# Predation on scyphozoan polyps and selective nematocyst incorporation dynamics in the aeolid, *Caloria militaris*

Hila Dror[1], Tamar Lotan[2], Dror Angel[1]*

[1]The Leon Recanati Institute for Maritime Studies, University of Haifa, Mt. Carmel, Haifa 3103301, Israel

[2] Marine Biology Department, The Leon H. Charney School of Marine Sciences, University of Haifa, Mt. Carmel, Haifa 3103301, Israel

*Corresponding author e-mail: dangel@univ.haifa.ac.il

## Abstract

Aeolid nudibranchs are known to prey on various cnidarians and incorporate nematocysts from their prey into their cerata (dorsal appendages) for self-defense. Nematocyst incorporation is selective, and is based on species, diet, prey availability, and predation pressure. This study investigated the interactions between two nudibranch species, *Caloria militaris* and *Flabellina affinis*, and scyphozoan polyps from common eastern Mediterranean jellyfish species, including *Rhopilema nomadica*, *Cassiopea andromeda*, *Phyllorhiza punctata*, and *Aurelia* sp. Laboratory experiments were used to assess whether these nudibranchs feed on scyphozoan polyps, and if they incorporate the prey nematocysts into the cerata. Results indicate that while *F. affinis* avoids scyphozoan polyps, *C. militaris* consumes all tested species, and can subsist on them for extended durations (up to 255 days). Predation rates varied among prey species tested, ranging from a mean of 8 to 43.3 polyps day$^{-1}$. However, *C. militaris* does not store scyphozoan nematocysts. These findings contribute to understanding nudibranch feeding ecology and the potential roles these predators play in regulating jellyfish blooms. Identification of scyphozoan nematocysts in the cerata of predator aeolid nudibranchs is discussed as a means to locate cryptic scyphozoan polyps in the marine environment.

**Keywords**

Scyphozoa polyp, *Rhopilema nomadica*, jellyfish blooms, aeolid nudibranch, nematocyst, kleptocnidae

## 1. Introduction

Aeolid nudibranchs (Gastropoda: Opisthobranchia) are marine gastropods that prey on cnidarians such as jellyfish, anemones, and hydroids[1–5]. Many are highly specialized feeders, targeting specific prey, and their larvae settle where adult prey is abundant[2,3,6,7]. Nudibranchs have evolved defenses against the cnidarian stinging mechanism, which consists of syringe-like capsules known as nematocysts[8,9]. These defenses include protective gut linings, epithelia, and mucus secretion[1,10–14]. Through kleptocnidae, nudibranchs retain and use their prey's nematocysts for defense, storing them in cnidosacs at the tips of their cerata (dorsal appendages)[10,12,15]. Not all nematocysts are retained, indicating selective sequestration[16–18], which may vary with prey availability and predator presence, with some species preferring scyphozoan nematocysts when multiple prey types are available[19].

The retained nematocysts may persist within the nudibranch's body for extended periods, ranging from days to weeks. Since the inventory of nematocysts (termed cnidome) facilitates taxonomic identification of Cnidaria[20], the presence and composition of nematocysts within the cerata can provide insights into the nudibranch's dietary history, serving as a record of the past and more recently consumed prey[10,17,21,22].

Here, we concentrated on two aeolid species, *Flabellina affinis* (Family: Flabellinidae) (Gmelin, 1791) (Fig. 1a), a native aeolid to the Mediterranean, and *Caloria militaris* (Family: Facelinidae) (Alder and Hancock, 1864) (Fig. 1b), a Lessepsian migrant[23]. *F. affinis*, measuring up to 40 mm in length, is present throughout the Mediterranean and along the Atlantic African coasts (http://www.seaslugforum.net/find/flabaffi). It is known to inhabit various habitats including seaweed beds, rocky reefs, and soft bottom, up to 10 meters deep, and was found to feed on hydroids of the genus *Eudendrium*[24]. *C. militaris* was originally described in the Bay of Bengal,

India, and has been recorded throughout the Indo-West Pacific (http://www.seaslugforum.net/factsheet/phidmili). This species is known to inhabit natural hard substrates, although it can also be found on artificial substrates up to 30 meters deep. *C. militaris*, measuring up to 40 mm in length, is known to feed on hydroids such as *Calyptospadix cerulea* (Clarke, 1882), *Ectopleura larynx* (Ellis & Solander, 1786), and *Pennaria disticha* (Goldfuss, 1820)[3,25]. Along the Israeli Mediterranean coast, *C. militaris* is now commonly found in large numbers during winter and spring, often in association with the hydroid *P. disticha* (Dror, personal observation).

