

Article

Feeding Habits of the Invasive Ctenophore *Mnemiopsis leidyi* in the Gulf of Trieste (Adriatic Sea)

Borut Mavrič ^{1,*} , Danijel Ivajnsič ^{2,3} , Davor Lučić ⁴ , Alenka Malej ¹  and Lovrenc Lipej ¹

¹ Marine Biology Station Piran, National Institute of Biology, Fornače 41, SI-6330 Piran, Slovenia; alenka.malej@nib.si (A.M.); lovrenc.lipej@nib.si (L.L.)

² Department of Biology, Faculty for Natural Sciences and Mathematics, University of Maribor, Koroška cesta 160, SI-2000 Maribor, Slovenia; dani.ivajnsic@um.si

³ Faculty of Arts, University of Maribor, Koroška cesta 160, SI-2000 Maribor, Slovenia

⁴ Institute for Marine and Coastal Research, University of Dubrovnik, Kneza Damjana Jude 12, P.O. Box 83, HR-20000 Dubrovnik, Croatia; davor.lucic@unidu.hr

* Correspondence: borut.mavric@nib.si

Abstract: The diet of the invasive ctenophore *Mnemiopsis leidyi* in the Gulf of Trieste was examined during its peak occurrence in the summer and early-autumn months (July to October) from 2017 to 2019, through the analysis of stomach contents. Altogether 506 specimens were individually caught for the analysis. A total of 3215 prey items were isolated and identified. Copepods emerged as the primary prey (relative abundance 66.7%), followed by cladocerans (7.7%), and bivalve larvae (6%). Notably, specimens of *M. leidyi* constituted a significant portion of the diet (5.4%), providing further evidence of cannibalism within this species. Copepods were also the most commonly occurring prey items in the diet of *M. leidyi*. Most of them were represented by calanoid and cyclopoid nauplii (48.2%), followed by a harpacticoid *M. norvegica* (28.3%), and calanoids (26.8%). Other frequently occurring taxa were bivalve larvae (19.3%), *M. leidyi* (18.7%), and cladoceran *Penilia avirostris* (16.1%). The rate of cannibalism peaked in July, coinciding with a period of limited food availability. Additionally, the study revealed that fish eggs and larvae were infrequently found in the stomachs of *M. leidyi*. However, the presence of massive aggregations of *M. leidyi* may impact microzooplankton populations in late summer or autumn, potentially leading to competition with small pelagic fish.



Academic Editor: Genuario Belmonte

Received: 8 January 2025

Revised: 26 January 2025

Accepted: 30 January 2025

Published: 7 February 2025

Citation: Mavrič, B.; Ivajnsič, D.; Lučić, D.; Malej, A.; Lipej, L. Feeding Habits of the Invasive Ctenophore *Mnemiopsis leidyi* in the Gulf of Trieste (Adriatic Sea). *Water* **2025**, *17*, 470. <https://doi.org/10.3390/w17040470>

Copyright: © 2025 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

Keywords: bioinvasion; cannibalism; comb jelly; competition; diet; Mediterranean Sea

1. Introduction

Due to its potential threat to fish stocks, there is an increasing body of research focused on the feeding habits of the invasive comb jelly *Mnemiopsis leidyi* A. Agassiz, 1865, in the Black Sea, Mediterranean Sea [1], and other regions of Eurasian waters [2–4]. The ctenophore has been shown to have a significant ecological impact by preying on both fish eggs and larvae [5], leading to a notable decline in fish stocks, particularly in the Black Sea [6–8]. Kamakin and Khodorevskaya [9] report a significant reduction in zooplankton abundance—by factor of four to ten—and changes in species structure in the Caspian Sea, attributed to the presence and high density of *M. leidyi*. Similarly, Riisgård and colleagues [2] reported a decrease in zooplankton in the Limfjord channel (Denmark), which resulted in an increase in phytoplankton abundance. A recent study by Stoltenberg et al. [10] demonstrated that *M. leidyi* can efficiently consume herring yolk-sac larvae under laboratory conditions.

In the Gulf of Trieste, *M. leidy* was initially documented by Shiganova and Malej [11] in 2005, with a subsequent record emerging only in 2016 [12]. Since then, the ctenophore has been regularly observed in the Gulf of Trieste, particularly during the warmer months from July to November [13]. A key factor contributing to the successful colonization of this species in the region is its high fecundity, which is notably greater in the coastal areas of the northern Adriatic Sea [12]. During the colder months, sightings of individuals are infrequent, as also noted by Budiša et al. [14] for the northern Adriatic. This scarcity may also be attributed to the fact that seasonal refugia [15,16] and deeper layers [17], where *M. leidy* overwinters, remain unmonitored. The species is native along the Atlantic coast of both Americas and prefers shallow temperate to subtropical estuaries [7] as well as bays and coastal waters in general [18].

This paper aims to shed some light on the feeding habits of the invasive ctenophore *M. leidy* in the Gulf of Trieste. Furthermore, it offers valuable insights into the potential effects of predators on the local plankton community.

2. Materials and Methods

2.1. Sampling

In the summer and autumn sampling periods of 2017, 2018, and 2019, 506 specimens of *Mnemiopsis leidy* were collected by SCUBA diving or snorkeling in surface water (0–2 m depth) in different localities in the Slovenian part of the Adriatic Sea (Table 1).

Table 1. Sampling dates and stations with corresponding longitude and latitude, where samples of *Mnemiopsis leidy* were taken in the period from 2017 to 2019 (MBS—abbreviation for Marine Biology Station).

Sampling Date	Site	Longitude, Latitude
23 August 2017	Piran, MBS	45°31'3.31" N, 13°34'5.47" E
29 September 2017	Piran, MBS	45°31'3.31" N, 13°34'5.47" E
29 September 2017	Piran, Piranček	45°31'16.20" N, 13°33'58.21" E
2 October 2017	Bele skale (3.5 km north)	45°33'30.56" N, 13°37'57.93" E
2 October 2017	Mariculture facility Strunjan	45°31'47.77" N, 13°35'33.54" E
19 July 2018	Piran, northern coast	45°31'56.70" N, 13°33'54.43" E
30 August 2018	Piran, MBS	45°31'3.31" N, 13°34'5.47" E
12 September 2018	Oceanographic buoy Vida	45°32'57.86" N, 13°33'3.28" E
11 October 2018	Pacug	45°31'34.38" N, 13°35'24.06" E
30 July 2019	Cape Madonna, Piran	45°31'43.60" N, 13°33'47.90" E
22 August 2019	Piran, MBS	45°31'3.31" N, 13°34'5.47" E
22 August 2019	Piran, Piranček	45°31'16.20" N, 13°33'58.21" E
28 August 2019	Oceanographic buoy Vida	45°32'57.86" N, 13°33'3.28" E
29 August 2019	Piran, northern coast	45°31'56.70" N, 13°33'54.43" E
5 September 2019	Piran, MBS	45°31'3.31" N, 13°34'5.47" E
14 October 2019	Piran, MBS	45°31'3.31" N, 13°34'5.47" E
24 October 2019	Piran, MBS	45°31'3.31" N, 13°34'5.47" E

