Journal of Marine Systems 83 (2010) 99–103

Contents lists available at ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

Reconciling end-to-end and population concepts for marine ecosystems

John H. Steele [a,*], Dian J. Gifford [b]

[a] Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA
[b] Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA

ARTICLE INFO

Article history:
Received 6 May 2010
Accepted 17 June 2010
Available online 1 July 2010

Keywords:
Marine ecosystem
Energy flow
Food webs
Resilience

ABSTRACT

The inherent complexities in the structure and dynamics of marine food webs have led to two major simplifying concepts, a species-centric approach focused on physical processes driving the population dynamics of single species and a trophic-centric approach emphasizing energy flows through broad functional groups from nutrient input to fish production. Here we review the two approaches and discuss their advantages and limitations. We suggest that these concepts are complementary: their applications involve different time scales and distinct aspects of population and community resilience, but their integration is necessary for ecosystem-based management.

Contents

1. Introduction

The close coupling of physical dynamics and ecological processes is a defining feature of marine ecosystems (Steele, 1985; Wiebe et al., 2001). Analysis of these relationships has generally followed two approaches: focus on the direct effects of physical processes at the individual species or population level versus focus on indirect effects through physical control of nutrient availability and transmission up the food web to top predators. The first, species-centric approach takes advantage of major advances in modeling advection and mixing in environments with complex topography. Here physical models are combined with simple formulations of the lower trophic levels or with descriptions of individual populations of pelagic species. This approach, depicting the non-linear dynamics of a few food-web components, is the basis for the successful JGOFS (Joint Global Ocean Flux Study) and GLOBEC (Global Ocean Ecosystems) modeling programs. The use of detailed simulations of spatial dynamics requires some limitation on biology and led DeYoung et al. (2004) to propose that "rather than model the entire ecosystem we should focus on key target species and develop species-centric models". In the second, trophic-centric, approach analysis focuses on the overall processes within food webs from nutrient uptake to fish production. On continental shelves the close coupling between pelagic and benthic food webs (Steele and Collie 2005) determines the structure of higher trophic levels. The diverse trophic components, with their large range in time scales and complicated links within the food web, pose quite different challenges to modelers, including accounting for the direct effects of mixing and transport on individual organisms.

Past food-web studies have tended to treat the upper and lower trophic levels separately, and for different purposes. The microbial web in the open ocean was studied intensively in the JGOFS program (e.g., Buesseler, 2001) where the focus was on export of carbon, defined as downward transport out of the euphotic zone. For studies emphasizing the upper trophic levels, the focus is on predatory interactions based on fish diet data (Garrison and Link, 2000; Heath, 2005). Linear steady-state, food-web models have been used to encompass these complex interactions (Christensen and Pauly, 1993). This trophic-centric approach does not include the dynamics of individual species. Recently, in response to the desire for ecosystem-based management, end-to-end models combining bottom-up and top-down components have been

* Corresponding author. Marine Policy Center, Woods Hole Oceanogr. Instn., Woods Hole, MA 02543, USA. Tel.: +1 508 289 2220; fax: +1 508 457 2184.
E-mail addresses: jsteele@whoi.edu (J.H. Steele), dgifford@gso.uri.edu (D.J. Gifford).

0924-7963/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.jmarsys.2010.06.006

used to portray continental shelf ecosystems (Aydin et al., 2005: Steele et al., 2007).

The "horizontal", species-centric, approach proposed by DeYoung et al. (2004) emphasizes the processes that link individual species or single trophic guilds directly to their physical environment. The "vertical" trophic-centric approach focuses on the flux of nutrients from inorganic states to the upper levels of the food web and can use complicated optimizations with large matrix inversions to resolve fluxes in linear steady-state systems (Vezina and Platt, 1988). The former has complex physical processes and relatively simple population dynamics; the latter combines complicated food webs with linear steady-state descriptions of processes.

In this paper, we illustrate the two approaches from work on the Georges Bank ecosystem. We 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 trophic communities. We review briefly some other methods that can be categorized as focusing on species or community structure. The relevant 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.

