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Review

Diversity of Feeding in Anthozoa (Cnidaria): A Systematic Review

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Abstract: In this study, we performed a bibliographical review examining the scientific literature on "feeding in Anthozoa" for the period from 1890 to 2019, using the scientific database Google Scholar, supplemented with additional literature. This study categorized published scientific papers on this topic by decade of publication, target taxa, variability of species studied in each order and main themes studied. As a result, 153 studies were found, and based on their content, it was observed that within Anthozoa, there has been a concentration of feeding studies on species in the orders Actiniaria (Hexacorallia), Scleractinia (Hexacorallia), and Alcyonacea (Octocorallia). This indicates that the other remaining orders of the group have been comparatively neglected with regards to their feeding aspects. Therefore, as data on feeding in some groups of Anthozoa are scarce, studies need to be carried out to fill the gaps that permeate this important benthic group, in order to better understand their ecology.

Keywords: feeding behavior; feeding habits; physiology; Hexacorallia; Octocorallia; Ceriantharia

1. Introduction

The phylum Cnidaria is comprised of three major clades: Anthozoa, Endocnidozoa and Medusozoa [1]. The distinction between these clades is supported by anatomy, life history, genome structure and phylogenetics. The class Anthozoa is considered the largest group in Cnidaria, with at least 7200 described species [1]. The representatives of this group have polypoid forms without a medusa stage in their life cycle, and are solitary or colonial [2,3]. Although the evolutionary history of Anthozoa is still under discussion, currently three subclasses are recognized: Hexacorallia, Octocorallia, and Ceriantharia [4].

There are several aspects that distinguish Anthozoa (=Anthozoaria) from Medusozoa. One aspect is related to the trophic level and behavior of the two groups. In Medusozoa, many studies on feeding behavior have been carried out examining different species, due to their potential impacts on commercial organisms. On the other hand, studies of this topic in the Anthozoa are much more limited [5]. This may be because most studies on anthozoan species have been more focused on their ecology and preservation, especially in coral reef ecosystems [6].

The understanding of diet and trophic levels and behaviors of Anthozoa are essential for a better comprehension of the ecology and evolution of species, as energy and nutrients derived from feeding habits are vital for reproduction, development and growth [7,8]. In this way, recognition of feeding habits is extremely important, as this behavior directly affects the survival of these organisms [9,10].

Despite the importance of obtaining data for food webs and dietary information for detailed examinations of trophic performance, until now there has been no summary of research related to these topics for Anthozoa. Thus, we here perform a literature review on the theme of "diversity of feeding in Anthozoa".

2. Materials and Methods

This study was performed as a bibliographic review, aiming to gather information to create a database of the studies that have emphasized anthozoan feeding over the years. The data presented in this bibliographic review were collected from Google Scholar, covering publications that appeared in English, Spanish and Portuguese languages until August 2019. Other relevant publications not covered by Google Scholar were also added from the reference lists of the studies collected and based in our knowledge of the literature. Google Scholar was chosen as it is the most comprehensive among citation search services [11], and potential problems with so-called "gray literature" were avoided via subsequent quality filtering. The search was conducted with a combination of the following keywords: "feeding", "diet" and "food web" combined with "Anthozoa", between the dates of August 8 to 24, 2019.

In total, 339 pieces of literature were identified, and, after duplication exclusion and quality filtering removal of gray literature, 270 pieces of literature were initially included in our review. Subsequently, every title, abstract and methodology section were analyzed to confirm that each work truly examined anthozoan feeding. Thus, some studies were excluded as they focused other animal groups, or they were not focused on feeding topics. After this filtering, 153 papers remained in our dataset (see Supplementary Materials). From each study the following data were extracted: (1) decade of publication; (2) Anthozoa groups found in articles; (3) observations of the species studied in each order; (4) approaches utilized in the studies.