Generally, *M. leidy* occurs in the Gulf of Trieste throughout the year [13]; however, its pick occurrence is observed from early July to November, aligning with patterns seen in other regions of the northern Adriatic Sea [14]. Nelson [19] stated that the stomodeum of the ctenophore is emptied of all its contents in less than half an hour after capture. To prevent the loss of stomach contents that may be ejected into the water, divers collected *M. leidy* specimens individually (Figure 1) and kept them separately in plastic containers, which were sealed with a secure screw cap immediately after capture. Care was taken to ensure that only active and unharmed specimens were collected. The total length of each specimen, including lobes, was subsequently measured to the nearest millimeter using a caliper.

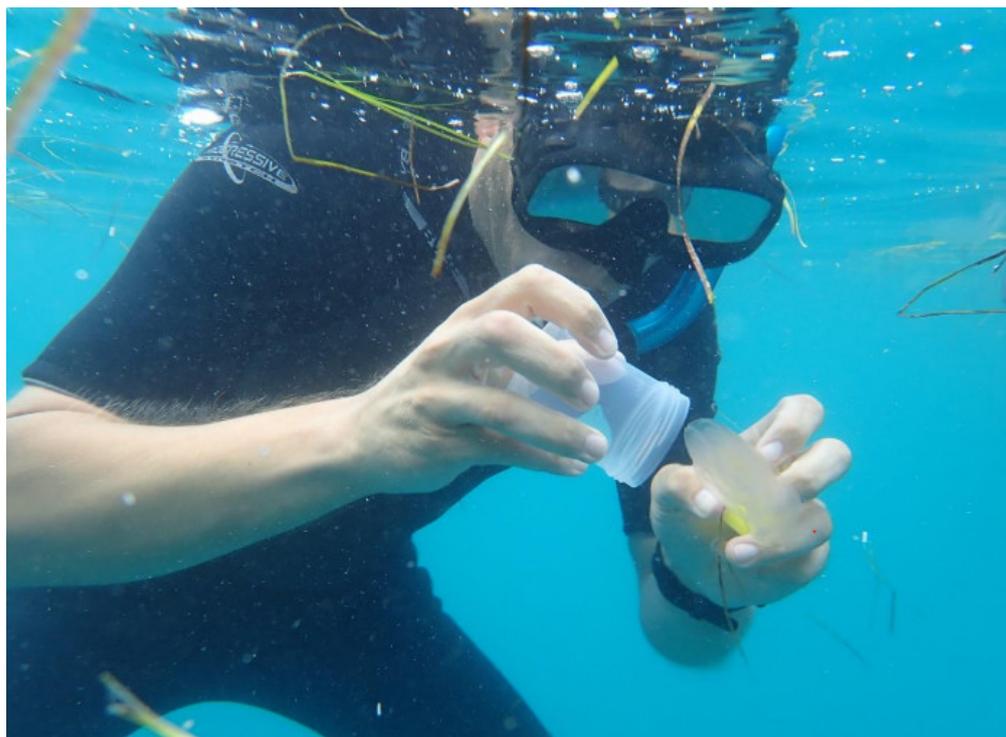


Figure 1. One of the authors (B.M.) is collecting specimen of *Mnemiopsis leidyi* in a plastic container (Photo credit: Tina Mirt).

In the container, the ctenophores regurgitated their stomach contents. The specimens were transferred to the Marine Biology Station lab in Piran within 1–2 h of sampling. In the laboratory, the expelled stomach contents were separated from containers and prepared for analysis. The stomachs contents were preserved in 5% alcohol solution and examined under Olympus SZX16 stereomicroscope. All identified organisms were isolated and classified to the lowest taxonomic category using appropriate identification keys (e.g., [20–22]).

2.2. Data Analysis

To assess the diet characteristics of the studied species, several indices were used. The relative importance of each prey item in the diet of *M. leidyi* was described with frequency of occurrence (F%), expressed as a percentage of analyzed stomachs' contents, and with relative abundance (N%), expressed as number of prey items of different species in the analyzed stomachs.

In addition, the vacuity index (VI), which is a percentage of empty stomachs, was calculated (sensu [23]). To test and visualize possible temporal (year and month) differences in prey abundance and composition, a non-metric multidimensional scaling (NMDS) analysis was performed by applying `vegdist` (method = bray) and `metaMDS` functions within the `vegan` package [24] in the R statistical environment [25]. Additionally, the `betadisper` algorithm was utilized to test multivariate homogeneity of groups (factors). The statistical analysis continued with the multivariate permutation analysis of variance (PERMANOVA; 999 permutations) and the `permutest` function, to objectively evaluate if the considered temporal variables significantly contributed to *M. leidyi* diet differentiation. Next, the `SIMPER` function was implemented to identify key contributors to the discovered temporal differences or similarities in the *M. leidyi* diet in the study area. Finally, to link and understand the relationship between environmental conditions (prey availability) and *M. leidyi* diet content, a generalized linear model (a GLM function in the R environment [Rcmdr package]) was fitted with prey number per stomach as the dependent variable

and number of empty stomachs and factor month as independent (predictor) variables (family=poisson, link function=logit).

Finally, relations between *M. leidyi* size, prey number (empty stomachs), and composition (especially cannibalism) by month were estimated. Variable *M. leidyi* size was tested for homogeneity of variances per month category with the Levine's test in the R statistical environment. Accordingly, a one-way analysis of variance (ANOVA) followed to test potential differences in mean *M. leidyi* size. Mean monthly values of *M. leidyi* size, proportion of Ctenophora in the stomachs, and vacuity index values were then analyzed with simple linear regression statistics.

3. Results

Between 2017 and 2019, a total of 506 stomach contents of *M. leidyi* were examined, revealing that 99 of these were empty, representing 19.6% of the total. The proportion of empty stomachs fluctuated between 4.2% and 48.7% across different sampling campaigns. The highest vacuity index was observed in July, followed by a gradual decline in the subsequent months. The full stomachs contained between one and eighty-three prey items, with nearly one-third (32%) of the stomachs having only one or two prey items (Figure 2).

