Interdisciplinary Studies on Environmental Chemistry—Marine Environmental Modeling & Analysis,
Eds., K. Omori, X. Guo, N. Yoshie, N. Fujii, I. C. Handoh, A. Isobe and S. Tanabe, pp. 57–63.

Investigating Alternate Trophic Pathways through Gelatinous Zooplankton and Planktivorous Fishes in an Upwelling Ecosystem Using End-to-End Models

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(Received 21 October 2010; accepted 20 December 2010)

Abstract—Evidence is accumulating that gelatinous zooplankton populations have increased recently in many regions of the world. Jellyfish are generally detrimental to fisheries because they feed on zooplankton and ichthyoplankton, and so are both predators and potential competitors of fish. In the upwelling region of the NCC, jellyfish are extremely abundant and can often comprise the majority of biomass in the pelagic ecosystem. Both empirical and modeling studies suggest that jellyfish can negatively impact many pelagic fishes through resource competition. Using top-down (ECOPATH) and bottom-up (End-to-End) models, we examine interannual variability in the transfer of energy through alternate planktivore (jellyfish and small fish) pathways and use this to project possible changes in the food web in the coming decades. Interannual changes in the Northern California Current (NCC) food web structure were examined using both documentary and alternate scenario strategies. Jellyfish have a major impact (large footprint) on lower trophic levels but translate relatively little production to higher levels in the food web (small reach) compared to forage fishes. Thus, a system dominated by jellyfish is not desirable and will actually decrease production of animals of interest to humans (fish, seabirds, marine mammals).

Keywords: upwelling ecosystem, jellyfish, pelagic fishes, California Current, food web modeling

INTRODUCTION

Evidence is accumulating that gelatinous zooplankton populations have increased recently in many regions of the world (Purcell *et al*., 2007; Richardson *et al*., 2009). Jellyfish are generally detrimental to fisheries because they feed on zooplankton and ichthyoplankton, and so are both predators and potential competitors of fish (Purcell and Arai, 2001; Lynam *et al*., 2005). Jellyfish

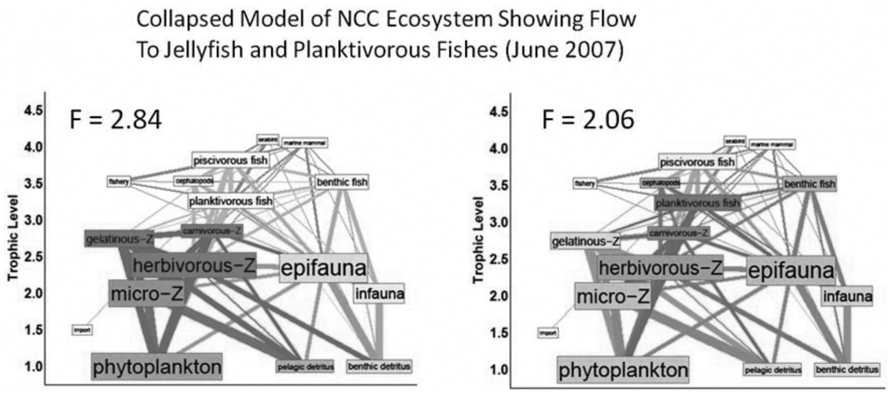

Fig. 1. Simplified end-to-end trophic models of the Northern California Current ecosystem for June 2007 showing flow up to jellyfish (gelationous-Z) in left panel and planktivorous fish in right panel. The relative intensity of shading indicates the importance of other components (boxes) and flows (connecting lines) to each consumer. The calculated values of the footprint (F) for the two consumers is given in the upper left of each panel.

populations are opportunistic, responding quickly to environmental changes by increasing their feeding, growth, and reproduction in optimal conditions; therefore, jellyfish have been suggested as key indicator species of changing climate conditions (Hay, 2006; Richardson *et al.*, 2009).

