Time scales of top-down and bottom-up processes in a coastal upwelling system

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Definitions

Definitions from Menge (1992):

- Top-down control
  Structure (abundance, distribution, &/or diversity) of lower trophic levels depends directly or indirectly on activities of higher trophic levels.
- Bottom-up control
  Direct or indirect dependence of community structure on factors producing variation at lower trophic levels or their resources.

Abstract

There is presently some debate as to whether food limitation or predation limits the populations of marine organisms. As part of the U.S. GLOBEC Northeast Pacific Program, we have begun to address this issue in the California Current System (CCS).

Here, I approach the problem through a simple lower and middle trophic model. The model is a multi-component food web model for a single upper pelagic box in the CCS, with compartments ranging from dissolved nitrogen through piscivorous fish. The model is driven by seasonal upwelling, and incorporates information on sunlight, mixed-layer depth, and temperature to predict primary, secondary, and tertiary production, expressed as nitrogen content of biomass. The model has been parameterized to represent a section of the CCS near Newport, Oregon, USA, allowing comparison of model output with several years of biweekly observations of water properties and zooplankton abundance.

In this simple model, within-season patterns are largely driven by physical (bottom-up) processes, with some modification by fish predation. Lower trophic species composition is largely determined by the presence/absence of fish (top-down control). Under a constant environment, the presence of fish induces multi-year variation that is absent in the absence of fish. Both top-down and bottom-up processes are important, but their apparent prevalence may depend on the trophic levels and time scales observed.

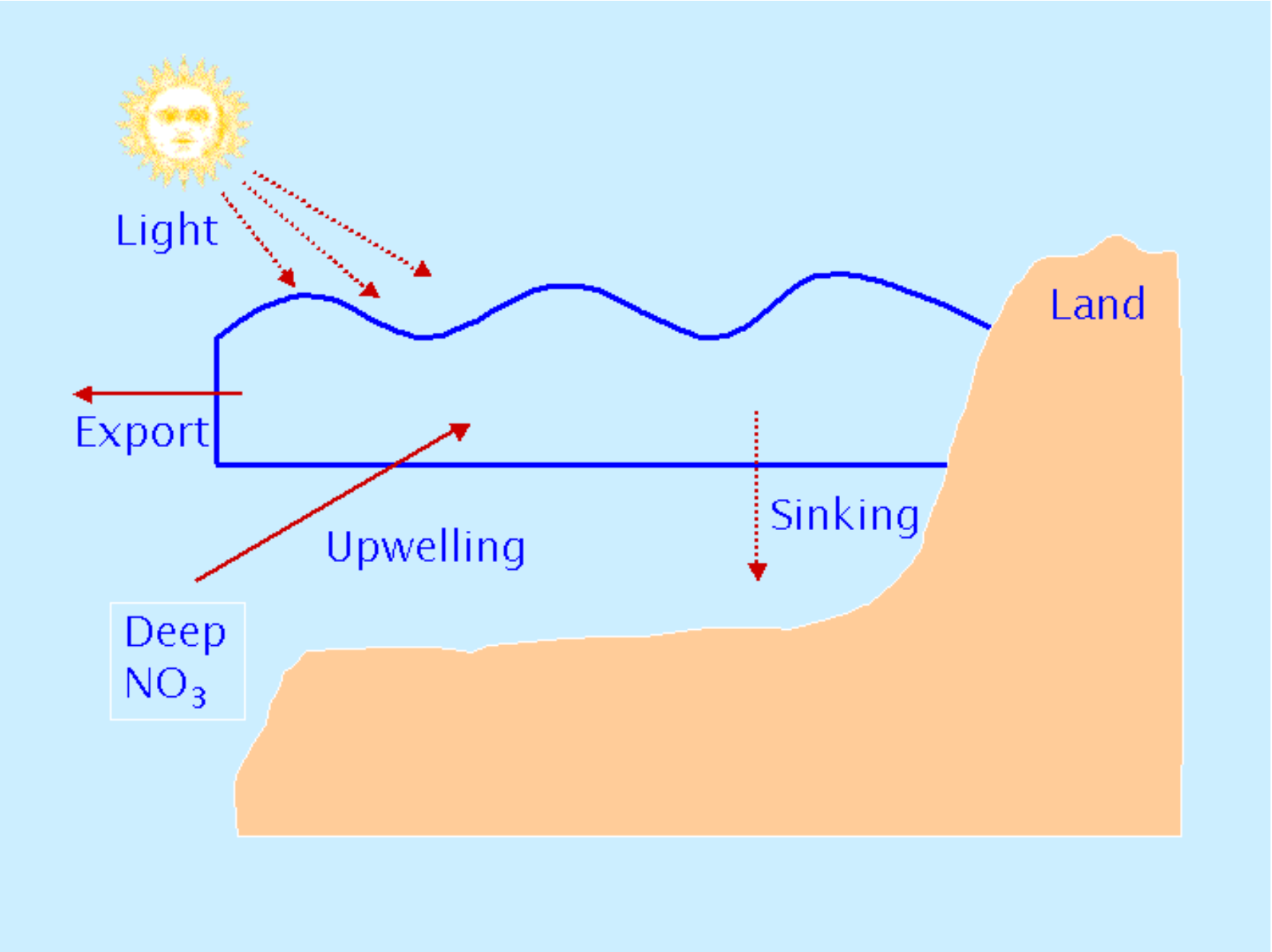

Figure 1. Schematic of the model physical setting.

Approach

The model

I approached the problem with a lower-to-middle trophic model coupled to an extremely simplified physics model.

The physical model used is a single box model representing the California Current System (CCS) upper pelagic zone at approximately 45 N (Fig. 1). The system is driven by Ekman transport which induces upwelling of nitrate-rich water and offshore advection. The model also incorporates seasonal changes in light, temperature, and mixed-layer depth. Gravity is also included as particle sinking. Data for Ekman transport (Bakun upwelling index), surface temperature, and mixed-layer depth were obtained from the NOAA Pacific Fisheries Environmental Laboratory (at http://www.pfeg.noaa.gov). Light was calculated based on a latitude-driven model (Brock 1981) modified by cloud cover and sea-surface transmission.

The biological model is more complex, tracking the flow of nitrogen through the lower end of the coastal pelagic food web—Nutrients through small fishes (Fig. 2). The full model has 12 components: four nutrients (nitrate, ammonium, dissolved organic N, and detritus), two primary producers (small phytoplankton and diatoms), bacteria, 2 zooplankters (copepods and euphausiids), and two fishes (planktivore and piscivore). The model is a modification of that used for Monterey Bay by Olivieri and Chavez (2000), which in turn was based on the model of Fasham, Ducklow, and McKelvie (1990). A full description of the model and its parameters are available from the author (via email: thomas.wainwright@noaa.gov).

Analysis

To examine the effects of top-down and bottom-up processes, two approaches were used. First, short term dynamics of the system were examined by comparing two versions of the biological model (the full model, and a lower-trophic model with fish and euphausiids removed) under two sets of physical environment conditions (real upwelling and temperature vs. climate mean seasonal cycles.) Second, time-scales of variation were examined by comparing the same two models over longer time periods (25 years) using the mean climate physics. Methods and results for these two approaches are described below.

