A Trophodynamic Model of the California Current System
First Year Progress

Tom Wainwright, NOAA/NWFSC, Newport, Oregon

Purpose

Our purpose is to develop a formal, empirically-based description of food-web structure in the California Current System (CCS), then estimate trophic dynamics for seasons/years with adequate data, and finally to develop a multi-species population model of the CCS and apply the model in examining hypothesized linkages with lower trophic and physical processes. In particular, the model will be used to identify the relative importance of marine food-web processes (food supply, predation, competition) in controlling salmonid population dynamics, with particular focus on defining the magnitude of potential predation rates by piscine, avian, and mammalian predators.

Accomplishments

First year work was proposed to consist of (1) describing food-web structure for the system from literature, (2) compiling existing data on standing biomass and bioenergetics for major food web components, then (3) incorporating this information into a trophic flux estimate, based on an ECOPATH-type model.

The literature review (tasks 1 & 2) has been substantially completed. This focused on compiling all available literature on prey composition, bioenergetics, and growth of seven important pelagic fish genera (*Clupea, Engraulis, Merluccius, Oncorhynchus, Sardinops, Scomber, Trachurus*) in the northeast Pacific (NEP). Because there was limited information for several particular species, literature covering entire genera were used to provide analogous information when data for local species was lacking. Additional literature was obtained relating to prey of CCS invertebrates, birds and mammals; review for these groups was not extensive as they are covered largely by other GLOBEC projects. We have begun the task of entering predator-prey information from this literature into a NEP-wide predator-prey database that will be used to construct detailed food-web diagrams for the region. An (incomplete) example of such a web is in Figure 1.

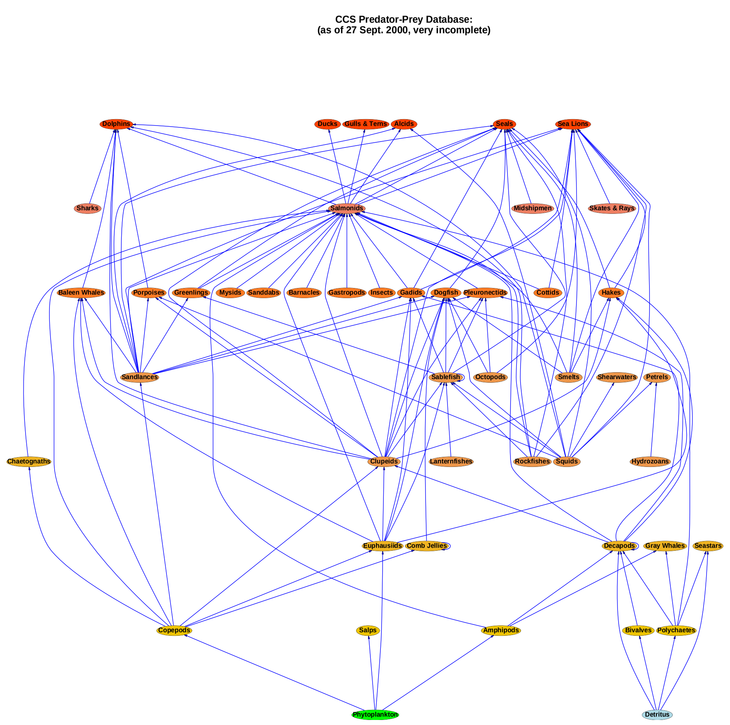

Figure 1. Example food-web diagram, based on the current state of the CCS predator-prey database. Arrows connecting nodes summarize predator-prey relations in the database in low-resolution taxonomic groupings (family-level for vertebrates, order- or class-level for invertebrates, and kingdom-level for plants). Note the incomplete state of the database, which has a strong bias toward salmonids (many connections) and little information on the prey of many taxa.

Modeling work (task 3) began with an attempt to apply the ECOPATH model (Christensen & Pauly 1992) to the major components of the CCS pelagic food web. However, this model proved impossible to "tune" with reasonable parameters for this system, and it soon became obvious that the steady-state assumptions implicit in this model were substantially violated by the strong seasonal and inter-annual dynamics of the CCS. For this reason, we began early on work originally proposed for year 2: the development of a trophodynamic model for the system. An initial prototype of this model has been completed and tested with a simplified upper trophic web. This prototype model is a single spatial box model 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. It is a modification of the Juan de Fuca eddy model developed by Robinson and others (Robinson et al. 1993; Robinson & Ware 1994). The lower trophic portion of our model is also similar in structure to the PICES CCCC NEMURO model (PICES 2000; Kishi 2000), although the present model tracks only N, not N and Si as does the NEMURO model.