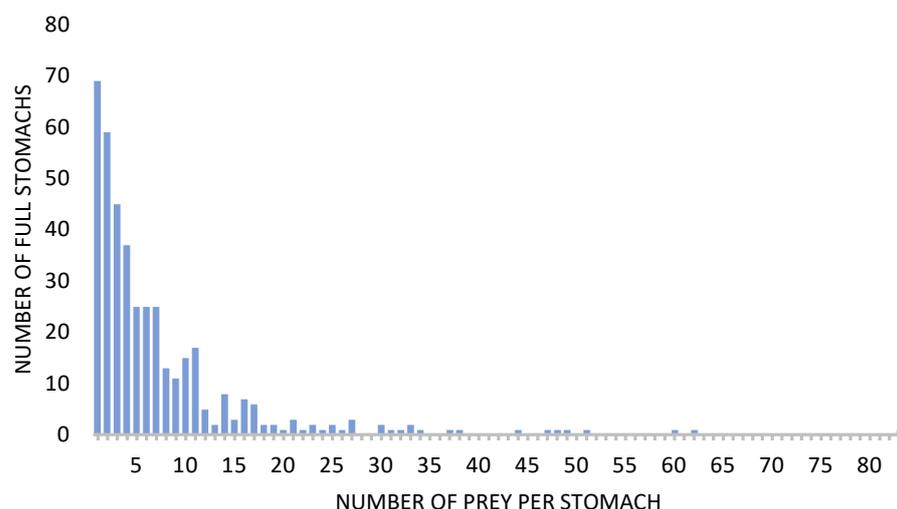


Figure 2. Number of prey items per full stomach (n = 407) in the examined specimens of *Mnemiopsis leidy* from the Gulf of Trieste in the period between 2017 and 2019.

A total of 3,215 prey items were isolated and identified (see Tables 2 and 3). The prey items found in the stomach contents primarily consisted of summer zooplankton species, although some benthopelagic taxa, such as Mysidacea, Cumacea, and benthic gastropods, were also present. Copepods dominated the stomach contents in terms of relative abundance, accounting for 66.7%, followed by cladocerans at 7.7%, bivalve larvae at 6.0%, and ctenophores at 5.4% (Figure 3a). The most frequently preyed adult copepod was the harpacticoid *Microsetella norvegica*, comprising 8.8% of the total. Other groups represented less than 5% of the relative abundance, including cirriped nauplii (Cirripedia), pteropods (Euthecosomata), various gastropods, dinoflagellates, diatoms, and tintinnid ciliates (Choreotrichida). Among the tintinnids, species from the genera *Eutintinnus*, *Tintinnopsis*, *Codonellopsis*, and *Dictyocista* were recorded. Notably, only seven prey items consisting of fish larvae and eggs were found in the stomachs of *M. leidy*.

Table 2. Basic data dealing with the number of stomachs analyzed and prey items isolated in the specimens of *Mnemiopsis leidyi* in the period between 2017 and 2019.

Sample Set	Date	Stomachs	Empty Stomachs	% of Empty Stomachs	Σ Prey Items	Preys per Stomach	Preys per Full Stomach
1	23 August 2017	20	4	20.00	137	6.85	8.56
2	29 September 2017	17	1	5.88	140	8.24	8.75
3	29 September 2017	31	0	0.00	329	10.61	10.61
4	2 October 2017	18	0	0.00	145	8.06	8.06
5	2 October 2017	16	0	0.00	130	8.13	8.13
6	19 July 2018	35	16	45.71	53	1.51	2.79
7	30 August 2018	13	5	38.46	101	7.77	12.63
8	12 September 2018	29	13	44.83	73	2.52	4.56
9	11 October 2018	29	9	31.03	79	2.72	3.95
10	30 July 2019	28	12	42.86	70	2.50	4.38
11	22 August 2019	10	0	0.00	229	22.90	22.90
12	22 August 2019	74	11	14.86	358	4.84	5.68
13	28 August 2019	39	19	48.72	66	1.69	3.30
14	29 August 2019	41	2	4.88	189	4.61	4.85
15	5 September 2019	48	2	4.17	616	12.83	13.39
16	14 October 2019	30	2	6.67	148	4.93	5.29
17	24 October 2019	28	3	10.71	202	7.21	8.08

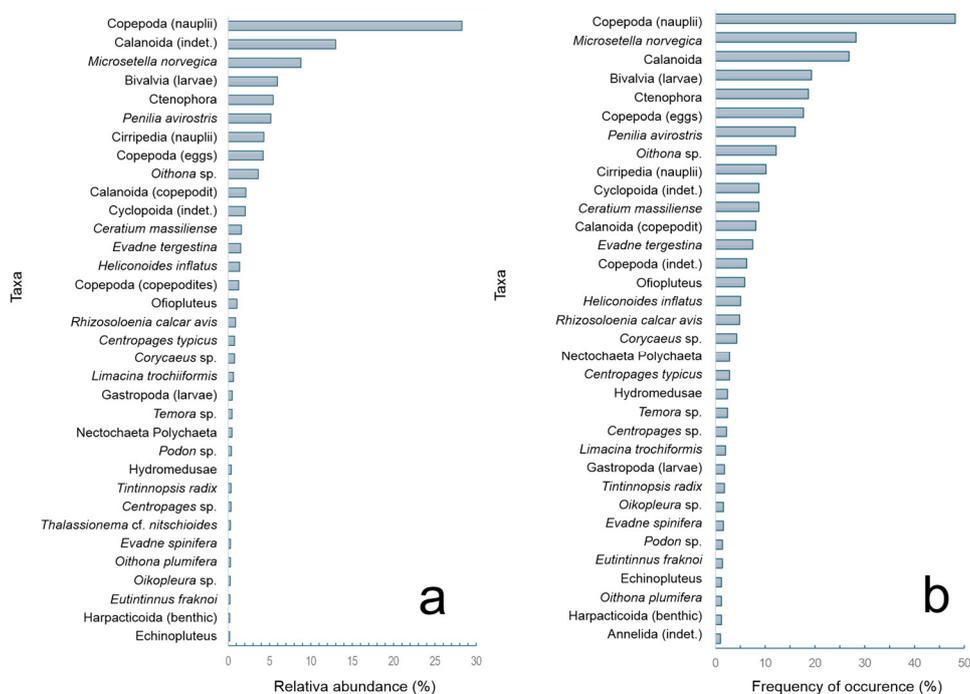


Figure 3. Relative abundance (a) and relative frequency of occurrence (b) of various prey items in the diet of *Mnemiopsis leidyi* in the period 2017–2019 in the Gulf of Trieste. Only prey categories with more than 0.2% of relative abundance and more than 1% of a frequency of occurrence are depicted.

