Diet composition and some observations on the feeding ecology of the rhizostome *Rhopilema nomadica* in Israeli coastal waters

Z. Kuplik1,2 and D. L. Angel3

1Department of Maritime Civilizations, Charney School of Marine Sciences & Recanati Institute for Maritime Studies, University of Haifa, Mt. Carmel, Haifa 31905, Israel and 2Department of Biodiversity and Conservation Biology, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa

Abstract

Since the mid-1980s, swarms of the rhizostome *Rhopilema nomadica* have been an annual phenomenon in Israeli Mediterranean coastal waters during the summer months. Despite its annual prominence and the potential impact on food webs and ecosystem services, studies concerning its feeding ecology and its interactions with other biota in the marine food web have not been conducted. During summer 2015 gut contents of 41 *R. nomadica* were analysed as well as ambient plankton assemblages. More than 60% of the medusae diet was found to consist of microzooplankton <150 μm. Size correlations revealed that larger *R. nomadica* consumed faster swimming prey while smaller medusae relied more on the slower swimming taxa. The medusan diet reflected most of the ambient plankton taxa, but no statistically significant correlations between the relative abundance in diet and ambient plankton were found. As summer progressed, there was a gradual decrease in both mean medusa bell diameter (from 42.2–16 cm) and integrity of feeding structures. These findings suggest that *R. nomadica*, at least at the time of its appearance in Israeli coastal waters, may exert less predatory pressure on the plankton than we might otherwise expect.

Introduction

Over the past three decades there has been an apparent increase in the occurrence and spread of jellyfish outbreaks (Legovic, 1987; Mills, 2001; Attrill et al., 2007; Brotz et al., 2012). Whether this increase is a global trend or a phenomenon restricted to certain areas, the ecological consequences associated with the presence of large numbers of these voracious planktivores may be extensive. Predation on fish eggs and larvae (Purcell, 1985; Cowan & Houde, 1993; Paradis et al., 1996; Cao et al., 2015; Tilves et al., 2016) and competition with fish for zooplankton (Purcell & Arai, 2001; Purcell & Sturdevant, 2001; Brodeur et al., 2008) were shown to have both top-down and bottom-up effects which could lead to ecosystems dominated by jellyfish (Lynam et al., 2006). Moreover, massive consumption of zooplankton by medusae could potentially alter phytoplankton dynamics (Stibor et al., 2004; Moller & Riisgard, 2007) and even trigger a cascade effect on the food web, all the way down to the microbial communities (Riemann et al., 2006).

Since the mid-1980s, the Mediterranean coastal waters of Israel have experienced jellyfish swarms on an annual basis, dominated by the scyphomedusa *Rhopilema nomadica*. These swarms, of what is believed to be a Lessepsian migrant (Spanier & Galil, 1991), are estimated to consist of hundreds of thousands of individuals per square nautical mile and many of the medusae are large, weighing as much as 40 kg, with bells up to 80 cm in diameter (Lotan et al., 1992). In general, these swarms appear towards the end of May/beginning of June and disappear by the end of July/beginning of August (Edelist et al., 2020). This abundance has a negative effect on many coastal and marine operations, including local fisheries (Nakar, 2011; Angel et al., 2016), industrial enterprises such as power and desalination plants (Rilov & Galil, 2009) and recreational activities (Ghermandi et al., 2015). Despite its annual prominence in Israeli Mediterranean coastal waters and the potential impact medusae may have on food webs, studies concerning the ecology of *R. nomadica* are few and have focused mainly on its life cycle and expanding distribution (Lotan et al., 1992, 1994; Kideys & Gucu, 1995; Yahia et al., 2013). Moreover, studies concerning its interactions with other members of the marine food web have not been conducted. This study is a first attempt to characterize *R. nomadica*’s feeding patterns and to explore its role within the Israeli Mediterranean coastal food web. An assessment of *R. nomadica*’s diet will be presented and compared with the composition of major ambient plankton taxa and considered with respect to this medusa’s proliferation in a highly oligotrophic environment such as the Levant.