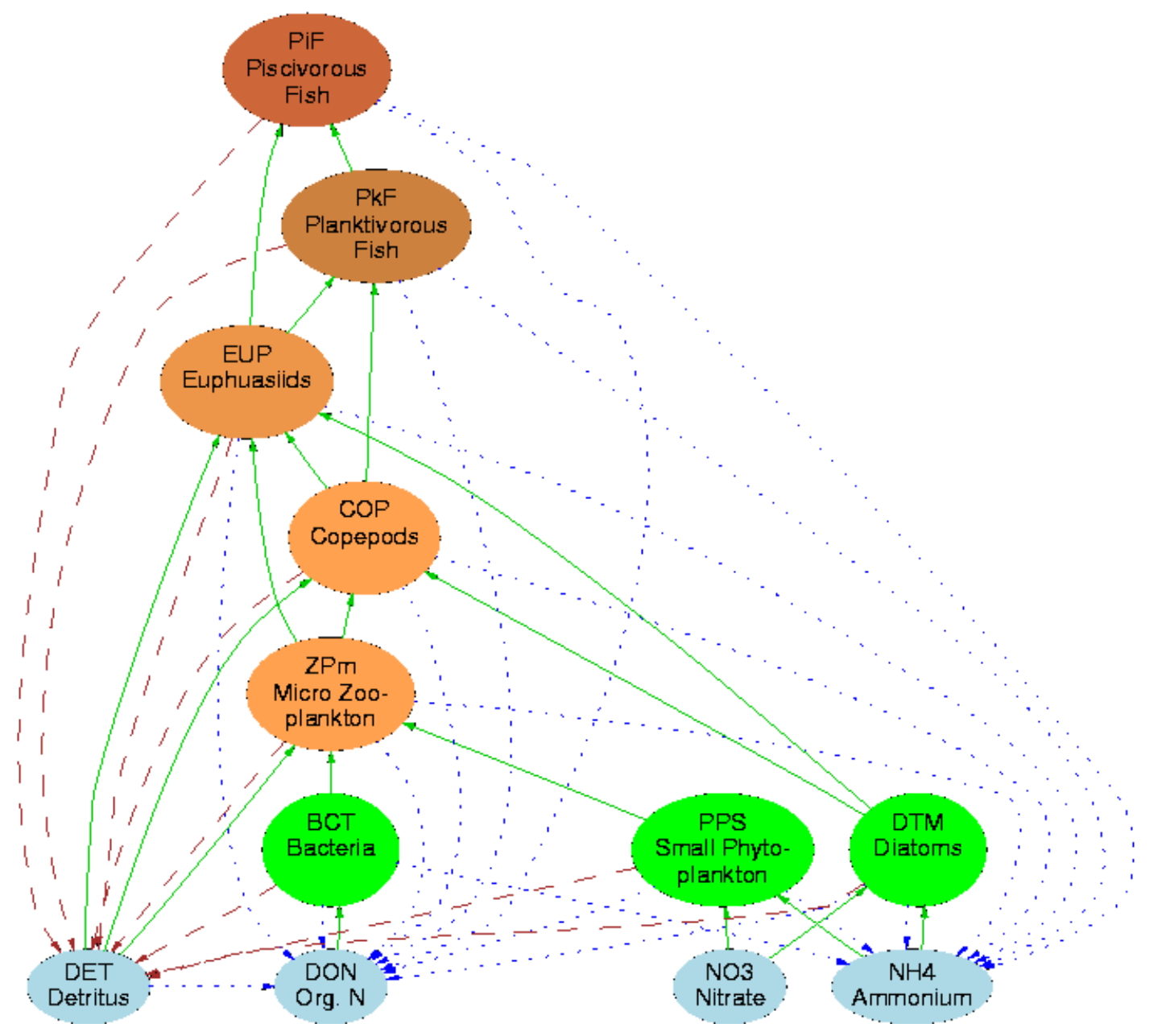

Figure 2. Structure of the biological model, showing the 12 model components (ellipses) and the main flow pathways (arrows: solid green—consumption, dashed red—egestion, dotted blue—respiration).

Short-Term Dynamics

Methods

Two versions of the biological model were run, each with two scenarios of physical inputs. The biological models contrast a lower-trophic (NPZD) case which has primarily bottom-up control, with one including larger zooplankton and fishes to allow a degree of top-down control. The first physical scenario has constant seasonality represented by root-transformed cosine functions fitted to monthly mean climate data. The second physical scenario (Fig. 3) uses real daily observations (1995-2000) for upwelling and surface temperature, combined with the mean climate models for mixed layer depth and light (for which daily observations were unavailable). Initial biomasses were equilibrium values based on the end values of 20-year mean-climate simulations.

Results

Annual summaries of biomass and production patterns for the mean climate scenario are shown in Figures 4 (full model) and 5 (lower trophic model). Detailed dynamics for both these and the “real” data scenario are shown in Figures 6-9.