In the upwelling region of the Northern California Current (NCC), large jellyfish are extremely abundant and can often comprise the majority of biomass in the pelagic ecosystem (Shenker, 1984; Suchman and Brodeur, 2005; Ruzicka *et al.*, 2007). Both empirical and modeling studies suggest that jellyfish can negatively impact many pelagic fishes through resource competition in this highly productive upwelling ecosystem (Ruzicka *et al.*, 2007; Brodeur *et al.*, 2008).

Our hypothesis is that climate-induced changes in ocean biotic and abiotic conditions can cause variations in the amount of production that flows through the jellyfish population in the NCC, thereby affecting the survival and growth of pelagic planktivores such as sardines, anchovies and herring. Using bottom-up (End-to-End) models, we examine relative importance of the transfer of energy through alternate planktivore (jellyfish or forage fish) pathways and use this bottom-up model to examine potential scenarios of varying flow through the jellyfish component of the food web.

MATERIALS AND METHODS

Spring and summer hydrographic, plankton, pelagic fish, and seabird surveys conducted off Oregon and Washington provide data on pelagic community composition from several oceanographically-contrasting years (2003–2007).

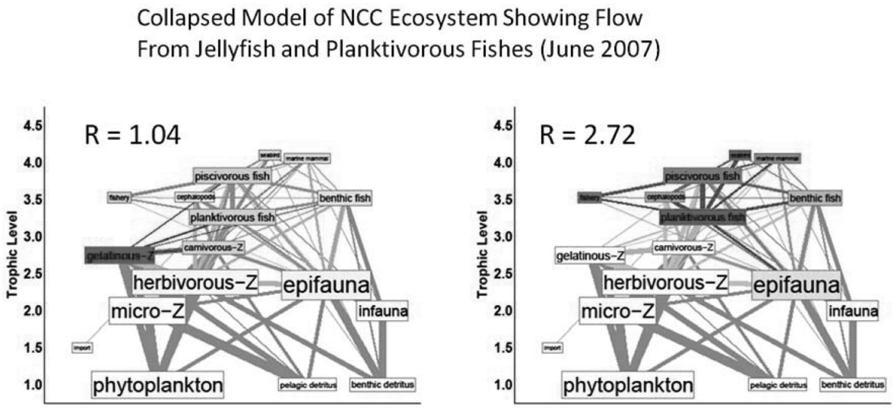

Fig. 2. Simplified end-to-end trophic models of the Northern California Current ecosystem for June 2007 showing flow from jellyfish (gelationous-Z) in left panel and planktivorous fish in right panel to higher trophic levels including fisheries. The relative intensity of shading indicates the importance of other components (boxes) and flows (connecting lines) from each consumer. The calculated values of the reach (R) for the two consumers is given in the upper left of each panel

Top-down ECOPATH models have been developed for the Northern California Current (NCC) ecosystem (Field *et al.*, 2006; Ruzicka *et al.*, 2007). For our analyses of variability in the pelagic system, we use modifications of the seasonal models of Ruzicka *et al.* (2007). This model has been used to look at seasonal changes in production of jellyfish and forage fishes during an earlier study period (2000 and 2002) when productivity was higher than the climatological average. Since we were interested in examining two-way interactions between components of the model and to look at potential effects of climate forcing, the top-down ECOPATH model was transformed to a bottom-up end-to-end model (Travers *et al.*, 2007; Steele, 2009; Rose *et al.*, 2010). This new model, called ECOTRAN, has been used to examine different energy flow scenarios for the NCC (Ruzicka *et al.*, submitted; Steele and Ruzicka, in revision).

For the purposes of the present study, we used a simple 17-box model that includes phytoplankton, pelagic and benthic detritus at the lowest levels up to top trophic levels including marine mammals and a commercial fishery. A more fully-resolved, 77-box model has been constructed and is presently being used for more detailed interannual comparisons (Ruzicka *et al.*, submitted). The contribution of jellyfish and planktivorous fish production to higher trophic levels was calculated using a metric termed "reach": the summed contribution of the group of interest to the production of all higher trophic level groups (via direct and indirect pathways). Their effect on lower trophic level was calculated as the "footprint": the fraction of producer group production, summed across all groups, supporting the group of interest. Our analyses are based upon a simulation of the June 2007 food web (see Ruzicka *et al.* (submitted)).

