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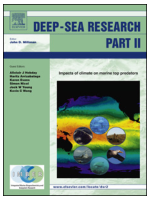

A coupled stable isotope-size spectrum approach to understanding pelagic food-web dynamics: A case study from the southwest sub-tropical Pacific

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ABSTRACT

This study investigated the food web structure of the oligotrophic picophytoplankton-dominated pelagic ecosystem in the vicinity of New Caledonia, within the Archipelagic Deep Basin (ARCH) province of the southwest sub-tropical Pacific. Nitrogen stable isotope ($\delta^{15}N$) data were collected for mesozooplankton (0.2–2 mm), macrozooplankton (2–20 mm), micronekton (20–200 mm) and nekton (> 200 mm) during 2002–2004 and 2011. Using a coupled $\delta^{15}N$ size-spectrum approach, we estimated (1) organism trophic level (TL); (2) food chain length (FCL); (3) predator prey mass ratio (PPMR); and (4) transfer efficiency (TE). The role of phytoplankton size structure in determining these parameters was investigated. Applying a trophic enrichment factor (TEF) of 3.4, maximum TL was calculated at ~5. The number of TLs spanned by each length class was 1.97 for mesozooplankton, 2.07 for macrozooplankton, 2.75 for micronekton, and 2.21 for nekton. Estimated PPMR was 10,099:1 for mesozooplankton, 3683:1 for macrozooplankton/micronekton, and 2.44×10^5:1 for nekton, corresponding to TEs of 6.3%, 8.5% and 2.4%, respectively. PPMR and TE were strongly influenced by the TEF used, and TEF 3.4 likely over and underestimated PPMR and TE, respectively, for mesozooplankton and macrozooplankton/micronekton. Comparatively low PPMR for mesozooplankton and macrozooplankton/micronekton indicated longer food chains and higher connectivity within these groups than for the nekton. Conversely, the high PPMR yet high trophic niche width for the nekton indicated that they prey primarily on macrozooplankton/micronekton, with a relatively high degree of dietary specialisation. Our results are discussed in the context of other marine food webs. The ARCH food chain was found to be 1–1.5 trophic levels longer than the eutrophic micro-/nanophytoplankton-dominated Californian upwelling system, providing empirical support for the role of phytoplankton size in determining FCL. Group specific PPMR estimates demonstrated that it is changes in trophic pathways across the mesozooplankton/macrozooplankton/micronekton groups that are primarily responsible for higher FCL under oligotrophic conditions. Finally, we discuss consistently low $\delta^{15}N$ values to the east of New Caledonia, and implications for the contribution of diazotroph nitrogen to the pelagic food web in this region.

1. Introduction

Food web dynamics are fundamental drivers in the response of pelagic ecosystems to perturbations ranging from bottom up forcing such as nutrient supply to primary producers (Doney et al., 2012; Sarmiento et al., 2004), to top down forcing such as fisheries removal of top predators (Polovina and Woodworth-Jefcoats, 2013).

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A detailed knowledge of food web dynamics is therefore essential to understanding both the short term and long term impacts of anthropogenic and climate induced change in marine ecosystems. However, high species richness of pelagic food webs and a correspondingly wide array of trophic strategies and behaviours (Duffy and Stachowicz, 2006) make this a challenging task.

An approach to dealing with the complexity of trophic interactions has been to simplify food webs into component parts that aggregate species exhibiting similar trophic traits. One such aggregation tool for food web studies is body size. Trophic data collected across a range of habitats, from terrestrial to marine, show that in $>90\%$ of feeding links predators are larger than prey (Barnes et al., 2010; Cohen et al., 1993). In marine ecosystems an organism's body size can be a better predictor of trophic position than its taxonomy (Jennings et al., 2001). Emergent from size-based trophic interactions is the theory of size spectra, which observes that normalised biomass vs log body mass class yields a slope of -1 in the majority of aquatic ecosystems, describing the loss of energy from one trophic level to the next and average predator prey mass ratios (PPMR), the size of a predator relative to its prey (Kerr and Dickie, 2001). In combination with allometric scaling of physiological rates, temperature and primary production, size spectrum theory is being increasingly used to parameterise models of marine food web processes (Blanchard et al., 2011, 2012; Jennings et al., 2008; Maury et al., 2007). Although this approach does not necessarily provide insights into species level interactions, an advantage is that it is based on ecological and physiological relationships that are broadly applicable across taxa and regions (Polovina and Woodworth-Jefcoats, 2013).