For compilation of the articles' approaches, publications were analyzed and separated into the following categories: "Feeding behavior", "Feeding ecology" and "Physiology". Studies categorized into "Feeding behavior" examined one or more of these subjects: prey capture, feeding rates, feeding performances, feeding mechanisms, and feeding strategies. In the category "Feeding ecology", studies examined the following topics: analyses of the gastral cavity contents, diet, feeding patterns, feeding characteristics, food spectrum, and the index of filling of the gastral cavity. In the last category, "Physiology" studies reported on: digestion processes, feeding regimes, digestive enzymes that influence the feeding process, nutritional aspects, and histological and/or morphological analyses of gastral cavity structures. Some studies analyzed more than one category and were counted for every category they represented.

3. Results

3.1. Decade of Publication

Based on this analysis, we were able to verify a growing interest in this topic from 1970 to 2019, with a total of 135 (=88.1%) studies conducted during this period (Table 1). Despite the increase in publications from the early 1970s, the table shows that after this time, the number of publications on the subject slowly declined. We also observed that by the most recent decade (2010–2019), the number of articles published on this topic in the class Anthozoa (n = 24) had decreased considerably when compared to the 1970s, period with the largest number of publications (n = 33).

Table 1. List of published papers per decade related to feeding in Anthozoa.

Decade	Number of Published Papers	Percentage (%)
1890–1899	1	0.7
1900–1909	1	0.7
1910–1919	2	1.3
1920–1929	2	1.3
1930–1939	4	2.6
1940–1949	1	0.7
1950–1959	2	1.3
1960–1969	5	3.3
1970–1979	33	21.6
1980–1989	25	16.3
1990–1999	28	18.3
2000–2009	25	16.3
2010–2019	24	15.6
Total	**153**	**100.0**

3.2. Anthozoa Groups Found in the Selected Papers

Table 2 summarizes articles by subclasses and orders. The absolute number of orders in the articles was larger than the total number of publications examined, as some studies were conducted on species from more than one order. Thus, the absolute number of orders (n = 163) was different from the absolute number of studies (n = 153). The papers in which this occurred were: [12] (Alcyonacea and Zoantharia); [13] (Scleractinia, Alcyonacea and Zoantharia); [14] (Zoantharia, Actiniaria and Scleractinia); [15] (Scleractinia and Alcyonacea); [16] (Actiniaria and Alcyonacea); [17] (Zoantharia, Scleractinia and Alcyonacea); and [18] (Scleractinia and Alcyonacea).

Table 2. Anthozoa orders found in selected publications considering the search "feeding", "diet" and "food web" terms from 1890–2019.

Subclass	Order	Absolute Number	Percentage (%)
Hexacorallia	Actiniaria	56	34.4
	Antipatharia	1	0.6
	Corallimorpharia	2	1.2
	Scleractinia	54	33.1
	Zoantharia	11	6.8
Octocorallia	Alcyonacea	35	21.5
	Helioporacea	0	0.0
	Pennatulacea	1	0.6
Ceriantharia	Spirularia	3	1.8
	Penicillaria	0	0.0
	Total	**163**	**100.0**

Hexacorallia was shown to be the most investigated anthozoan subclass with a total of 124 studies (76.1%). This was the only subclass that had scientific papers for all its constituent orders. In this subclass, Actiniaria (n = 56) and Scleractinia (n = 54) were the two orders with the largest number of studies, (total 110 studies = 67.5% of absolute number of examined articles).

The subclass Octocorallia was second, with 36 studies (=22.1% of total number of examined articles). Within Octocorallia, although the order Helioporacea did not have any publications and Pennatulacea had only a single study, the order Alcyonacea was well represented (n = 35). Finally, the subclass Ceriantharia had only a very limited number of studies on feeding topics, with the order Spirularia having three publications in total (1.8% of total number of articles), and no studies in existence for the order Penicillaria.

