# Theme session G

## Marine food webs from end-to-end and back again, a theme session in honor of John Steele

Conveners: Jeremy Collie (USA) Manuel Barange (Italy) Mariano Koen-Alonso (Canada)

During a career spanning 50 years, John Steele played a dominant role in broadening Biological Oceanography from an essentially descriptive science to a quantitative discipline. He had an uncommon knack for explaining general ecological principles with elegant mathematical representations. With his seminal monograph, "The Structure of Marine Ecosystems," John pioneered the application of network models to marine food webs. With network models of the North Sea, John demonstrated that most of the production (~85%) is recycled through the microbial loop; only the remainder (new production) is passed on to the upper trophic levels. John stressed the importance of functional groups as ecological units and advocated their use in Ecosystem Based Fisheries Management. This theme session recognized John Steele's contributions to marine ecology, while highlighting the links between his pioneering ideas and the continuing development and application of food-web models.

The presentations made during this session provided examples on how relatively simple representations of food webs, based on functional groups and/or size distributions aimed at mapping the main energy flows within ecosystems (e.g. microbial loop, benthic and pelagic pathways), provide a practical avenue for using first principles to represent the organization of real marine ecosystems. These representations not only provide a suitable platform for exploring the connections and level of dependency between primary production, and trophic levels of interest to fishing, but also allow for effective comparisons across different marine ecosystems.

Contributions were received on most, but not all, of the topics listed in the theme session proposal. Bottom-up network models are constructed from the diet composition of consumers, their ecological efficiency, and the input of primary production at the base of the food web. An Ecopath model being developed for the Gulf of Mexico used Monte Carlo simulations to investigate the consequences of an uncertain diet composition matrix. Three of the studies compared food webs across ecosystems. The structure and function of marine food webs is remarkably similar among ecosystems in different regions of the world (Fig. 1). Different taxa can play the same functional role in different ecosystems. Never-the-less, ecosystems with a higher level of omnivory have a higher network efficiency and pass more of the primary productivity to higher trophic levels. The supply and recycling of nutrients and advection of planktonic taxa are the two most important physical determinants of food-web dynamics. These cross-system comparisons show that while general patterns can emerge at broader scales, processes at regional/local scales also play important roles in modulating the linkages between primary production and fisheries productivity, most notably regional physical/oceanographic characteristics of the ecosystem.

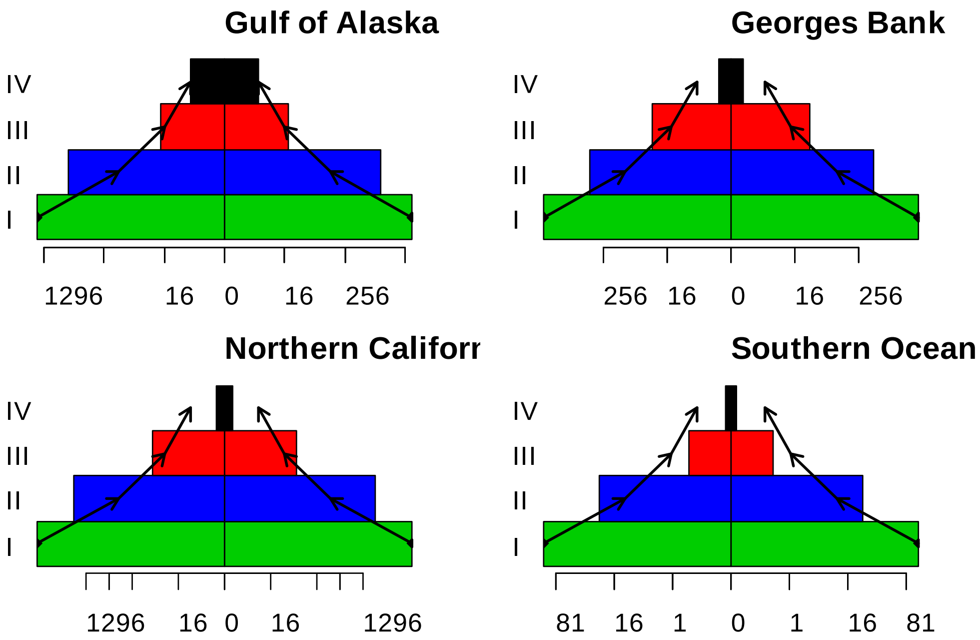


**Figure 1. Production (gWW m$^{-2}$ yr$^{-1}$) of the four ecosystems studied in the US GLOBEC Program). Production is grouped by trophic level and plotted on a geometric axis. Black arrows indicate expected production with a 10% trophic efficiency.**