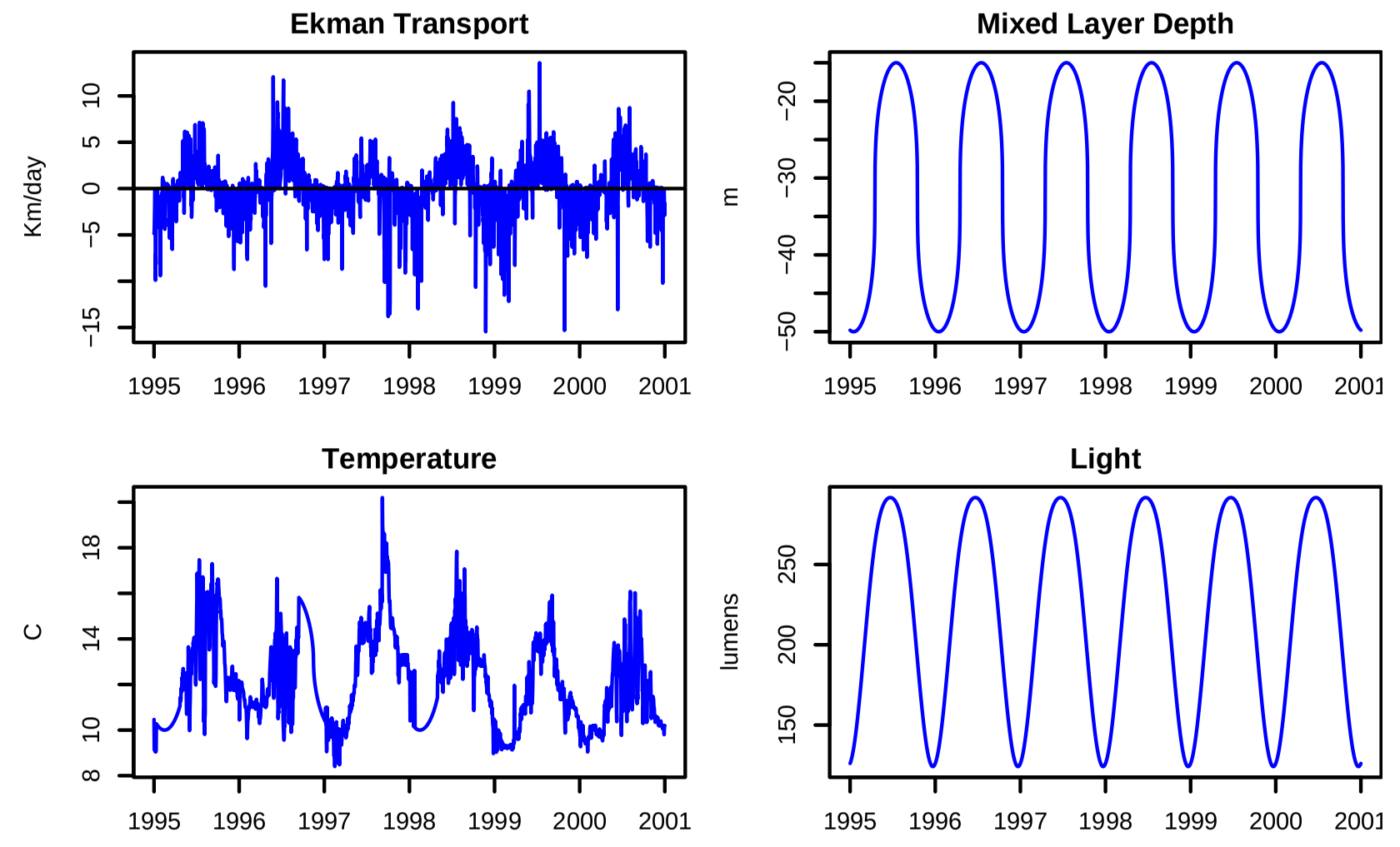

Figure 3. Physical inputs to the “real” physics scenario. The “climate mean” scenario was similar, but with smooth curves for all series.

Full Model

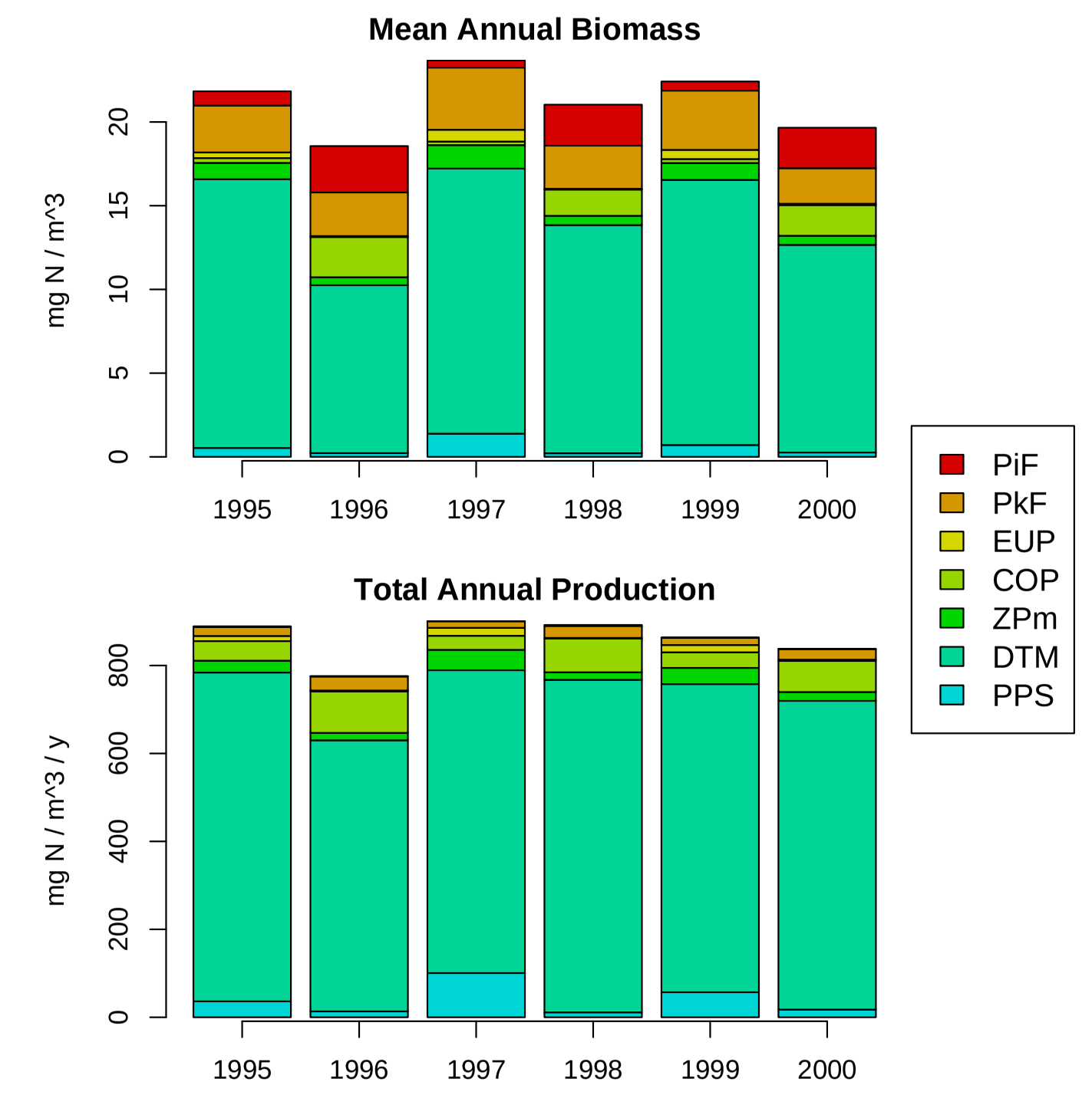

Figure 4. Annual summary of biomass (upper panel) and production (lower panel) for full model with the mean climate scenario.