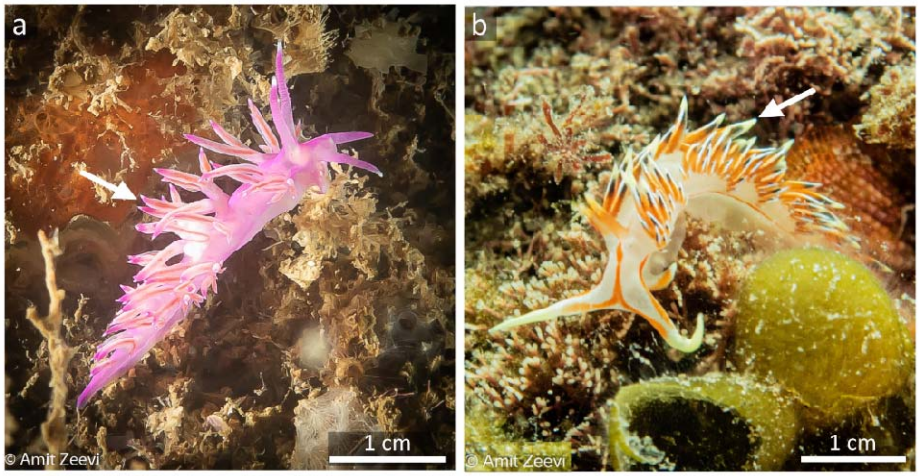


Fig. 1: The aeolid nudibranchs (a) *F. affinis* and (b) *C. militaris*. Arrows mark the tips of the cerata. Photos: Amit Zeevi.

The eastern Mediterranean has been experiencing massive jellyfish blooms during the last several decades, which have negative ecological, economic and societal effects[26]. We wanted to explore the interactions between nudibranchs and Scyphozoa species common to the region. *Rhopilema nomadica* (Galil, Spanier & Ferguson, 1990), *Cassiopea andromeda* (Forskål, 1775), and *Phyllorhiza punctata* (von Lendenfeld, 1884) are Indo-Pacific species that occur in the eastern Mediterranean[27], whereas *Aurelia* sp. is a cosmopolitan genus[28]. Since the 1980's, *R. nomadica* has become the dominant jellyfish species in the eastern Mediterranean, with population present most of the year[29]. It is considered one of the "100 worst invasive species" in the Alien Invasive Species Inventories for Europe[30] due to its negative ecological and economic effects and rapid expansion westward[26,31].

Most Scyphozoa have a complex life cycle, consisting of both a pelagic medusa stage and a benthic polyp stage. Polyps are regarded as the driving force behind jellyfish outbreaks since they reproduce asexually and can persist for extended periods, releasing numerous young medusae each season[2,32]. The polyps of most of the Scyphozoa are cryptic and their location at sea remains unknown. Nudibranchs have been found to effectively consume scyphozoan polyps[2,33–36], leading to a significant reduction in polyp populations[2]. Therefore, understanding the feeding behavior of nudibranchs and their predation on scyphozoan polyps is important in our quest to understand the dynamics of scyphozoan populations[2,33–36].

We examined the interactions between aeolid nudibranchs and scyphozoan polyps, focusing on species commonly found in the eastern Mediterranean. First, we tested which nudibranch species can feed on scyphozoan polyps and whether these can serve as a primary food source for extended periods. We hypothesized that certain nudibranch species exhibit a more generalist feeding behavior than previously reported, capable of surviving solely on scyphozoan polyps when their preferred food (Hydrozoa) is scarce. Next, we examined whether these nudibranchs can incorporate the nematocysts of prey scyphozoan polyps into their cerata. We found that predation by *C. militaris* may serve as an important factor regulating scyphozoan polyp populations.

