Journal of the Marine Biological Association of the United Kingdom

cambridge.org/mbi

Original Article

Cite this article: Kuplik Z, Angel DL (2020). Diet composition and some observations on the feeding ecology of the rhizostome *Rhopilema nomadica* in Israeli coastal waters. *Journal of the Marine Biological Association of the United Kingdom* **100**, 681–689. https://doi.org/10.1017/S0025315420000697

Received: 26 September 2019
Revised: 14 June 2020
Accepted: 13 July 2020
First published online: 11 August 2020

Key words:
Annual swarms; eastern Mediterranean; jellyfish; predation; senescence; zooplankton

Author for correspondence:
D. L. Angel, E-mail: drorleonard@gmail.com

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

Z. Kuplik[1,2] and D. L. Angel[1]

[1]Department of Maritime Civilizations, Charney School of Marine Sciences & Recanati Institute for Maritime Studies, University of Haifa, Mt. Carmel, Haifa 31905, Israel and [2]Department 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 m^2 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 ml 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 subsamples) 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 medusa'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).

https://doi.org/10.1017/S0025315420000697 Published online by Cambridge University Press

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.

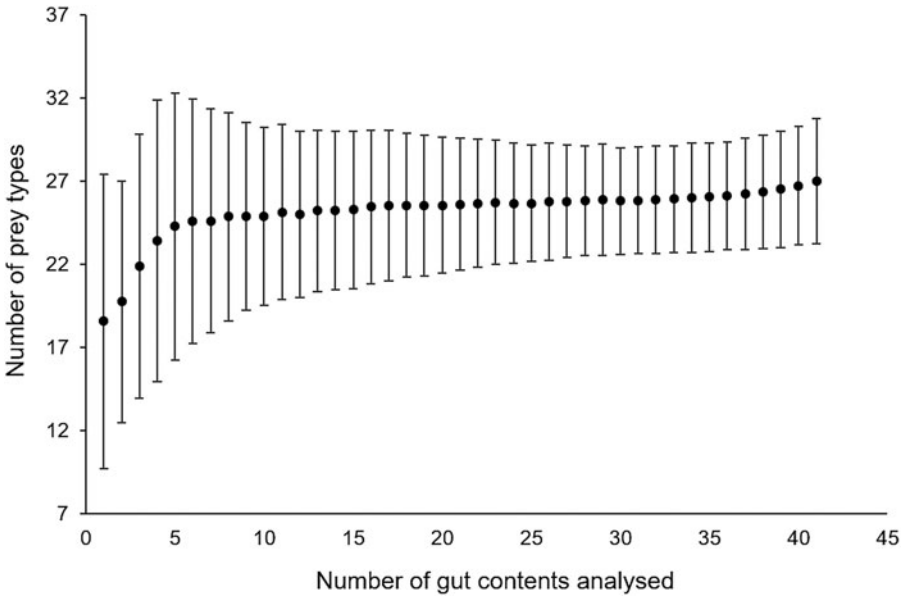

Fig. 1. Cumulative prey type curve (Chao1) to evaluate the required sampling effort (number of medusa guts analysed) to reliably estimate diet composition.

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	1.7.2015	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 (*Creseis* 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).

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

https://doi.org/10.1017/S0025315420000697 Published online by Cambridge University Press

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	1.7.2015	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.