Materials and methods

Medusa samplings and processing

Gut contents of 41 specimens of the scyphomedusa *Rhopilema nomadica* (bell diameter size range: 10–57 cm) were sampled during summer 2015. Sampling surveys began shortly after
medusae were first observed (end of May) and ended when they became scarce (end of July). Only individuals that appeared intact were sampled. Six sampling surveys on six different dates were executed 0.5–1 nautical mile offshore Mikhmoret, located on the central Mediterranean coastline of Israel (32°24′23″N 34°52′24″E). All samplings took place in the morning hours, 07–11:00 am, by means of a motor boat. Bottom depth at the sampling sites ranged from 12–35 m.

Medusae were captured individually and brought onboard by means of a 60 cm diameter dip net. Size (bell diameter, ±1 cm) and wet weight (±0.1 kg) of each medusa were recorded. Gut content of each medusa was collected immediately after bringing the jellyfish onboard. Sampling of the jellyfish gut to retrieve its prey was performed through the aboral surface; by dissecting and carefully removing the apex of the umbrella, thereby exposing the gastric pouches. The latter were then rinsed with 50 μm filtered seawater via squirt bottle and the retrieved content was fixed immediately in buffered formalin (4% v/v; final concentration). The fixed samples were stored in the laboratory at room temperature until processed for taxonomic classification and abundances, within 4 months.

Gut content composition was defined as the relative abundance (%) of each taxon out of total prey items retrieved from the pouches (taxa abundances and comparisons between medusae were based on these relative abundances). Extraction of food items from the gut was performed in a uniform manner for all medusae and was assumed to reliably represent the diet composition of each individual.

**Plankton tows**

On each of the six sampling excursions, a horizontal plankton tow was performed to characterize the local ambient plankton population and compare its taxonomic composition with that of the gut contents. Plankton was sampled using a 50 cm diameter (~0.2 m² opening), 150 μm mesh size plankton net, towed at ~1 knot, at depths of 2–10 m. Duration of each tow was ~10 min. A calibrated General Oceanics flowmeter was used to calculate the volume of water filtered.

Samples were fixed with buffered formalin (4% v/v final concentration) and stored at room temperature until they were processed for taxonomic classification, within 4 months.

Shortly before sorting, each plankton sample was concentrated onto a 100 μm mesh, rinsed with tap water to eliminate the fixative, and was then transferred to 70% EtOH.

Both gut contents and plankton samples were sorted using a 15 μl plexiglass counting chamber (Bogorov design), super-fine sorting needles and a Motic SMZ-171 stereomicroscope. Organisms were identified and classified to the lowest possible taxonomic level. Representative taxa were measured and photographed via Moticam 2 digital camera and software. Plankton from the tows were sub-sampled, using a 5 ml Stempel pipette, and a minimum of 500 plankters per tow (~3 or more sub-samples) were sorted and counted to determine their relative abundances.

**Histological analysis**

Male and female gonadal tissues were sampled and fixed in 4% formaldehyde/seawater solution for 24 h, after which samples were rinsed in running tap water, dehydrated in 70% ethanol and embedded in paraffin. Histological cross sections (7 μm thick) were cut with a Shandon M1R rotary microtome and were stained with Gill’s haematoxylin and eosin. The vertical distance between each cross section was more than 300 μm. Five histological slides were prepared for each sample containing several slices of the gonadal tissues. The histological sections were examined under a light microscope (Olympus BX43) fitted with a digital camera (Olympus DP72).

**Data analysis**

In order to test whether the number of *R. nomadica* analysed was sufficient for describing its diet, a cumulative prey type curve was generated by plotting the cumulative number of prey types identified in the medusan guts against the cumulative number of gut contents analysed. An adequate sample size is assumed when the curve approaches an asymptote (Hurtubia, 1973; Ferry & Cailliet, 1996). PRIMER-e v6 software was used to generate the curve (Chao1).

A Spearman’s rank-order correlation was run to assess: (1) the relationship between the relative abundance of various prey types ≥150 μm ingested by the medusae (% prey type out of total >150 μm prey items) and their relative abundance in the plankton (% prey type in the plankton samples) and (2) the relationship between size of the medusa (bell diameter) and the relative abundance of each of its major dietary components.