## 2. Results

### 2.1. Short-term predation of nudibranchs on various cnidarian

All nudibranchs that were placed in the bowls explored the bottom, sides, water surface, and the slide with polyps. However, *F. affinis* avoided contact with *R. nomadica* polyps, and no polyps were consumed during the 24 h experiment (Supp. Fig. S1). In contrast, *C. militaris* retracted when its oral tentacles first contacted the polyp, as if stung, and either moved away or remained still. To avoid being stung when feeding, the nudibranch elevated its head, and engulfed the polyp from the top, consuming the goblet and leaving the stalk (Supp. material S2). During the close-up observation, three out of the four *C. militaris* individuals were observed feeding on *R. nomadica* polyps. Twenty-four h later, between 58% and 100% of the polyps that were offered had been consumed by *C. militaris* nudibranchs (19 ± 8.83 polyps day$^{-1}$).

However, when *C. militaris* were offered adult *R. nomadica* tentacles, they kept their distance. Upon contact, the nudibranch would get stung, curl up, roll and quickly crawl away. Predation of *C. militaris* on *C. andromeda* polyps was less efficient than on *R. nomadica* polyps. Upon first contact, the polyp attacked the nudibranch causing it to retreat. The first *C. andromeda* polyp was approached only 82 min after *C. militaris* was added to the experimental bowl, and it took nearly 30 min for the nudibranch to fully swallow it. By the end of the 24 h experiment, the nudibranch had consumed only three *C. andromeda* polyps (37.5% predation). In contrast to the behavior of *C. militaris* offered scyphozoan polyps, when presented with the hydrozoan, *P. disticha*, it began feeding immediately, and continued throughout the observation period. The nudibranch would crawl on the hydrozoan branch, reach a polyp, remove it from the stalk, and swallow it whole. The sting of the polyps did not seem to affect the nudibranch as it didn't retract when coming into contact with the polyp tentacles. Unlike the hydrozoan and scyphozoan polyps, none of the anemone (*E. diaphana*) and coral (*O. patagonica*) polyps were consumed by *C. militaris.* The nudibranch made some attempts to approach the anemone but was severely stung and kept away. Our findings indicate that scyphozoan and hydrozoan polyps may serve as prey for *C. militaris* nudibranchs in the wild.

### 2.2. Long-term predation of *C. militaris* on scyphozoan polyps

*C. militaris* nudibranchs were offered four species of scyphozoan polyps as prey. The mean (and maximum) number of polyps consumed by the nudibranchs per day was 8 $\pm$ 10.2, 32.8 $\pm$ 23.7, 44 $\pm$ 45.3, 43.3 $\pm$ 24.1 (49, 130, 192, and 105) for *Aurelia* sp., *C. andromeda*, *R. nomadica*, and *P. punctata,* respectively (Table 1). The predation rate and the predation proportion was significantly lower for the *Aurelia* sp. polyps compared to the other species (*C. andromeda*, *R. nomadica*, and *P. punctata*) ($F_{(3,217)} = 19.3$, $p < 0.0001$) (Fig. 2). Whereas thousands of *R. nomadica* polyps were consumed during the experiment, the podocysts of *R. nomadica* were left untouched. Nudibranch survival was longest when feeding on *C. andromeda* polyps (146 - 255 days) and the shortest when feeding on *P. punctata* polyps (34 - 40 days) (Supp. video S2-S4: and Supp. Table S5). The nudibranchs started feeding almost immediately upon encounter with prey and no ingestive conditioning to a certain prey was observed (no change in predation rate over time). To better understand the potential effect of predation of *C. militaris* on

132 scyphozoan polyps, we scanned the literature for nudibranch species known to feed on
133 scyphozoan polyps (Table 1), and found that *C. militaris* predation rate is within the range of
134 predation rates reported for other nudibranch species. These results indicate that *C. militaris*
135 may be a prominent predator of scyphozoan polyps.
136
137 Table 1: Nudibranch species that prey on scyphozoan polyps and predation rate (when
138 available). * Predation rates are presented as polyps day$^{-1}$, unless otherwise stated. **
139 Dependent on body size.
140

