Expanded trophic complexity among large sharks

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ABSTRACT

To understand the effects of predator removal in marine ecosystems requires accurate estimates of trophic position and trophic structure that have been difficult to obtain to date. For example, most sharks are classified as diet generalists that feed around trophic position 4, but this classification contradicts observations of diverse feeding behaviour among large species, suggesting that trophic structure has been oversimplified among upper trophic level species. To test this assumption, bulk $\delta^{15}N$ and $\delta^{13}C$ values of 13 shark species constituting the large shark assemblage off southern Africa were integrated into (i) a hierarchical Bayesian model, accounting for body size and variable sample sizes among species, and (ii) a dietary $\delta^{15}N$-dependent enrichment model to quantify individual and assemblage-wide trophic position and structure. Compound specific isotopic analysis of amino acids (CSIA-AAs) for a subset of species was used to verify results. Although discrepancies occurred between methods, overall these data confirm that large sharks, including several globally threatened species, feed at markedly higher trophic positions and across a broader trophic range than is currently assumed. This identifies a lower degree of functional equivalence among the assemblage. Such complex trophic structure among large sharks suggests that cascading effects from species-specific removals in food webs may be weaker but more pervasive than currently assumed. Reassignment of the trophic structure of large marine predators has important consequences for any potential regulatory and stabilizing roles in marine food webs.

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1. Introduction

The removal of top predators and purported adverse effects on ecosystem structure, function, and resilience among ecosystems is widely debated. In terrestrial systems, trophic cascades, defined as 'predator regulated top down control of community structure with conspicuous indirect effects transferring to lower linkages', are well documented (McLaren and Peterson, 1994; Crooks and Soule, 1999; Terborgh et al., 2001) and the occurrence of trophic cascades in low diversity marine systems is widely accepted (Paine, 1966; Strong, 1992; Shurin et al., 2002). However among more diverse marine environments, where a higher number of complex trophic linkages exist, the impact of predator removal remains largely unknown. With documented declines in marine predator populations (Christensen et al., 2003; Myers and Worm, 2003; Estes et al., 2011) and current concern over the status of global fish stocks (Pauly et al., 1998; Pauly et al., 2005; Worm et al., 2009),

there is a heightened interest in the strength of top down control and its pervasiveness in the marine environment (Heithaus et al., 2008).

The occurrence and strength of predator removal effects within food webs are dependent on the functional equivalence within a given ecosystem. Functional equivalence assumes that guilds of species have similar effects on community or ecosystem processes, such as equivalent ecological or trophic roles, and are frequently defined by functional groups (Loreau, 2004; Petchey and Gaston, 2006). Removal of a species where functional equivalents co-occur is presumed to minimise interference to food web structure, buffering potential trophic cascades as species are assumed interchangeable and compensatory (Yachi and Loreau, 1999; Loreau, 2004).

Among whole marine ecosystem models, large predatory fishes are typically defined as generalist feeders, implying that species within the group have similar regulative effects on lower trophic position (TP) species in the food web (TP range 4.1–4.5; Cortés, 1999). Yet empirical evidence suggests that many species viewed as functional equivalents and assigned a priori into functional groups is often inaccurate (Chalcraft and Resetarits, 2003a,b; Loreau, 2004; Resetarits and Chalcraft, 2007), including for large sharks (Matich et al., 2011;

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Heithaus et al., 2013; Hussey et al., 2014a). In contrast, species with similar life histories and morphology can have diverse functional roles that generate complex intra-guild functional diversity (Chalcraft and Resetarits, 2003a,b; Resetarits and Chalcraft, 2007; Heithaus et al., 2013).

Potential misclassification of functionally diverse species into a single trophic group raises concerns about studying top-down predator effects and fisheries exploitation (Pauly et al., 1998; Branch et al., 2010; Christensen and Pauly, 1992; Williams and Martinez, 2004) using the conventional designation of large predators as largely secondary consumers (primary piscivores; TP = 4). For example, while some large sharks feed predominantly on small schooling zooplanktivorous fish, other species feed preferentially on piscivorous fish (Dudley and Cliff, 1993; Wetherbee and Cortes, 2004; Dudley et al., 2005), elasmobranchs (Cliff et al., 1990; Cliff and Dudley, 1991a, 1991b), and marine mammals (Tricas and McCosker, 1984; Hussey et al., 2011). Consequently, even with high levels of omnivory, large sharks would feed above TP 4, with species potentially feeding upwards of TP 6, revealing more complex trophic structuring than the current 'generalist' feeding paradigm (Hussey et al., 2014a,b; Fig. 1).