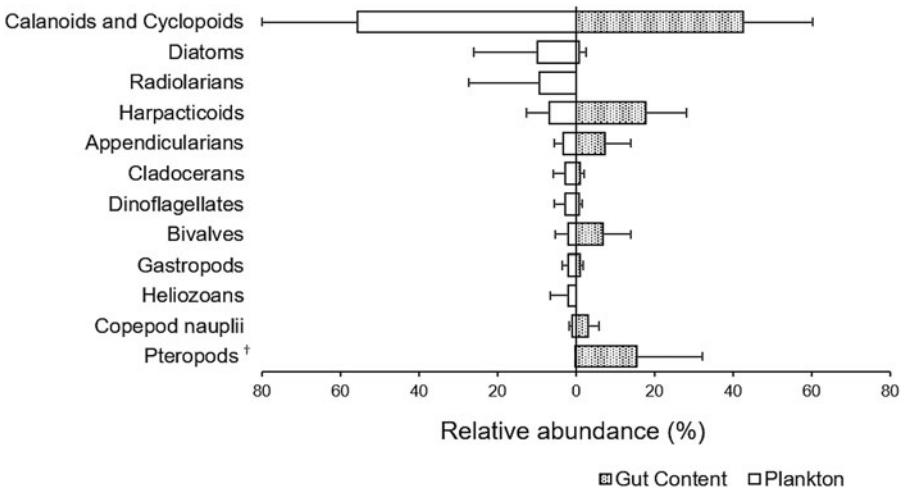

Fig. 2. Abundance of plankton >150 µm in ambient water and in the guts of *R. nomadica*. Presented are taxa which were found to comprise at least 1% of the plankton composition. Taxa appear in descending order according to their abundance in ambient water samples. Mean and standard deviation, N = 6. †*Creseis* sp.

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.

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

https://doi.org/10.1017/S0025315420000697 Published online by Cambridge University Press

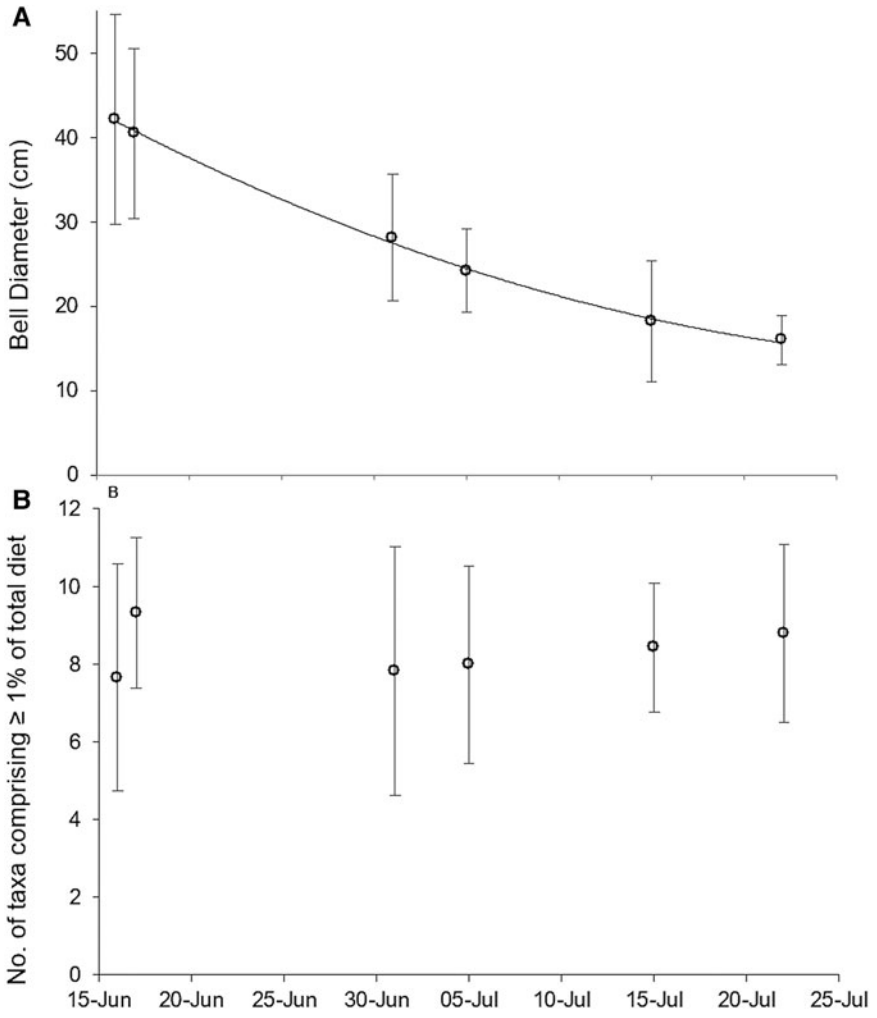

Fig. 3. (A) the temporal shift of sampled *R. nomadica*'s population towards smaller specimens; (B) the number of taxa found to contribute at least 1% to the diet of *R. nomadica* during June–July 2015. For (A), $R^2 = 0.9985$, $y = 0.0113x^2 - 950.13x + 2E + 07$. For (B), $F_{(1,5)} = 1.34$, $P = 0.27$, Power = 0.42 (one-way ANOVA).

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.