3.3. Observations of the Species Studied in Each Order

Despite the Actiniaria being the order that had the largest number of studies related to feeding patterns (=56 studies), the variety of species studied within these publications were not the biggest among the Anthozoa groups. In total, 44 different species were observed in the publications, with the most analyzed species were *Actinia equina*, analyzed in seven studies, followed by *Anthopleura elegantissima* examined in five studies, and *Metridium senile* in four studies.

On the other hand, for some orders that had a smaller number of publications than Actiniaria, such as Scleractinia (=54 studies) and Alcyonacea (=35 studies), the number of species studied was actually higher, as some studies covered a large number of species. For example, in one study of Scleractinia (Hexacorallia), 47 species were analyzed [18], and in a single study of the group Alcyonacea (Octocorallia), 30 species were examined [19]. In total, Scleractinia had 137 different species examined and Alcyonacea 69 species.

In the orders that had a very small number of studies, few species were analyzed. In Hexacorallia, the order Corallimorpharia had two studies with one species each (*Paracorynactis hoplites* and *Amplexidiscus fenestrafer*), Antipatharia had a single study with three species (*Stichopathes lutkeni*, *Antipathes pennacea*, and *Antipathes* sp.) and Zoantharia had 11 studies examining 10 different species. In some studies of the order Zoantharia, more than one species was analyzed, and four species were the most investigated: *Zoanthus sociatus* (=five studies), *Palythoa caribaeorum* (=three studies), *Parazoanthus axinellae* (=two studies) and *Palythoa psammophilia* (=two studies). The order Pennatulacea (Octocorallia) had a single study examining *Ptilosarcus gurneyi*. In Spirularia (Ceriantharia), of a total of three publications, two species were observed: *Pachycerianthus fimbriatus* (=two studies) and *Cerianthus lloydii* (=one study).

In total, the number of species analyzed in the class Anthozoa regarding feeding topics were 268 species. This number represents approximately 3.7% of the total described species for the class (~7200 described species; [1]).

3.4. Approach Observed in the Studies

Figure 1 summarizes the approaches observed in the compiled studies, sorted by categories: "Feeding behavior", "Feeding ecology" and "Physiology".

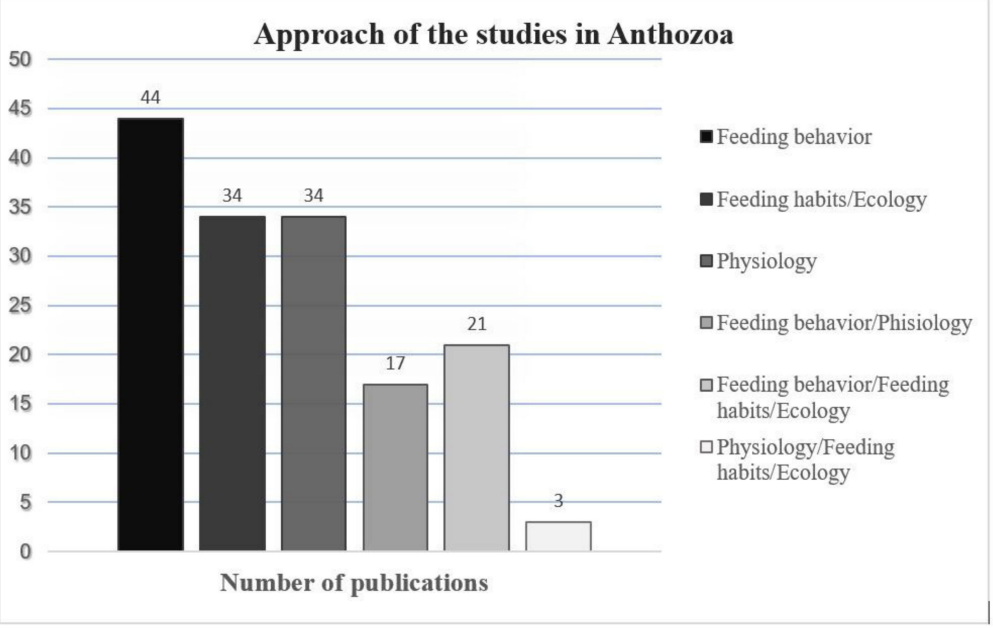

Figure 1. The number of published articles on each approach category in studies of feeding topics in Anthozoa.

