Interdisciplinary Studies on Environmental Chemistry—Environmental Pollution and Ecotoxicology,
Eds., M. Kawaguchi, K. Misaki, H. Sato, T. Yokokawa, T. Itai, T. M. Nguyen, J. Ono
and S. Tanabe, pp. 419–425.

A Mini-Review of Spatial Segregation of Aquatic Food Webs: Stable Isotope Technique and Human Impact

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(Received 3 October 2011; accepted 11 October 2011)

Abstract—Organisms that comprise food webs inhabit areas that are spatially heterogeneous in productivity, resource abundance, and habitat structure, thus the spatial structure in a food web should be considered. Here I reviewed the spatial structure of aquatic food webs. The sub-web structure in a food web should be recognized in understanding the whole food web structure. Also, I reviewed the human impact on spatial structure of aquatic food webs due to species invasion, habitat fragmentation and aquaculture. These human impacts induce the changes in spatial segregation patterns of aquatic food webs. To estimate spatial structure of food webs, the stable isotope technique will be particularly useful because the technique can detect the spatial changes in food sources and links of food web along with environmental and biological gradients in an ecosystem.

Keywords: stable isotope, spatial scale, habitat, segregation, lake, stream, coastal marine

INTRODUCTION

In many ecosystems, the organisms that comprise food webs inhabit areas that are spatially heterogeneous in productivity, resource abundance, and consumer demography (Paine, 1966; Pimm, 1982; Fahrig, 2003). Thus, a current focus in ecological studies is the interaction among spatially heterogeneous and segregated habitats (Polis *et al*., 1997; Thompson *et al*., 2001). Food webs within habitats comprise trophic interactions from primary producers to top predators (Pimm, 1982) and can be predicted to be spatially heterogeneous and coupled with each other (e.g., Polis *et al*., 1997; Schindler and Scheuerell, 2002).

Spatial scale of ecological processes has been recognized as an important view in ecology, and yet has presented an enormous challenge for ecologists (Levin, 1992). A current emphasis in ecology stresses the interactions among spatially segregated habitats (Polis *et al*., 1997). Discontinuous habitats are coupled by organism movements, gravity, water flow and air flow, which generate fluxes of predators and prey, detritus and nutrients among spatially distinct habitats (Polis *et al*., 1997; Schindler and Scheuerell, 2002; Doi, 2009).

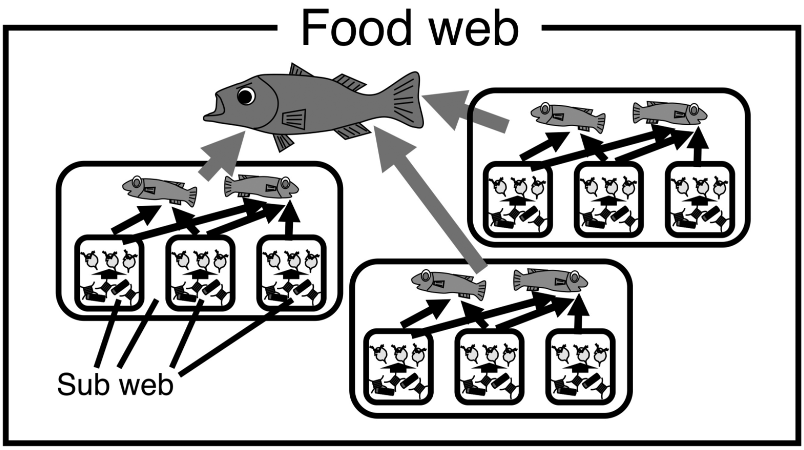

Fig. 1. A conceptual illustration of a food web with sub web components.

The producers and consumers that comprise food webs inhabit areas that are spatially heterogeneous in nutrients, productivity, resource abundance, and habitat structure, thus the spatial structure in a food web should be considered.

The purpose of this proceeding paper is to briefly review the spatial structure of food webs in aquatic ecosystems, especially focusing on the segregation in aquatic food webs. In addition, I review the human impact on spatial structure of aquatic food webs due to species invasion, habitat fragmentation and aquaculture.