Lower Trophic Model

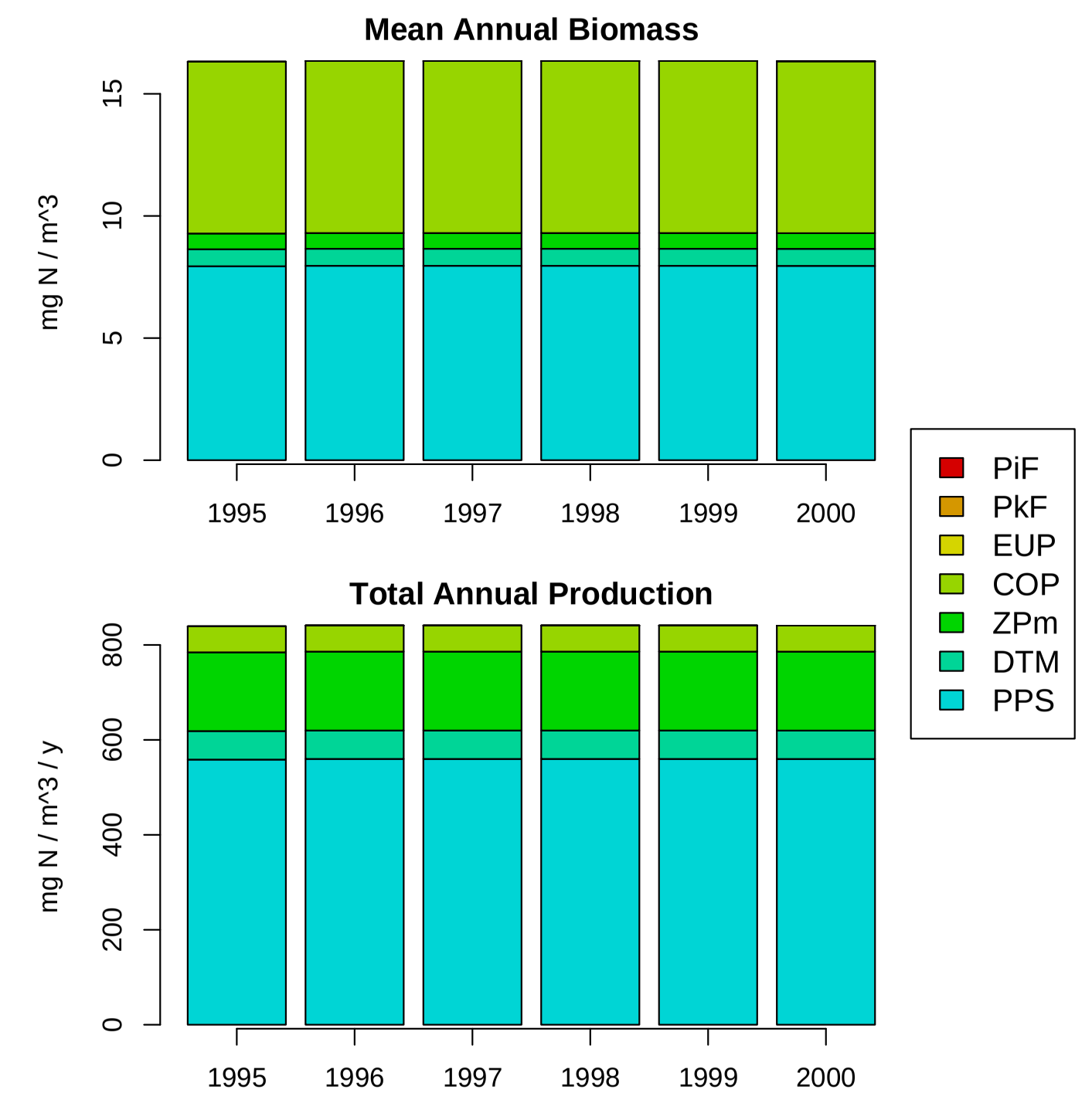

Figure 5. Annual summary of biomass (upper panel) and production (lower panel) for lower trophic model with the mean climate scenario.

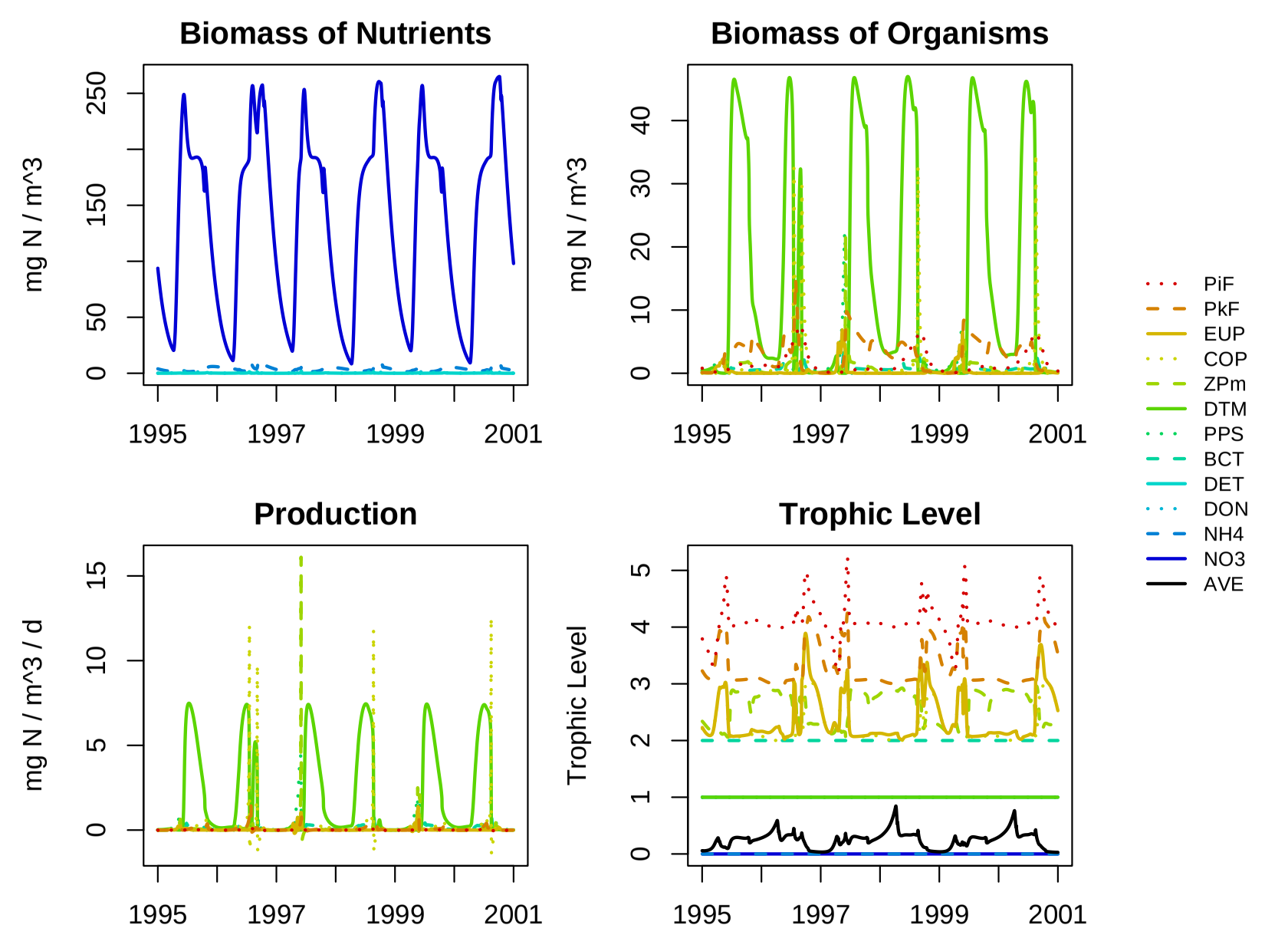

Figure 8. Detailed dynamics of the full model with mean climate inputs.