Subjects related to the topic of "Feeding behavior" were observed in the most publications, with a total of 82 studies (=53.6% of the total) using this approach. Of these, 44 studies (=28.8%) featured only topics related to "Feeding behavior", with the others including multiple topics. For "Feeding ecology", a total of 58 publications (=37.9%) were related to this approach, with 34 of these studies (=22.2%) including subjects only in this category. Studies related to "Physiology" had the lowest number of publications, with a total of 54 studies (=35.3%), with publications analyzing only aspects associated with this topic in 34 studies (=22.2%).

Some studies combined more than one category of study of the feeding topics: 21 studies (=13.7%) were related to "Feeding behavior" and "Feeding ecology", 17 studies (=11.1%) were related to "Feeding behavior" and "Physiology", and 3 studies (=2.0%) were related to "Physiology" and "Feeding ecology". None of these articles included all three approaches, "Behavior + Ecology + Physiology".

3.4.1. Hexacorallia

This subclass was the most investigated group in Anthozoa, with a total of 124 studies (=76.1% of total). In the analyses below, we examined which categories of studies were most conducted for each order.

- Actiniaria

This order had 56 studies related to feeding aspects (Table 3). We observed that studies related to the topic "Feeding ecology" were the most investigated, with 28 publications related to this topic (=50.0%). The "Feeding behavior" approach was the second-most common, with 24 studies (=42.9%). "Physiology" topics were present in 19 publications (=33.9%).

Table 3. Approaches of feeding studies examining Actiniaria.

Order	Methodology	Absolute Number	%
Actiniaria	Feeding behavior	11	19.7
	Feeding ecology	18	32.1
	Physiology	12	21.4
	Feeding behavior/Physiology	5	8.9
	Feeding behavior/Feeding ecology	8	14.3
	Physiology/Feeding ecology	2	3.6
	Total	**56**	**100.0**

- Scleractinia

This order had a total of 54 studies (Table 4). Of these studies, most were related to aspects of "Feeding behavior" (32 studies; =59.2%). "Physiology" and "Feeding ecology" were less common in the studies, with 22 (=40.8%) and 13 publications (=24.1%), respectively.

Table 4. Approaches of feeding studies examining Scleractinia.

Order	Methodology	Absolute Number	%
Scleractinia	Feeding behavior	20	37.0
	Feeding ecology	6	11.1
	Physiology	15	27.8
	Feeding behavior/Physiology	6	11.1
	Feeding behavior/Feeding ecology	6	11.1
	Physiology/Feeding ecology	1	1.9
	Total	**54**	**100.0**

- Zoantharia, Anthipatharia and Corallimorpharia

The order Zoantharia had 11 studies, with three related to the topic "Feeding ecology" (=27.3%), three to "Feeding behavior/Physiology" (=27.3%), two to "Feeding behavior" and "Physiology" categories (=18.2%), and one to "Feeding behavior/Feeding ecology" (=9.0%). Studies on the combined topics "Physiology/Feeding ecology" were not observed.

The order Anthipatharia had only a single study related to "Feeding behavior" (=100.0%). The order Corallimorpharia had two studies related to "Feeding behavior" (=100.0%).

3.4.2. Octocorallia

This subclass was the second most investigated group in Anthozoa, with a total of 36 studies (=22.1% of total studies). A summary of the studies on the three orders in this subclass is given below.

- Alcyonacea

There was a total of 35 studies on this order (Table 5). The topic "Feeding behavior" consisted of 19 studies (=54.3%), "Feeding Ecology" had 16 studies (=45.7%) and "Physiology" had 8 publications (=22.9%).