Table 3. Relative abundance (N%) of prey items arranged in higher taxonomical groups in the diet of *Mnemiopsis leidyi* in the period between 2017 and 2019 in the Gulf of Trieste evaluated per single year and altogether.

Prey Taxon	2017	N%	2018	N%	2019	N%	Overall	N%
Diatoms and dinoflagellates	18	1.87	9	2.98	73	3.74	100	3.11
Tintinnina	11	1.14	2	0.66	15	0.77	28	0.87
Ctenophora	40	4.16	8	2.65	127	6.50	175	5.44
Hydrozoa	5	0.52	2	0.66	7	0.36	14	0.44
Annelida	7	0.73	4	1.32	10	0.51	21	0.65
Bivalvia	103	10.71	4	1.32	85	4.36	192	5.97
Gastropoda	34	3.53	1	0.33	51	2.61	86	2.67
Cladocera	68	7.07	3	0.99	177	9.07	248	7.71

Table 3. Cont.

Prey Taxon	2017	N%	2018	N%	2019	N%	Overall	N%
Cirripedia	84	8.73	19	6.29	36	1.84	139	4.32
Copepoda	550	57.17	249	82.45	1345	68.09	2144	66.69
Mysidacea	2	0.21	0	0	0	0	2	0.06
Amphipoda	0	0.00	0	0	1	0.05	1	0.03
Stomatopoda	1	0.10	0	0	0	0	1	0.03
Cumacea	4	0.41	0	0	0	0	4	0.12
Decapoda	1	0.10	0	0	2	0.10	3	0.09
Echinodermata	26	2.70	0	0	14	0.72	40	1.24
Appendicularia	5	0.52	0	0	5	0.26	10	0.31
Teleostei	3	0.31	1	0.33	3	0.15	7	0.22
sum	962	100	302	100	1951	100	3215	100

Copepods emerged as the predominant prey items in the diet of *M. leidyi*, in terms of their frequency of occurrence (Figure 3b). The majority of these were represented by calanoid and cyclopoid nauplii, accounting for 48.2%, followed by the harpacticoid *M. norvegica* at 28.3%, and calanoids at 26.8%. Other notable taxa included bivalve larvae (19.3%), *M. leidyi* itself (18.7%), and the cladoceran *Penilia avirostris* (16.1%).

No other taxonomic group exceeded 10% representation: cladocerans accounted for 8.2%, particularly *P. avirostris*; bivalve larvae made up 6.7%; and cirriped nauplii represented 4.5%. The most frequently preyed upon adult copepod was the harpacticoid *M. norvegica*. The significant presence of copepods, cirriped nauplii, bivalve larvae, tintinnids, and other organisms indicates that *M. leidyi* primarily preys on microzooplankton (size range from 20 to 200 μm).

The highest vacuity index was observed in July and August (Table 2). Copepods constituted the primary food category, accounting approximately from 43.9% to 76.7% of the total diet (Figure 4a). In July, cannibalism comprised nearly one-third of the diet of *M. leidyi*, but this percentage steadily declined through the next months. Regarding dietary diversity, only 17 prey categories were identified in July, while subsequent months revealed between 36 and 46 distinct taxa. This temporal feeding pattern is further illustrated in Figure 4b. The NMDS space and PERMANOVA analysis demonstrated similarities in prey abundance and composition during August, September, and October. These three months exhibited significant differences from July, when the diet of *M. leidyi* was predominantly composed of *M. leidyi*, Calanoida, bivalve larvae, and copepodites.

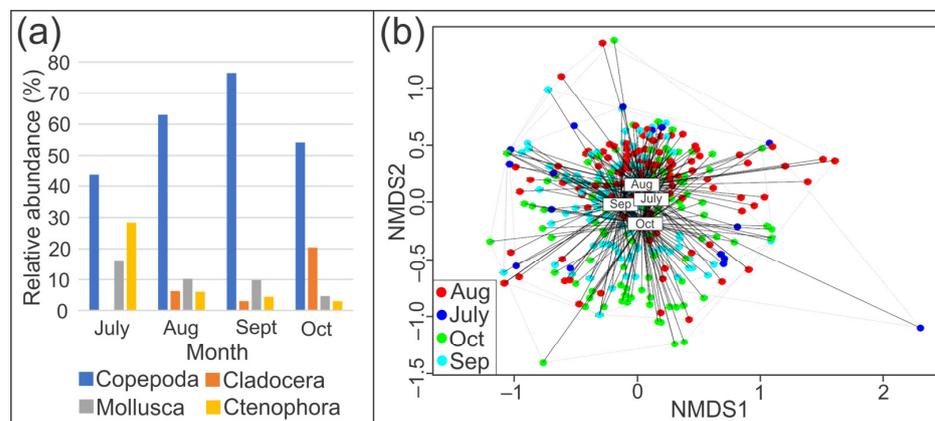


Figure 4. Relative abundance (%) of four main zooplankton groups in the diet of *Mnemiopsis leidyi* in different months in the period 2017–2019 in the Gulf of Trieste (a) and visualization of differences in abundance and compositions of prey (b).

The analysis of various years revealed that only two prey categories—copepods and bivalve larvae—accounted for more than 10% of the diet (see Figure 5a). The proportion of copepods fluctuated between 57.2% and 82.5%, while bivalve larvae ranged from 1.3% to 10.7%. Additionally, cirriped nauplii constituted between 1.8% and 8.7% of the diet. Cannibalism percentages varied from 2.7% to 6.5%.

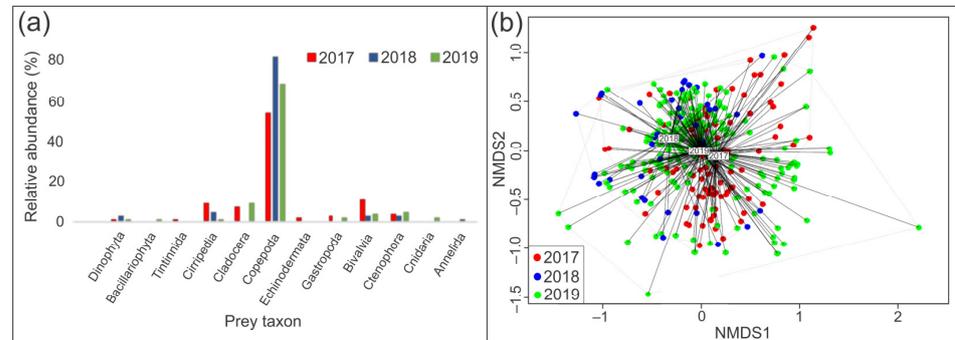


Figure 5. Percentage (%) of prey categories in the diet of *Mnemiopsis leidyi* in years 2017, 2018, and 2019 (a) and the NMDS visualization of prey composition and abundance in different years (b).