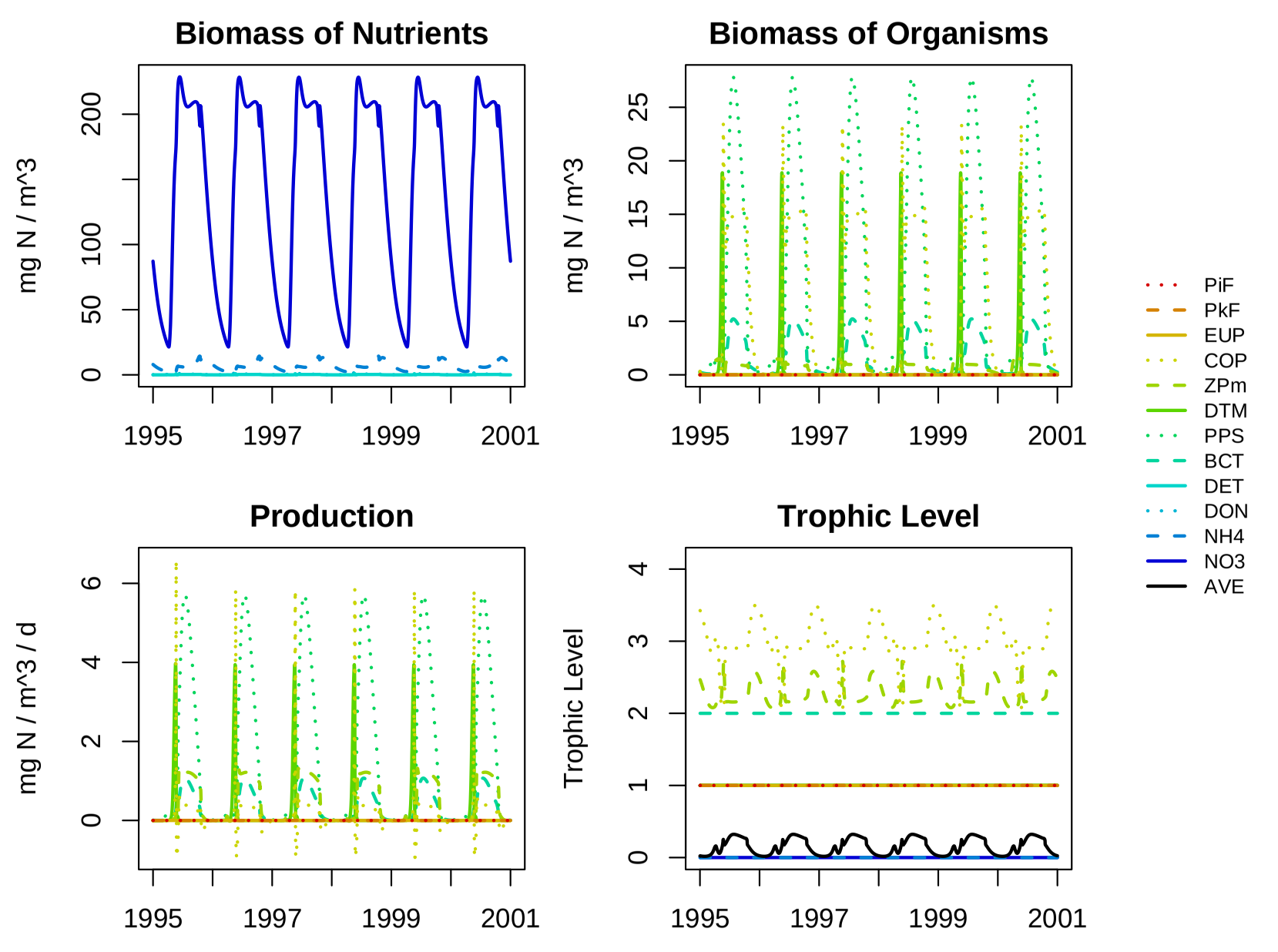

Figure 9. Detailed dynamics of the lower trophic model with mean climate inputs.

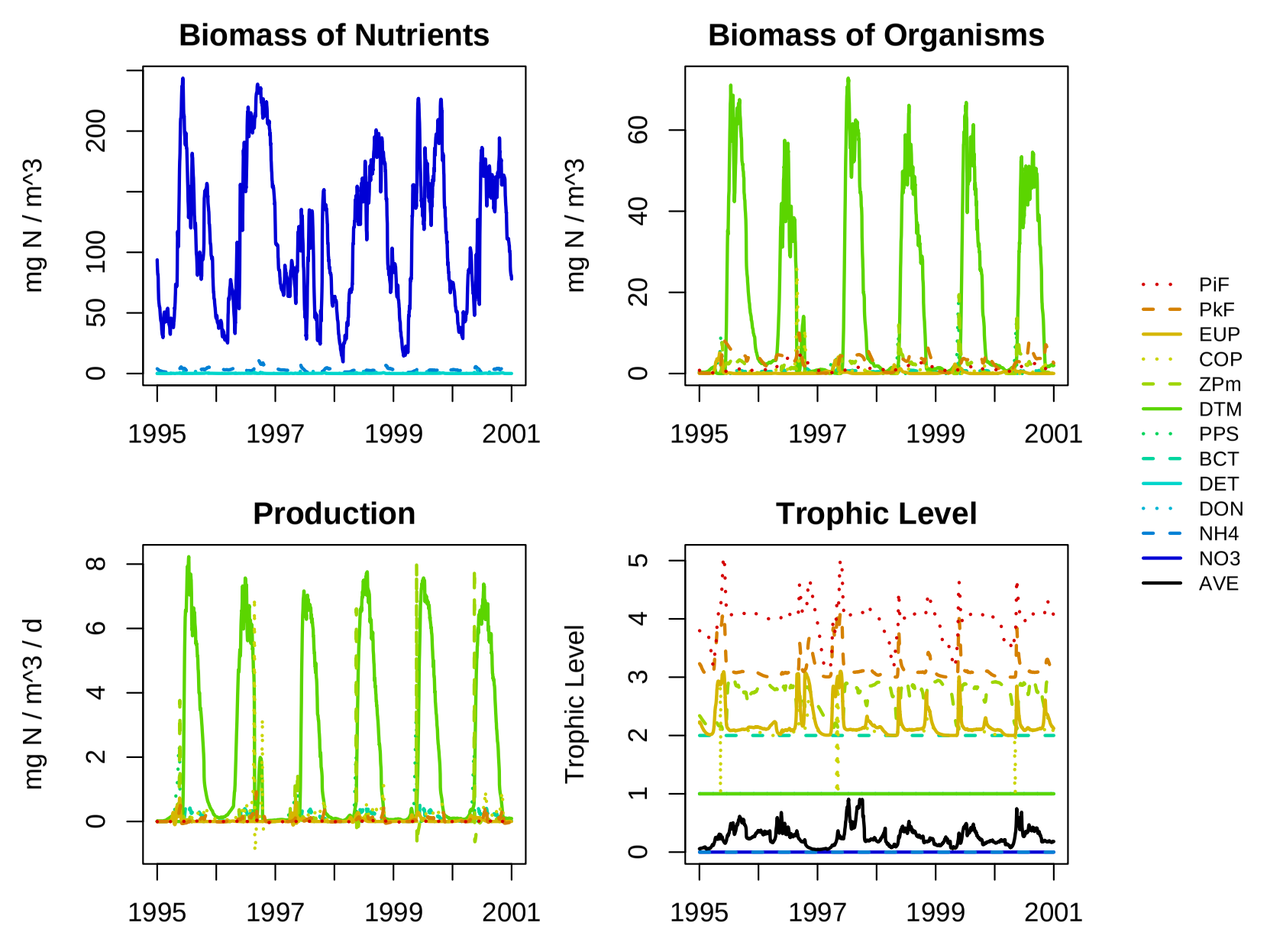

Figure 6. Detailed dynamics of the full model with 1995-2000 data.