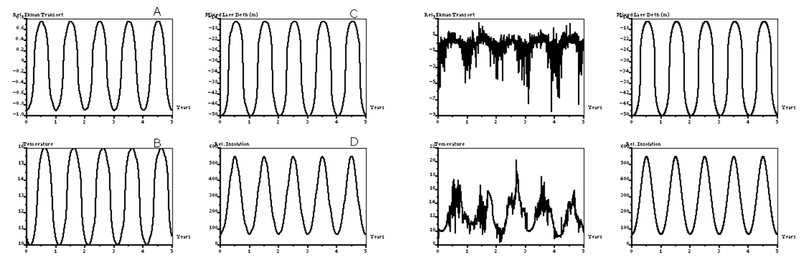

Figure 3. Environmental variables (inputs) for the mean climate condition 5-year run of the prototype model. Variables are continuous functions approximating monthly climate means at 45 deg. N for : A-Bakun upwelling index (m^3s^{-1} per m of coastline), B-Temperature (C), C-Mixed layer depth (m), and D-Relative insolation (arbitrary units).

Figure 4. Environmental variables (inputs) for the 1995-1999 5-year run of the prototype model. Here, year 0 corresponds to calendar year 1995, and year 4 to 1999. Variables as in Figure 3.

Modeling Methods

Model structure

The prototype model is a seven-component food web model (Figure 2) for a single upper pelagic region, assumed to be a rectilinear box. Boundaries of the boxed are at fixed positions, except for the lower boundary, which is set to the mixed-layer depth (MLD) and varies seasonally. Four physical factors drive the model: currents, temperature, mixed-layer depth, and insolation. Within the food-web, nitrogen (N) is used as the fundamental currency which is tracked through physical transport, feeding, egestion, and respiration flows. All uptake and feeding interactions follow modified Michaelis-Menten dynamics, as in Robinson et al. (1993).

Physical Conditions (Inputs)

To date, the prototype model has been configured to approximate upper pelagic zone conditions off the northern Oregon coast (ca. 45 deg. N) and has been applied to two physical condition scenarios: mean climatic conditions and observed 1995-1999 conditions.

In the prototype model, currents are represented only as offshore Ekman transport, as approximated by the Bakun Upwelling Index, and flow occurs across only the lower and western boundaries of the modeled box.

In the mean climate scenario, seasonal variation in physical processes are represented by sine or square-root-sine functions with a 365 d period. Mean value, amplitude, and phase shift of these functions were estimated to provide a good approximation to observed monthly climate means (Table 1). Upwelling index, surface temperature, and mixed-layer depth climatic means were obtained from the World Ocean Database 1998 via the PFEL Live Access Server (Available on the web at http://salmonid.pfeg.noaa.gov/las.html). Insolation was based on a model for the mouth of the Strait of Juan de Fuca (Robinson et al. 1993).

The 1995-1999 scenario used the same functions for MLD & light (for which there is no regular local data series), but used daily observations of upwelling and surface temperature, obtained from PFEL.

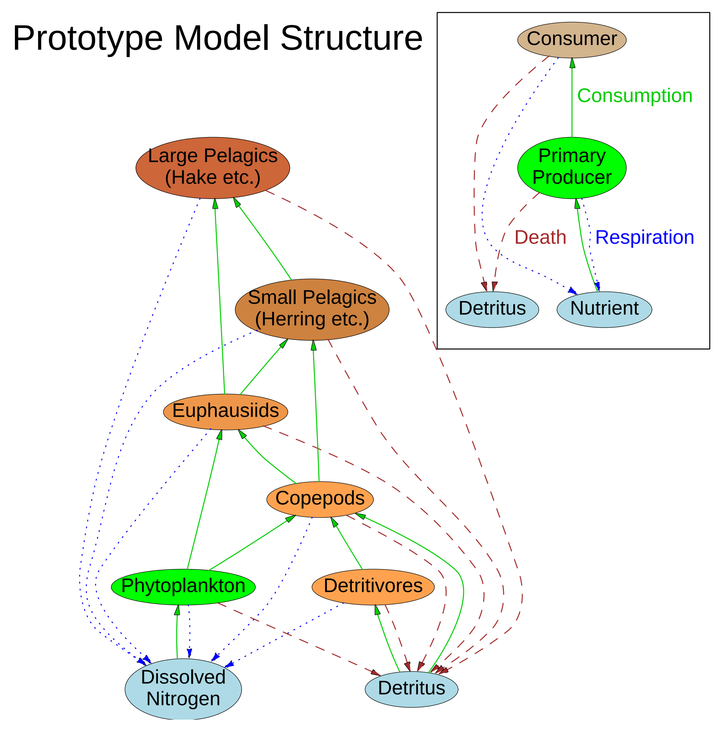

Figure 2. Structure of biological interactions in the prototype model, with flow arrows representing consumption (solid green), death or egestion (dashed brown), and respiration (dotted blue).