However, by comparing the *M. leidyi* diet data of all three years in the multivariate space, no significant differences ($p > \alpha$; $\alpha = 0.05$) in prey abundance and composition were detected between the years 2018 and 2019 (Figure 5b). Instead, some variation in prey composition was noticed by comparing those years against 2017, when following taxonomic groups were significantly more abundant as a prey: *M. norvegica*, ophiopluteus larvae, gastropod larvae, Cyclopoida (indet.), and *Oikopleura* spp.

Moreover, the assumption about the linkage between temporal prey distribution and *M. leidyi* diet was tested with a generalized linear model (GLM). The effect plots in Figure 6 let us conclude that there is a significant negative linear relation (estimate value = -0.39 ; $p = 0.01$; $\alpha = 0.05$) between prey frequency per stomach and empty stomachs. In other words, when the proportion of empty stomachs (=starvation) is higher, the stomachs with food also contain fewer prey items. In addition to that, the temporal prey frequency pattern plays an important (statistically significant) role as well. It increases from July to September, when it reaches maximum value. Again, prey abundance and composition in August, September, and October are comparable, while they differ significantly in July.

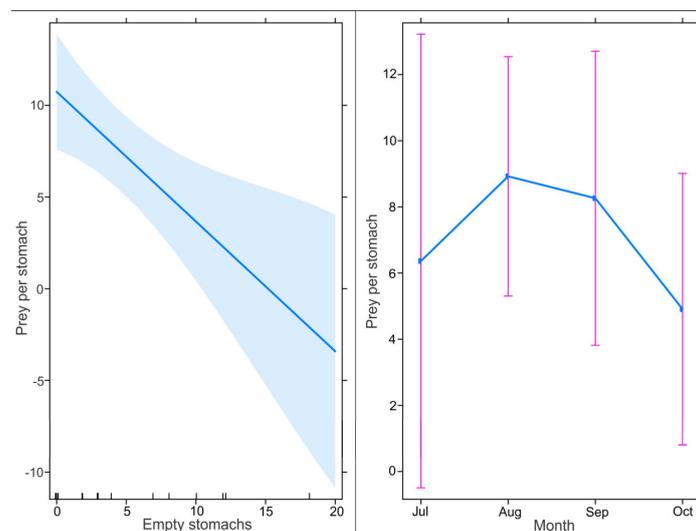


Figure 6. GLM effect plots for the predicting variables of the number of empty stomachs and time (months).

In accordance with the findings in Figure 6, during the starvation period in July, notably smaller individuals of *M. leidyi* were associated with observed cannibalism. These individuals exhibited less fullness in their stomachs, and their diet contained the highest proportion of ctenophores (refer to Figure 7). No significant statistical differences were found among the months of August, September, and October.

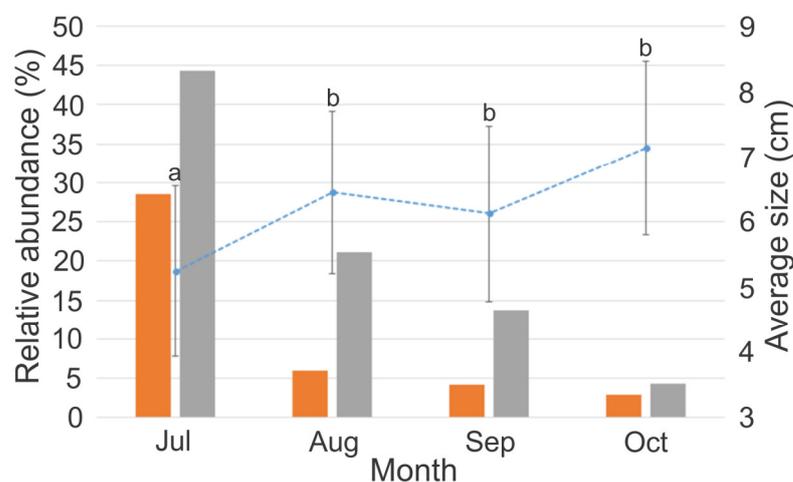


Figure 7. The relationships between *M. leidyi*'s size (blue dashed line; different small letters indicate statistically significant differences in size per month category [$p < \alpha$; $\alpha = 0.05$], error bars = standard deviations), the percentage of ctenophore in their stomachs (orange bars), and vacuity index (grey bars).

The collected specimens of *Mnemiopsis leidyi* varied in size between 3.62 and 8.27 cm, with an average size of 6.17 cm. Although there were differences in the average sizes of specimens across the four relevant months, these differences were not statistically significant (see Figure 7). The smallest ctenophores were observed in July, while the largest were recorded in October. Notably, the size of *M. leidyi* was inversely related to the percentage of ctenophores found in the stomachs and the vacuity index value (refer to Figure 7). In simpler terms, larger specimens observed in autumn exhibited a reduced tendency for cannibalism and had fewer empty stomachs, which were primarily filled with two taxonomic groups: Copepoda and Cladocera.

4. Discussion

As *Mnemiopsis leidyi* occurs in dense aggregations during warm-water periods, this may cause ecological and economic problems in the new environment. These aggregations may impose considerable predatory pressure on the zooplankton organisms (*sensu* [7]). Various studies indicate that *Mnemiopsis* preys on a wide range of zooplankton organisms, ranging in size from less than 100 μm to a maximum 5 mm [3], which was also corroborated in our research.

Dietary studies of predators are essential for understanding their ecological roles within their environments. Nelson [19] studied the food habits of *M. leidyi* in the inland waters of New Jersey, discovering that its primary prey consisted of various crustaceans, as well as gastropod and bivalve larvae. Sullivan and Gifford [26] characterized *M. leidyi* as an omnivorous predator that preys on zooplankton, while Costello et al. [18] noted its broad dietary niche, feeding on microplankton, mesozooplankton, and ichthyoplankton. Our study, with over 500 specimens examined, revealed that in the Gulf of Trieste, *M. leidyi* acts as an opportunistic predator, consuming a significant portion of microzooplankton, particularly copepod nauplii. Microzooplankton, defined by the classification of Sieburth et al. [27] as a group of heterotrophic and mixotrophic organisms ranging from 20 to 200 μm

in size, encompassing various protists, such as ciliates, dinoflagellates, foraminifers, and small metazoans, such as copepod nauplii, some copepodites, and certain meroplanktonic larvae. Budiša et al. [14], who analyzed 155 specimens of *M. leidyi* in nearby waters along the west Istrian coast, reported an average of from 1.2 to 2.5 zooplankton specimens found in the stomachs of the *M. leidyi*, which is significantly lower than our values of from 2.8 to 22.9 prey items per full stomach, with an average of 7.5 prey items. Additionally, the mean vacuity index in our study was considerably lower (61.3% vs. 19.6%). The presence of tintinnine ciliates and dinoflagellates is not surprising, as Sullivan and Gifford [26] previously noted their ingestion by *M. leidyi* larvae. The dominant mesozooplankton taxa in the diet of *M. leidyi* reflects the general situation in the Gulf of Trieste, characterized by late summer period swarms of *Penilia avirostris*, and the significant role of copepods in other seasons [28]. The zooplankton community is notably unique, as it is predominantly composed of a few strictly coastal species of copepods [29].