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 zooplankton 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

https://doi.org/10.1017/S0025315420000697 Published online by Cambridge University Press

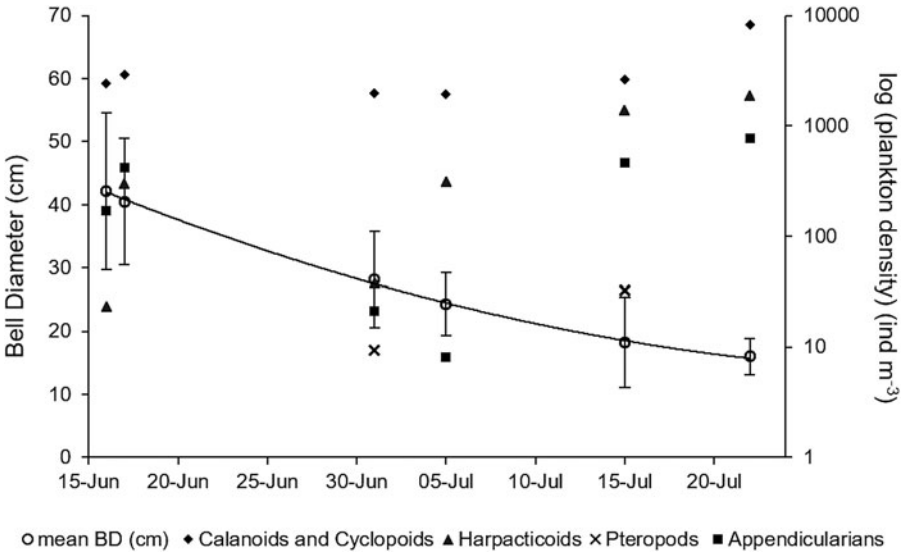

Fig. 4. Time dependence of size (bell diameter) of *R. nomadica* and ambient concentrations of the four most contributing taxa (>150 μm) to the medusa's diet.

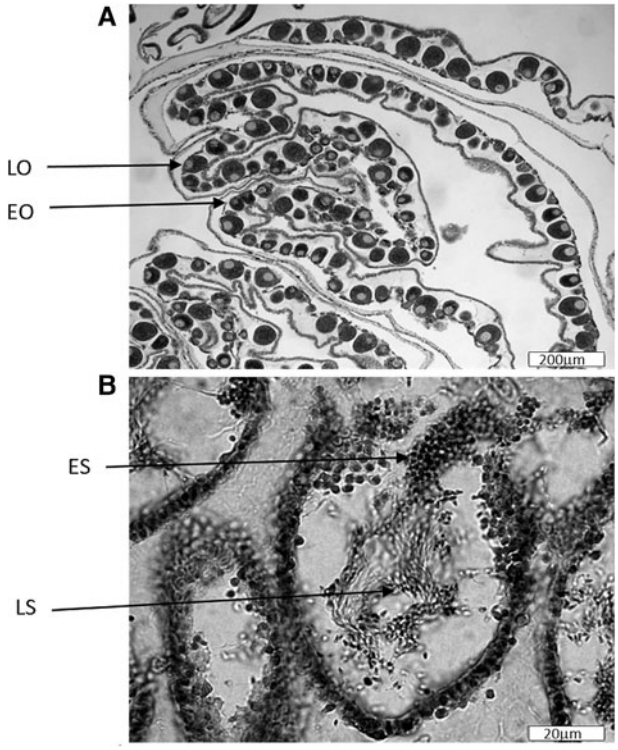

Fig. 5. Histological sections of *R. nomadica*'s gonads in advanced stages of sexual maturity. (A) female gonad; (B) male gonad. EO, Early oocyte; LO, Late oocyte; ES, Early spermatid; LS, Late spermatid.

