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Understanding What Drives Food Web Structure in Marine Pelagic Ecosystems

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Abstract—Coastal ecosystems constitute <3% of the world ocean area yet contributes to >80% to world fisheries catch. Understanding food web structure is essential in ecosystem-based management, predicting impacts of global climate change, and in determining trophic pathways of certain bioaccumulation pollutants. Within the Pacific Ocean the northern California Current ecosystem off western North America and the Kuroshio-Oyashio transition zone exhibit very high levels of primary production and secondary production, whereas the southern California and Kuroshio Currents have relatively lower levels of production. Because levels of base production can vary between ecosystems but yet many of the same fish taxa reside within these systems, a natural comparison of the relative trophic levels between conspecifics can help determine the importance of the prey community in structuring higher-level trophic interactions. In this study we hypothesized that ecosystems of high primary and secondary production will have shorter food chains due to greater omnivory by the consumption of plankton by fish; this should be expressed as lower relative trophic levels, as determined by nitrogen stable isotope values. Results showed fish from low production zones showed significantly higher relative trophic levels to those from high production zones. Overall, food webs from highly productive ecosystems are likely more web-like and non-linear compared to those from lower-production ecosystems.

Keywords: stable isotopes, food webs, trophic structure, marine

INTRODUCTION

Coastal ecosystems contribute to most of the world's fisheries catch and are subject to overharvest but also eutrophication and climate change (FAO, 1999). The trophic pathways by which energy flows through these large marine ecosystems is therefore germane to how multiple trophic levels may respond to such perturbations. In particular, eastern boundary current ecosystems are of the most productive of marine systems (FAO, 1999), yet they also exhibit high temporal variation in primary and secondary production and community structure and biomass of fishes (Ware and Thomson, 2005). Because of this there has been considerable interest in understanding how these changes occur, whether they are mediated through fisheries harvest (e.g., Yodzis, 2000) or through trophic interactions (Ware and Thomson, 2005). Attempts to examine the trophic structure of has been limited to direct observation by diet analyses (Brodeur and Pearcy, 1992; Miller and Brodeur, 2007), and through stable isotope analysis of some portion of the food web (Bode *et al.*, 2007; Miller *et al.*, 2011).

Coastal marine ecosystems vary considerably throughout the world but there are some generalities. Eastern boundary current (EBCs) upwelling ecosystems are on the eastern sides of the large ocean basins of the Atlantic (Canary and Benguela Currents) and the Pacific (California and Humboldt Currents) and are typified by having very high primary and secondary production, and a nekton community represented by a relatively few number of baitfish species that constitute much of the nekton biomass (Cury *et al.*, 2000). Although upwelling-induced production in other systems is not uncommon, it is not at production scale observed in typical EBC systems. Another system are western boundary currents which exhibit considerably lower levels of production and are typically warmer coming from southern waters. Although the nekton community is different in these systems, some fishes such as the sardines (*Sardinops* sp.), anchovies (*Engraulis* sp.) and the globally distributed blue shark (*Prionace glauca*) are common members in both upwelling and non-upwelling ecosystems. The presence of these species in multiple systems provides an opportunity to compare ecosystems with regard to their respective trophic behavior.

Trophic relationships within large pelagic ecosystems have been examined through diet and stable isotope analysis, however most of these studies are highly internal within their respective systems and fail to provide meaningful comparative analyses. Stable isotope analysis using ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) are now a common tool in elucidating relative trophic position and source of base production of an organism (Post, 2002). The stable isotope approach is based on an organism's differential retention of the heavier isotope over the lighter relative to its diet. Over time, the relative distribution of isotope ratio values effectively acts as a time-averaged signature of the organism's assimilated diet (Peterson and Fry, 1987; Post, 2002). The trophic-related shift in the differential retention of the heavier and lighter forms is generally termed trophic enrichment (Peterson and Fry, 1987), and can be used to examine relative trophic position. Stable isotopes are measured as the ratio of the heavy (^{15}N) to the lighter (^{14}N) isotope of an element using the following equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3$ where X is ^{15}N and R is the ratio of the heavy to the light isotope (Peterson and Fry, 1987). For nitrogen, a predator preferentially retains the heavier (^{15}N) isotope over the lighter (^{14}N) of its diet, with each trophic level accounting for an approximate enrichment of 3.4‰ relative to its prey (Post, 2002). In comparative analyses using stable isotopes it is important to consider the value of $\delta^{15}N$ for the base of the food web, because ecosystems can vary in their dominant sources of nitrogen such as from upwelling or from offshore

Table 1. Number of fishes from each system analyzed for stable isotope analysis. System abbreviations are denoted as the following: Kuroshio Current (KC), Oyashio Current (OC), Oyashio-Kuroshio Transition (OKT), southern California Current (SCC) and northern California Current (NCC).