The portion of larvae and small specimens of *M. leidyi* in the diet was recorded at 5.4%, with a frequency of occurrence of 18.8%, indicating that preying on conspecific specimens is relatively frequent. Cannibalism was particularly noticeable in July, when it constituted nearly one-third of the overall diet. Budiša et al. [14] identified some cydippid larvae in the diet of *M. leidyi*, but did not quantify the extent of cannibalism. Since their study did not take place in July, they may have overlooked the timeframe characterized by the most significant cannibalistic behavior. Javidpour et al. [3,30] proposed that cannibalism is more likely to occur during peak ctenophore densities. Furthermore, the authors suggest that cannibalism serves as a regulatory mechanism for ctenophore population dynamics. By forming large summer blooms, the ctenophores effectively deplete the available prey, displace competitors, and utilize these bloom events to accumulate energy reserves for times of food scarcity. Our study corroborates this pattern.

This study revealed that fish eggs and larvae were infrequently found in the stomachs of *M. leidyi* from the Gulf of Trieste. The occurrence of fish eggs and larvae was negligible, with percentages of 0.12% for eggs and 0.09% for larvae. Similarly, Budiša et al. [14] reported that fish eggs constituted less than 1% of the prey items consumed by *M. leidyi* near the west Istrian coast. These observations align with earlier findings by Hamer et al. [31], who indicated that *M. leidyi* poses little threat to ichthyoplankton, potentially serving only as a competitor. Based on the abovementioned, the direct impact of *M. leidyi* can be considered negligible in the area. On the other hand, large aggregations of *M. leidyi* may influence microzooplankton populations during late summer or autumn. Since microzooplankton is crucial as a food source for the larval stages of certain target fish species, *M. leidyi* could negatively affect those fishery resources. In September copepod nauplii and copepodites may comprise nearly 80% of the ctenophore diet, while in October, a significant portion of prey is represented by cladocerans, particularly *Penilia avirostris*. Among the commercially important species, a single specimen of the pseudozoea of *Squilla mantis* was discovered in the stomach of *M. leidyi*, alongside numerous mytilid bivalve larvae. Given this context, the potential impact of the comb jelly on local mussel mariculture should not be overlooked, as previously noted [32,33].

The rare instances of direct predation on ichthyoplankton by ctenophores may nonetheless significantly affect small fish populations, such as small pelagics, through indirect competitive interactions with fish larvae that compete for mesozooplankton and microzooplankton as food sources (sensu [34] for *Pelagia noctiluca*; [35]). Research by Borme et al. [36] has demonstrated that anchovy (*Engraulis encrasicolus*), a vital fisheries resource, primarily preys on calanoid copepods in the Gulf of Trieste. Budiša et al. [14] noted, that the coinciding timing of *M. leidyi* blooms and shifts in anchovy distribution may be mutually influential. Furthermore, recent findings by Piccardi et al. [37] indicate a decline in landings

within the Venice lagoon, attributed to ctenophore blooms, which are exacerbated by rising water temperatures. These blooms of *M. leidy* appear to be a contributing factor to the decreased landings of *Gobius ophiocephalus* and *Sepia officinalis*, the primary target species in the artisanal fisheries of the lagoon.

To elucidate the real impact of *M. leidy* on the environment of the Gulf of Trieste and the adjacent northern Adriatic Sea, a study examining the competition between small pelagic fishes, particularly anchovy, and *M. leidy* could provide valuable insights into the extent of ctenophore influence on native competitors. It is plausible that the similar feeding habits of *M. leidy* and small pelagics, such as anchovy (*Engraulis encrasicolus*) [36], may result in intense competition. This conclusion aligns with findings by Budiša et al. [14], who noted a declining trend in anchovy abundance in the northern Adriatic coinciding with *M. leidy* blooms in the same region. Additionally, we cannot dismiss the potential for competition for food with *Aurelia* spp., which are prevalent and abundant scyphozoans in the area. However, the peaks in abundance of *Aurelia* and *Mnemiopsis* do not align in the studied area [38]. Evidence from Kertinge Nor cove in Denmark indicates that *A. aurita* can outcompete *M. leidy* for food [39]. In this location, *A. aurita* polyps produce a significant number of ephyrae in early spring, leading to a large population of small medusae [39]. Conversely, the coexistence of both species in another Danish environment, the Limfjorden, has resulted in considerable predation pressure, severely depleting zooplankton stocks [39].

Despite the increasing body of research on *M. leidy* in the Mediterranean and Adriatic Seas, the environmental factors influencing its sporadic presence remain ambiguous. (sensu [40]). Consequently, a long-term monitoring program for *M. leidy* and other carnivorous gelatinous zooplankton, as suggested by Luskov ([38]), is essential. This initiative should encompass investigations into predation impacts to better understand potential competition with other zooplankton predators and their effects on the plankton community. Future research should also examine the competition dynamics between microzooplankton and mesozooplankton predators. Additionally, innovative methods for dietary assessment, such as molecular tools like DNA metabarcoding, should be employed to address the challenges of identifying partially digested prey [1]. However, it is important to note that such tools cannot detect instances of cannibalism.

