

Comparison of Marine Food Webs across Environmental Gradients—A Tool for Unraveling Environmental Factors Driving Trophic Structure

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Abstract—Stable isotopes of carbon and nitrogen are a commonly applied tool in ecology to elucidate relative trophic level and source production. Marine ecological studies have largely applied stable isotope analysis to understanding within-ecosystem trophic dynamics; however across-ecosystem comparisons have largely been ignored. Here I review the use of comparative analyses in freshwater and marine systems, and provide some examples of marine systems where this approach may be effective in addressing the role of the environment in shaping food webs. Specific systems where isotopes have been underutilized are coral reefs, where high species diversity and underlining trophic complexities have likely limited their use. However hypothesis-based analysis of conspecifics across environmental gradients can help to simplify the importance of specific biotic and abiotic factors controlling food web structure. Because stable isotopes have progressively been applied to marine systems since the 1980's, a substantial record of values from nearly all ecosystem types and trophic levels has been accrued in the published literature. A current project linking stable isotope data to other ecological databases of FishBase and SeaLifeBase is presented.

Keywords: food webs, environment, stable isotopes, marine, comparative analyses

INTRODUCTION

Stable isotopes of carbon and nitrogen are commonly used in ecology to elucidate food web dynamics and sources of primary production (Fry, 2006). For nitrogen the difference in $\delta^{15}\text{N}$ between a consumer and its diet (termed trophic fractionation $\Delta\delta^{15}\text{N}$) is approximately 3.4‰ (Minagawa and Wada, 1984; Post, 2002), whereas carbon is more fractionated at source production (Peterson and Fry, 1987). As a result one can use the relative isotopic position of all organisms measured to provide a $\delta^{15}\text{N}$ – $\delta^{13}\text{C}$ isoscape of the food web. Although informative, this single-system approach only provides a limited view as to the trophic plasticity which may occur in species and the food web. In addition, considerable variation in the trophic enrichment of ^{15}N has been a major limitation in the interpretation of

results, because evidence suggests that the trophic fractionation factor is not uniform between lower and upper trophic levels. Fractionation factors have been shown to be higher with larger, higher trophic level organisms, which may be attributed in-part to the amount protein in the diet (McCutchan *et al.*, 2003). Uncertainties in the trophic enrichment factor therefore greatly limits interpretation of results and its use as a tool in understanding food web dynamics. Here I suggest a more comparative analysis approach, using the relative trophic positions of same species (i.e., conspecifics) across environmental gradients to understand trophic plasticity and the major biotic and abiotic factors shaping food web structure of marine ecosystems. I provide an overview of this approach in aquatic ecology, and provide examples of where this approach would be most effective in marine systems.

MATERIALS AND METHODS

A literature review was performed on the use of stable isotope analyses and comparative analyses across marine and aquatic ecosystems. Suggestions for comparative analyses within marine systems of coral reefs, seamounts, and coastal pelagic zones are presented and discussed.

RESULTS AND DISCUSSION

Application to freshwater and marine systems

The comparative analysis approach is not new, and has been effectively used in freshwater ecosystems where the systems are relatively well-constrained, and ecosystem characteristics can be easily defined. Examples of ecosystem characteristics include ecosystem size, complexity (ratio of shoreline area to volume), community diversity and level of primary production. In a study to examine the importance of lake size (volume), level of primary production, and production-size in shaping food chain length, Post *et al.* (2000) measured the $\delta^{15}\text{N}$ -based relative trophic position of top predatory fish species from 25 lakes in northeastern US. Their results indicated that ecosystem size was the major factor for increasing food chain length. In a similarly-structured experiment Doi *et al.* (2009) examined the importance of size, primary production and resource availability (edible microalgal carbon) in driving food chain length in 15 ponds in Japan. Their results showed that a combination of pond size and resource availability drove food chain length. There are fewer and less-clear results from marine systems where comparative analyses have been applied. From the western Mediterranean Marine Protected Area, Vizzini and Mazzola (2009) examined the relative trophic level of fish species across various zones of high and low protection from fisheries. Their results showed slightly lower trophic levels from highly-protected areas, but that other factors such as food availability and the potential for site-specific differences in feeding preferences of fish (e.g., preference for ichthyoplankton or zooplankton) may be more important. From an extensive literature review Vander Zanden and Fetzer (2007) examined food chain length

in both freshwater and marine ecosystems, in which they observed streams having shorter lengths than lakes and marine systems. Interestingly, they observed no difference in food chain length between lakes and marine systems, and no difference among estuarine, coastal and pelagic systems. Despite the success of comparative analyses from freshwater systems, it has been to a largely underutilized in marine ecosystems where stable isotopes may be effective in refining food webs from more open (e.g., pelagic) or more complex (coral reef) systems.

