## OLM 9.9. Application of the energy pathway method to modules of complex food webs

Populations are embedded in complex ecosystems with a large number of various interactions between and within species. In order to determine their fates in the face of changing environmental conditions – such as climate change – it is crucial to find ways for simplification, i.e. to identify the core interactions that are shaping the community. Keeping this in mind, we present two examples here illustrating that the approach focusing on the energy pathways from resources to top consumers (p. 197) can be applied to understand the behaviour of some isolated parts of complicated food webs in artificial or natural ecosystems.

Persson and his co-workers (2001) set up water tanks harbouring aquatic communities of different compositions in order to investigate the effects of resource enrichment. The communities differed in their numbers of trophic levels and their species compositions on the top level. Even though the trophic webs included many branches and loops, they exhibited the behaviour expected on the basis of simple food chain or coupled food chain models. For example, under resource enrichment the increase of the algal population unpalatable for the consumers of the community shows the typical behaviour of species not regulated from above (Figure 9.9.1.a). The steady biomass of algae and the increase of the dominant herbivore *Daphnia* populations with resource enrichment fit well to the predicted pattern of a 3-node food chain (Figure 9.9.1b.). Similarly, fish densities increased and small grazer densities remained essentially unchanged (while the *Daphnia* populations went to extinction) in the tanks with fish and added nutrients (not shown on the figure). This is the outcome expected under the exclusive resource limitation hypothesis, i.e., under top down control.



Figure 9.9.1: Resource enrichment experiment in water tanks with different communities

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- a. Increased nutrient content (proportion phosphorus 1%, ammonium 2%, nitrate 3.1%) lead to the increase of the population of unpalatable algae where small grazers kept the edible populations under control, thus their biomass did not change while that of the grazer populations increased, possibly due to the bacteria-HNF side loop.
- b. *Daphnia* populations could persist only in tanks with increased resource supply rate. *Daphnia* species consumed both types of algae thus total algal biomass did not change with resource enrichment. figures after (Persson et al. 2001). HNF: heterotrophic nanoflagellates

Occasionally, indirect effects of unexpected direction are found in thoroughly studied systems. The bald eagle (*Haliaetus leucocephalus*) population was expected to decrease as a consequence of the shrinking sea otter population, because the high intensity of sea urchin grazing decimates kelp forests, the home of prey fish which eagles feed on (Figure 9.9.2). However, contrary to the expectation, on a group of islands from among those around the Bering Sea, the Aleutian Islands, both the number of bald eagle nests and the reproductive success of the birds increased (Anthony et al. 2008). A feasible explanation to the surprising data might be that the density of prey better for the eagles than fish – sea birds feeding on sea urchin – increased. Separating the sub-web consisting of sea urchins, sea otters, sea gulls and bald eagles from the larger food web and considering it as a (3:2) loop web may explain the dynamics observed (Wollrab et al. 2012).



Figure 9.9.2: The food web consisting of some species of the North Pacific Ocean and the Southern Bering Sea (Estes et al. 2009), with the sub-web explaining the increase in bald eagle population size separated. b) The behaviour of a 2:3 type network due to the increased mortality of an apex consumer. P1: sea otter, H: sea urchin, P2: sea gull, SP bald eagle

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## References

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