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Feeding ecology of common demersal elasmobranch species in the Pacific coast of Costa Rica inferred from stable isotope and stomach content analyses

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ABSTRACT

Knowledge of the feeding ecology and trophic interactions of marine species is essential to understanding food web dynamics and developing ecosystem-based management approaches. Given that many top predatory fishes have experienced large population declines from coastal ecosystems, it is critical to understand the role of smaller, mesopredators in coastal food webs. This study used stomach content (SCA) and stable isotope analyses (SIA) of muscle tissue ($\delta^{13}C$, $\delta^{15}N$) to examine the feeding ecology of four common demersal elasmobranchs (*Mustelus henlei*, *Raja velezi*, *Zapteryx xyster* and *Torpedo peruana*) from the Pacific coast of Costa Rica, Central America. Specifically, we investigated: (*i*) size- and sex-related changes in diet; (*ii*) dietary changes between seasons; (*iii*) dietary changes across depth and latitudinal gradients; and (*iv*) the degree of diet overlap among species. SCA showed that *M. henlei*, *R. velezi* and *Z. xyster* were feeding on a wide range of teleost and decapod species, whereas teleosts dominated the diet of *T. peruana*. *Torpedo peruana* had a lower prey diversity and dietary breath than the other species. Interestingly, SIA revealed a significantly larger isotopic niche breath in *Z. xyster*, indicating that SIA can provide a broader perspective of diet than SCA. Both SCA and SIA showed relatively low dietary overlap among species, except between *R. velezi* and *Z. xyster* which have a similar size, mouth morphology and potentially feeding behaviour. Latitude and size were identified as important drivers of the feeding ecology of elasmobranchs; however, their effect varied considerably among species and was often influenced by other factors such as sex and depth. Season had little influence on elasmobranch diet, but our data suggested that isotopic baseline values differ between geographic regions due to differences in local biogeochemical processes and/or prey availability, and possibly in response to seasonal nutrient fluctuations. This may also indicate that some of these elasmobranchs tend to use more localized habitats along the coast. The present study increased our understanding of the feeding ecology of common demersal elasmobranch species. Moreover, trophic information of elasmobranchs provided an important baseline record to understanding how trawling fisheries may impact demersal ecosystems in Costa Rica and the Central American region.

1. Introduction

Large population declines of top predatory fishes have been widely documented (Dulvy et al., 2014; Lotze and Worm, 2009; Myers and Worm, 2003). This has raised concern as large marine predators such as sharks are thought to have an important role in the structure and function of marine communities through direct and indirect interactions with prey, and their removal may result in trophic cascading effects (Heithaus et al., 2008, 2014; Myers et al., 2007; Stevens et al., 2000). Therefore, given that many top predatory fishes have experienced large population declines in coastal ecosystems, knowledge of the feeding ecology and trophic interactions of mesopredators is essential to understanding food web dynamics (Ferretti et al., 2010; Trueman et al., 2014; Vaudo and Heithaus, 2011). Detailed trophic information of a species is also essential to defining its role in the ecosystem and developing ecosystem-based management approaches.

Ecological theory predicts a high level of separation among coexisting sympatric species along at least one of three niche dimensions: food, habitat, and/or time (Heithaus et al., 2013; Knickle and Rose, 2013). Trophic niche partition (e.g., separation in the use of different food resources) is presumed to reduce overlap within and among

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elasmobranch species (Heithaus et al., 2013; Papastamatiou et al., 2006; Platell and Potter, 2001; White et al., 2004). Elasmobranchs typically change their diet with size because of changes in cranial morphology throughout ontogeny (Dean et al., 2007; Lowry et al., 2007) or due to higher metabolic requirements (Kim et al., 2012; Lowe et al., 1996). As a result, body size is an important driver reducing the degree of dietary overlap (Espinoza et al., 2012; Papastamatiou et al., 2006; White et al., 2004). Many coastal elasmobranchs also segregate spatially by sex, size and depth during specific times of the year (Clarke et al., 2014; Mollet and Cailliet, 2002; Springer, 1967); therefore, detailed knowledge of the spatial and seasonal distribution of a species is critical to understanding its feeding ecology.

The diet and trophic ecology of sharks and rays have traditionally been studied using stomach content analysis (SCA) (Cortés, 1997; Ebert and Bizzarro, 2007; Hyslop, 1980). The use of SCA can provide high taxonomic details on the diet of a species but is often time consuming, typically lethal, and only provide a "snap shot" of what a species has recently consumed (Hussey et al., 2011). In contrast, stable isotope analysis (SIA) provides long-term integrated dietary information using methods that are generally cost-effective and potentially non-lethal. This information is also valuable to examine broader dietary changes and trophic dynamics (Fisk et al., 2002), habitat utilization (Heithaus et al., 2013; Hussey et al., 2011), and movement patterns of sharks and rays (Carlisle et al., 2012; Couturier et al., 2013). Stable isotopes of carbon ($^{13}C/^{12}C$ expressed relative to a standard as $\delta^{13}C$) provide a useful tool to track movements between isotopically distinct habitats, whereas stable isotopes of nitrogen ($^{15}N/^{14}N$ expressed relative to a standard as $\delta^{15}N$) are often used to examine dietary shifts and trophic relationships in food webs (Hussey et al., 2011; Post, 2002). Long-term integrated stable isotope values also provide important information on the ecological role of elasmobranchs within a food web (Vaudo and Heithaus, 2011).