Opportunities in marine systems

There are some conditions where stable isotope analysis and the comparison of relative trophic positions within a species may be most effective, as in the case of environmental extremes that would have a reasonable effect on organism feeding behavior and therefore food web structure. The following are some specific examples of where systems exhibit environmental extremes, and therefore may be highly suited for comparative analysis of relative trophic level using $\delta^{15}\text{N}$, but in some instances the differences in sources of primary production by $\delta^{13}\text{C}$ can also be explored.

Coral reefs

Coral reef ecosystems are highly sensitive to perturbations from human activities (development, fishing, and tourism) and climate change, which have resulted in coral bleaching on a global scale (Selig *et al.*, 2010). Coral reefs also exhibit major phase-shifts between highly diverse coral-dominant systems to algal-dominant systems (Bruno *et al.*, 2009). Surprisingly, no study has examined the difference in food web structure of coral-rich and highly impacted reefs, and in general the use of stable isotopes in understanding coral reef food webs is very low. From a cursory literature review only several studies have examined coral reef trophic relationships. Yamamuro *et al.* (1995, 2003) has mainly examined sources of primary production to reef systems of Japan using both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. More recently Kolasinski *et al.* (2009) examined size-specific diet and isotope-based relationships in yellowstriped goatfish (*Mulloidichthys flavolineatus*) from the southwestern Indian Ocean, and Bruno *et al.* (2009) examined the trophic niche in damselfishes (Pomacentridae) off Madagascar. Although useful these studies are limited to very specific sites and do not incorporate geographical variability in trophic behavior, therefore restricting their interpretation of results. Given the global concern for coral reefs, more structured studies of these systems are needed to help understand the underlying changes in energy flow that may occur with phase shifts and climate change. This could be done by comparing the $\delta^{15}\text{N}$ -based trophic position of dominant fish species between impacted and unimpacted sites (Fig. 1), but also the assessment of whether there is a shift in the source of primary production from pelagic to more benthic algae using $\delta^{13}\text{C}$. Such studies should carefully measure or account for habitat complexity (structure and relief), level of algal cover, nutrient loading and/or proximity to nutrient sources (upwelling or anthropogenic) as well as physical exposure to wave and tidal

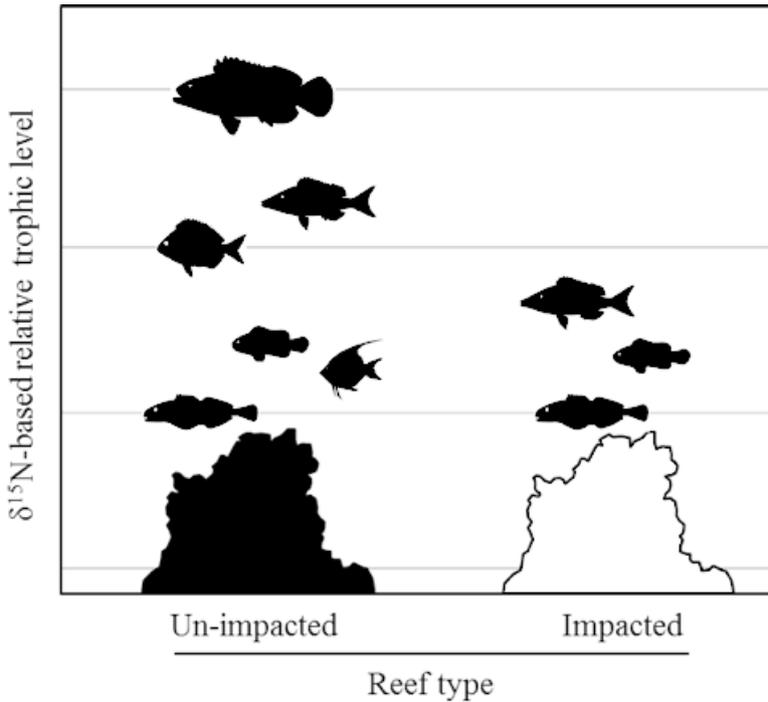


Fig. 1. Schematic diagram of how coral reef systems may be compared by changes in the relative trophic positions of conspecifics in un-impacted natural and impacted (e.g., bleached, or crown-of-thorns) systems.

energy.