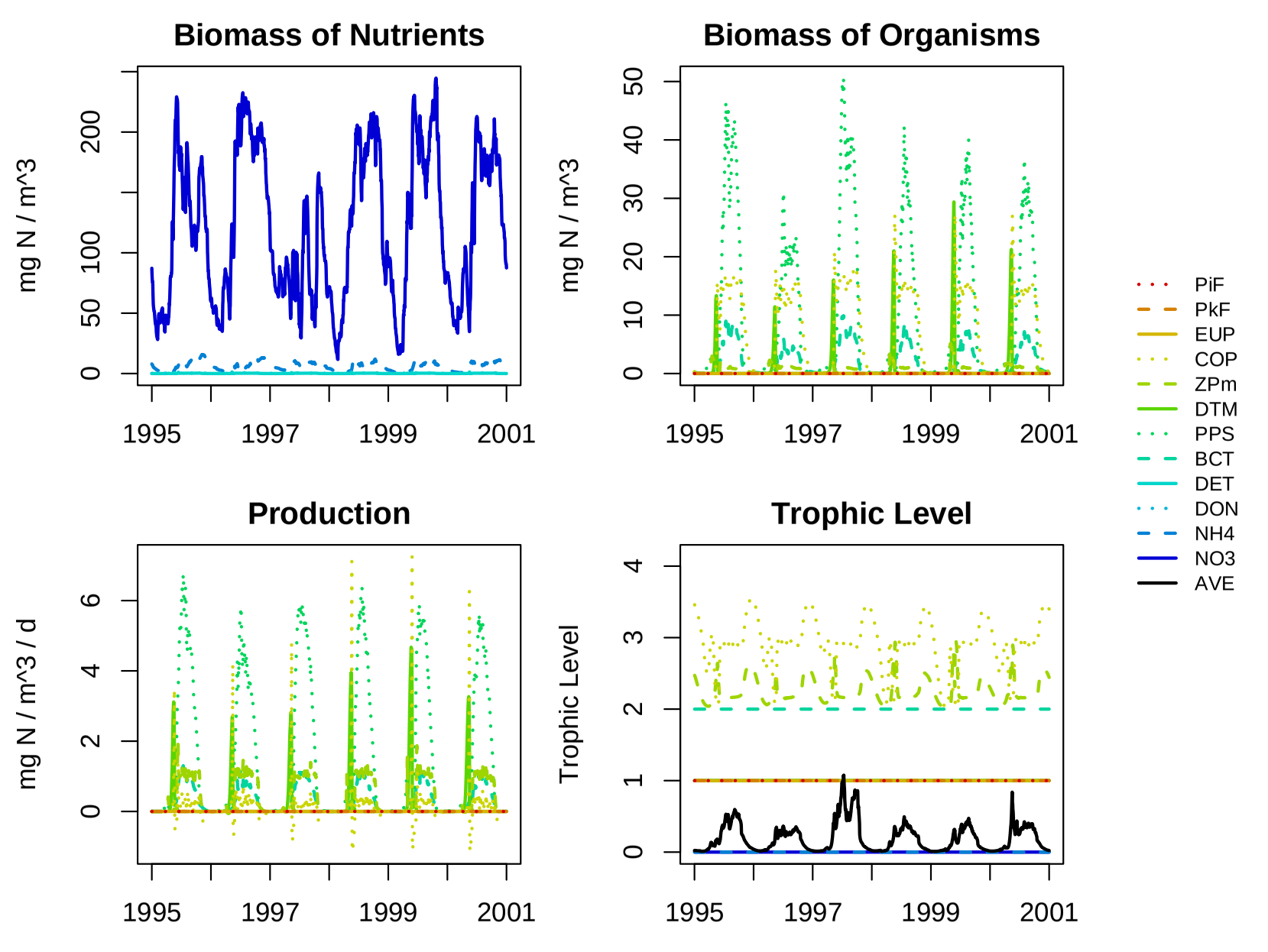

Figure 7. Detailed dynamics of the lower trophic model with 1995-2000 data.

Time Scales of Variation

Methods

This analysis used the same two biological models (full and lower trophic) as the short-term analysis. These models were run for 25 years with the mean climate seasonal change scenario (i.e. with no year-to-year variation). As before, initial biomasses were the end-points of 20-year runs of the mean climate scenario.

Results of the simulations were then analyzed via spectral analysis (Fourier transform method). All spectra were standardized to have a maximum power of zero dB. Because the raw periodograms were dominated by the 1-year cycle of physical inputs, residual periodograms were calculated by dividing the upwelling spectrum out of the biological component spectra.

Results

The raw periodogram for physical variables and biological components for the full model simulations are shown in Figure 10. Figures 11 and 12 present the residual periodograms (effect of upwelling removed) for both biological models.

