**Running header:** Whitehead et al.- Feeding Behaviors of Whale Sharks

**The influence of zooplankton communities on the feeding behaviors of whale shark in Bahia de La Paz, Gulf of California**

**La influencia de las comunidades de zooplancton en el comportamiento de alimentación del tiburón ballena en Bahía de La Paz, Golfo de California**

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**Abstract**

The whale shark is the world’s largest filter feeding shark and holds international protection as an endangered species. It is known to form seasonal aggregations linked to blooms of zooplanktonic organisms. The aim of this study was to investigate whether whale shark foraging behaviors are related to the density or concentration of available prey items. Zooplankton samples were obtained between October-2016 and March-2017 from Bahia de La Paz in the presence (n=12) and absence (n=32) of foraging whale sharks. Results indicated that zooplankton biomass was 1.6 times significantly greater (t=-3.21, p<0.05) when sharks were observed feeding and the mean number of individuals of all taxonomic groups in the presence of feeding whale sharks was 2.5 times greater than in the absence of feeding, although it was not significantly different (t=-1.70, p>0.05). The dominant taxonomic groups were copepods and chaetognaths with no significant differences found in the mean number of copepods (t=-1.81, p>0.05), chaetognaths (t=-1.70, p>0.05), euphausiids (t=-0.12, p>0.05) and decapods (t=-1.80, p>0.05), between the presence and absence of feeding whale sharks. In conclusion, whale sharks feeding behaviors occur during higher concentrations of zooplankton biomass and the species may potentially target dense patches of both copepods and chaetognaths.

**Keywords:**

Bahia de La Paz, Ecology, Zooplankton communities, Foraging behaviors

**Resumen**

El tiburón ballena es el tiburón filtrador más grande del mundo y tiene protección internacional como especie en peligro de extinción. Forman agregaciones estacionales vinculadas a floraciones de organismos zooplanctónicos. El objetivo de este estudio fue investigar si el comportamiento de alimentación del tiburón ballena está relacionado con la densidad o concentración de presas disponibles. Las muestras de zooplancton fueron obtenidas entre octubre-2016 y marzo-2017 en Bahía de La Paz en la presencia (n=12) y ausencia (n=32) de tiburones ballena alimentándose. Los resultados indicaron que la biomasa de zooplancton fue 1.6 veces significativamente mayor (t=-3.21, p<0.05) y el número de individuos promedio de todos los grupos taxonómicos fue 2.5 veces mayor, aunque sin diferencias significativas (t=-1.70, p>0.05) en presencia de tiburones ballena alimentándose. Los grupos taxonómicos dominantes fueron copépodos y quetognatos, sin diferencias significativas en el número promedio de copépodos (t=-1.81, p>0.05), quetognatos (t=-1.70, p>0.05), eufáusidos (t=-0.12, p>0.05) y decápodos (t=-1.80, p>0.05), entre la presencia y ausencia de tiburones ballena alimentándose. En conclusión, el comportamiento de alimentación del tiburón ballena se produce durante las concentraciones más altas de biomasa de zooplancton y las especies potencialmente pueden dirigirse a parches densos tanto de copépodos como de quetognatos.

**Palabras clave:**

Bahía de la Paz, Ecología, Comunidades de zooplancton, Comportamientos de alimentacion.

**Introduction**

The whale shark is the world’s largest filter feeding shark, with individuals sighted in numerous regions across the globe (Compagno, 2001; Rowat & Brooks, 2012). The species in the main are solitary, spending the majority of their lives migrating from tropical to sub-tropical waters seemingly navigating along scent trails that lead them to areas of intense productivity, such as coastal upwelling zones, continental shelf’s and submerged seamounts (Beckley et al., 2007; Ketchum et al., 2013). In spite of this solitary lifestyle, these sharks are known to regularly form almost sex-segregated aggregations in coastal waters (Colman, 1997; Rowat et al., 2011). These aggregations are usually on a seasonal basis, but at times can be sporadic, and typically lie between latitudes of 30°N and 35°S of the equator (Compagno*,* 2001). From current research, it seems to be clear that these aggregations are often linked to certain productivity events such as a fish spawning (Heyman et al.,2001) or blooms of zooplanktonic species (Clark & Nelson, 1997; Hacohen et al.,2006; Hernández-Nava & Álvarez-Borrego, 2013; Lavaniegos et al., 2012; Wilson et al., 2001). Bahia de La Paz is located in the southern part of Baja California peninsula and is an almost entirely enclosed bay with high levels of both primary (Reyes-Salinas et al., 2003) and secondary productivity (De Silva-Dávila & Palomares-García, 1998) supporting an array of filter feeding marine fauna such as: sardines, manta rays and whale shark (De Silva-Dávila & Palomares-García, 1998; Ketchum et al., 2013). The circulation of water within this enormous bay is distributed by a central mesoscale cyclonic eddy, which is suspected to influence the complete horizontal distribution of all trophic groups of zooplankton in the bay (Duran-Campos et al., 2015). Additionally, the bay is known to have seasonal tendencies, which rotate this eddy in an anti-clockwise direction during the winter months (November – March) and in the summer months (May – August) in a clockwise direction, leavening a somewhat transitional period between these two (Duran-Campos et al., 2015; Palomares-García et al., 2003).