The reasons for why stable isotopes have not been more widely applied to coral reef systems is that they are of the most complex of aquatic systems, and some of the limitations of stable isotopes such as only using two isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) when there are overwhelmingly more sources can be problematic. The comparative analysis of common species across these systems however would remove much of this complexity and would provide a better understanding of how the source of base production changes, and the relative trophic position and trophic complexity are altered between phase shifts. For phase shifts between algae dominated and coral dominated systems, the overwhelming physical and ecological presence of algae can cause major shifts in the benthic prey available to consumers and we would expect a concomitant predictable shift in nitrogen and possibly carbon of the consumer based on whether they are an omnivore, herbivore or top predator. Differences may also provide an early warning method in how organisms may respond to such phase shifts.

Seamount systems

Seamounts are submarine mountains which reach close to but not breaking the surface of the ocean. They are often biological hotspots, providing structure and habitat for fishes and enhanced primary production through turbulent mixing and upwelling (Morato and Pauly, 2004). Many benthic and epibenthic species are also largely constrained to their respective seamount systems due to their sessile nature or as in the case of many fish species, expressing site fidelity through territorial behavior. Therefore trophic relationships are likely an important attribute of system structure and function that can be explored through stable isotope analysis. Similar to coral reefs, food web structure can be compared between seamount systems with respect to environmental characteristics but also in terms of exploitation level by fisheries. The comparison between seamount systems can provide a relatively effective platform for understanding trophic links within these systems and sources of primary production that may be driving the food web. The overall implementation of stable isotopes would also greatly enhance our understanding of reef census data and community and population shifts over time.

Pelagic food webs

Pelagic ecosystems can be highly variable in their level of base and higher trophic level production. Eastern boundary current ecosystems such as the Peru and California Current are of the most productive, and have historically been the largest fisheries (FAO, 1999). In contrast there are other regions that are relatively low production, with low nutrients such as the Kuroshio Current off Japan. The obvious influence of primary production in driving higher trophic level production (e.g., bottom-up control, Ware and Thomson, 2005) underscores the importance of trophic links in these food webs. Comparative analyses between these systems has been performed using satellite-derived measures of chl-*a* (Carr, 2001) which is closely tied to potential fisheries production. If trophic relationships are important in driving these systems, than a comparative analysis of $\delta^{15}\text{N}$ -based trophic level between these systems using conspecifics may reveal major trophic connections, but also the environmental characteristics driving food web structure. Many species of marine fishes and invertebrates are globally distributed, and presumed to have a similar trophic role in their respective ecosystems. For pelagic species, comparative analyses should focus on those that are dominant in the food web wherever present. Some examples include lower trophic level fishes of sardine (*Sardinops* spp.) and anchovy (*Engraulis* spp.), mid-trophic levels of horse mackerel (*Trachurus* spp.) and Loligo squid, and higher trophic levels of hake (*Merluccius* spp.), mackerel (*Scomber* spp.), blue shark (*Prionace glauca*).

Future directions

As the use of stable isotopes progresses and we accumulate more isotope data covering a broad range of species and over space and time, there will become

a need to bring together data for comparing food web structure of ecosystems, but also more applied uses such as in ecosystem models for management and as a precursor monitor of eutrophication (Miller *et al.*, 2010) and in pollution studies. A project by the author and members of the Fish Information Network are currently establishing a global database of isotope values by species and region, where published isotope literature is integrated into a comprehensive database that includes species and environmental characteristics. The data will eventually be integrated with well-established databases on species (FishBase and SeaLifeBase) that will be fully accessible to researchers on the web. Further plans are to integrate results from studies incorporating compound-specific nitrogen isotope analysis, which can provide greater certainty in trophic level assignment and as a potential indicator of source production (Popp *et al.*, 2007).

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