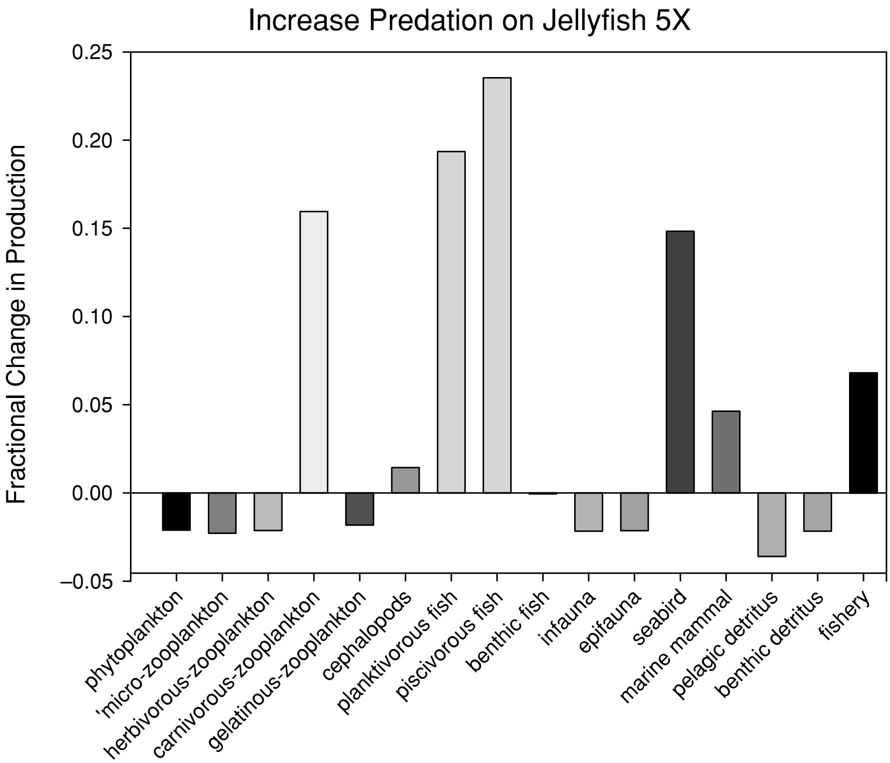

Fig. 3. Output (fractional change in production of each trophic group) of a scenario where predation on jellyfish is increased five-fold compared to the base model.

RESULTS

During June 2007, jellyfish were estimated have a major impact on lower trophic levels (footprint = 2.84) compared to planktivorous fishes (2.06, Fig. 1). However, relatively little of the jellyfish production was transferred to higher trophic levels in the food web (reach = 1.04) compared to forage fishes (2.76; Fig. 2).

When we altered the model to impose a five-fold increase in the predation rate on gelatinous zooplankton keeping all other rates the same, we see a marked increase in the production rate of carnivorous zooplankton due to release of predation pressure from jellyfish, along with corresponding increases in planktivorous and piscivorous fishes, seabirds, marine mammals, and fisheries (Fig. 3). Conversely, increasing the flow of production to jellyfish without increasing the overall productivity of the system negatively affects all these groups, but particularly planktivorous fishes and seabirds (Fig. 4).