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 medusae 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

https://doi.org/10.1017/S0025315420000697 Published online by Cambridge University Press

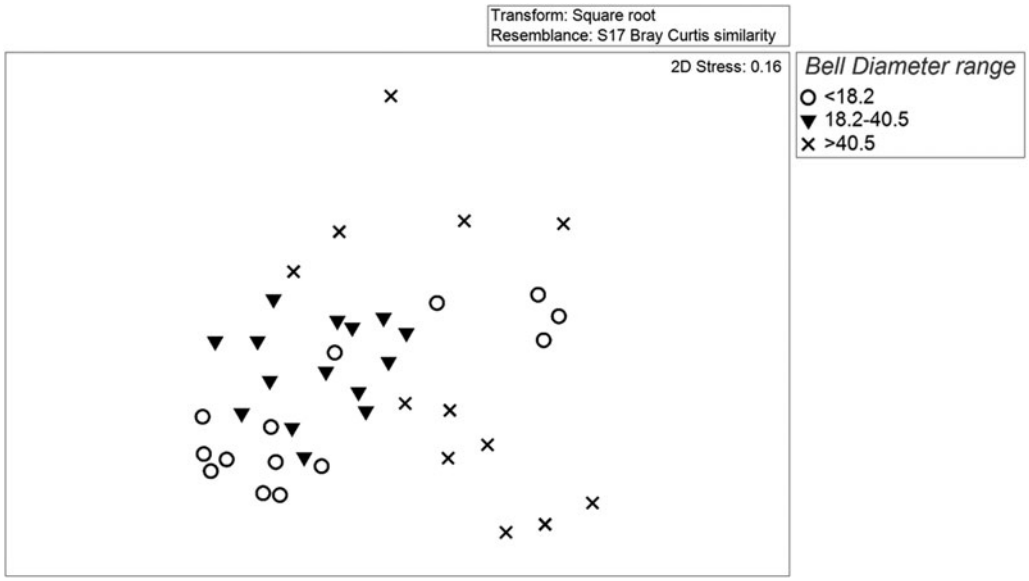

Fig. 6. A non-parametric multidimensional scaling (nMDS) of the relative abundance of prey types in the gut content of *R. nomadica*, in relation to its bell diameter size group.

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

ANOSIM pairwise test			SIMPER	
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.

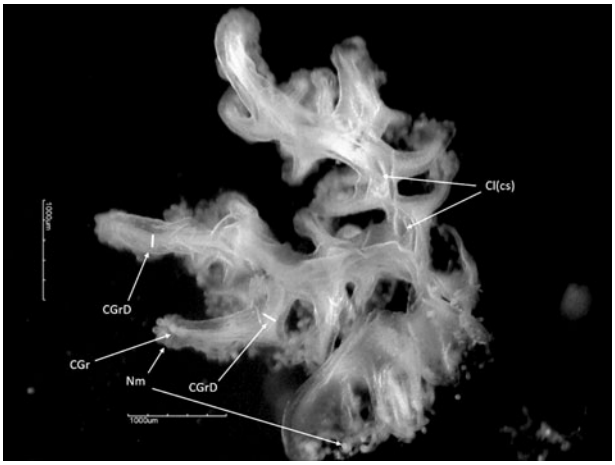

Fig. 7. Distal part of one of the branched oral arms of *R. nomadica*. Prey is captured by batteries of nematocytes (Nm) located on the club-shaped structures and transferred through the ciliated grooves (CGr) to canals leading to the gastric cavities. CGrD, ciliated groove diameter; Cl(cs), canals (cross-section).

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

https://doi.org/10.1017/S0025315420000697 Published online by Cambridge University Press

only one of several variables affecting prey capture and since other factors, such as predator and prey behaviour and contact rate (Graham & Kroutil, 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 & Jenssen, 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; Hagiwara *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 swarming events (Edelist *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 medusa 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 zooplankton species-specific digestion times, night-time sampling to examine a possibly different diet composition and plankton tows 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

Acknowledgements. First and foremost, we would like to thank Dr Dani Kerem who contributed greatly to this study. This study would not have been possible without the tremendous help of the Maritime Aquaculture Department staff, Mevoot-Yam School, Michmoret; Rafi Yavetz, Gal Belogolovsky, Arik Weinberger, Ifat Mazoz and David Halfon, who assisted in so many ways. We would also like to thank Prof. Gitai Yahel for assisting with the statistics, Dr Itzchak Brickner for his help with histology, and the School of Marine Sciences, Ruppin Academic Center, for providing marine laboratory facilities.

Financial support. The authors gratefully acknowledge support from the University of Haifa, the Helmsley Charitable Trust Mediterranean Sea Research Center, and the Maurice and Lady Hatter Fund of the Leon Recanati Institute for Maritime Studies (RIMS) at the University of Haifa.