After ensuring normality (Shapiro–Wilk test) and equality of variances (Levene’s test), one-way ANOVA was used to determine whether there are any statistically significant differences between the number of ingested prey groups on the different sampling dates.

To test the null hypothesis that there was no significant difference in prey composition among medusae of varying bell diameter, an analysis of similarity (ANOSIM) was performed (Clarke, 1993). Prey groups which contributed most to the dissimilarities between diet compositions were identified through similarity percentages (SIMPER) (Clarke, 1993). Diet compositions were visualized by means of non-parametric multidimensional scaling (nMDS).

**Results**

**Gut content composition**

A total of 15,192 prey items were found in 41 gut contents and sorted into 28 different prey types. Bell diameter of the sampled medusae ranged from 10–57 cm and wet weight from 0.11–9.1 kg (Table 1). Cumulative prey type curves plotted for the gut contents indicated that the overall number of gut contents sampled was sufficient for a reliable characterization of *Rhopilema nomadica*’s diet (Figure 1). In fact, the curve starts to plateau after 5 gut contents, which was the minimum number sampled on a given date.

While processing jellyfish gut contents, we found that *R. nomadica* feeds primarily on micro-planktonic prey <150 μm (65% of total prey ingested). In order to compare diet composition to that of plankton sampled by means of a 150 μm mesh net, prey items were sub-divided into two size groups, <150 and >150 μm, and all comparisons with plankton composition (e.g. gut content analysis, below) were performed on the latter.

On average, 12 prey types were found to comprise ≥1% of the medusae’s diet (Table 2), and 10 prey types were regular dietary components found in medusae guts on all sampling dates (Supplementary Table S1).

Of the 12 prey types, four groups contributed more than 70% of the pooled *R. nomadica* diet: bivalves (<150 μm), various eggs (<150 μm), calanoid and cyclopoid copepods (all >150 μm), and copepod nauplii (<150 μm), comprising 24, 18, 17 and 14% of the diet, respectively. Occasional prey, found at a mean overall relative abundance of less than 1% in the gut contents, included ascidian larvae, nematodes, hydromedusae and platyhelminthes (Supplementary Table S1).
Plankton composition

Plankton samples were sorted into 22 organism groups, of which on average 11 were found to comprise ≥1% of the plankton assemblage (Table 3). The four most abundant groups: calanoid, cyclopoid and harpacticoid copepods, diatoms and radiolarians comprised more than 80% of the plankton. Taxa found in low abundances (<1%) included various unidentified eggs, polychaetes, hydromedusae and ciliates.

Gut content analysis

The prey consumed by the medusae reflect most of the taxa found in the plankton (Supplementary Table S2), but there was no

Table 1. Summary of the data collected for gut content analyses on six sampling excursions during June–July 2015

| Sampling date | N (sampled medusae) | Mean bell diameter, cm (± SD) | Mean wet weight, kg (± SD) | Mean no. of prey medusa−1 (± SD) | Mean plankton abundance, ind. m−3 (± SD) | Seawater temperature (°C) |
|---------------|---------------------|------------------------------|---------------------------|----------------------------------|----------------------------------------|--------------------------|
| 16/6/15       | 6                   | 42.2 ± 12.5                  | 5.4 ± 3.1                 | 114 ± 94                         | 3329 ± 369                             | 25.5                     |
| 17/6/15       | 6                   | 40.5 ± 10.1                  | 5.0 ± 2.5                 | 220 ± 164                        | 8654 ± 450                             | 25.7                     |
| 01/7/15       | 6                   | 28.2 ± 7.5                   | 2.1 ± 1.1                 | 537 ± 428                        | 2813 ± 122                             | 26.5                     |
| 05/7/15       | 9                   | 24.2 ± 5.0                   | 1.5 ± 1.0                 | 385 ± 344                        | 2536 ± 156                             | 27.3                     |
| 15/7/15       | 9                   | 18.2 ± 7.2                   | 0.8 ± 0.9                 | 603 ± 367                        | 14,566 ± 1250                          | 27.5                     |
| 22/7/15       | 5                   | 16.0 ± 2.9                   | 0.5 ± 0.2                 | 217 ± 99                         | 13,803 ± 1537                          | 28.1                     |

SD, standard deviation; ind., individuals.