Bulk nitrogen isotopes in animals' tissues provide an empirical tool for calculating TP and trophic structure in aquatic systems that have generated novel insights into ecosystem dynamics (Fry, 1988; Madigan et al., 2012; Hussey et al., 2014a,b). However the approach can be confounded by its dependence on the isotopic value of a reliable baseline organism (Cabana and Rasmussen, 1996) and variable isotopic discrimination between predator and prey groups (Caut et al., 2009) that may bias TP estimates. Alternatively, recent compound specific nitrogen isotope analysis of individual amino acids (CSIA-AAs) provides an autogenous, within-web measure of the system baseline (source) and consumer TP for each individual consumer (McClelland and Montoya, 2002; Popp et al., 2007). Differences between trophic AA $\delta^{15}N$ values (which enrich during trophic processing) and source AA $\delta^{15}N$ values (which show minimal fractionation) can be used to calculate TP, negating the need for independent baseline organism nitrogen isotope values. This increases confidence in estimates for the isotopic

structuring of aquatic assemblages and provides an absolute measure of TP (Chikaraishi et al., 2009).

Using a combined bulk tissue and CSIA-AA nitrogen isotopic approach, we show that members of a large shark assemblage feed across a higher and broader trophic range than is conventionally assumed. Specifically we identify more complex species-specific roles and lower levels of functional equivalence among so-called generalist predators.

2. Materials and methods

2.1. Sampling and stable isotope analysis

Thirteen species of sharks (n = 271) comprising the 'large shark assemblage' off southern Africa, and including common large sharks and IUCN threatened species, were sampled from captures in beach protection nets along the KwaZulu-Natal (KZN) coast between 2005 and 2009 (for details see Dudley et al., 2005). All samples were processed for bulk stable isotope analysis, $\delta^{15}N$ and $\delta^{13}C$ values, following standard procedures (see electronic online supporting materials, Method S1). A subset of seven species (n = 18), spanning the range from low to high bulk $\delta^{15}N$ values were selected for CSIA-AA and prepared as described in Popp et al. (2007) (see electronic online supporting materials, Method S2).

2.2. Trophic position and trophic structure (BULK SIA–TP$_{SIA}$)

As ontogenetic diet shifts to higher TP prey have been widely reported in large sharks, resulting in ^{15}N enrichment with size (Estrada et al., 2006; Hussey et al., 2011; Rabehagasoa et al., 2012), we developed a Bayesian hierarchical model to estimate species-level $\delta^{15}N$ values ($\delta^{15}N_{species}$) given individual body size (precaudal length − PCL). Specifically, we modelled $\delta^{15}N$ values for individual i, as;

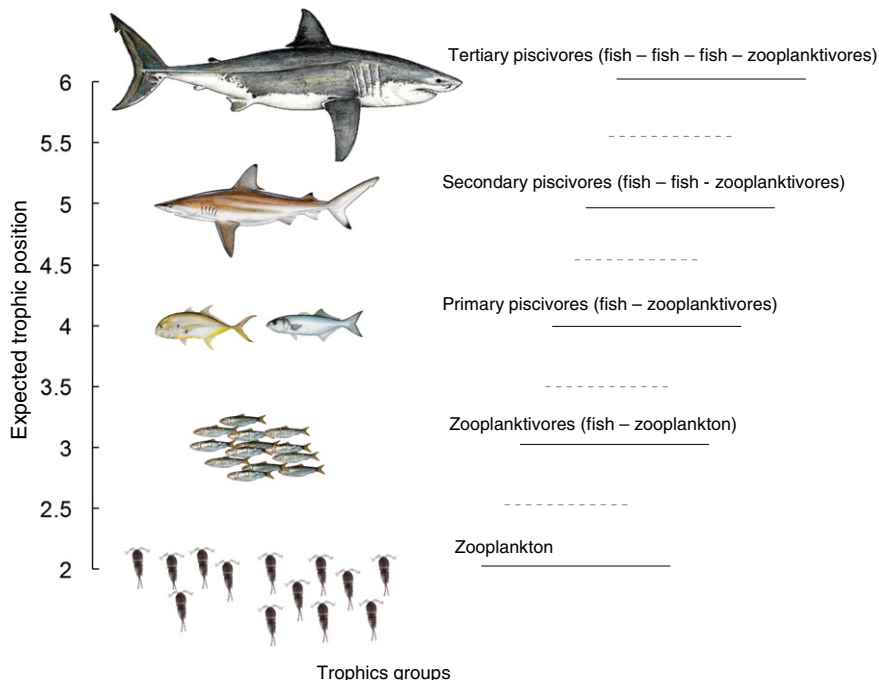$$\delta^{15}N_{is} \sim N\left(\mu_{is}, \varepsilon_s\right) \tag{1}$$

Fig. 1. Expected marine food web with extended upper trophic levels to accommodate known feeding behaviours of the large shark assemblage.