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# Topological constraints on the dynamics of wasp-waist ecosystems

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## Abstract

Small pelagic fish species like anchovy or sardines are of high ecological and economical importance. As marine food webs are fished down, these small pelagics tend to be more exploited and overfished. It is not yet very well known what the possible effects of their collapse can be, therefore there is an urgent need to outline a theoretical framework for understanding their dynamics. These fish occupy very special position in food webs, ensuring energy transfer between species lower and higher levels, while forming narrow “wasp-waists” poor in number of species (but very abundant). Our purpose was to quantify the interaction structure of model food webs of equal complexity but different levels of “wasp-waistedness”. We analysed the topological properties of the webs by characterising every direct and indirect interactions between individual species, as well as by assessing the relative positional importance of each species in each web. We found that (1) the shorter the interaction pathways considered, the weaker the predictive power of node degree for positional importance, (2) the importance of species varies more in wasp-waist food webs, (3) if longer indirect chain effects are considered, indirect effects can well be stronger than direct ones, (4) interactions between coexisting wasp-waist species are stronger than the average, and (5) the “self-regulatory” looping effects are also stronger for wasp-waist species. Based on the topological properties of the networks, our results describe constraints acting on the dynamical behaviour of wasp-waist ecosystems. We give explanations, from this viewpoint, for regime shifts in which one WW species replaces another, and for the unpredictable dynamics of these fish stocks. From a marine conservation viewpoint, we illustrate that as the abundance of wasp-waist species decreases, the architecture of energy flows becomes highly vulnerable and unreliable. We provide an approach for quantifying these structural changes.

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*Keywords:* Food web; Indirect effect; Wasp-waist ecosystem; Keystone species; Regime shift; Sardine; Anchovy; Dynamical predictions

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## 1. Introduction

It is widely recognised that heavy exploitation of particular fish species may have serious effects on

other species, and that fisheries should be considered in multispecies contexts (May et al., 1979). Recent investigations on indirect species interactions also call for a community context in understanding the possible secondary effects of disturbing a single species (Menge, 1995; Abrams et al., 1996; Yodzis, 2000). However, the whole community of living organisms is highly complex in itself, and we also have to take into account abiotic factors, ecosystem engineering and, for example, nutrient stocks and cycles. The conventional wisdom that “No fish is an island” (<http://www.ecopath.org>) is evident, but makes fisheries ecology extremely complicated. In recent decades, the need for outlining an ecological context for the theory of fishing has emerged (Caddy, 1993).

Complexity can be treated either by data aggregation or by developing new methods to cope with huge databases. Both methodologies are problematic. Strong aggregation of data makes it possible to analyse a relatively simple system, which might not reflect the real characteristics of the original system, and important ecological information can be lost. If rich databases are not aggregated, or only lightly, we retain more reality but the outcome of simulation of such complex systems depend heavily on initial conditions (May, 1979). If the dynamics of a complex system is to be studied, two solutions can be considered. A more experimentally based possibility is to analyse the time-series of fish stocks (based on catch data), which is descriptive and of less generality. A more general approach is the structural analysis of interaction networks (e.g., trophic webs), which provides insights into the topological constraints on dynamics. (Note that physicists understand the electron structure of small molecules like  $H_2$ , but chemists have to use graph theory to understand and characterise giant molecules, like RNAs, cf. Plavsic et al., 1993). Strongly aggregated food web data may serve the traditionally rich methodology of population and community dynamics (instead of reflecting biological needs), but there is a recent trend in treating complex networks with more emphasis on structure. The two kinds of analyses have to complement each other, for example, in studying the dynamical consequences of connectedness (p. 137 in Ashby, 1954; Pimm, 1982; Christensen, 1995; Jordán and Scheuring, 2002; Jordán et al., 2002).

Here, a helpful context is the network perspective on ecology: the properties and behaviour of the studied entities (e.g., a fish population) are understandable only if a larger set of entities, preferably the “whole” system is taken into account (cf. Margalef, 1991). The mathematical description of networks makes quantitative approaches possible, which are, for example, strongly needed in keystone research (Power et al., 1996). Thinking in a network context is the practical side of a fundamental topological view: network indices help to define, quantify and understand how subsystems are connected to each other, i.e., how parts form the whole (Thom, 1975). This interest might be of basic importance in ecology if we want to understand how species are functionally linked in ecosystems (Jones and Lawton, 1995).

In this paper, we quantitatively characterise the interaction structure of hypothetical food webs in order to probe the wasp-waist architecture typical of some marine ecosystems (Cury et al., 2000). The expression “wasp-waist ecosystem” was coined by Rice (1995) to characterize those where the intermediate trophic role is performed by one or a few species while the lower and upper trophic levels are species rich (Fig. 1A). The canonical wasp-waist ecosystems are those of upwelling regions where one trophic level is represented mainly by small pelagic fish like sardines or anchovies (Bakun, 1996), but there are other examples. For instance, species of herbivorous (or omnivorous) copepods such as *Calanus finmarchicus*, are often seasonally dominant in the boreal Atlantic; while other copepod species like *Drepanotus pectinatus*, dominate the herbivorous biomass in Morbihan Bay, Kerguelen, where it sometimes exceeds 99% of copepod numbers (Razouls et al., 1996). Another example is the Manila clam, *Tapes philippinarum*, which has become a wasp-waist species in Venice lagoon (Pranovi et al., 2003), as has the invading zebra mussel, *Dreissena polymorpha*, in parts of its new range. Also, the juvenile forms of jellyfish at higher trophic levels such as *Balistes* (Bakun, 1996) or other copepods (Bocher et al., 2001, 2002), often occupy the wasp-waist positions in marine ecosystems. In such systems, if the component species are grouped into say four trophic levels and only first order trophic interactions are considered, then the responses to

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