References

Angel DL, Edelist D and Freeman S (2016) Local perspectives on regional challenges: jellyfish proliferation and fish stock management along the Israeli Mediterranean coast. *Regional Environmental Change* **16**, 315–323.

Attrill MJ, Wright J and Edwards M (2007) Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography* **52**, 480–485.

Boero F, Bouillon J, Gravili C, Miglietta MP, Parsons T and Piraino S (2008) Gelatinous plankton: irregularities rule the world (sometimes). *Marine Ecology Progress Series* **356**, 299–310.

Brewer RH (1989) The annual pattern of feeding, growth, and sexual reproduction in *Cyanea* (Cnidaria, scyphozoa) in the Niantic River estuary, Connecticut. *Biological Bulletin* **176**, 272–281.

Brodeur RD, Suchman CL, Reese DC, Miller TW and Daly EA (2008) Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. *Marine Biology* **154**, 649–659.

Brotz L, Cheung WWL, Kleisner K, Pakhomov E and Pauly D (2012) Increasing jellyfish populations: trends in Large Marine Ecosystems. *Hydrobiologia* **690**, 3–20.

Cao L, Liu J, Yu X, Zhao B, Shan X, Zhuang Z and Dou S (2015) Size-dependent predation of fish larvae by jellyfish: an experimental evaluation exemplified with the flounder *Paralichthys olivaceus* larvae and the moon jellyfish *Aurelia aurita* medusae. *Hydrobiologia* **754**, 135–146.

Clarke KR (1993) Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117–143.

Costello JH and Colin SP (1994) Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. *Marine Biology* **121**, 327–334.

Costello JH and Colin SP (1995) Flow and feeding by swimming scyphomedusae. *Marine Biology* **124**, 399–406.

Cowan JH and Houde ED (1993) Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. *Marine Ecology Progress Series* **95**, 55–65.

D'Ambra I, Costello JH and Bentivegna F (2001) Flow and prey capture by the scyphomedusa *Phyllorhiza punctata* von Lendenfeld, 1884. *Hydrobiologia* **451**, 223–227.

Edelist D, Guy-Haim T, Kuplik Z, Zuckerman N, Nemoy P and Angel DL (2020) Phenological shift in swarming patterns of *Rhopilema nomadica* in the Eastern Mediterranean Sea. *Journal of Plankton Research* **42**, 211–219.

Fancett MS (1986) Species composition and abundance of scyphomedusae in Port Phillip Bay, Victoria. *Australian Journal of Marine and Freshwater Research* **37**, 379–384.

Ferry LA and Cailliet GM (1996) Sample size and data: are we characterizing and comparing diet properly? In Mackinlay D and Shearer K (eds) *Feeding Ecology and Nutrition in Fish. Proceedings of the Symposium on the Feeding*

Ecology and Nutrition in Fish, International Congress on the Biology of Fishes, San Francisco, California. San Francisco, CA: American Fisheries Society, pp. 70–81.

Galil BS, Spanier E and Ferguson WW (1990) The scyphomedusae of the Mediterranean coast of Israel including two Lessepsian migrants new to the Mediterranean. *Zoologische Mededelingen* **64**, 95–106.

Ghermandi A, Galil B, Gowdy J and Nunes PALD (2015) Jellyfish outbreak impacts on recreation in the Mediterranean Sea: welfare estimates from a socioeconomic pilot survey in Israel. *Ecosystem Services* **11**, 140–147.

Glamuzina B, Skaramuca B, Glavic N and Kozul V (1998) Preliminary studies on reproduction and early life stages in rearing trials with dusky grouper, *Epinephelus marginatus* (Lowe, 1834). *Aquaculture Research* **29**, 769–771.

Graham WM and Kroutil RM (2001) Size-based prey selectivity and dietary shifts in the jellyfish, *Aurelia aurita*. *Journal of Plankton Research* **23**, 67–74.

Guadalupe Padilla-Serrato J, Lopez-Martinez J, Acevedo-Cervantes A, Alcantara-Razo E and Hiram Rabago-Quiroz C (2013) Feeding of the scyphomedusa *Stomolophus meleagris* in the coastal lagoon Las Guasimas, northwest Mexico. *Hidrobiológica* **23**, 218–226.

Hagiwara A, Wullur S, Marcial HS, Hirai N and Sakakura Y (2014) Euryhaline rotifer *Proales similis* as initial live food for rearing fish with small mouth. *Aquaculture* **432**, 470–474.