| **Nudibranch** | **Schyphopolyp** | **Citation** | **Predation rate (polyps d$^{-1}$) *** |
|---|---|---|---|
| ***Caloria militaris*** (Alder & Hancock, 1864) | *Aurelia* sp. | This study | 8 ± 10.2 |
| | *Cassiopea andromeda* | This study | 32.8 ± 23.7 |
| | *Phyllorhiza punctata* | This study | 43.3 ± 24.1 |
| | *Rhopilema nomadica* | This study | 44 ± 45.3 |
| ***Ceratodoris plana*** (*as Okenia plana*) (Baba, 1960) | *Nemopilema nomurai, Aurelia coerulea, Rhopilema esculentum* | Tang et al. 2021 | 30 - 118 ** |
| ***Coryphella verrucosa*** (Sars, 1829) | *Aurelia aurita* | Hernroth & Gröndahl 1985 a, b | 200 |
| | *Cyanea capillata* | Gröndahl & Hernroth 1987 | |
| | *Aurelia* | Östman 1997 | |
| (as *Flabellina verrucosa*) | *Aurelia* | Frick 2005 | |
| ***Cratena pilata*** (Gould, 1870) (as *Coryphella* sp.) | *Chrysaora quinquecirrha* | Cargo & Schultz 1967 | 11 polyps in 10 min |
| | *Chrysaora quinquecirrha* | Vogel 1969 | |
| | *Chrysaora quinquecirrha* | Oakes & Haven 1971 | |
| ***Cuthona sp.*** (Alder & Hancock, 1855) | *Chrysaora quinquecirrha* | Soranno 2016 | |
| ***Dendronotus dalli*** (Bergh, 1879) | *Aurelia labiata* | Hoover et al. 2012 | |
| ***Dendronotus rufus*** (O'Donoghue, 1921) | *Aurelia labiata* | Kozloff 1983 | |
| | *Aurelia labiata* | Hoover et al. 2012 | |
| ***Eubranchus spp.*** | *Chrysaora quinquecirrha* | Soranno 2016 | |

| | | | |
|---|---|---|---|
| ***Facelina bostoniensis*** (*as Facelina drummondi*) (Couthouy, 1838) | *Aurelia aurita* | Thiel 1962 | |
| ***Flabellina fusca*** (Bergh, 1894) | *Aurelia labiata* | Hoover et al. 2012 | |
| ***Goniobranchus tinctorius*** (*as Chromodoris tinctoria*) (Rüppell & Leuckart, 1830) | *Nemopilema nomurai, Aurelia coerulea, Rhopilema esculentum* | Tang et al. 2021 | |
| ***Hermissenda crassicornis*** (Eschscholtz, 1831) | *Aurelia aurita* | Keen 1991 | <120 |
| | *Aurelia labiata* | Hoover et al. 2012 | 8.6 - 31.3 polyps h-1 ** |
| | *Aurelia aurita* | Takao et al. 2014 | 43 - 535 ** |
| ***Pleurobranchaea maculata*** (*as Pleurobranchaea novaezealandiae*) (Quoy & Gaimard, 1832) | *Aurelia* sp.1 | Feng et al. 2017 | 393.8 |
| | *Nemopilema nomurai, Aurelia coerulea, Rhopilema esculentum* | Tang et al. 2021 | 27 - 78 ** |
| ***Sakuraeolis enosimensis*** (Baba, 1930) | *Chrysaora quinquecirrha* | Takao et al. 2014 | 8 - 45 ** |
| | *Aurelia* sp.1 | Feng et al. 2017 | 26.6 |
| ***Sakuraeolis sakuracea*** (Y. Hirano, 1999) | *Chrysaora quinquecirrha* | Takao et al. 2014 | 26 - 131 ** |