Table 2. Relative abundance (% ± standard deviation) of the 12 prey types found in R. nomadica’s gut contents which comprised ≥1% of its diet

| Sampling Dates/Taxa | 16.6.2015 | 17.6.2015 | 17.7.2015 | 5.7.2015 | 15.7.2015 | 22.7.2015 | Mean ± SD |
|---------------------|-----------|-----------|-----------|----------|-----------|-----------|-----------|
| Bivalves (<150 μm)  | 23 ± 19   | 11 ± 9    | 26 ± 9    | 34 ± 18  | 41 ± 11   | 10 ± 9    | 24 ± 13   |
| Various eggs (<150 μm) | 15 ± 19 | 9 ± 7     | 24 ± 8    | 22 ± 10  | 24 ± 8    | 11 ± 13   | 18 ± 7    |
| Calanoids and cyclopoids (>150 μm) | 27 ± 14 | 18 ± 6 | 13 ± 9 | 11 ± 9 | 2 ± 1 | 30 ± 9 | 17 ± 11 |
| Copepod nauplii (<150 μm) | 6 ± 10 | 39 ± 20 | 9 ± 4 | 11 ± 6 | 12 ± 9 | 6 ± 2 | 14 ± 12 |
| Harpacticoids (>150 μm) | 3 ± 3 | 4 ± 1 | 2 ± 1 | 6 ± 4 | 4 ± 2 | 19 ± 8 | 6 ± 6 |
| Pteropods (Cresseis sp.) (>150 μm) | 0 | 0 | 16 ± 7 | 5 ± 5 | 2 ± 1 | 13 ± 12 | 6 ± 7 |
| Gastropods (>150 μm) | 15 ± 12 | 4 ± 4 | 2 ± 1 | 7 ± 5 | 2 ± 1 | 4 ± 1 | 6 ± 5 |
| Appendicularians (>150 μm) | 5 ± 5 | 5 ± 1 | 3 ± 3 | <1 | <1 | 3 ± 2 | 3 ± 2 |
| Diatoms (>150 μm) | <1 | 1 ± 1 | <1 | <1 | 9 ± 3 | 1 ± 2 | 2 ± 4 |
| Bivalves (>150 μm) | 1 ± 1 | 1 ± 0 | 1 ± 0 | 2 ± 1 | 2 ± 1 | 1 ± 0 | 1 ± 1 |
| Ciliates (<150 μm) | 0 | 6 ± 13 | <1 | <1 | <1 | 0 | 1 ± 2 |
| Copepod nauplii (>150 μm) | <1 | 2 ± 1 | <1 | 1 ± 0 | 1 ± 0 | <1 | 1 ± 1 |

Taxa presented in descending order of mean relative abundance of pooled contents (last column).
correlation between the cumulative gut content and the plankton tow yield of the major dietary items (Figure 2, Table 4). Notably radiolarians, the third most abundant taxa in the plankton, were not observed at all in the gut contents.

A shift in the population, from large to smaller medusae (i.e. smaller bell diameter), was recorded during the sampling period (Figure 3A). Larger specimens dominated the population at the beginning of the summer and the relative abundance of smaller medusae increased towards the last sampling excursion. Whereas the change in medusa bell diameter had no significant impact on the number of prey groups comprising the medusa diet (Figure 3B), positive and negative correlations were found between bell diameter and the relative abundance of a few of the ‘most consumed’ taxa in the GC (Table 5). Large mesozooplankton prey, such as appendicularians and copepods, were captured and ingested more frequently by larger medusae, while smaller medusae fed more on the small prey (e.g. bivalve larvae and small diatoms). Whereas there was a decrease in mean size of the medusae, the abundance in the plankton of the four most contributing taxa to the R. nomadica diet remained relatively stable for the entire study (Figure 4).