The feeding mechanism of whale sharks are designed to capture their food supply by the filtering of water through special filter pads (Motta et al., 2010). An early dissection of a whale shark in South Africa revealed that there is a transverse band of a spongy filtration tissue within each gill slit of the species (Beckley et al., 1997). Each pore in this uniquely designed tissue is effectively a tiny canal that is connected to another directly under the surface to form a much larger passage, which eventually opens into the branchial cavity underneath the branchial arches (Motta et al., 2010). The overall function of these filtration pads is based upon this pore structure, allowing smaller items of prey to pass through with the water as it is swept over the gills which are then discharged through the gill slits, while larger prey items are trapped and ultimately directed down the small central gullet.

Whale sharks are well-known to display multiple types of foraging behaviours presumably related to differing concentrations of available food sources (Hacohen-Domené et al., 2006; Ketchum et al., 2013; Motta et al., 2010). In many feeding aggregations, the most frequently observed feeding behaviour is active surface or surface ram feeding (Clark & Nelson, 1997). During this behaviour the species may swim almost at the surface with its mouth open and slightly lifted out of the water, repeatedly opening and closing its mouth driving water and food items over its filtering apparatus (Clark & Nelson, 1997; Heyman et al., 2001; Motta et al., 2010). Other occasions when food concentrations are higher, suction or vertical feeding might occur, where the species could be observed in a diagonal or an almost vertical position, while generating a suction in its pharynx drawing in large volumes of water and prey (Motta et al., 2010; Nelson & Eckert, 2007). Lastly, passive feeding can be witnessed within the species and may be simply described as the animal swimming slowly through the water with their mouth marginally open, presumably filtering the scarce prey items, closing its mouth every few minutes with the shark appearing to swallow (Heyman et al., 2001). Examinations of the composition of zooplanktonic organisms present in Bahia de la Paz have shown that a number of species show a higher level of dominance during certain times of the year (Clark & Nelson, 1997; Hacohen-Domené et al., 2006). An early study by Clark and Nelson (1997) observed the foraging of juvenile whale sharks in the southern parts of Bahia de La Paz. From this early observational study of whale sharks, feeding behaviours linked to high concentrations of copepod species comprised mainly of *Acartia clausi* and *Acartia* sp in the southern regions of the bay. Ketchum et al. (2013) examined the foraging ecology of whale sharks in Bahía de La Paz and observed that the zooplankton biomass varies seasonally, with the lowest being observed in May and June and peaks of biomass occurring in November and February. The aim of this study was to investigate whether or not whale shark foraging behaviours are related to the density or concentration of available zooplanktonic prey items within this known coastal aggregation site for this species.

**Materials & methods**

Zooplankton samples were monthly obtained from October 2016 to March 2017 from Bahía de La Paz in both the presence and absence of foraging juvenile whale sharks. A total of 32 surface plankton tows were taken in the absence of feeding whale sharks from four sample stations (8 at each station) and registered by the global positioning system (GPS). The sampling stations were distributed throughout the known aggregation area of where whale sharks are reported feeding (Figure.1), with observations of whale sharks sighted swimming in those areas during the routine absent tows. Zooplankton samples were collected using a 505 μm mesh plankton net, which was towed for five minutes behind the boat in a circular motion at approximately 1-1.5 km h−1. Upon the net being removed from the water, collected zooplankton were washed down into the collecting container at the end, fixed with 4% formalin solution, labelled for identification and stored in plastic screw top containers.