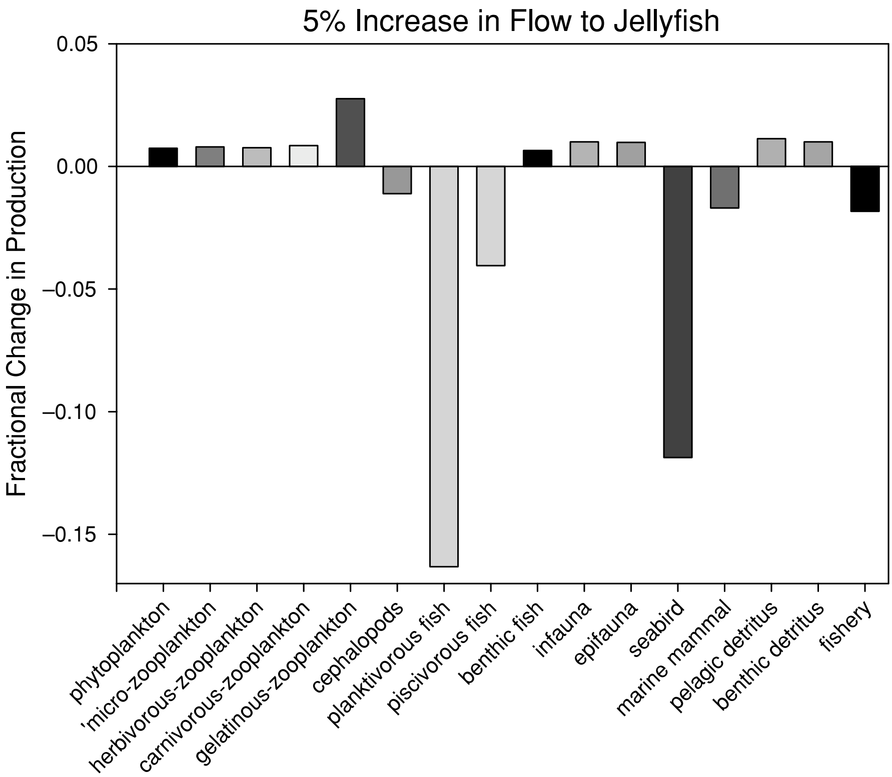

Fig. 4. Output (fractional change in production of each trophic group) of a scenario where the amount of food going to jellyfish is increased 5% compared to the base model, without any increase in the total productivity of the model.

DISCUSSION

Although our bottom-up model is quite simplified compared to some of the ECOPATH models available (e.g., Ruzicka *et al.*, 2007; see Pauly *et al.*, 2009 for a review), our simulations reveal the important role of gelatinous zooplankton as a reservoir of production in a system, with very little of the energy consumed being passed up to higher trophic levels and fisheries. The ecological impacts of jellyfish in our model are likely to be an underestimate as we ran our model with June data, when the dominant schyphomedusae (*Chrysaora fuscescens*) has not reached its annual peak in biomass (Shenker, 1984; Suchman and Brodeur, 2005). Had our model been run for late summer or fall when the biomass of this species increases dramatically and forage fish biomass actually decreases (Ruzicka *et al.*, 2007), then the relative flow into jellyfish would have been even more important.

Although jellyfish have yet to become the dominant component of the pelagic ecosystem in the NCC as they have in other areas (Lynam *et al.*, 2006;

Uye, 2008), expected changes in this ecosystem such as climate change, eutrophication, fishing, and coastal hypoxia may all favor promoting jellyfish production at the expense of planktivorous fish production (Purcell *et al.*, 2007; Richardson *et al.*, 2009; Uye, 2010). Presently, very few food web models include jellyfish due to their lack of their perceived importance or, more likely, the paucity of good quantitative data on biomass and vital rates of gelatinous zooplankton necessary for modeling (Pauly *et al.*, 2009). We recommend that jellyfish be included as an integral part of any food web model in future modeling exercises. Our simulations showed that a system dominated by jellyfish is not desirable and will actually decrease production of higher trophic level animals of interest to humans (fish, seabirds, marine mammals), and will likely affect overall fisheries production in this system.

Acknowledgments—This research was funded by the National Marine Fisheries Service (Northwest Fisheries Science Center), Bonneville Power Administration, and a grant from US GLOBEC Pan Regional Synthesis Program. We thank Professors Takeoka of CMES and Tanabe of COE for support for the first author to present this work at the symposium.

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