Hamner WM (1988) Behavior of plankton and patch formation in pelagic ecosystems. *Bulletin of Marine Science* **43**, 752–757.

Hamner WM and Jenssen RM (1974) Growth, degrowth, and irreversible cell differentiation in *Aurelia aurita*. *American Zoologist* **14**, 833–849.

Hurtubia J (1973) Trophic diversity measurement in sympatric predatory species. *Ecology* **54**, 885–890.

Ishii H and Tanaka F (2001) Food and feeding of *Aurelia aurita* in Tokyo Bay with an analysis of stomach contents and a measurement of digestion times. *Hydrobiologia* **451**, 311–320.

Kideys AE and Gucu AC (1995) *Rhopilema nomadica*: a Lessepsian Scyphomedusan new to the Mediterranean coast of Turkey. *Israel Journal of Zoology* **41**, 615–617.

Kohno H, Ordonio-Aguilar RS, Ohno A and Taki Y (1997) Why is grouper larval rearing difficult? An approach from the development of the feeding apparatus in early stage larvae of the grouper, *Epinephelus coioides*. *Ichthyological Research* **44**, 267–274.

Larson RJ (1987) A note on the feeding growth and reproduction of the epipelagic scyphomedusa *Pelagia noctiluca* Forskål. *Biological Oceanography* **4**, 447–454.

Larson RJ (1991) Diet, prey selection and daily ration of *Stomolophus meleagris*, a filter feeding scyphomedusa from the NE Gulf of Mexico. *Estuarine, Coastal and Shelf Science* **32**, 511–525.

Lee HE, Yoon WD and Lim D (2008) Description of feeding apparatus and mechanism in *Nemopilema nomurai* Kishinouye (Scyphozoa: Rhizostomeae). *Ocean Science Journal* **43**, 61–65.

Legovic T (1987) A recent increase in jellyfish populations: a predator-prey model and its implications. *Ecological Modelling* **38**, 243–256.

Lilley MKS, Ferraris M, Elineau A, Berline L, Cuvilliers P, Gilletta L, Thiery A, Gorsky G and Lombard F (2014) Culture and growth of the jellyfish *Pelagia noctiluca* in the laboratory. *Marine Ecology Progress Series* **510**, 265–273.

Liu CY, Wang B, Li YP and Dong J (2011) The feeding methods and feeding habit of jellyfish *Rhopilema esculentum* at different developmental phases. *Fisheries Science* **8**, 014.

Lotan A, Benhillel R and Loya Y (1992) Life cycle of *Rhopilema nomadica*: a new immigrant scyphomedusan in the Mediterranean. *Marine Biology* **112**, 237–242.

Lotan A, Fine M and Benhillel R (1994) Synchronization of the life cycle and dispersal pattern of the tropical invader scyphomedusan *Rhopilema nomadica* is temperature dependent. *Marine Ecology Progress Series* **109**, 59–65.

Lynam CP, Gibbons MJ, Axelsen BE, Sparks CAJ, Coetzee J, Heywood BG and Brierley AS (2006) Jellyfish overtake fish in a heavily fished ecosystem. *Current Biology* **16**, R492–R493.

Malej A (1989) Behavior and trophic ecology of the jellyfish *Pelagia noctiluca* (Forsskal, 1775). *Journal of Experimental Marine Biology and Ecology* **126**, 259–270.

Martinussen MB and Bamstedt U (2001) Digestion rate in relation to temperature of two gelatinous planktonic predators. *Sarsia* **86**, 21–35.

Mills CE (2001) Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* **451**, 55–68.

Moller LF and Riisgard HU (2007) Population dynamics, growth and predation impact of the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa*, and *Aequorea vitrina* in Limfjorden (Denmark). *Marine Ecology Progress Series* **346**, 153–165.

Morand P, Carre C and Biggs DC (1987) Feeding and metabolism of the jellyfish *Pelagia noctiluca* (Scyphomedusae, Semaeostomae). *Journal of Plankton Research* **9**, 651–665.

Nakar N (2011) *Economic Evaluation of Jellyfish Effects on the Fishery Sector – Case Study from the Eastern Mediterranean* (MA thesis). University of Haifa, Haifa, Israel.

Omori M and Hamner WM (1982) Patchy distribution of zooplankton: behavior, population assessment and sampling problems. *Marine Biology* **72**, 193–200.