The application of stable isotope analyses provides an empirical method to measure the trophic relationships between food web components. The enrichment of nitrogen isotopes from one trophic level to the next provides a means to estimate the trophic level of individual taxa/size classes, assuming knowledge of the enrichment factor between trophic levels (Post, 2002; Post et al., 2000). Stable nitrogen isotopes can also be used to infer nitrogen sources in marine food webs (Montoya et al., 2002), providing insights into the role of these sources and processes cycling in food web structuring. An advantage of using stable isotope data to analyse trophic interactions is that they integrate an organism's diet over time scales of days to months, and as a result require lower intensity sampling to capture natural dietary variation than do gut content studies (Hobson and Welch, 1992). In addition to simple trophic level estimates, $\delta^{15}N$ values can be coupled with biomass spectra theory to estimate the food web parameters of PPMR (Jennings et al., 2001) and transfer efficiency (Barnes et al., 2010; Jennings et al., 2002). Since in a food web of given size structure, a reduction in the predator–prey body size ratio must result in an increase in food chain length, i.e., the number of steps between primary producers and top predators, (Cousins, 1987), PPMR can be used as a measure of relative food chain length (Jennings and Warr, 2003). Coupling of $\delta^{15}N$ values with biomass spectra theory therefore provides a means to investigate the role of environmental conditions in structuring food webs (Jennings and Warr, 2003), the efficiency of transfer of primary production to higher trophic levels (Barnes et al., 2010; Cabana and Rasmussen, 1996), and, given the greater stability of longer and more diffuse food chains, the susceptibility of food webs to perturbation (Jennings and Warr, 2003; Thompson et al., 2007; Yodzis, 2000).

In the case of pelagic food webs, one of the key drivers of lower trophic level dynamics, with implications for the food web as a whole, is the size structure of phytoplankton at the food web base (Finkel et al., 2010; Legendre and Rassoulzadegen, 1995; Maranon et al., 2012). Phytoplankton can broadly be ordered into three size classes: pico- (PP; $<2\ \mu m$), nano- (NP; 2–20 μm) and micro- (MP; 20–200 μm) (Azam et al., 1983). The majority of zooplankton species are unable to effectively graze PP (Fortier et al., 1994). A predominance of PP therefore favours smaller crustacean zooplankton and specialist small particle grazers such as gelatinous tunicates, an increased importance of microbial pathways to mesozooplankton predators, and increased omnivory by mesozooplankton as a whole (Calbet et al., 2005; Calbet and Saiz, 2005; Sommer et al., 2002). Such systems are expected to yield longer, less efficient food webs (Ryther, 1969). Conversely, MP favours large copepod and euphausiid grazers, which enable rapid transfer of energy to higher trophic levels via short, efficient food chains. Globally, PP dominate in oligotrophic (nutrient poor) regions and nutrient-rich regions that are light and/or iron limited, while MP dominate in naturally eutrophic (nutrient rich) regions (Kiorboe, 1993; Uitz et al., 2010). Consequently, phytoplankton size composition has significant implications for regional differences in food web structure. It is also an important consideration in the context of long term change as enhanced stratification and decreased nutrient supply to the photic zone, favouring PP, is predicted with ongoing ocean warming (Ganachaud et al., 2013; Moran et al., 2010; Polovina et al., 2011).

The potential role of phytoplankton size composition in structuring pelagic food webs lends itself to size-based analyses. In this study we present the application of a coupled stable isotope-size spectrum approach to investigate the pelagic food web structure of the Archipelagic Deep Basin (ARCH) of the southwest subtropical Pacific (Longhurst, 1998). The ARCH is characterised as highly oligotrophic, with nitrate generally being at limiting levels in the photic zone but nitrogen levels being augmented by diazotrophs, nitrogen-fixing bacteria (Le Borgne et al., 2011). We developed and analysed a database of nitrogen stable isotopes, spanning zooplankton to top predators, making estimates of the food web properties of 1. trophic level; 2. food chain length; 3. predator prey mass ratios and; 4. transfer efficiencies, for the food web as a whole, as well as for the size based components of mesozooplankton (0.2–2 mm), macrozooplankton (2–20 mm), micronekton (20–200 mm) and nekton (>200 mm) (Table 1). We compare our data with data from the eutrophic micro/nanophytoplankton dominated Californian upwelling system to test the hypothesis that phytoplankton size structure is a key driver of food chain length, yielding a shorter food chain in the latter region. Using group specific PPMR data from the ARCH we investigate which components of the food web are most susceptible to change following shifts in phytoplankton size structure. Finally we assess our results in the context of the oligotrophic/diazotrophic nature of ARCH and future climate change projections.

2. Methods

2.1. Sampling of food web components for isotope analysis

The locations of all samples collected during this study are illustrated in Fig. 1, and the details of sampling are presented in Table 1 and in the text below. Mesozooplankton were collected in August and December of 2011 during the NECTALIS 1 and 2 surveys using a vertically hauled 200 μm mesh multi-net (Hydrobios, Kiel, Germany). Samples were collected from 4 discreet depth layers: 0–100 m, 100–200 m, 200–400 m, and 400–500 m. For the purpose of stable isotope analysis, two stations to the east of New Caledonia were completed in August 2011, and four stations (two to the east and two the west of New Caledonia) in December 2011 (Fig. 1). Samples were immediately frozen onboard and returned to the laboratory for processing. In the laboratory the sample from each depth was separated into 5 size classes with a sieve column: 125–250, 250–500, 500–1000, 1000–2000, and 2000–4000 μm. As the multi-net mesh size was 200 μm, zooplankton $<200\ \mu m$ were under represented in the 125–250 μm size class. Zooplankton