SPATIAL STRUCTURE AND SEGREGATION OF FOOD WEB

Although the resources and organisms in food webs may be distributed patchily and gradually, little evidence exists for the spatial heterogeneity of food webs. The sheer water mass in certain lakes may cause spatial heterogeneity and segregation, since planktonic species have low mobility and short life cycles (Wetzel, 2001). The predator with high mobility and a longer life cycle, such as fish, may connect segregated food webs (e.g., Vander Zanden and Vadeboncoeur, 2002). In fact, evidence for spatial heterogeneity of aquatic food webs has been shown by δ^{15}N isotope analyses results of fish habitat heterogeneity in a lake (Harvey and Kitchell, 2000) and from vertical food web data in an ocean (Jennings *et al*., 2008).

If food webs are spatially heterogeneous, they would individually have their own boundaries. Here I hypothesized that the spatial segregation of food webs exists due to the limited movement of the species. Such a segregated food web is called a “sub web” (Fig. 1), and the hierarchical structure of sub web and whole food web should be recognized. Despite the increasing number of studies in the field, the spatial segregation patterns in the food webs have remained unclear. However, stable isotope techniques should be effective in testing the sub-web hypothesis in aquatic habitats. Next, I review the methodology of stable isotopes to estimate spatial structure of aquatic food webs.

METHODOLOGY: STABLE ISOTOPE TECHNIQUE TO ESTIMATE FOOD WEBS

In the past decade, ecologists have increasingly used natural stable isotope compositions to evaluate ecological interactions within ecosystems. Stable isotopes can provide a continuous measure of trophic position that integrates the assimilation of energy or mass flow through all the different trophic pathways leading to an organism (Post, 2002; McCutchan *et al.*, 2003). Carbon and nitrogen stable isotope ratios have been increasingly used to analyze food web structures in aquatic ecosystems. Generally, isotopic data are reported in the conventional δ notation;

$$\delta^{13}C \text{ or } \delta^{15}N = (R_{sample}/R_{standard} - 1)\cdot 1000(‰)$$

where, R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio for $\delta^{13}C$ or $\delta^{15}N$, respectively. Pee Dee Belemnite and N_2 in air were used as international standards for $\delta^{13}C$ and $\delta^{15}N$, respectively. $\delta^{13}C$ typically becomes enriched by 0.5‰ relative to their prey (McCutchan *et al.*, 2003) and $\delta^{15}N$ by 3.4‰ relative to their prey (Post, 2002).

Stable isotopes can track the fates of different sources of energy and materials if those sources have distinct isotopic signatures and if the isotopic signatures change in a predictable fashion as the material moves though the food web. In general, primary producers, including phytoplankton, benthic algae and higher vascular plants, have distinct isotopic signatures in lake and marine ecosystems (Vander Zanden and Vadeboncoeur, 2002; Doi *et al.*, 2003, 2008b). Also, in stream ecosystems, primary producers, including benthic algae and higher vascular plants, have distinct isotopic signatures (Finlay, 2001, 2004; Finlay *et al.*, 2002; Doi *et al.*, 2007). Thus, carbon and nitrogen stable isotopes can provide a robust measure to examine spatial segregation of aquatic food webs.

HUMAN IMPACTS ON CONNECTION AND SPATIAL STRUCTURES OF AQUATIC FOOD WEBS

There are various human impacts on aquatic food webs. It is well known that human-driven modifications such as removing of habitats, can strongly affect the food web structure and functioning. Here I review the following human impacts; species invasion, ecosystem fragmentation, and aquaculture on food-web segregation (or fragmentation), which have been a recent focus by aquatic ecologists. To assess these human impacts on aquatic food webs, we have used stable isotopes as an effective technique because they can quantitatively reveal degree the of human impact on the food web.

Species invasion

Species invasions can have a strong impact on food webs (e.g., Vander

Zanden *et al*., 2000; Maezono *et al*., 2005). Vander Zanden *et al*. (2000) found the historical impact of invasion on lake food webs. In this instance, the trophic position of a native top-predator fish (lake trout) decreased after invasion of another top-predator fish (largemouth bass). The decreasing of trophic position reflected a shift in the diet of native trout towards zooplankton and reduced dependence on littoral fish, because littoral fish were consumed predominantly by the invading bass species. Such a top-predator invasion changed the connection between littoral and pelagic food webs. In North America, the invasion by the zebra mussel also had an influence on lake food webs (e.g., Mills *et al*., 2003). Due to filtration by zebra mussels, phytoplankton and then zooplankton density were decreased, and the food web structure has progressively changed over the last 30 years. In addition the spatial structure of food webs also modified by the invaded zebra mussel (Mills *et al*., 2003). Invasive salt cedar has also changed stream food webs, especially through decreasing densities of herbivores in salt cedar habitats by greatly reducing the availability of algae by heavy shading (Kennedy *et al*., 2005). Invasive plants also indirectly affect food webs through changes in light condition of the ecosystems. Thus, invasive species directly and indirectly influence the spatial structures of food webs.