It was also observed that the medusa population transitioned from one with intact (oral arms and appendages) individuals to a population that consisted of a larger number of medusae with damaged bells, reduced oral arms and even complete loss of external as well as internal feeding structures (Supplementary Figure S1). Almost all of the medusae had gonads, most of which were in advanced stages of sexual maturity (Figure 5). It is noteworthy that despite the apparent physical deterioration, the medusae were swimming vigorously. Based on these observations (size and physiological state), medusae were divided

### Table 3. The relative abundance (% ± standard deviation) of plankton groups found within the plankton samples which comprised ≥1% of total plankton assemblage

| Taxa/Sampling Dates | 16.6.2015 | 17.6.2015 | 17.7.2015 | 5.7.2015 | 15.7.2015 | 22.7.2015 | Mean ± SD |
|---------------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| Calanoids and cyclopoids | 74 ± 6 | 34 ± 4 | 71 ± 1 | 77 ± 4 | 18 ± 1 | 60 ± 4 | 56 ± 24 |
| Diatoms | 1 ± 1 | 2 ± 0 | 10 ± 0 | 2 ± 1 | 42 ± 6 | <1 | 10 ± 16 |
| Radiolarians | 2 ± 2 | 46 ± 2 | 0 | 5 ± 4 | 4 ± 1 | 0 | 9 ± 18 |
| Harpacticoids | <1 | 4 ± 1 | 1 ± 1 | 12 ± 2 | 9 ± 3 | 14 ± 3 | 7 ± 6 |
| Appendicularians | 5 ± 3 | 5 ± 2 | <1 | <1 | 3 ± 2 | 6 ± 2 | 3 ± 2 |
| Cladocerans | 8 ± 3 | <1 | <1 | <1 | 3 ± 1 | 5 ± 3 | 3 ± 3 |
| Dinoflagellates | <1 | 3 ± 2 | 1 ± 0 | <1 | 6 ± 3 | 6 ± 2 | 3 ± 3 |
| Bivalves | <1 | 1 ± 0 | <1 | <1 | 8 ± 3 | 1 ± 2 | 2 ± 3 |
| Gastropods | 4 ± 2 | <1 | 1 ± 0 | <1 | 2 ± 1 | 3 ± 2 | 2 ± 1 |
| Heliozoans | 0 | 0 | 11 ± 2 | 0 | 0 | 0 | 2 ± 5 |
| Copepod nauplii | <1 | 2 ± 1 | 0 | <1 | <1 | 1 ± 2 | 1 ± 1 |

Taxa presented in descending order of mean relative abundance of the plankton groups. <1 represents relative abundance of less than 1%. Taxa in bold represent prey found within R. nomadica’s gut contents at a mean relative abundance ≥1%. Standard deviation presented for each sampling date was calculated through counting a minimum of three sub-samples of the date’s sample.

### Table 4. Correlation test results (Spearman’s rho) between prey types >150 μm ingested by R. nomadica (comprising ≥1% of its total diet composition) and their relative abundance in plankton samples

| Taxa | Correlation coefficient | P |
|------|-------------------------|---|
| Calanoids and cyclopoids | 0.31 | 0.54 |
| Harpacticoids | 0.77 | 0.07 |
| Appendicularians | 0.37 | 0.47 |
| Bivalves | 0.09 | 0.87 |
| Pteropods | 0.51 | 0.30 |
| Copepod nauplii | 0.09 | 0.87 |

P (two-tailed) significance <0.05.
for further analysis into three size groups, each group representing two sampling dates: ≥40.5 cm (N = 12; 16/06 and 17/06), 18.2–40.5 cm (N = 15; 01/07 and 05/07) and ≤18.2 cm (N = 14; 15/07 and 22/07).

A non-parametric multidimensional scaling (nMDS) and analysis of similarity (ANOSIM) of the gut content samples, where bell diameter size group is the independent factor (Figure 6, Table 6) indicates that significant dissimilarities exist between gut content compositions (P < 0.05). Pteropods, copepod nauplii and calanoid and cyclopoid copepods were found to contribute most to the observed differences.