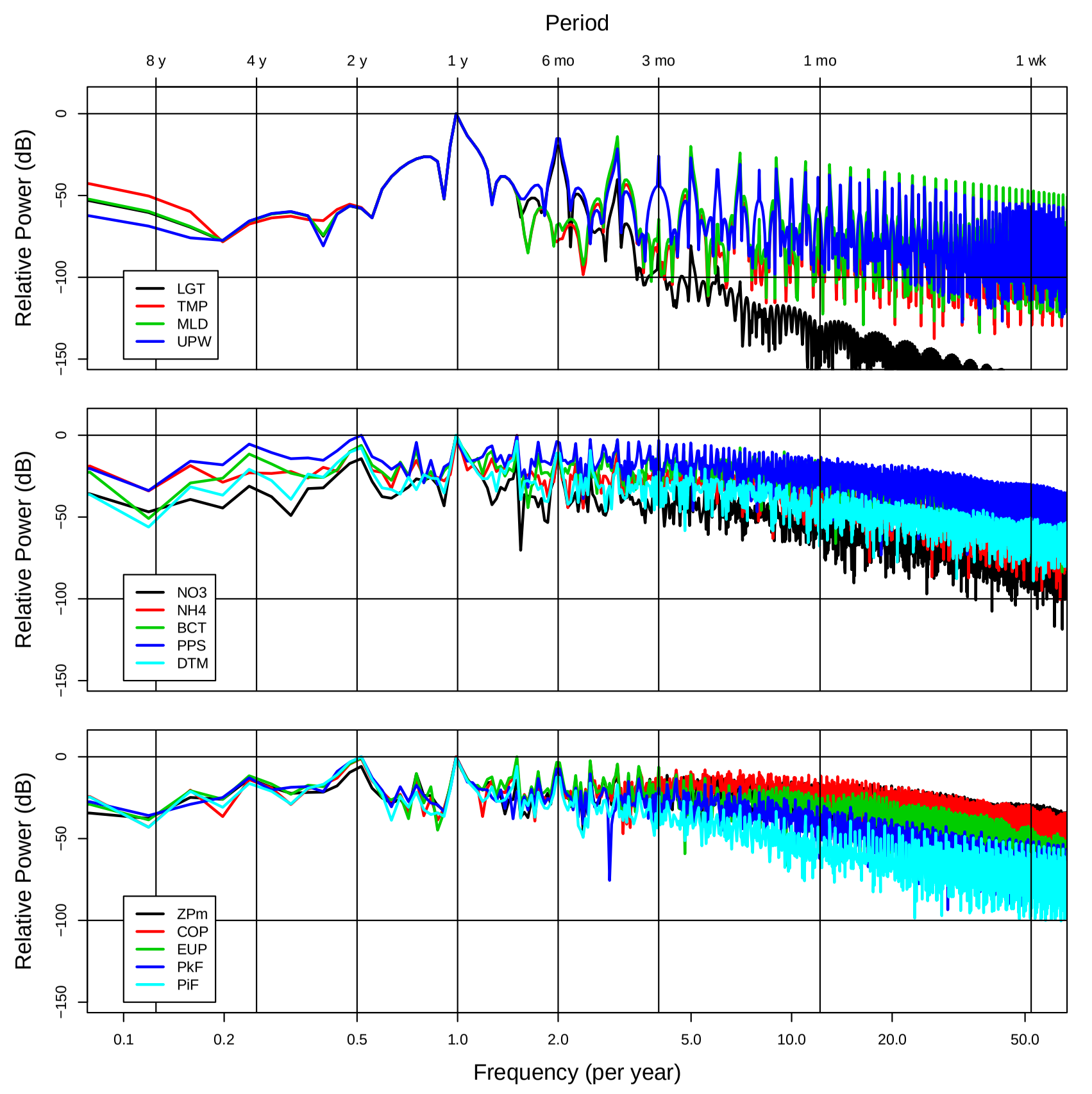

Figure 10. Raw periodogram for the full model, showing periodicities in physical inputs (upper panel) and biological components (middle and lower panels.

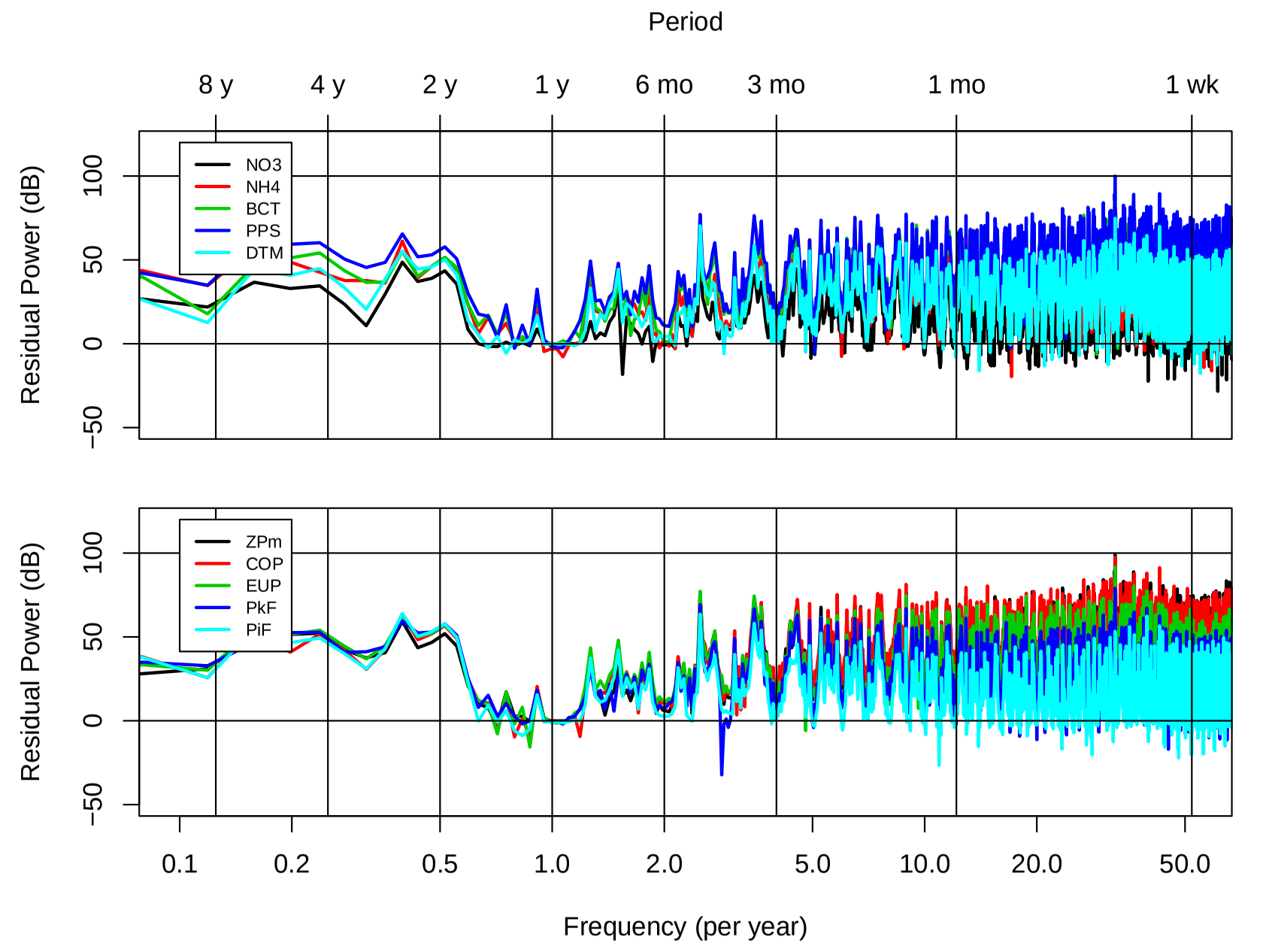

Figure 11. Residual periodogram (upwelling spectrum removed) for the full model.