Zooplankton samples were also taken in the presence of foraging whale sharks. A total of 12 samples were taken during the presence of feeding whale sharks in the same area as previously mentioned (Figure.1). Once encountering a whale shark, observers on-board confirmed that the animals were feeding either actively on the surface or in a vertical position. Following the confirmation of the sharks feeding, the research boat approached slowly and the animals GPS position was registered. Next the plankton net was lowered into the water and for vertical feeding events, a tow for five minutes was conducted in a circular motion around the animal at a distance of 5-10m. For incidences of active surface feeding the net was towed alongside the sharks for the same amount of time.

The total biomass of zooplanktonic organisms was determined by using the displacement method (Beers, 1976) and standard biomass calculations (Smith & Richards, 1977). Zooplankton was grouped into five main taxonomic groups: Copepoda, Chaetognatha, Euphausiidae, Decapoda, and “Other”, following previous plankton work from the same region and other sites in Mexican waters (Franco-Gordo et al., 2016; Ketchum et al., 2013). After zooplankton was assembled into groups, individuals were counted to obtain the total number of individuals for each sample and ultimately an overall relative abundance of each groups for each sample collected. Qualitative analysis of zooplankton samples was focused on zooplankton biomass (g m-3) and the number of individuals (no. m-3) present in each taxonomic group within each sample, to gain information on the composition of zooplankton members between present and non present samples. Differences in zooplankton biomass and number of individuals between the presence and absence of feeding whale sharks were tested using a Welch two sample *t*-test for unequal sample sizes and unequal variances (Zar, 2010). All statistical analyses were conducted in the statistical program R (R Development Core Team, 2018).

**Results**

Zooplankton biomass was 1.6 times greater and the mean zooplankton biomass was significantly greater for samples where whale sharks were observed feeding compared to samples where sharks were not feeding (Table. 1, *t* = -3.21, *p* < 0.05). Individuals for the taxonomic groups of copepods and chaetognaths were predominant in all samples, both in the presence and absence of feeding whale sharks. In the presence of feeding whale sharks chaetognaths were the most predominant, followed by members of copepods, while in the absence of feeding whale sharks’ copepods were the most predominant, followed by chaetognaths (Figure. 2; Table. 1). While the mean number of individuals of all zooplankton taxonomic groups per m3 in the presence of feeding whale sharks was 2.5 times greater than in the absence of feeding whale sharks, it was not significantly different (Table 1, *t* = -1.70, *p* > 0.05). In the presence of feeding whale sharks the number of copepods, chaetognaths, euphausiids and decapods was 2.8, 3.3, 1.06 and 3.4 times greater than in the absence of feeding whale sharks, respectively. No significant differences were observed in the mean number of individuals of copepods (*t* = -1.81, *p* > 0.05), chaetognaths (*t* = -1.70, *p* > 0.05), euphausiids (*t* = -0.12, *p* > 0.05) and decapods (*t* = -1.80, *p* > 0.05) between the presence and absence of feeding whale sharks. Ultimately, the taxonomic group “other” was observed to be 4.2 times greater in absence of feeding whale sharks than in the presence of feeding whale sharks with significant differences in the mean number of individuals (*t* = 3.93, *p* < 0.05).

**Discussion**

From the majority of work focused on the prey preference of whale sharks, it is correct to assume that seasonal aggregations of whale sharks are often linked or related to productivity and the availability of zooplanktonic organisms (Clark & Nelson, 1997; Hacohen et al., 2006; Heyman et al.,2001; Ketchum et al., 2013; Motta et al., 2010). In our results, we observed that the total biomass of zooplankton was significantly greater with as much as 1.6 times during feeding events, over non-feeding events. This confirms the theory that whale shark feeding events are related to the densities of available food and theoretically the species search out patches of high concentration of prey to ensure optimal feeding. In numerous other sites, aggregations of whale sharks have been linked or somewhat in response to zooplankton blooms or fish spawning events such as in the Seychelles (Rowat et al., 2011), Belize (Heyman et al., 2001), Australia (Meekan et al., 2009) Tanzania (Rohner et al., 2015), Qatar (Robinson et al., 2012) as well as the Mexican Caribbean (De la Parra et al.,2011). From early work on the diet of whale sharks, we know that foraging events may to some degree related to concentrations of prey items and feeding behaviours are intriguingly different with varying densities of planktonic food sources (Clark & Nelson, 1997; Motta et al., 2010; Nelson & Eckert, 2007; Rohner et al., 2015).