Discussion

The rhizostome Rhopilema nomadica has been described as one of the '100 worst invasive species in the Mediterranean' (Streftaris & Zenetos, 2006). Despite its negative impact on human activities and interests along the Israeli coast, information concerning its ecology is limited and, in this regard, the results presented here are the first to describe its diet and its possible impacts on the ecosystem.

The first notable observation that emerged from examination of R. nomadica’s gut contents was the size distribution of the ingested prey. In five of the six excursions, more than 60% of the identified prey in the medusan gut were smaller than 150 μm (Table 2, Supplementary Table S1). These findings are not unusual: although scyphomedusae are known to be opportunistic predators (Larson, 1987; Brewer, 1989; Ishii & Tanaka, 2001) able to consume a wide variety of zooplanktonic prey that they encounter, their feeding preferences may vary greatly. While members of the Semaeostomeae (e.g. Pelagia noctiluca, Aurelia aurita and Cyanea capillata) are able to consume prey larger than several millimetres, including large copepods and fish larvae (Purcell, 2003; Purcell et al., 2014; Cao et al., 2015), rhizostomes feed mainly on microplankton (20–200 μm), including larval zooplankon and even small taxa such as ciliates (Liu et al., 2011).

This size-dependent prey selectivity is probably related to the anatomy of the feeding structures of the Rhizostomeae (Larson, 1991; Lee et al., 2008). Whereas semaeostome medusae have a flexible central mouth opening which enables them to ingest even relatively large prey, rhizostome medusae lack a defined

Table 5. Correlation test results (Spearman’s rho) between size (bell diameter) of R. nomadica specimen and the relative abundance (%) of major taxa found in their gut content

| Taxa                             | Correlation coefficient | P  |
|----------------------------------|------------------------|----|
| Calanoids and cyclopoids (>150 μm) | 0.34                   | 0.03 |
| Appendicularians (>150 μm)       | 0.54                   | <0.01 |
| Bivalves (>150 μm)               | -0.34                  | 0.03 |
| Diatoms (<150 μm)                | -0.40                  | 0.01 |
| Bivalves (>150 μm)               | -0.34                  | 0.03 |
| Pteropods (>150 μm)              | -0.34                  | 0.03 |
| Harpacticoids (>150 μm)          | -0.32                  | 0.04 |

P (two-tailed) significance <0.05.
mouth. Instead, ciliated grooves located at the distal end of their branched oral arms transfer the captured prey into a set of canals towards the gastric cavities (Smith, 1934). Stereomicroscope images show that the diameter of the openings of the ciliated grooves and the adjacent canals extending towards the gastric cavities in *R. nomadica* are 100–200 μm wide (Figure 7). It is likely that these ciliated openings can expand to a certain extent since larger prey were also found in the gut contents. Nevertheless, prey at the micro-size scale is probably 'preferred' due to the physical constraints of the feeding structures.