Table 5. Approach of the feeding studies in Alcyonacea.

Order	Methodology	Absolute Number	%
Alcyonacea	Feeding behavior	11	31.4
	Feeding ecology	9	25.7
	Physiology	7	20.0
	Feeding behavior/Physiology	1	2.9
	Feeding behavior/Feeding ecology	7	20.0
	Physiology/Feeding ecology	0	0.0
	Total	**35**	**100.0**

- Helioporacea and Pennatulacea

There were no papers focusing on feeding for the order Helioporacea. However, there was one single publication on "Feeding behavior" for the order Pennatulacea (=100.0%).

3.4.3. Ceriantharia

The subclass represented by the tube anemones was the focus of only three publications (=1.8% of total studies) related to the feeding aspects. The order Spirularia had two studies focused on the topic "Feeding behavior/Physiology" (=66.7%) and one study on the topic "Feeding behavior/Feeding ecology" (=33.3%). No studies focused on the order Penicillaria.

4. Discussion

Understanding the feeding patterns of organisms can help inform a wide variety of other ecological and evolutionary studies [7,20]. Due to the importance of such research, many studies regarding feeding aspects in Cnidaria have been conducted [21]. For example, several studies have been carried out on feeding and trophic performances in Medusozoa (e.g., [22–24]), including freshwater species [25], due to their impacts on commercial marine and freshwater species [5]. Although members of Anthozoa also have great ecological importance, as they help in the maintenance of aquatic ecosystems [26], fewer feeding-related studies have been performed on this class. In the present bibliographic review, we observed that over recent past decades the numbers of studies on this theme, although they are increased compared to pre-1970s numbers, are still not so large (n = 24 to 33), particularly considering that Anthozoa is the largest class in the phylum Cnidaria in terms of numbers of species [27].

Our results show that feeding-related research in Anthozoa has focused on three taxonomic groups: orders Actiniaria and Scleractinia, in the subclass Hexacorallia, and order Alcyonacea, in subclass Octocorallia. We also observed a tendency for studies on trophic activities in Anthozoa to be linked to aspects of behavior, ecology and preservation, especially in shallow water tropical and subtropical coral reef ecosystems (e.g., [6]). Thus, taxonomic groups that are more abundant in coral reefs have a corresponding larger number of feeding-related studies. Thus, the other orders in the class Anthozoa, which are often less common in shallow coral reefs, have had comparatively less research conducted on feeding-related topics. Additionally, many species of these other taxonomic groups may inhabit ecosystems where the collection of specimens is logistically more challenging such as the deep sea [28], making it difficult to obtain specimens and data.

Some feeding strategies are already recognized in Anthozoa: there are species that are filter-feeders (e.g., [29]), others that perform the feeding process in symbioses with other organisms (e.g., [10,30]), and some species that can incorporate dissolved organic matter (e.g., [31]), while others are clearly polyphagous opportunists (e.g., [32,33]). However, since members of the class Anthozoa have a wide variety of feeding strategies, studies carried out on some groups may not match the dietary and behavior patterns present in others [27]. Thus, conducting further studies on the varied taxa in this class would help to comprehensively increase the pool of knowledge on their diets and feeding habits, and thus allow for better methodologies to study these groups, particularly when combined with the use of newer techniques such as stable isotope trophic relationship studies [34,35]. Another topic rarely addressed that deserves more research attention is the trophic position of different species of anthozoans. According to the studies [13,36,37] the vast majority are primary or secondary consumers, but other species appear to at least be occasional higher-level predators [38]. Once again, the overall lack of information for many anthozoan taxa does not allow for the broader profiling of the class.

In conclusion, while our review clearly shows that relevant research has been and continues to be conducted regarding the feeding habits of Anthozoa, there are several research areas that lack information. In particular, we observed a small number of studies examining two orders of Octocorallia and for the subclass Ceriantharia. Such relatively neglected anthozoan groups clearly need more research attention.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/12/10/405/s1.

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