries

1. INTRODUCTION

Understanding the drivers that dictate productivity of fishery ecosystems continues to be a major goal of oceanographers, marine ecologists and fishery scientists. Marine ecosystems are highly divergent with respect to both rates of primary production (Mann & Lazier 1996) and production capacity as gauged by fishery landings data (Pauly *et al.* 2005; FAO 2007). Three main processes that may regulate production dynamics of marine fishery ecosystems have been identified: biophysical, exploitative and trophodynamic. We refer to these as the production ‘triad’, as they represent dominant themes of research that have sought to understand variation in productivity within and across ecosystems. There is ample evidence for each of these acting singly. For example, it is well known that biophysical conditions can dictate survivorship of early life-history stages of fishes (Beaugrand *et al.* 2003; Platt *et al.* 2003), that climatic regime shifts may profoundly alter communities (Anderson & Piatt 1999; Chavez *et al.* 2003), and that fisheries production is linked to primary production (Ware & Thomson 2005; Chassot *et al.* 2010). The important roles that fisheries exert on marine ecosystems is well understood through characterization of the extent and magnitude of direct impacts on exploited stocks (Pauly & Christensen 1995; Worm *et al.* 2009) and also their attendant indirect effects (Jackson *et al.* 2001). Trophodynamic processes are also widely recognized as potentially dominant drivers in marine ecosystems (Frank *et al.* 2005; Daskalov *et al.* 2007). Rarely is the impact of multiple drivers assessed simultaneously.

We held a workshop in Woods Hole, MA, USA from 10–14 May 2010 involving 28 scientists from Canada, Norway and the USA to quantify the importance of biophysical processes, trophodynamics and fishing on productivity in 11 northern marine ecosystems (figure 1). These ecosystems represent many of the major Northern Hemisphere ecosystems that support significant fisheries. Our approach presumed that no single process among the triad need have primacy and attempts to establish such primacy present a false dichotomy (Hunt & McKinnell 2006); rather than view the dominance of each single driver as strict alternatives, we hypothesized that all act simultaneously, and the relative importance of each varies depending on fundamental ecosystem characteristics and interactions among the drivers. Further, we recognized that the taxonomic resolution of any analysis may affect the perceived importance of any particular driver (Fulton *et al.* 2003). Thus, we also explored the effect of taxonomic aggregation on model results through simulation modelling.

Placing these ecosystem responses into a broader context has been suggested as an approach to elucidating both common generic patterns and those processes that are unique to particular ecosystems. The inherent complexity, multiple drivers and large scale of marine ecosystems preclude experimentation at appropriate spatio-temporal scales; thus, a comparative approach is ideally suited to these types of issues.

2. ANALYTICAL CONTEXT

An essential element in comparative ecosystem analysis is the development of a common analytical platform

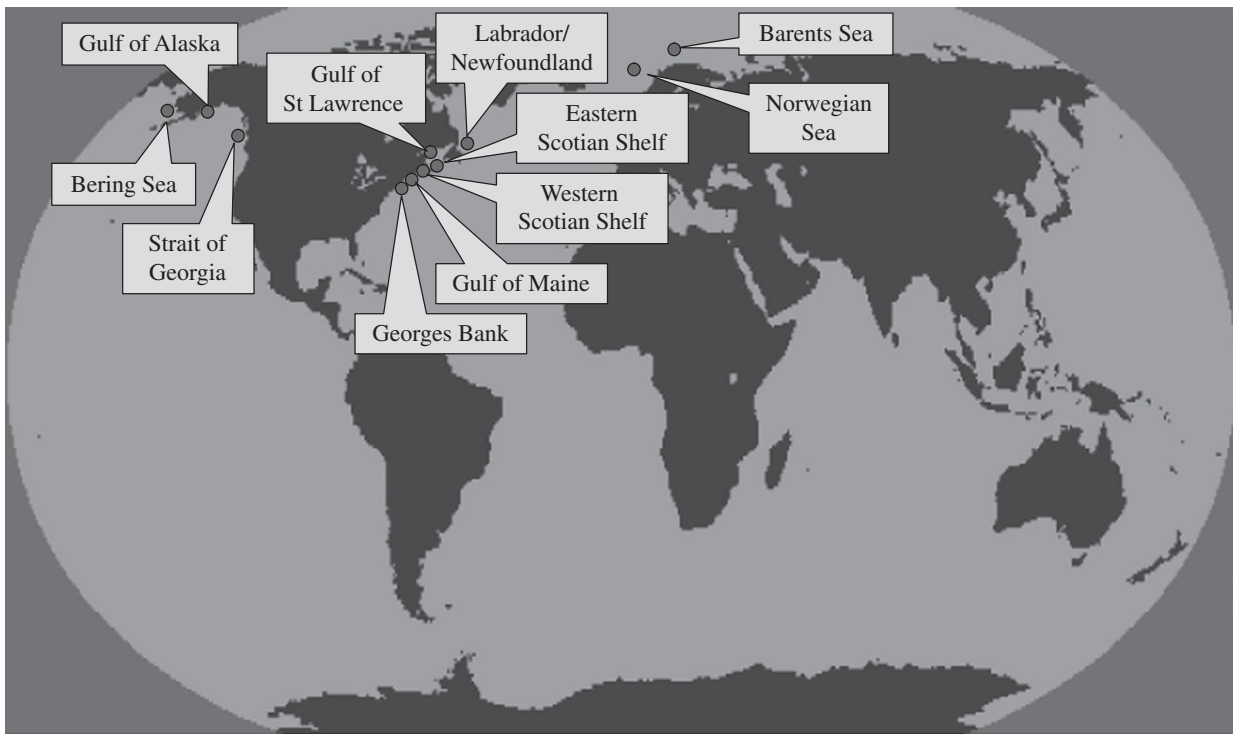


Figure 1. Ecosystems studied at this workshop.