A diet similar to the one described here for *R. nomadica* was also described by Liu et al. (2011), where larvae and early developmental stages of crustaceans and molluscs comprised most of the diet of *Rhopilema esculentum* in South-east Asian waters. In comparison to the dominance of zooplankton in both *Rhopilema* spp. diets, *Rhizostoma pulmo*, studied at the Mar Menor coastal lagoon in Spain (Mediterranean waters), consumed mainly microphytoplankton (Perez-Ruzafa et al., 2002). While it is only reasonable to assume that different species of rhizostomeae prefer to feed on different plankters, intraspecific differences in the diet of two populations of cannonball jellyfish, *Stomolophus meleagris*, were shown to occur (Larson, 1991; Guadalupe Padilla-Serrato et al., 2013). Seeing as those two populations were found in different oceans (NE Gulf of Mexico and NW Mexico) with different plankton communities, Guadalupe Padilla-Serrato et al. (2013) hypothesized that the observed differences in feeding may be related to the relative abundance of the available prey in the studied environments. In the absence of dietary data on other populations of *R. nomadica*, we are unable to speculate on the effect of prey availability on the feeding of this medusa. No correlation was found between the proportions of major prey types >150 μm ingested by the medusa and their relative abundance in the plankton (Table 4). For example, while it appeared that there was a preference for pteropod prey (they comprised 6%, on average, of the medusa gut contents in four of the six samplings), pteropods were generally found in very low abundances (<1%) in the plankton. This dietary mismatch may be real but may also be related to the limitations involved with studying a gelatinous organism's diet through its gut contents and trying to deduce its feeding preferences by comparing the contents to the plankton community in the surrounding waters. The patchy nature of plankton (Omori & Hamner, 1982; Hamner, 1988; Ritz, 1994) and the lack of knowledge concerning medusan digestion rates for the different prey types (Martinussen & Bamstedt, 2001) may bias the comparisons. Gut content composition may be different from the composition of plankton in our samples simply due to the fact that the medusa encountered prey patches different in composition than the patches we sampled. With respect to digestion times, since soft-bodied plankton (e.g. medusae, appendicularians) are digested faster than shelled ones, such as molluscs (Suchman et al., 2008), remains of the hard-bodied organisms are likely to be found in greater proportions. As discussed in Sheppard & Harwood (2005), biochemical and/or molecular techniques are probably superior to visual inspection when attempting to identify prey remains in gut contents, but these were not employed in this study.

What is more puzzling, however, is the apparent selectivity of prey ingested. Radiolarians were one of the dominant taxa in the plankton, yet they were entirely absent in the *R. nomadica* gut.
samples. If radiolarians were gelatinous (indeed, many are) it may be that this taxon was ingested but that its remains were not recognizable in the gut material. On the other hand, it is possible that medusae are not ‘passive feeders’ and are able to select which plankters they ingest and digest in the surrounding waters. In a laboratory culture of young *R. nomadica* that were offered *Artemia* sp., dozens of medusae (2–3 cm in diameter) fed on the Artemia prey, yet one individual was observed swimming through the ‘cloud’ of prey without capturing any brine shrimp on its feeding appendages or in its gastric tracts. This behaviour repeated itself during several feeding sessions (for 48 h) until this specimen started feeding like all other individuals in the aquarium (Z. Kuplik, unpublished observations). As mentioned above, perhaps medusae can choose whether or not they capture available prey, but in order to test this accurately, additional field sampling and controlled feeding trials must be conducted. An intriguing dominant prey found within the gut contents were ‘various eggs’ of unknown organisms. Since copepods are the most abundant taxon in the plankton, the eggs may have been ingested by the medusae while consuming copepods with egg clutches as by-catch. However, whether or not the eggs were copepod eggs, their large number in the gut contents supports our finding of selectivity for prey at the micro-scale.

In general, the gut contents of larger *R. nomadica* contained larger (and faster) prey (i.e. adult copepods and appendicularians, Table 5). This corresponds with the findings of Costello & Colin (1994, 1995) and D’Ambra et al. (2001) who showed that the velocity of the marginal flow, i.e. the flow around the bell margins created by bell pulsation, was positively correlated with the size of the medusa. Assuming that medusae can only capture prey with escape speeds slower than the marginal flow velocity, this should enable larger medusae to capture faster prey. Contrary to expectation, however, harpacticoids (rapidly moving copepods) in gut contents were negatively correlated with medusa bell diameter. This anomaly was observed in a plankton sample collected on 22 July 2015, with an unusually large number of harpacticoids in the plankton and in the medusae gut content samples when medusae were mostly small (16 cm mean bell diameter). But, since medusa body size is

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### Table 6. ANOSIM (Analysis of Similarity) of the diet compositions in relation to the medusa’s bell diameter

| Bell diameter (cm) | R statistic | P  | Taxa                        | Contribution to dissimilarity (%) |
|--------------------|-------------|----|-----------------------------|-----------------------------------|
| >40.5 vs 18.2–40.5 | 0.57        | 0.001 | Pteropods (>150 μm)        | 12.90                             |
| >40.5 vs <18.2     | 0.46        | 0.001 | Copepod nauplii (<150 μm)  | 10.87                             |
| 18.2–40.5 vs <18.2 | 0.30        | 0.001 | Calanoids and cyclopoids (>150 μm) | 12.02                             |

The most contributing taxa to the differences found via ANOSIM were identified via SIMPER (similarity percentages) analysis and are specified on the two right columns.
only one of several variables affecting prey capture and since other factors, such as predator and prey behaviour and contact rate (Graham & Krountil, 2001) were not assessed in the present study, the above assumption could not be ascertained.