Table 1: Physical factor models for climatic mean conditions.

Factor	Units	Function	Mean	Amplitude	Day of min. value
Upwelling	$m^3s^{-1}m^{-1}$	sqrt(sin(t))	-7.5	82.5	5
Temperature	C	sqrt(sin(t))	13.0	3.0	45
Mixed-Layer Depth	m	sqrt(sin(t))	-32.5	17.5	15
Insolation	arbitrary	sin(t)	500	300	2

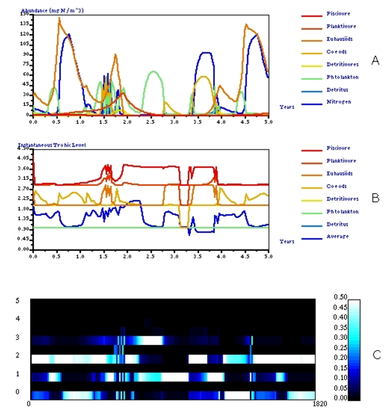

Figure 5. Results for the mean climate condition 5-year run of the prototype model. A-Abundance of nitrogen (mg N m^{-3}) in the 8 model compartments. B-instantaneous trophic level of the 7 biological compartments, plus the mean trophic level (dark blue). C-Distribution of biomass across trophic levels; x-axis is days from 1 January of year 1, y-axis is instantaneous trophic level, scale represents proportion of biomass at a given trophic level, with all proportions greater than 0.5 shown in white.

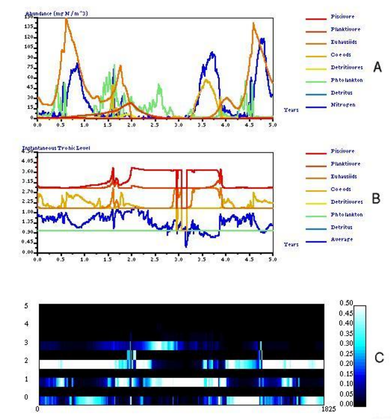

Figure 6. Results for the 1995-1999 5-year run of the prototype model, as in Figure 5. Here, year 0 corresponds to calendar year 1995, and year 4 to 1999.

Results & Discussion

Mean Climate Conditions

Figure 3 illustrates the physical inputs and Figure 5 illustrates the outputs of the mean climate condition runs. While these results are not a realistic view of the CCS system, the model was parameterized so that the behavior of the model is within the realm of possibilities for that system. The first noteworthy result is that while the physical system (Fig. 3) is identical in all years, the biological system (Fig. 5-A) is not: Biomass in years 0 & 4 is dominated by euphausiid biomass, year 1 exhibits rapid shifting of dominance among phytoplankton, copepods, and euphausiids, year 2 is phytoplankton-dominated, and year 3 is copepod-dominated. Note also that when there is a high abundance of zooplankton, there is also a high level of dissolved nitrogen. These changes are also reflected in patterns of distribution of biomass among trophic levels (Fig. 5-C). From sensitivity experiments with the model, it appears that the relative abundance of different plankton in any given year is defined by two things: the relative starting abundance of the plankton organisms and the abundance of piscivorous fishes. This suggests that "top-down" control is very important in this model, at least if there is no environmental variation.

Another noteworthy result is the pattern of instantaneous trophic levels over time. (Instantaneous trophic level of an organism is the level at which the organism is feeding at a particular instant in time: it changes as prey composition varies.) For most heterotrophs the trophic level varies over an entire trophic level in the course of the model run; for example, euphausiids vary between level 2 and level 3 depending on if they are feeding on copepods or phytoplankton, and on what the trophic level of copepod prey is at any given time. There is also a "trophic collapse" in this run, between time 3.1 and 3.2 when phytoplankton become so rare that copepods stop feeding.

1995-1999 Conditions

While upwelling and temperature patterns during 1995-1999 (Figure 4) differ substantially from mean climate conditions, the mid- to long-term biological dynamics (Figure 6) do not. The most obvious difference is the somewhat greater dominance of phytoplankton relative to copepods in the second year (1996). At short time scales (days), there is substantially more variability at the lower trophic levels (nutrients, phytoplankton, and copepods) than in the mean climate runs, but this variability does not carry through to the upper trophic levels (euphausiids and fish).