that can produce metrics which are standardized and comparable across ecosystems. The need for standardized methods across ecosystems precludes complex, detailed methods tailored to the specifics of any particular ecosystems but instead favours simpler, abstract representations of key ecological processes. In ecology, simple density-dependent population models have commonly proved to be useful in this type of application; in fisheries ecology, these approaches are easily adapted to also account for removals from fisheries, through models commonly called surplus production models. These models relate the production of a population to current population size, intrinsic rates of productivity, and density-dependent effects. Although there has been debate about the applications of such modelling approaches to specific applications (Mohn 1980; Ludwig & Walters 1985, 1989; Punt 2003), there is consensus that they play a useful and important role in ecology in general (Mangel 2006) and fisheries science in particular (Ludwig & Walters 1985, 1989; NRC 1998).

Given these considerations, surplus production models were deemed to be a useful, unifying theme as a basis for the workshop as they: (i) require the simplest of readily available input data, (ii) are robust to various assumptions and behave favourably or even more accurately than more complicated (i.e. stage or age-structured) fisheries models, (iii) produce standard outputs that are readily and easily comparable and that can be easily related to commonly used fishery management reference points, (iv) are eminently scalable to different levels of organization, (v) can readily incorporate covariates, and (vi) can be applied through existing software packages and code or through simple *de novo* applications.

3. WORKSHOP APPROACH

The workshop sought to compile the data required and to develop production models at multiple organizational levels (e.g. species, guild, ecosystem) across these ecosystems (figure 1). The specific objectives of the workshop were to: (i) create a novel database, (ii) use production modelling as a platform for initiating comparisons across species and ecosystems, and (iii) undertake simulation modelling to assess the impact of different levels of aggregation on the inferences drawn.

To meet the workshop objectives, five activities were undertaken: (i) database development; (ii) simulation modelling to explore effects of aggregation; (iii) application of production modelling to stock-specific cases for species that are functionally analogous and commonly found across ecosystems (e.g. cod, herrings, etc.), incorporating both environmental and trophic covariates with fisheries landings; (iv) application of production to total system fish biomass, with and without covariates, executed for all species in aggregate; and (v) analysis of empirical relationships among fish biomasses, fisheries landings and environmental/lower trophic level drivers. The focus on production models was valuable in that metrics derived from these models can be compared across populations and ecosystems, and also be used for living marine resource management.

4. RESULTS AND OUTCOMES

Several important outcomes were noted from this workshop. These included the cross-training of several staff from all the institutes involved on aspects of the development of the multi-ecosystem database structures and computer code to extract and analyse the

said data. After appropriate quality controls and final updates, the database should represent a sizeable collection of integrated physical, lower trophic level, biomass and fisheries data. The development of several analytical tools, in open-source code, was also an important outcome. Combined, these outcomes resulted in unanticipated capacity building that will have a wider impact beyond just those involved in this workshop and its associated tri-lateral collaborations.

Empirical analyses were supported by the development and exploration of several simulation models. These models explored a range of issues associated with production models, specifically the impact of data aggregation on estimated biological reference points (BRPs), the types of conclusions that can be drawn and the extent to which production models can be used to simultaneously estimate species interactions and catchabilities. Ultimately, these simulation models provided further information regarding the robustness of production modelling.

The ability of production models to estimate commonly used fishery management BRPs, and explore them across a range of aggregations, ecosystems, drivers and covariates is significant. Production models provide a common management 'currency' (BRPs) that can be and often are used directly in living marine resource management by several fisheries management bodies. Thus, the direct link to management and the associated scientific theory explored by these models are likely to have a large programmatic benefit for emerging research initiatives.

Preliminary results were developed for production models across total fish biomass for these ecosystems and for a few, example functionally analogous species across these ecosystems. These initial results suggest that there are some common patterns driving overall fisheries production in these Northern Hemisphere ecosystems, but that the prominence of any particular driver varies among these systems. Empirical, multivariate analyses were conducted and confirmed the modelling results. Further, the range of simulation model applications developed showed important differences across ranges of aggregations. Additional effort remains to verify some portions of the assembled database, although it is largely populated.

5. CONCLUSIONS

Our focus on quantifying production dynamics in marine fishery ecosystems is of direct relevance to calls for ecosystem-based fisheries management (EBFM; Garcia *et al.* 2003; Pikitch *et al.* 2004). Sound management of fisheries, and more generally coastal resources, requires an improved understanding of the drivers of ecosystem dynamics. Several laws and treaties have called for an evaluation of ecosystem science as it pertains to the management of marine ecosystems and their associated fisheries, and how best to incorporate such ecosystem considerations into management. The work and analyses executed at this workshop provides an important step to that end by using three key ways in which EBFM can be more fully implemented—the comparative approach, the

development of ecosystem (production) models and ultimately the evaluation of BRPs for systems management (Link 2005; Samhuri *et al.* 2009).

Aside from the application for fisheries management, this approach allows us to explore the relative prominence among the triad of drivers that dictate the productivity of fishery ecosystems, a major area of interest for oceanographers, marine ecologists and fishery scientists. The theoretical considerations involved in production modelling are generally understood (Mangel 2006), but the theoretical considerations with respect to various applications at this range of taxonomical hierarchies, covariates and exploitation—that are all at varying levels across such a wide array of ecosystems—have not been previously explored. As the productivity of marine ecosystems is highly variable, this work and subsequent follow-ups should further elucidate those key drivers of marine ecosystem production.

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