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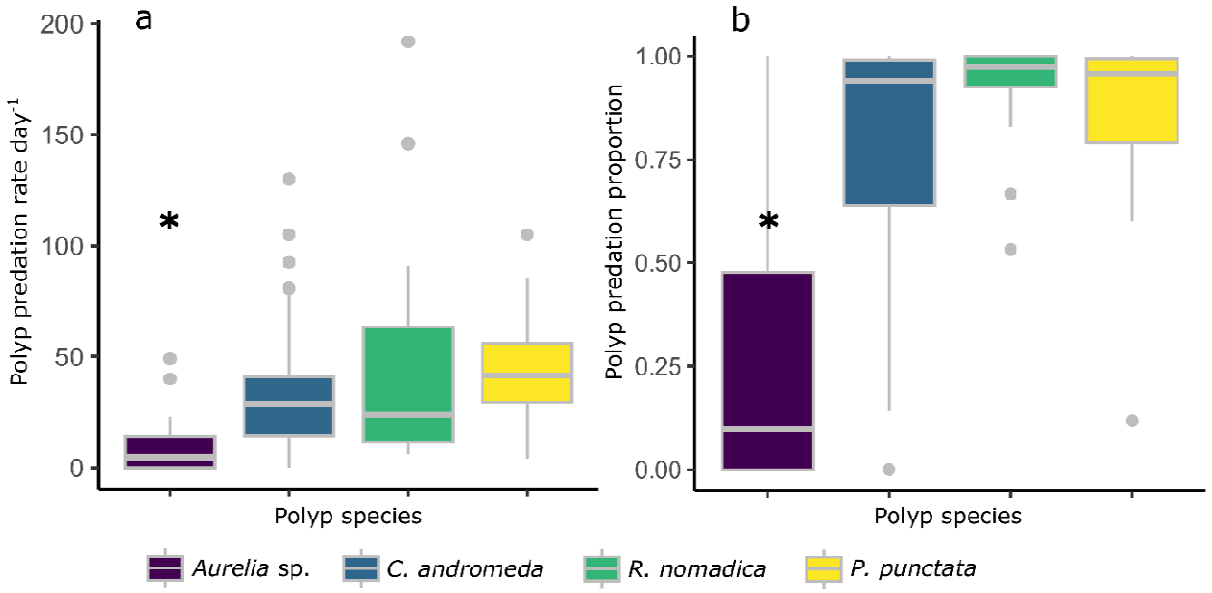


Fig. 2: Predation of *C. militaris* on *Aurelia* sp., *C. andromeda*, *R. nomadica,* and *P. punctata* polyps. (a) Predation rate presented as polyps day$^{-1}$ (b) Predation proportion. Asterisk (*) indicates significant difference between prey species at $P < 0.0001$. Number of nudibranchs tested for each prey species: 5, 4, 2, and 4 for *Aurelia* sp., *C. andromeda*, *R. nomadica,* and *P. punctata,* respectively.

### 2.3. Morphological identification of prey nematocysts in the predator's cerata

*C. militaris* nudibranchs were offered polyps of various Scyphozoa (*R. nomadica*, *C. andromeda*, and *Aurelia* sp.) and Hydrozoa (*A. pluma* and *P. disticha*) as prey, and the incorporation of nematocysts into the cerata was examined. In order to clear the cerata from previously incorporated nematocysts, and examine the time-line for nematocyst incorporation, nudibranchs were immersed in 5% KCl. As a result, the nudibranchs recoiled and raised their cerata, ejecting a mix of mucus and nematocysts without autotomizing their cerata. However, ten minutes after returning to seawater, the animals resumed normal behavior. While the cerata of freshly collected nudibranchs, at sea, contained hundreds of nematocysts (Fig. 3a),

159 most cerata examined after the treatment were completely empty of nematocysts and in
160 others, between 0 and 3 nematocysts were detected (Fig. 3b).