Conclusions

In this model, the following patterns are apparent:

- Interannual patterns in species abundance are largely determined by top-down processes and depend more on past biological patterns than present physical patterns.
- Bottom-up (physical) processes are apparent in short-term (daily-weekly) patterns in lower trophic levels. These short-term fluctuations are filtered out of the dynamics of mid- to upper-trophic organisms.

However, it is at this point unclear how well this simplified prototype model reflects reality.

Future Work

The next task is to incorporate more upper trophic complexity in the model, with all important marine species included explicitly. As more refined physical and lower trophic models (GLOBEC NEP projects by Haidvogel et al.; Huntley & Zhou; Powell & Haidvogel; Botsford, Hastings, & Largier; Murphree et al.; Peterson; and Powell & Batchelder) are developed, these will be incorporated as driving functions for the higher trophic levels. As data sets are improved, spatial structure, fish migration patterns, ontogeny, and size-structure within species will need to be incorporated to accurately describe processes affecting salmonid growth and survival. These new features will be prioritized in year 2, and implemented in years 2-4 of the project.

As the model develops, we will apply it to make comparisons with three data sets: historic Oregon coast, GLOBEC surveys of the California and Oregon coasts, and BPA studies of the Columbia plume region. This will provide comparisons of trophic structure in both space (Columbia Plume to south of Cape Blanco) and time (early 1980s vs. late 1990s and early 2000s). We will also be able to compare the outputs of our models to those of Pauly and Christensen (1996) and Robinson and Ware (1994) for off Vancouver Island. Environmental conditions are likely to be different for these comparisons and we can use the model to examine the influence of oceanographic features/conditions on the food web (Robinson 1994). From these comparisons, particularly noting where along trophic pathways production may exceed consumption, we will also be able to consider the conditions under which salmon production may be controlled by prey availability and/or predator abundance. The ultimate application of this work is in extending our understanding of how trophic relationships control the production of salmonids and other pelagic fishes. The full model will be used in a projection mode to study the community-level consequences of changes in physical and lower trophic-level driving mechanisms, as well as anthropogenic changes in trophic structure through harvest or predator management.

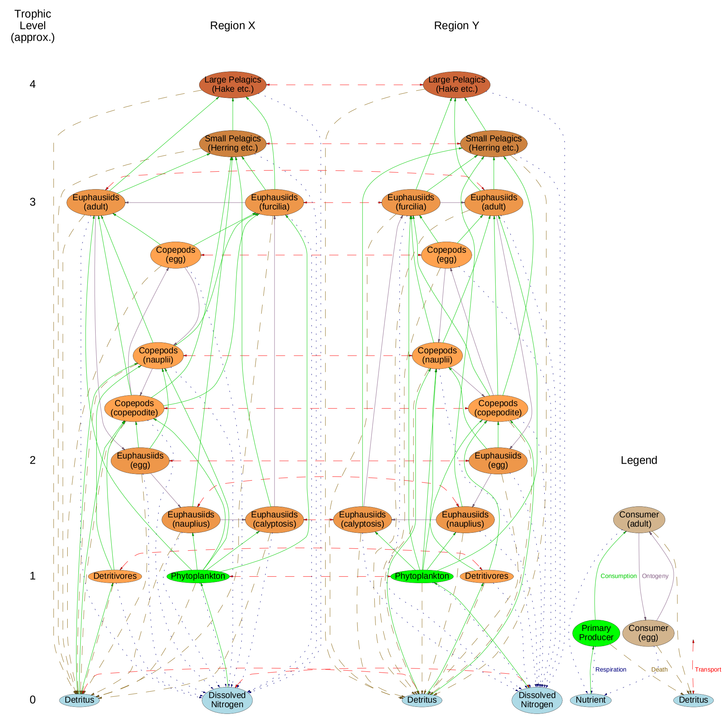

Figure 7. A partial representation of the complete model, with spatial structure represented here by only two of many spatial cellse, and foodweb structure greatly simplified. Compared to the prototype model (Figure 2), note the addition of transport/migratory flows (dashed red) connecting spatial regions and ontogenic flows (solid lilac) connecting different life-history stages within a single organism.

Acknowledgements

We thank NOAA's Pacific Fisheries Environmental Laboratory for providing environmental data, Cliff Robinson for sharing code of his model, Yong-Woo Lee for literature compilation, AT&T Research for providing the GraphViz software package, and the INRIA-Rocquencourt Scilab Group for providing Scilab software.

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