Another intriguing observation was the consistent decrease in mean bell diameter of R. nomadica observed and captured during the 5 weeks of this study. Other scyphomedusae (e.g. Rhopilema esculentum, Aurelia aurita and Pelagia noctiluca) have also been observed to decrease in size over time, and a decrease in available food was the most common explanation for this phenomenon (Hamner & Jensen, 1974; You et al., 2007). In a detailed study of Pelagia noctiluca, Lilley et al. (2014) suggested that insufficient prey availability, coupled with high metabolic rates due to temperature-dependent functions such as pulsation and respiration (Morand et al., 1987; Malej, 1989) and intense reproductive efforts could all be involved in the decrease in medusa size. Since R. nomadica is considered a tropical invasive species (Galil et al., 1990), it is unlikely that the seawater temperatures recorded during this study (25.5–28.1°C) were involved in the decrease in bell diameter as a result of metabolic stress. In addition, abundances of key plankton prey did not decrease during this period, as observed in the plankton tow samples (Table 1; Figure 4). One factor that could be associated with the reduction in medusa size is the advanced reproductive state of the sampled medusae, since sexual maturity may be correlated with the degeneration of feeding structures following spawning (Fancett, 1986). Indeed, many of the medusae observed were shown to lack part or even all of their feeding structures (see Supplementary Figure S1), especially during the last two excursions in this study. It is possible that the reduction in size was related to increased energy investment in reproduction, a loss in feeding efficiency (reduced feeding structures) or is an indication that R. nomadica is a senescent species where sexual reproduction is followed by death (Boero et al., 2008; Uye, 2008). This hypothesis (i.e. senescence) seems to be supported by the large number of dead medusae and medusa parts washed ashore towards the end of the blooming period. However, lack of additional data prevents us from drawing such a conclusion at this stage.

Conclusions

The findings of this study provide new information toward our understanding of the ecology and the role R. nomadica plays in the eastern Mediterranean ecosystem. Despite massive swarms of this species, it is not clear that it depletes plankton stocks indiscriminately, as might be assumed based simply on the conventional diet of medusae. The apparent preferential feeding of R. nomadica on prey smaller than 150 μm, at least at the stage of sexual maturity, should diminish its role as a significant predator of fish eggs and larvae and thus as a major competitor with large fish which rely on mesozooplanktonic rather than microplanktonic prey. However, it may compete over smaller prey with organisms such as larval fish, the survival of which depends on microscopic food due to their small mouth opening (Kohno et al., 1997; Glamuzina et al., 1998; Hagwara et al., 2014). In light of the notable observed changes in the medusae (i.e. gonadal maturation, loss of feeding structures and the reduction in bell size), and the fact that a large proportion of the medusae are washed to shore at the end of the annual swimming events (Edelst et al., 2020), we suggest that R. nomadica is a sexually senescent species. The loss of feeding apparatus could imply that during the time of this study the medusae were not feeding to their full potential.

In summary, through this study we have managed to shed some light on the diet and feeding preferences of the rhizostome R. nomadica. Nevertheless, more study is required: year-round gut content sampling (e.g. inspection of intact and possibly less sexually mature medusae), feeding trials in order to obtain zoo-plankton species-specific digestion times, night-time sampling to examine a possibly different diet composition and plankton tow at the micro and meso size scale. Additionally, by applying techniques such as stable isotopes and fatty acids, we may identify other sources to the medusae diet that are not detectable by gut content analyses (Pitt et al., 2008). All these could provide us with valuable information for a better resolution of R. nomadica’s role and trophic position in the marine food web.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315420000697

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