Recent studies have shown that twenty-five species of sharks and rays are captured as by-catch in the commercial trawling fishery of Costa Rica, representing over 36% of the elasmobranch richness reported for the entire Pacific coast (Bussing and Lopéz, 2009; Clarke et al., 2014). From these, the brown smooth-hound (*Mustelus henlei*), rasptail skate (*Raja velezi*), southern banded guitarfish (*Zapteryx xyster*) and Peruvian torpedo (*Torpedo peruana*) represent four of the most common species caught in waters deeper than 50 m (Clarke et al., 2014; Espinoza et al., 2012, 2013). These species are commonly found in the Eastern Tropical Pacific (ETP), have wide depth distributions (approx. 18–300 m), and are subjected to various levels of fishing (Allen and Robertson, 1994; Clarke et al., 2014; Mejía-Falla and Navia, 2011). All except *T. peruana* are relatively small (<1 m total length), slow-moving, demersal species that feed primarily on epibenthic prey (Allen and Robertson, 1994; Bussing and López, 1993).

Despite the common occurrence and high spatial interaction with commercial trawling fisheries, little is known about the feeding ecology of common demersal elasmobranchs in ETP (Clarke et al., 2014; Mejía-Falla and Navia, 2011; Navia et al., 2007). Previous studies showed that *R. velezi* and *Z. xyster* have similar diets, which consist primarily of decapod shrimps during early life-stages and teleost and/or larger prey as they mature (Espinoza et al., 2013; Navia et al., 2007). *Mustelus henlei* is a more opportunistic epibenthic mesopredator with a highly diverse diet consisting of larger proportions of teleosts and cephalopods (Cortés, 1999; Espinoza et al., 2012; Navia et al., 2007). Although these studies reported detailed information about the diet composition of *M. henlei*, *R. velezi* and *Z. xyster*, our knowledge about how other factors (e.g., season, depth and latitude) influence their feeding ecology is scarce. The diet of *T. peruana* remains poorly known throughout their distribution, but based on studies from a closely-related species (*Torpedo californica*; Lowe et al., 1994), this species is presumed to feed more on epipelagic teleosts. Catch data from the Costa Rican trawling fishery revealed sex and size segregation patterns associated with depth in some of these elasmobranchs (Clarke et al., 2014). Therefore, depth is expected to be an important factor influencing their diet. Here we combined information from SCA and SIA of muscle tissue to examine the feeding ecology of *R. velezi*, *M. henlei*, *Z. xyster* and *T. peruana* along the Pacific coast of Costa Rica, Central America. Specifically, we investigated: (*i*) size- and sex-related changes in diet; (*ii*) dietary changes between seasons; (*iii*) dietary changes across depth and latitudinal gradients; and (*iv*) the degree of diet overlap among species.

2. Materials and methods

2.1. Study site and sampling

The Pacific coast of Costa Rica has a highly irregular coastline and a continental shelf of approximately 15,600 km^2 (Fig. 1; Wehrtmann and Cortés, 2009). Based on geographic features, the Pacific coast was divided in three regions: North, Central and South (see Wehrtmann and Cortés, 2009). The North Pacific region has limited freshwater input due to the absence of large rivers and is influenced by strong seasonal upwelling that occurs between December and April (Jiménez, 2001). The Central Pacific is bordered by two large estuarine systems (Golfo de Nicoya and the Humedal Nacional Térraba-Sierpe — HNTS). The South Pacific region has a steep continental slope, and is adjacent to the Golfo Dulce, a large tropical fjord (Quezada-Alpizar and Cortés, 2006). Costa Rica has a pronounced dry (December–May) and rainy (June–November) season. Seasonal changes in the amount of nutrient input from large rivers are known to influence coastal productivity, particularly in the central and southern Pacific regions (Wehrtmann and Cortés, 2009).

Fieldwork was conducted on-board commercial shrimp trawlers along the entire Pacific coast of Costa Rica (Fig. 1). Vessels were 22.5 m long and equipped with two standard epibenthic nets (20.5 m long; mouth opening: 5.35 × 0.85 m; mesh size: 4.45 cm; cod-end mesh size: 3.0 cm). The duration of each haul varied between 15 min to 6 h, and trawling speed fluctuated between 2 and 3 knots. Both fishery-independent and dependent surveys were conducted between March 2010 and December 2011 along the entire Pacific coast. However, fishing effort was concentrated in the Central Pacific region at depths between 25 and 250 m (Fig. 1). Captured elasmobranchs were identified, sexed, weighed, and measured (stretch total length — STL: tip of the snout to posterior tip of the tail, with the tail flexed down; disc width — DW: distance between the wing tips). Hereafter, elasmobranch size referred to TL in *M. henlei* and DW in *R. velezi*, *Z. xyster* and *T. peruana*. Individuals were classified as immature (neonates and juveniles) or mature (adults) based on the stage of calcification of the claspers (males), and the development of the oviductal gland, uterus and egg development stage (females) (see Clarke et al., 2014).

2.2. Diet composition and overlap

Stomachs were extracted at sea, placed in labelled plastic bags, stored on ice and frozen upon returning to the laboratory. Stomach contents were emptied on a 500-μm mesh sieve, rinsed with water, and identified to the lowest taxonomic level possible under a dissecting microscope. Prey items were counted, weighted and when possible measured to the nearest mm. Unidentified prey items were excluded from subsequent analyses. An index of vacuity was used to express the number of empty stomachs encountered as a percentage of the total stomachs examined. Net feeding was not considered an issue as most prey items examined showed an advanced stage of digestion (see Espinoza et al., 2012, 2013). The diet composition of elasmobranchs was analysed at two taxonomic levels. First, prey items were pooled at the family and/or order level. Second, all prey items were pooled into six major categories: (1) teleosts, (2) shrimps, (3) crabs, (4) stomatopods, (5) cephalopods, and (6) other invertebrates (this category included other crustaceans, polychaetes and unidentified worms).