Composition of the different groups of prey items in our results for both samples where sharks were observed feeding and not feeding, showed the dominance of two taxonomic groups (copepods and chaetognaths) in all collected samples. This may provide more evidence that verifies that in Bahia de La Paz for the most part, two main taxonomic groups of zooplankton are the most abundant on a seasonal basis and an important dietary item for whale sharks. Previous work in the same area (Hacohen et al., 2006; Ketchum et al., 2013) and studies in the southern regions of the bay (Clark & Nelson, 1997) also observed seasonal aggregations of whale sharks foraging on copepods. Furthermore, studies from other sampling sites in the Gulf of California, where whale sharks were also witnessed foraging, similarly confirms the species to be drawn to dense patches of plankton, primarily composed of copepods (Nelson & Eckert, 2007).

Taking a closer look at the mean values of the number of individuals of all zooplankton taxonomic groups during the presence of feeding whale sharks. We learned that although the biomass was 2.5 times greater during the presence than in the absence of feeding whale sharks, it was not significantly different (Table. 1, *t* = -1.70, *p* > 0.05). This may simply indicate that in such a focused small sample area with sample stations separated by only a short distance, environmental factors such as sea surface current and wind direction may influence the biomass and composition tendencies of available prey items. Previous work that examined environmental factors present in this region, demonstrated that its connectivity with the Gulf of California and an important central mesoscale cyclonic eddy in the bay itself, may be highly influential in the complete horizontal distribution of all trophic groups of zooplankton (Duran-Campos et al., 2015; Monreal-Gomez et al., 2001). We did observe that in the presence of feeding whale sharks the number of copepods, chaetognaths, euphausiids and decapods species were 2.8, 3.3, 1.06 and 3.4 times greater than in the absence of feeding whale sharks, supporting existing evidence that whale shark opt to forage on certain taxonomic groups (Nelson & Clark, 1997; Hacohen et al., 2006; Ketchum et al., 2013; Rohner et al., 2015). While our study and previous studies (Hacohen et al., 2006; Ketchum et al., 2013; Rohner et al., 2015) did observe whale sharks clearly feeding in patches of food dominated by a certain food source it must be taken with caution. As the species may not show prey selectivity, but rather foraging habits that solely target high concentrations of available food in areas where the composition changes on a seasonal or even daily basis, due to constantly changing environmental factors. In conclusion, we can report that within Bahia de La Paz whale sharks feeding behaviours occur during higher concentrations of zooplankton biomass and that the species may potentially target dense patches of both copepods and chaetognaths species as a primary prey source.

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Table 1. Mean (SE) zooplankton biomass (g m-3) and mean (SE) number of individuals (no. m-3) present in each taxonomic group of non-feeding stations (Stations A-D) and whale shark feeding samples.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Station** | **Copepods (no. m-3)** | **Chaetognaths (no. m-3)** | **Euphausiidae (no. m-3)** | **Decapoda (no. m-3)** | **Other (no. m-3)** | **All taxonomic groups (no. m-3)** | **Biomass (g m-3)** | **n** |
| A | 2441.25 (1164.03) | 1252.5 (311.29) | 123.75 (41.44) | 705 (194.67) | 731.25 (225.99) | 5253.75 (1068.92) | 65.54 (2.68) | 8 |
| B | 3022.5 (2072.86) | 2583.75 (837.93) | 232.5 (134.13) | 686.25 (248.51) | 915 (347.13) | 7440 (2471.5) | 69.41 (3.52) | 8 |
| C | 686.25 (298.73) | 1136.25 (428.46) | 453.75 (172.19) | 825 (396.7) | 1155 (155.78) | 4256.25 (1172.5) | 62.35 (3.9) | 8 |
| D | 1976.25 (1244.36) | 2433.75 (823.85) | 457.5 (110.77) | 1218.75 (550.6) | 1717.5 (475.17) | 7803.75 (2018.41) | 58.39 (3.39) | 8 |
| All Non-feeding stations | 2031.56 (659.84) | 1851.56 (328.42) | 316.87 (64.4) | 858.75 (181.95) | 1129.68 (168.06) | 6188.43 (887.55) | 63.92 (1.77) | 32 |
| Whale shark feeding | 5869.16 (2011.41) | 6186.58 (2525.86) | 336.66 (141.5) | 2955.08 (1144.73) | 266.33 (141.29) | 15628.33 (5454.50) | 103.83 (12.26) | 12 |