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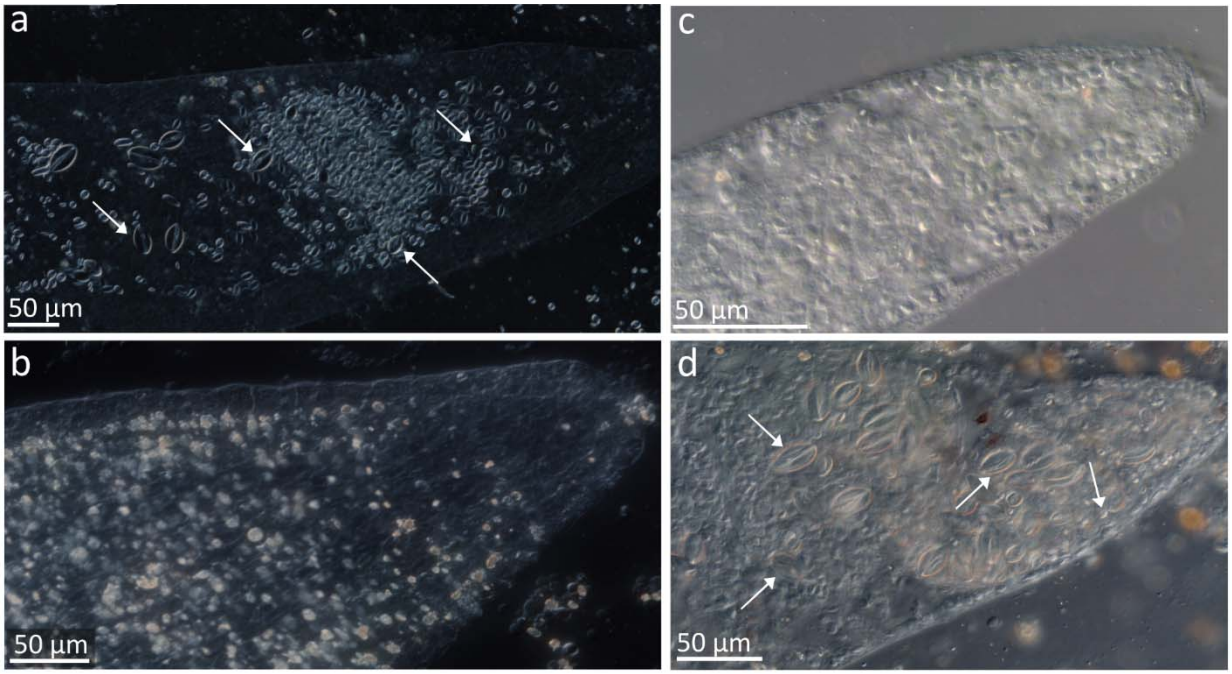


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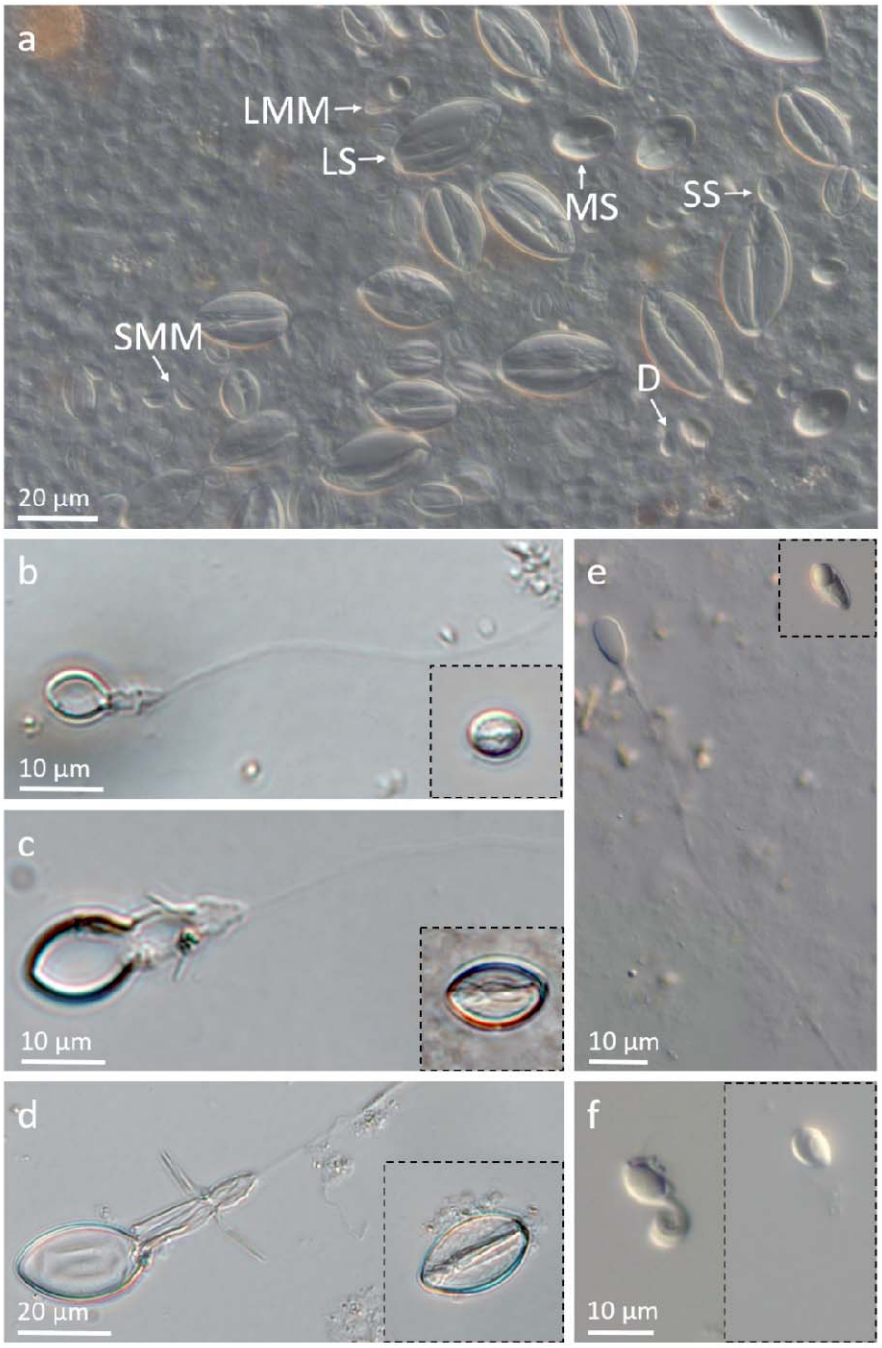
163 Fig. 3: Cerata of *C. militaris* nudibranchs. (a) Naturally feeding (b) After treatment with 5% KCl.
164 (c) Fed with polyps of the scyphozoan, *R. nomadica* on day 12. (d) Fed with the hydrozoan *P.*
165 *disticha* on day 9.