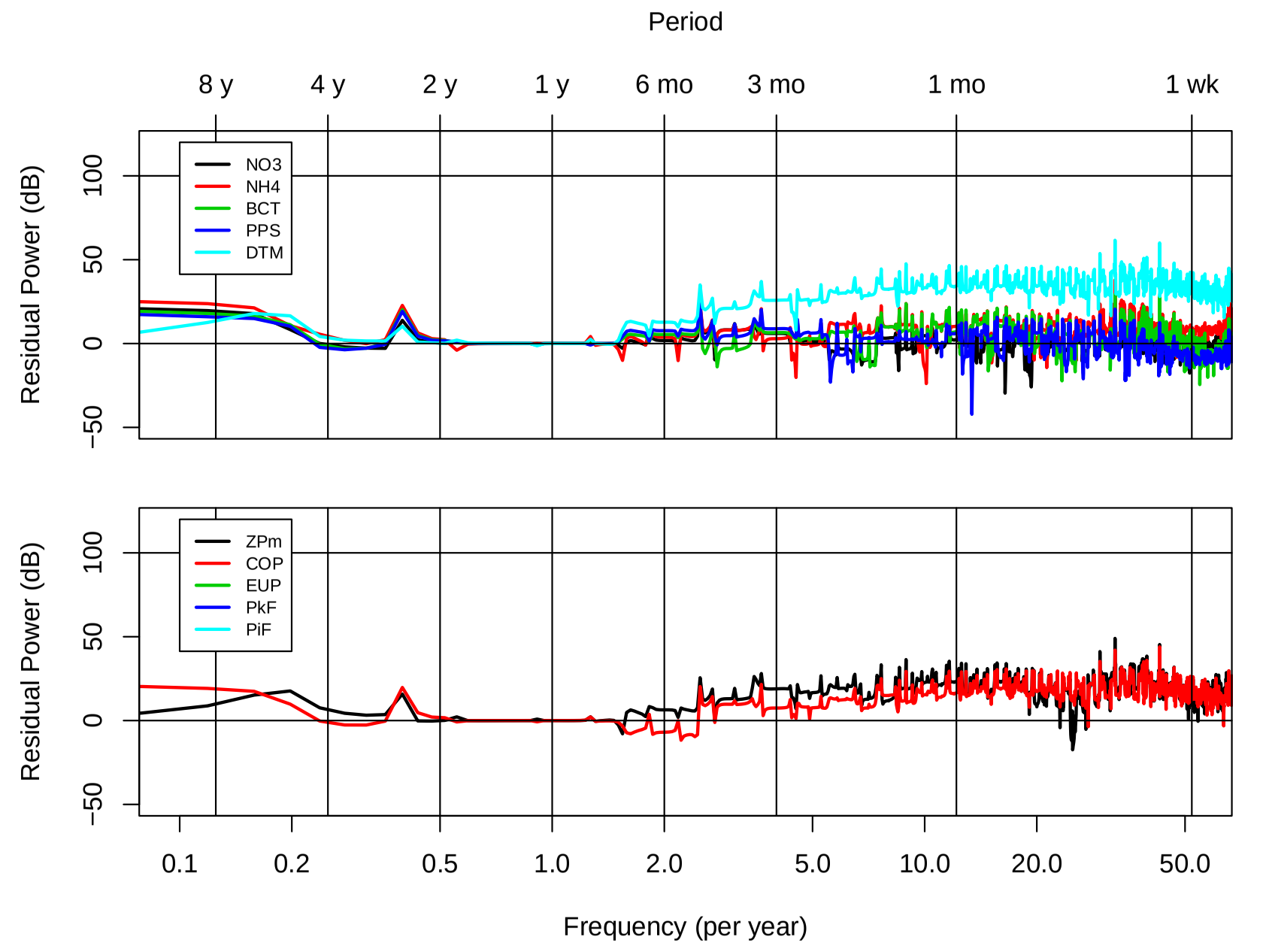

Figure 12. Residual periodogram (upwelling spectrum removed) for the lower trophic model.

Discussion

Realism

The current model is not expected to closely reflect reality. The physics are extremely simplified, and biological parameters are taken from the plankton modeling literature (Fasham et al. 1990, and others) with no adjustment for local conditions or species composition. That said, for the full model and “real” physics scenarios, summer peak values of nitrate, phytoplankton, and copepod abundance are reasonably close (+/- 50%) to observed values from biweekly surveys along the Newport Line (B. Peterson, NMFS, pers. comm.). The general seasonal pattern of plankton abundance is also captured, although fine-scale event-driven peaks and valleys in abundance curves are not reproduced. A spatially-explicit model is under development which should improve the predictive power of the trophic model.

Top-Down and Bottom-Up Processes

The model structure allows a great deal of experimentation with biological structure and physical forcing. The work presented here is essentially a simple experiment examining the potential role of fish as top-down controls on plankton abundance and production.

The short-term dynamics simulations illustrate the dramatic effect that fish may have on lower trophic structure and dynamics. Under constant seasonal inputs (mean climate scenario), the lower-trophic model (Fig. 5 & 9) has no interannual variation, dominance of small phytoplankton in primary production, and dominance of microzooplankton in secondary production. In contrast, the full model (Fig. 4 & 8) has considerable interannual variation (notably in phytoplankton biomass), with diatoms dominating primary production and either microzoo-plankton or copepods dominating secondary production in different years. Clearly, fish grazing can restructure lower trophic species composition and the multi-year cycles in fish abundance can drive changes in lower trophic production.

Time scales of bottom-up and top-down processes can be seen by examining the periodograms derived from 25-year simulations. Physical variables are clearly dominated by a seasonal cycle with a one-year period (Fig. 10, upper panel). This cycle is also dominant or co-dominant in all the biological components (Fig. 10, middle and lower panels). However, the biological components have more spectral structure than the physical inputs, especially at multi-year time scales; notably the zooplankton and fishes all have a strong peak at a period of 2 years.

The full model is best compared with the lower trophic model by examining the residual periodograms with the influence of upwelling removed. For the full model (Fig. 11), all components have interannual dynamics that are absent from the lower trophic model (Fig. 12). Surprisingly, the full model also exhibits stronger within-season (period < 1 year) variation for all components than the lower-trophic models.

Conclusions

For this idealized system, the following conclusions can be drawn:

- The seasonal pattern of total primary production is largely driven by physical processes, with some modification by top-down (fish) processes.
- Lower trophic species composition is largely determined by the presence/absence of top-down controls.
- In a constant environment, the presence of fish induces low-frequency (interannual) variation and increases the magnitude of high-frequency (within season) variation in lower trophic components.
- In general, bottom-up processes drive high-frequency variation in primary production, while top-down processes affect low-frequency variation in primary production.
- Both top-down and bottom-up processes are important in lower trophic dynamics. The likelihood of detecting these processes in field studies will depend on the focus of the studies: within-season plankton studies will predominantly perceive bottom-up control, while interannual-scale studies that include higher predators will perceive top-down control.

References

Brock, T. D. 1981. Calculating solar radiation for ecological studies. Ecol. Modelling 14:1-9.

Fasham, M. J. R., H. W. Ducklow, and S. M. McKelvie. 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. J. Marine Res. 48:591-639.

Menge, B. A. 1992. Community regulation: Under what conditions are bottom-up factors important on rocky shores? Ecology 73(3):755-765.

Olivieri, R. A., and F. P. Chavez. 2000. A model of plankton dynamics for the coastal upwelling system of Monterey Bay, California. Deep-Sea Res. II 47:1077-1106.