

Benthic-pelagic couplings as key determinants of food web structure along environmental gradients

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Trophic relationships play a crucial role in shaping community structure and ecological functions in marine ecosystems. Studying food-web variation along environmental gradients is still in its infancy and provides new insights in understanding how abiotic variables shape species interactions. In epicontinental seas, benthic-pelagic couplings modify predator-prey relationships and lead to entangled trophic networks. Here, we assumed that depth affects benthic-pelagic couplings' strength and we investigated depth-related changes in the feeding patterns of fish in the whole English Channel (EC) used as a case study. Gut content and stable carbon and nitrogen isotopes of 33 fish species were collected between 5-100 m depth in 2009 and in 2014. Samples from additional compartments of the ecosystem were also collected to delineate the whole food web. First, analyses on the general topology of the EC food-web indicated that it forms a continuum of four trophic levels with species falling into functional groups characterized by varying contributions of pelagic and benthic food sources. Further studies using Bayesian isotope mixing models (Isoweb) quantified that, at the whole EC scale, the main food sources for all fish functional groups were of benthic origin (>50%). However, a significant decrease in upper consumers' $\delta^{13}\text{C}$ variance and a significant increase in their $\delta^{15}\text{N}$ variance as depth increases suggested a reorganization of the trophic network along the depth gradient. Then, mixing models including depth as a continuous covariate (MixSIAR) successfully deciphered depth-related variation in feeding strategies that differed between fish functional groups. In shallow waters, fish species benefited from both pelagic and benthic prey whereas, in deeper waters, they fed predominantly on either benthic or pelagic sources depending on their habitat preferences. Benthic food contribution to the diet of pelagic and benthic species varied from 10 to 50% and from 50 to 100%, respectively. A focus on the isotopic niche (Niche Rover) of a subset of 10 species confirmed that depth structured species' niche position, breadth and overlap. Environmental gradients such as depth gradient should be used as proxies of benthic-pelagic couplings' strength to understand spatial variation in consumers' resource use and highlight varying energy pathways structuring marine food webs.