Ecosystem fragmentation

Ecosystem fragmentation is one of the major factors to biodiversity loss (Fahrig, 2003). Many studies on ecosystem fragmentation have focused on terrestrial ecosystems (Fahrig, 2003), however, aquatic ecosystem fragmentation is also widespread and can significantly change the food web structure (Nilsson *et al*., 2005; Layman *et al*., 2007). Layman *et al*. (2007) showed shifts in the trophic role of a top predator induced by ecosystem fragmentation in tidal creeks. The fragmentation of tidal creeks was caused by bridge and culvert constructions. They measured trophic niche width of top-predator fish based on stable isotope ratios, to assess the effects of aquatic ecosystem fragmentation on food webs. They demonstrated a collapse in trophic niche width of the predator from fragmented systems which was related to decreasing diversity of potential prey. Thus, ecosystem fragmentation will reduce food sources in food webs, because of limiting exchanges of materials in the system.

Ecosystem fragmentation also increases food sources for food webs. Drifting plankton from lake and reservoir outflows are thought to be a high-quality food source for river organisms (Richardson and Mackay, 1991), and can also subsidize downstream food webs. Doi *et al*. (2008a) showed that the drifting plankton from a dam reservoir altered the food web and community structure in the dammed river. Dams fragmented the continuous systems of rivers and alter downstream ecosystems (e.g., Ward and Stanford, 1983; Poff and Hart, 2002; Nilsson *et al*., 2005). Dam construction provides food subsidies for the downstream food webs and alters their respective community structure. Thus, the response of food webs to ecosystem fragmentation were different among systems. The effect of ecosystem fragmentation has scarcely been understood, and we need more empirical data to discuss the effects of ecosystem fragmentation on food webs.

Aquaculture

Recently, aquaculture has grown substantially in coastal areas (Black, 1998). Fish farms generally enrich surrounding waters and sediments with nutrients and organic matter, and this loading can cause a variety of environmental problems, such as algal blooms and sediment anoxia (e.g., Angel *et al*., 2002). Farms use many nets and ropes, and large amounts of algae and invertebrates are attached to these structures (e.g., Fukumori *et al*., 2008). Doi *et al*. (2008b) examined the planktonic food webs from fish and pearl oyster farms using stable isotopes. Based on isotope mixing model results, the attached microalgae contributed up to approximately 70% of the copepod food source, and the contribution of attached microalgae on farm structures to cyclopoid copepods was similar to their contribution to farm attached macroinvertebrates. This study shows that materials from attached microalgae play an important role in planktonic food webs around farm habitats. Thus, farming may modify the spatial structure of marine food webs through zooplankton communities. Such a “hot spot” of primary production on aquaculture-based structures would change the spatial structure of costal food webs.

CONCLUSION

I conclude that the spatial structure and segregation of aquatic food webs are influenced by various human impacts, which have been recently increasing in aquatic habitats. To conserve aquatic ecosystem structure including food web and to maintain ecosystem functions and services for human, we should recognize the impact of humans on food web structure. As I suggested above, stable isotope technique will be useful in detecting the spatial segregation of habitats, populations, communities, and ecosystems. In this review, I mainly focused on spatial structure and segregation of food webs in “aquatic” ecosystems using stable isotopes, because the study on the theme is only limited to aquatic systems. I encourage the study of the “sub-web” structure concept to terrestrial systems.

Acknowledgements—I am grateful to S. Tanabe and others who arranged the 6th Symposium of the Global COE program in Ehime University on 4–6 August 2011, and invited me to give the talk at the symposium. This study was supported by the Japan Society for the Promotion of Science to H. Doi.

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