Two presentations used size-based end-to-end models, which are complementary to network models organized by trophic compartments. Size-based models avoid the complication that some taxa belong in different trophic compartments depending on their life-history stage. For example, the diet composition of fish larvae, juveniles, and adults are very different. In size-based models, functional groups can be defined as taxa with similar asymptotic sizes. Size-based models were used to estimate the global fish biomass and production and to investigate the trophic consequences of fish stock recovery.

Variability in top-down forcing occurs with changes in consumer abundance. In ecosystems with a diversity of predators that vary asynchronously, predation pressure may remain fairly constant (e.g. some temperate communities). By contrast, with few predator species, or predators that vary synchronously, predation pressure varies with time. An empirical analysis of the Barents Sea investigated whether peaks and collapses of the capelin stock are induced from top-down predation or bottom-up food supply. Simple network models assume linear (Type-I) functional responses. However, an empirical analysis of diet data from the northwest Atlantic indicates that Type-I responses are the exception. Benthivores had mostly Type-II responses, planktivores Type-III, and piscivores had a mix of Type-II and Type-III functional responses.

Network models have now been constructed for all the world's Large Marine Ecosystems. Coupled with satellite-derived estimates of primary production, they are being used to estimate potential fisheries production at the global scale. Data presented in this session indicate declines in primary production in both the eastern and western North Atlantic. Primary production in the North Sea declined significantly from 1988 to 2013, mostly likely because of reduced riverine nutrient inputs and climate change. Significant correlations were found between primary production and the dynamics of higher trophic levels, including small copepods and recruitment of seven commercially important fish stocks (Engelhard et al.). Along the entire US northeast continental shelf there was a dramatic decline in chlorophyll *a* concentration between the decade from 1977-1987 and the contemporary period beginning in 1997 (Morse et al.). These changes in phytoplankton dynamics are reflected at all trophic levels. Conversely, analyses of Georges Bank, within the northeast shelf, appear to indicate an increase in the phytoplankton fraction that drives fisheries productivity in more recent years, although without reaching its former levels (Hyde and Fogarty). Changes in primary production can translate into measurable changes in fisheries productivity. At the same time that fish stocks are rebuilding and increasing their consumption, caps on total harvest may need to be adjusted downwards to account for declining productivity.

Not all topics solicited in the theme session proposal were addressed either because of lack of contributions, or last-minute withdrawals. There were no reconstructions of past food webs or future food webs under changing climate conditions, although an exploration of some expected changes in phytoplankton size composition using an ecosystem model suggested reduced fisheries productivity under climate change. Unfortunately, a study that linked a biophysical circulation model with end-to-end models of higher trophic levels was withdrawn, as was a study that used the Atlantis model to test the performance of Ecopath with Ecosim.

From a management and advice perspective, the results showcased during this session demonstrate that these end-to-end, food-web analyses are maturing, and can provide operational first-order approximations of potential fisheries production at the regional ecosystem scale, as well as support strategic analyses on how some of the potential impacts of climate change on lower trophic levels can affect fisheries productivity. These are promising lines of inquiry that can contribute to developing integrated perspectives of the bottom-up process influencing and regulating fisheries productivity at the ecosystem level. The use of food-web models to link primary production to fishery yields has been identified as a priority by SCICOM.

Even though current results indicate a level of development suggesting that practical management applications are possible, existing models and analyses would still benefit from efforts to better characterize transfer efficiencies, ideally including field studies. It is clear that important gaps in our understanding still exist in our simplified representations of energy flows through the microbial loop and the benthic-pelagic coupling at the functional ecosystem scale. Parallel changes in productivity argue for further comparative studies between the northeast and northwest Atlantic to disentangle the interaction between changing temperature and nutrients.

Overall, the evidence emerging from the presentations in this session further consolidates the enduring value of the path that John Steele laid for the study of marine ecosystems. They also provide hints of many exciting new scientific insights and practical applications that are currently being explored, and which will continue carrying his legacy into the future of marine science.