2. A case study: Georges Bank

The problem of reconciling the species-centric and trophic-centric approaches can be illustrated from studies of Georges Bank. Detailed simulations of the anti-clockwise circulation around the Bank describe the transport of cod and haddock larvae from spawning sites on the north-east peak to potentially rich food on the southern flank of the Bank, Fig. 1 (Werner et al., 1996; Lynch et al., 2001). Larval growth rates are correlated with copepod abundance, particularly *Pseudocalanus* spp. (Buckley and Durbin, 2006), but not with years of successful recruitment to the adult stocks. These studies demonstrate the way that broadcast spawners have evolved by adapting to the regularities in their physical environment. But the complexities in such processes and their inter-annual variability explain why very few environment–recruitment correlations survive re-examination (Myers, 1998). The only exceptions are for populations located at the latitudinal extremes of their range (Drinkwater, 2005). Friedland et al. (2008) proposed that successful recruitment of Georges Bank haddock depends on the food available to the adult spawners the previous fall, but this has been challenged (Payne et al., 2009). This controversy exemplifies the problems with the assumption that "recruitment" processes in the larval phase determine the year class strength of individual species (Rothschild, 1986) and with the hope that information about the physical system can predict future stocks (Myers, 1998).

A general problem with studies of declines in gadoid stocks such as cod, is the corresponding increases in other stocks — elasmobranchs followed by pelagic species on Georges Bank, Fig. 2; crustaceans on the Newfoundland and Nova Scotia continental shelves (Worm and Myers, 2003); and small pelagic fish in the North Sea (Heath, 2005). Some possible explanations of these patterns are phrased in terms of "cascades" (Frank et al., 2005) or "regime shifts" (Choi et al., 2004). These studies rely on comparisons or correlations of time series of a few selected species and do not consider the energetic implications of changes in the entire trophic web.

The alternative trophic-centric approach quantifies fluxes of energy, nutrients or carbon through the entire food web (Steele, 1974; Vezina and Platt, 1988; Heath, 2005). For Georges Bank, seminal studies were done by Sissenwine and colleagues (Cohen et al., 1982; Sissenwine et al., 1984). More recently Steele et al. (2007) combined data on the fish community and its diet (Garrison and Link, 2000), with detailed analyses of the microbial food web beginning with uptake of NO_3 (Bisagni, 2003) to determine end-to-end fluxes, Fig. 3. The model output was expressed in terms of production by three trophic guilds of fish – planktivores, benthivores and piscivores – described by the major components of their diet. Thus a critical physical constraint, flux of NO_3, determines the total abundance of the adult fish stocks in broadly defined communities but does not determine abundance of individual species such as cod or haddock.

This issue is illustrated by the response of the Georges Bank fish community to changes in ocean climate and fishing effort. There were two major stresses, decreased production during 1963–1972, and very high fishing effort during 1967–1976 (Fig. 2a). The lower levels

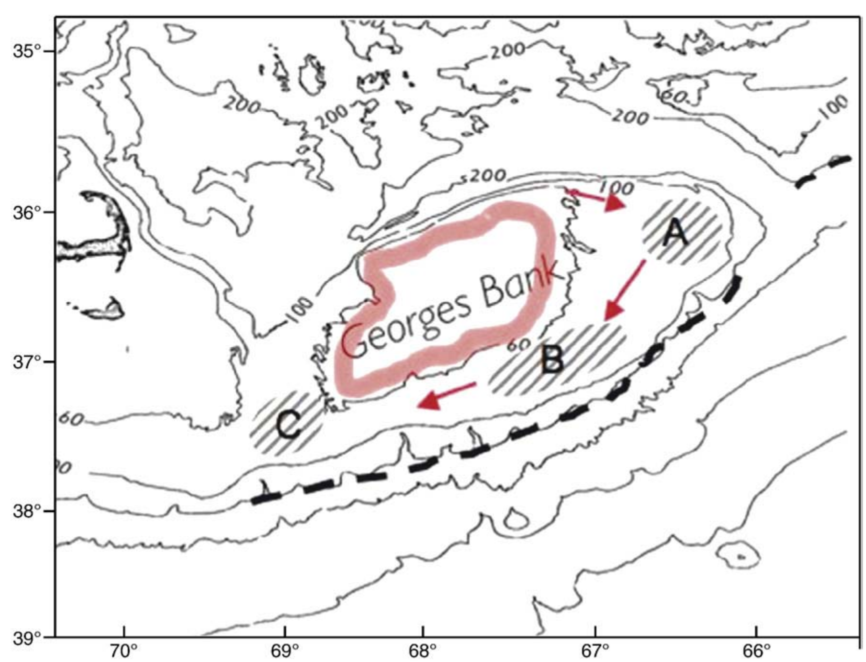

Fig. 1. Georges Bank in the northwest Atlantic showing the approximate location of A, eggs; B, larvae; and C, pelagic juveniles of cod and haddock in response to circulation between the tidal (red line) and shelf edge (dashed line) fronts.
Adapted from Lough and Manning (2001).