Paradis AR, Pepin P and Brown JA (1996) Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 1226–1235.

Perez-Ruzafa A, Gilabert J, Gutierrez JM, Fernandez AI, Marcos C and Sabah S (2002) Evidence of a planktonic food web response to changes in nutrient input dynamics in the Mar Menor coastal lagoon, Spain. *Hydrobiologia* **475**, 359–369.

Pitt KA, Clement AL, Connolly RM and Thibault-Botha D (2008) Predation by jellyfish on large and emergent zooplankton: implications for benthic-pelagic coupling. *Estuarine, Coastal and Shelf Science* **76**, 827–833.

Purcell JE (1985) Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. *Bulletin of Marine Science* **37**, 739–755.

Purcell JE (2003) Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska. *Marine Ecology Progress Series* **246**, 137–152.

Purcell JE and Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* **451**, 27–44.

Purcell JE and Sturdevant MV (2001) Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. *Marine Ecology Progress Series* **210**, 67–83.

Purcell JE, Tilves U, Fuentes VL, Milisenda G, Olariaga A and Sabates A (2014) Digestion times and predation potentials of *Pelagia noctiluca* eating fish larvae and copepods in the NW Mediterranean Sea. *Marine Ecology Progress Series* **510**, 201–213.

Riemann L, Titelman J and Bamstedt U (2006) Links between jellyfish and microbes in a jellyfish dominated fjord. *Marine Ecology Progress Series* **325**, 29–42.

Rilov G and Galil B (2009) Marine bioinvasions in the Mediterranean Sea - history, distribution and ecology. In Rilov G and Crooks JA (eds), *Biological Invasions in Marine Ecosystems*. Berlin: Springer, pp. 549–575.

Ritz DA (1994) Social aggregation in pelagic invertebrates. *Advances in Marine Biology* **30**, 155–216.

Sheppard SK and Harwood JD (2005) Advances in molecular ecology: tracking trophic links through predator-prey food-webs. *Functional Ecology* **19**, 751–762.

Smith HG (1934) The feeding mechanism and digestion in *Cassiopea frondosa*. *Yearbook of the Carnegie Institute of Washington* **33**, 261–262.

Spanier E and Galil BS (1991) Lessepsian migration: a continuous biogeographical process. *Endeavour* **15**, 102–106.

Stibor H, Vadstein O, Diehl S, Gelzleichter A, Hansen T, Hantzsche F, Katechakis A, Lippert B, Løseth K, Peters C, Roederer W, Sandow M, Sundt-Hansen L and Olsen Y (2004) Copepods act as a switch between alternative trophic cascades in marine pelagic food webs. *Ecology Letters* **7**, 321–328.

Streftaris N and Zenetos A (2006) Alien marine species in the Mediterranean – the 100 'worst invasives' and their impact. *Mediterranean Marine Science* **7**, 87–117.

Suchman CL, Daly EA, Keister JE, Peterson WT and Brodeur RD (2008) Feeding patterns and predation potential of scyphomedusae in a highly productive upwelling region. *Marine Ecology Progress Series* **358**, 161–172.

Tilves U, Purcell JE, Fuentes VL, Torrents A, Pascual M, Raya V, Gili J-M and Sabates A (2016) Natural diet and predation impacts of Pelagia noctiluca on fish eggs and larvae in the NW Mediterranean. *Journal of Plankton Research*, **38**, 1243–1254.

Uye S (2008) Blooms of the giant jellyfish *Nemopilema nomurai*: a threat to the fisheries sustainability of the East Asian Marginal Seas. *Plankton & Benthos Research* **3**(suppl.), 125–131.

Yahia MND, Kefi-Daly Yahia O, Gueroun S, Aissi M, Deidun A, Fuentes V and Piraino S (2013) The invasive tropical scyphozoan *Rhopilema nomadica* Galil, 1990 reaches the Tunisian coast of the Mediterranean Sea. *Bioinvasions Records* **2**, 319–323.

You K, Ma C, Gao H, Li F, Zhang M, Qiu Y and Wang B (2007) Research on the jellyfish (*Rhopilema esculentum* Kishinouye) and associated aquaculture techniques in China: current status. *Aquaculture International* **15**, 479–488.

https://doi.org/10.1017/S0025315420000697 Published online by Cambridge University Press