166

167 During the 12 days of the experiment, *C. militaris* nudibranchs preyed on all prey items
168 provided (supp. Table S6). However, the cerata of nudibranchs that fed on the polyps of *R.*
169 *nomadica*, *C. andromeda*, and *Aurelia* sp., and on the hydrozoan *A. pluma* showed no signs of
170 nematocysts during the experiment at days 3, 6, 9, and 12 (Fig. 3c, presenting a ceras of *C.*
171 *militaris* feeding on *R. nomadica*). In contrast, nudibranchs feeding on the hydrozoan, *P.*
172 *disticha,* incorporated the prey nematocysts into their cerata within 3-6 days, with increasing
173 numbers, temporally, until by day 9 of the experiment, several hundred nematocysts of various
174 types were concentrated at the tip of each ceras examined (Fig. 3d).

175 The nematocysts found in the cerata were identified as stenoteles (large, medium, and small),
176 desmonemes, and microbasic mastigophores (large and small) (Fig. 4a), the desmonemes being
177 the most abundant (35.9%), and the large microbasic mastigophores, the least (1.5%) (Table 2).
178 The same types and sizes of nematocysts were identified in the hydrozoan, *P. disticha*, as
179 published by Östman[47] (Fig. 4b-f) (Table 2). However, the relative abundance of the various
180 nematocyst types was significantly different than that found in the cerata of nudibranchs fed
181 with *P. disticha* (PERMANOVA, $R^2 = 0.56$, $p < 0.0001$). The small stenoteles were the main
182 contributors to the difference between the Hydrozoa and the cerata samples (SIMPER, 39%),
183 but only the desmonemes exhibited similar relative abundances in the cerata and in the
184 Hydrozoa.

185 A comparison between nudibranchs in the feeding experiments and wild-caught animals
186 showed that the cerata of naturally feeding nudibranchs contained various nematocyst types
187 and sizes. Many nematocysts found were small, medium, and large stenoteles (sizes: 5-9x4-8
188 µm, 13-17x7-14 µm, and 22-26X14-20 µm, respectively), similar in size and shape to the
189 cnidome described above in the cerata of nudibranchs feeding on the hydrozoan *P. disticha.*
190 The most abundant and distinct nematocysts found were bean-shaped microbasic euryteles
191 (ca. 10-16x5-8 µm) with a short shaft, divergent from the lateral capsule axis (Supp. Fig. S7),
192 matching the nematocyst complement of the hydrozoan, *Eudendrium merulum* (Watson,
193 1985)[48]. Additional nematocysts found in the cerata of naturally feeding *C. militaris* were round
194 stenoteles (9-12x8-11 µm) and small isorhizas (5.5-6.5x4-5 µm). These results show that *C.*
195 *militaris* selectively incorporates nematocysts into its' cerata.