Author Contributions: Conceptualization, L.L. and B.M.; methodology, L.L. and B.M.; software, L.L. and D.I.; validation, L.L., B.M. and D.I.; formal analysis, L.L. and D.I.; investigation, L.L., B.M. and D.I.; resources, B.M.; data curation, L.L.; writing—original draft preparation, L.L.; writing—review and editing, B.M., A.M., D.L. and D.I.; visualization, L.L. and D.I.; supervision, L.L. and B.M.; project administration, B.M.; funding acquisition, B.M. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Slovenian Ministry of Agriculture, Forestry and Food which financed the project “Overview of the status, assessment of the environmental impact and overview of possible measures to control the population of the non-indigenous species of ctenophoran *Mnemiopsis leidy* in the Slovenian Sea” (project no. 430-79/2018) and Slovenian national research corefunding No. P1-0237 (Coastal Sea Research) and P1-0143 (Cycling of substances in the environment, mass balances, modelling of environmental processes and risk assessment). The authors acknowledge also the role of the research project “Development of Research Infrastructure for the International Competitiveness of the Slovenian RRI Space-RI-SI-LifeWatch”, co-financed by the Republic of Slovenia, Ministry of Education, Science and Sport and the European Union from the European Regional Development Fund, as well as, the Research Program “Slovene Identity and Cultural Awareness in Linguistic and Ethnic Contact Areas in Past and Present (P6-0372)”, which was financially supported by the Slovenian Research Agency.

Data Availability Statement: The raw data supporting the conclusions of this article will be made available by the authors on request.

Acknowledgments: We would like to express our gratitude to our colleagues Tihomir Makovec, Leon Lojze Zamuda, Domen Trkov, Tina Mirt, and Milijan Šiško for their help during sampling operations. Special thanks also to anonymous reviewers who have improved the quality of the manuscript.

Conflicts of Interest: The authors declare no conflicts of interest.

References

- Schroeder, A.; Camatti, E.; Pansera, M.; Pallavicini, A. Feeding Pressure on Meroplankton by the Invasive Ctenophore *Mnemiopsis leidyi*. *Biol. Invasions* **2023**, *25*, 2007–2021. [CrossRef]
- Riisgård, H.U.; Bøttiger, L.; Madsen, C.; Purcell, J. Invasive Ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark) in Late Summer 2007—Assessment of Abundance and Predation Effects. *Aquat Invasions* **2007**, *2*, 395–401. [CrossRef]
- Javidpour, J.; Molinero, J.C.; Lehmann, A.; Hansen, T.; Sommer, U. Annual Assessment of the Predation of *Mnemiopsis leidyi* in a New Invaded Environment, the Kiel Fjord (Western Baltic Sea): A Matter of Concern? *J. Plankton Res.* **2009**, *31*, 729–738. [CrossRef]
- Shiganova, T.A.; Sommer, U.; Javidpour, J.; Molinero, J.C.; Malej, A.; Kazmin, A.S.; Isinibilir, M.; Christou, E.; Siokou-Frangou, I.; Marambio, M.; et al. Patterns of Invasive Ctenophore *Mnemiopsis leidyi* Distribution and Variability in Different Recipient Environments of the Eurasian Seas: A Review. *Mar. Environ. Res.* **2019**, *152*, 104791. [CrossRef]
- Purcell, J.; Nemazie, D.; Dorsey, S.; Houde, E.; Gamble, J. Predation Mortality of Bay Anchovy *Anchoa mitchilli* Eggs and Larvae Due to Scyphomedusae and Ctenophores in Chesapeake Bay. *Mar. Ecol. Prog. Ser.* **1994**, *114*, 47–58. [CrossRef]
- Shiganova, T.A. Invasion of the Black Sea by the Ctenophore *Mnemiopsis leidyi* and Recent Changes in Pelagic Community Structure. *Fish. Oceanogr.* **1998**, *7*, 305–310. [CrossRef]
- Purcell, J.E.; Shiganova, T.A.; Decker, M.B.; Houde, E.D. The Ctenophore *Mnemiopsis* in Native and Exotic Habitats: US Estuaries versus the Black Sea Basin. *Hydrobiologia* **2001**, *451*, 145–176. [CrossRef]
- Kideys, A.; Roohi, A.; Bagheri, S.; Finenko, G.; Kamburska, L. Impacts of Invasive Ctenophores on the Fisheries of the Black Sea and Caspian Sea. *Oceanography* **2005**, *18*, 76–85. [CrossRef]
- Kamakin, A.M.; Khodorevskaya, R.P. Impact of the Alien Species *Mnemiopsis leidyi* A. Agassiz, 1865 on Fish of the Caspian Sea. *Inland Water Biol.* **2018**, *11*, 173–178. [CrossRef]
- Stoltenberg, I.; Mittermayer, F.; Clemmesen, C.; Dierking, J.; Javidpour, J. Predation on Baltic Sea Yolk-Sac Herring Larvae (*Clupea harengus*) by the Invasive Ctenophore *Mnemiopsis leidyi*. *Fish. Res.* **2024**, *273*, 106973. [CrossRef]
- Shiganova, T.; Malej, A. Native and Non-Native Ctenophores in the Gulf of Trieste, Northern Adriatic Sea. *J. Plankton Res.* **2008**, *31*, 61–71. [CrossRef]
- Malej, A.; Tirelli, V.; Lučić, D.; Paliaga, P.; Vodopivec, M.; Goruppi, A.; Ancona, S.; Benzi, M.; Bettoso, N.; Camatti, E.; et al. *Mnemiopsis leidyi* in the Northern Adriatic: Here to Stay? *J. Sea Res.* **2017**, *124*, 10–16. [CrossRef]
- Mavrič, B.; Lipej, L.; Šiško, M.; Kogovšek, T. Review of the Status, Evaluation of the Impact on the Environment and Survey of Possible Measures to Control the Population of the Alien Species *Mnemiopsis leidyi* in the Slovenian Sea. Marine Biology Station NIB: Piran, Slovenia, 2019; Available online: <https://www.vliz.be/nl/imis?module=ref&refid=320344&printversion=1&dropIMISitle=1> (accessed on 26 January 2025).
- Budiša, A.; Paliaga, P.; Juretič, T.; Lučić, D.; Supić, N.; Pasarić, Z.; Djakovac, T.; Mladinić, M.; Dadić, V.; Tičina, V. Distribution, Diet and Relationships of the Invasive Ctenophore *Mnemiopsis leidyi* with Anchovies and Zooplankton, in the Northeastern Adriatic Sea. *Mediterr. Mar. Sci.* **2021**, *22*, 827. [CrossRef]
- Costello, J.H.; Sullivan, B.K.; Gifford, D.J.; Van Keuren, D.; Sullivan, L.J. Seasonal Refugia, Shoreward Thermal Amplification, and Metapopulation Dynamics of the Ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Limnol. Oceanogr.* **2006**, *51*, 1819–1831. [CrossRef]
- Marchessaux, G.; Faure, V.; Chevalier, C.; Thibault, D. Refugia Area for the Ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in the Berre Lagoon (Southeast France): The Key to Its Persistence. *Reg Stud Mar Sci* **2020**, *39*, 101409. [CrossRef]
- Costello, J.; Mianzan, H.W. Sampling Field Distributions of *Mnemiopsis leidyi* (Ctenophora, Lobata): Planktonic or Benthic Methods? *J. Plankton Res.* **2003**, *25*, 455–459. [CrossRef]
- Costello, J.H.; Bayha, K.M.; Mianzan, H.W.; Shiganova, T.A.; Purcell, J.E. Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) from a Native to an Exotic Species: A Review. *Hydrobiologia* **2012**, *690*, 21–46. [CrossRef]
- Nelson, T.C. On the Occurrence and Food Habits of Ctenophores in New Jersey Inland Coastal Waters. *Biol. Bull.* **1925**, *48*, 92–111. [CrossRef]
- Trégouboff, G.; Rose, M. *Manuel de Planctonologie Méditerranéenne*, 1st ed.; Centre National de la Recherche Scientifique: Paris, France, 1957; Volume 1.
- Trégouboff, G.; Rose, M. *Manuel de Planctonologie Méditerranéenne*, 1st ed.; Centre National de la Recherche Scientifique: Paris, France, 1957; Volume 2.