	Western Pacific (Japan)			Eastern Pacific (U.S.)	
Taxa	KC	OC	OKT	SCC	NCC
Sardine (*Sardinops sagax*)	45	64	20	45	55
Anchovy (*Engraulis* spp.)					
E. japonicus (Japan only)	25	53	21	—	—
E. mordax (U.S. only)	—	—	—	45	55
Pacific mackerel (*Scomber japonicus*)	—	10	—	8	3
Blue shark (*Prionace glauca*)	—	4	—	15	20

intrusion, and these values can differ markedly. Obtaining a $\delta^{15}N$ value of the base of the food web will therefore allow for the subsequent calculation of higher trophic levels, with $\delta^{15}N$ increasing by 3.4‰ for each trophic level. In marine ecosystem studies the base $\delta^{15}N$ can be measured from particulate organic matter (POM) and setting the base value from trophic level 1.0, or utilizing a primary consumer such as a copepod, to indicate trophic level 2.0.

In this study we examined the relative trophic structure of nekton and zooplankton from regions of high and low primary and secondary production. Areas of relatively high production were the Oyashio-Kuroshio Current transition (OKT), and the northern California Current (NCC), with relatively low production regions represented by the Kuroshio Current (KC), Oyashio Current (OC), and the southern California Current (SCC) ecosystem. We collected and compared the relative trophic levels of sardine, anchovy, Pacific mackerel and blue shark from these different systems using stable isotope analysis of nitrogen ($\delta^{15}N$).

MATERIALS AND METHODS

Field collection

Collections of fish and zooplankton occurred between July 2008 and August 2009, covering three major current systems (Kuroshio, Oyashio, and California Currents) which were further defined by sub-system variation in primary production, such as the northern and southern California Current, and the Kuroshio-Oyashio Transition (Fig. 1). Fish collected and analyzed were sardine (*Sardinops sagax*), anchovy (*Engraulis* spp.), Pacific mackerel (*Scomber japonicus*), and blue shark (*Prionace glauca*); total number by location are listed in Table 1. Upon collection fish were either quickly frozen whole and brought to the lab for processing, or as in the case of blue shark, had tissue removed immediately after capture and samples were frozen for later processing in the lab. All muscle tissue samples were obtained from the dorsal-anterior region of the fish.

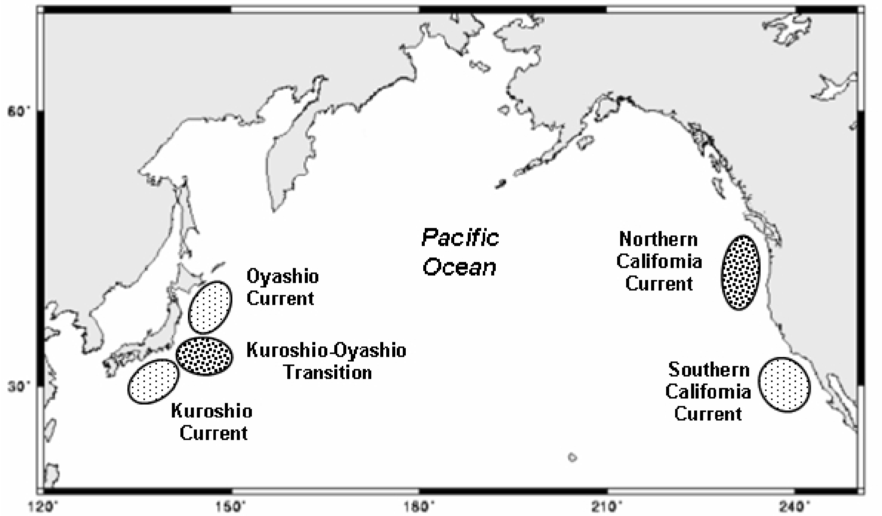

Fig. 1. Map of the Pacific Ocean showing regions of low (light dots) and high (dark dots) primary production off Japan and the U.S. Areas were sampled for zooplankton and nekton for this study Japan and U.S.

Laboratory analysis

Tissue samples were dried in a drying oven at 70°C for 24 hrs and subsequently ground to a fine powder using a mortar and pestle. Stable isotopes were measured for δ^{13}C (data not shown in this study) and δ^{15}N at the Center for Marine Environmental Studies, Ehime University (Japan) using a Carlo Erba Elemental Analyzer 2500 coupled to a Finnigan MAT Delta Plus stable isotope ratio mass spectrometer via a ConFlo-III continuous flow interface (measurement error for δ^{15}N ± 0.3‰). Calculation of the ratios relative to the standard for nitrogen (N_2) was done by the standard equation $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where R is the ratio of the heavy to light isotope for the sample (R_{sample}) and standard ($R_{standard}$) in units of parts per mil (‰).

Data analysis

Statistical comparisons were performed using a *t*-test (alpha 0.05) using *R* statistical package (version 2.10.1). Comparison between ecosystems with different δ^{15}N base values was performed by first subtracting the base δ^{15}N from the values of the fish. This allowed for direct comparison.