22. Newell, G.E.; Newell, R.C. *Marine Plankton: A Practical Guide*, 1st ed.; Hutchinson Educational: London, UK, 1963.
23. Hyslop, E.J. Stomach Contents Analysis—A Review of Methods and Their Application. *J. Fish. Biol.* **1980**, *17*, 411–429. [[CrossRef](#)]
24. Oksanen, J.; Kindt, R.; Legendre, P.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; Stevens, M.H.H.; Wagner, H. The Vegan Package. Community Ecology Package. 2023. Available online: <https://github.com/vegandevs/vegan> (accessed on 30 November 2024).
25. R Core Team. *R A Language and Environment for Statistical Computing*; The R Foundation: Vienna, Austria, 2023.
26. Sullivan, L.J.; Gifford, D.J. Diet of the Larval Ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). *J. Plankton Res.* **2004**, *26*, 417–431. [[CrossRef](#)]
27. Sieburth, J.M.; Smetacek, V.; Lenz, J. Pelagic Ecosystem Structure: Heterotrophic Compartments of the Plankton and Their Relationship to Plankton Size Fractions 1. *Limnol. Oceanogr.* **1978**, *23*, 1256–1263. [[CrossRef](#)]
28. Cataletto, B.; Feoli, E.; Fonda Umani, S.; Cheng-Yong, S. Eleven Years of Time-Series Analysis on the Net-Zooplankton Community in the Gulf of Trieste. *ICES J. Mar. Sci.* **1995**, *52*, 669–678. [[CrossRef](#)]
29. Specchi, M.; Fonda Umani, S. Copepods of the Gulf of Trieste. *Thalass. Jugosl.* **1983**, *19*, 339–341.
30. Javidpour, J.; Molinero, J.-C.; Ramírez-Romero, E.; Roberts, P.; Larsen, T. Cannibalism Makes Invasive Comb Jelly, *Mnemiopsis leidyi*, Resilient to Unfavourable Conditions. *Commun. Biol.* **2020**, *3*, 212. [[CrossRef](#)] [[PubMed](#)]
31. Hamer, H.H.; Malzahn, A.M.; Boersma, M. The Invasive Ctenophore *Mnemiopsis leidyi*: A Threat to Fish Recruitment in the North Sea? *J. Plankton Res.* **2011**, *33*, 137–144. [[CrossRef](#)]
32. Nowaczyk, A.; Vincent, D.; Curd, A.; Antajan, E.; Massé, C. Invasion along the French Atlantic Coast by the Non-Native, Carnivorous Planktonic Comb Jelly *Mnemiopsis leidyi*: Can an Impact on Shellfish Farming Be Expected? *Bioinvasions Rec.* **2023**, *12*, 371–384. [[CrossRef](#)]
33. McNamara, M.E.; Lonsdale, D.J.; Cerrato, R.M. Shifting Abundance of the Ctenophore *Mnemiopsis leidyi* and the Implications for Larval Bivalve Mortality. *Mar. Biol.* **2010**, *157*, 401–412. [[CrossRef](#)]
34. Milisenda, G.; Rossi, S.; Vizzini, S.; Fuentes, V.L.; Purcell, J.E.; Tilves, U.; Piraino, S. Seasonal Variability of Diet and Trophic Level of the Gelatinous Predator *Pelagia noctiluca* (Scyphozoa). *Sci. Rep.* **2018**, *8*, 12140. [[CrossRef](#)]
35. Camatti, E.; Acri, F.; De Lazzari, A.; Nurra, N.; Pansera, M.; Schroeder, A.; Bergamasco, A. Natural or Anthropogenic Variability? A Long-Term Pattern of the Zooplankton Communities in an Ever-Changing Transitional Ecosystem. *Front. Mar. Sci.* **2023**, *10*, 1176829. [[CrossRef](#)]
36. Borme, D.; Tirelli, V.; Brandt, S.; Fonda Umani, S.; Arneri, E. Diet of *Engraulis encrasicolus* in the Northern Adriatic Sea (Mediterranean): Ontogenetic Changes and Feeding Selectivity. *Mar. Ecol. Prog. Ser.* **2009**, *392*, 193–209. [[CrossRef](#)]
37. Piccardi, F.; Poli, F.; Sguotti, C.; Tirelli, V.; Borme, D.; Mazzoldi, C.; Barausse, A. Assessing the Impact of the Invasive Ctenophore *Mnemiopsis leidyi* on Artisanal Fisheries in the Venice Lagoon: An Interdisciplinary Approach. *Hydrobiologia* **2024**, 1–19. [[CrossRef](#)]
38. Hočevár, S.; Malej, A.; Boldin, B.; Purcell, J. Seasonal Fluctuations in Population Dynamics of *Aurelia aurita* Polyps in Situ with a Modelling Perspective. *Mar. Ecol. Prog. Ser.* **2018**, *591*, 155–166. [[CrossRef](#)]
39. Riisgård, H.U.; Barth-Jensen, C.; Madsen, C. High Abundance of the Jellyfish *Aurelia aurita* Excludes the Invasive Ctenophore *Mnemiopsis leidyi* to Establish in a Shallow Cove (Kertinge Nor, Denmark). *Aquat. Invasions* **2010**, *5*, 347–356. [[CrossRef](#)]
40. Riisgård, H.U. Invasion of Danish and Adjacent Waters by the Comb Jelly *Mnemiopsis leidyi*—10 Years After. *Open J. Mar. Sci.* **2017**, *7*, 458–471. [[CrossRef](#)]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.