RESULTS AND DISCUSSION

Results from our analysis show a general trend of relatively lower trophic levels in fishes from high-productive upwelling (NCC) and convergence zones (OKT) compared to lower productive marine systems (KC, OC, and SCC). The

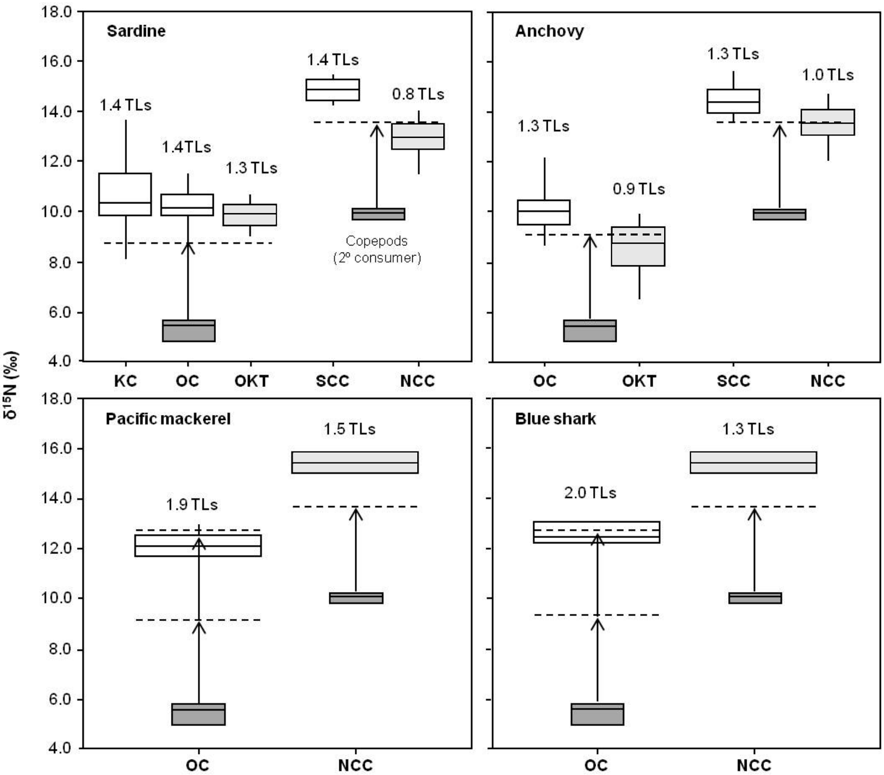

Fig. 2. Nitrogen stable isotope results from four nekton species collected from low-production ecosystems of the Kuroshio (KC) and Oyashio Current (OC) off the west Pacific, and the southern California Current (SCC) of S. California, and high production zones of the Oyashio-Kuroshio Transition (OKT) off central Japan and the northern California Current (NCC) off Oregon and Washington, U.S. Red lines denote mean δ^{15}N of copepods to adjust for differences in the base of the food web; stippled lines represent sequential trophic levels (TLs) above the baseline δ^{15}N.

largest differences were between the OC and NCC with respect to Pacific mackerel (*Scomber japonicus*) and blue shark (*Prionace glauca*), of which those from the OC were feeding at approximately 0.4 and 0.7 TLs, respectively, above their NCC counterparts ($p < 0.05$, mean difference in δ^{15}N). Sardine and anchovy followed a similar trend both within subsystems of the California Current (NCC and SCC) and between the KC, OC and OKT (Fig. 2). This pattern follows the prediction that nekton may be feeding lower on the food web due to a greater availability of lower trophic-level prey within high productive ecosystems, and that some evidence points to euphausiids as driving this pattern. From the NCC euphausiids are a major component of the zooplankton community are consumed by most of the dominant nekton species, such as jack mackerel, hake, salmonids, baitfish species (sardine and anchovy) and even blue sharks (Miller and Brodeur, 2007). Euphausiids are relatively large, conspicuous and exhibit schooling behavior which may allow relatively large visual predators to both view and consume en masse. Other major prey taxa may be decapod larvae (*Cancer* spp.), and larval-juvenile fishes which can make up a large proportion of zooplankton biomass.

Our study was based on only a few select taxa and only represent several trophic levels. Undoubtedly these relationships are more complex in space and time, however our study provides an effective method for comparing ecosystem differences in general trophic structure of major nekton species. This also provides some evidence for the relative dependence of fishes on certain prey. We can see from blue shark and Pacific mackerel (Fig. 2) that individuals from low-productive regions are dependent upon the adjacent lower trophic level whereas those from high-productive zones are most likely dependent upon zooplankton rather than fish. The stable isotope approach is based on temporal integration of an organisms diet, and we would predict that this method could be used to measure temporal variation in trophic level change within a particular ecosystem. For example the occurrence of strong el Niño events off the east Pacific have shown major shifts in the nekton and zooplankton community, as well as a corresponding shift in nekton diets from euphausiids typical of upwelling years to more gelatinous zooplankton during el Niño years (Brodeur and Pearcy, 1992). An ideal opportunity would be to examine the stable isotope shift between strong upwelling years to those from low production el Niño southern oscillation (ENSO) events. Future studies should take advantage of strong el Niño events to compare shifts in the trophic structure of the system.

In our study we compared the relative trophic levels from four nekton species representing low to high trophic levels from the eastern and western pacific. Current analysis will be on expansion of sampling to different areas of the Benguela Current ecosystem (South Africa and Namibia) and apply MODUS satellite data to quantify gross and net primary production and link to trophic characteristics of major nekton from each system.

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