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197 Fig. 4: Similar nematocyst types observed in the cerata of *C. militaris* feeding on the Hydrozoa *P.*
198 *disticha,* and occurring in *P. disticha* (a) Nematocysts in the cerata of *C. militaris* feeding on *P.*
199 *disticha* (day 9). SS, small stenoteles; MS, medium stenoteles; LS, large stenoteles; LMM, large
200 microbasic mastigophores; SMM, small microbasic mastigophores; D, desmonemes. (b-f)

201 Discharged and intact nematocysts types observed in *P. disticha.* (b-d) Small, medium, and large
202 stenoteles, (e) Microbasic mastigophores, (f) Desmonemes.

203 Table 2: Measurements and relative abundance of the various intact nematocyst types found in
204 the cerata of *C. militaris* nudibranchs after 9 days of preying on the hydrozoan *P. disticha* and in
205 *P. disticha*. Measurements are presented as mean ± SD (n = 10) and relative abundance is
206 presented as percent of >100 nematocysts counted (n = 7).

| | **Cerata of *C. militaris*** | | | **Hydrozoan *P. disticha*** | | |
|---|---|---|---|---|---|---|
| **Nematocyst** | **Length (µm)** | **Width (µm)** | **Relative abundance (%)** | **Length (µm)** | **Width (µm)** | **Relative abundance (%)** |
| **Small stenotele** | 7.3 ± 0.1 | 5.1 ± 0.2 | 18.2 ± 9.8 | 6.6 ± 0.6 | 5.2 ± 0.5 | 57.0 ± 10.5 |
| **Medium stenotele** | 13.6 ± 0.8 | 8.9 ± 0.7 | 11.9 ± 6.6 | 13. 7 ± 1.6 | 9.5 ± 0.8 | 4.1 ± 6.8 |
| **Large stenotele** | 30.1 ± 2.5 | 15.9 ± 1.2 | 19 ± 8.6 | 29.0 ± 2.1 | 16.1 ± 2.3 | 2.3 ± 3.2 |
| **Desmoneme** | 5.3 ± 0.1 | 3.5 ± 0.1 | 35.9 ± 14.5 | 5.1 ± 0.2 | 4.0 ± 0.2 | 27.1 ± 12.5 |
| **Small microbasic mastigophores** | 7.23 ± 0.5 | 3.8 ± 0.3 | 13.3 ± 10.1 | 10.1 ± 0.8 | 4.5 ± 0.5 | 2.3 ± 3.7 |
| **Large microbasic mastigophores** | 12.1 ± 0.5 | 6.3 ± 0.4 | 1.5 ± 2.0 | 11.1 ± 1.1 | 6.0 ± 0.5 | 2.8 ±3.1 |

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208

209 ## 3. Discussion

210 The aeolid nudibranch, *C. militaris,* is known to feed on several hydrozoan species[3,25]. Our study
211 examined whether this nudibranch can also prey on scyphozoan polyps and use these as a food
212 source. We show that *C. militaris* preys on various scyphozoan polyps of common eastern
213 Mediterranean species, and that these may serve as an exclusive food source for prolonged
214 periods of time. *C. militaris* exhibited broad predatory behavior, consuming all hydrozoan and
215 scyphozoan polyp species offered, with a maximum intake of 192 *R. nomadica* polyps $d^{-1}$.
216 Feeding on *C. andromeda* polyps facilitated the longest survival period (255 d), whereas
217 nudibranchs feeding on *P. punctata* survived only 40 d. *Aurelia* sp. was the least favorable prey
218 type, showing the lowest predation rate and proportion of polyps consumed (8 ± 10.2 and 27%

219 ± 34%, respectively), while *R. nomadica* was the preferred scyphozoan prey type (44 ± 45.3 and
220 92.8% ± 11.2% predation rate and proportion of polyps consumed, respectively).

221 The predation rate of *C. militaris* on jellyfish polyps is comparable with the rates reported for
222 other nudibranch species (see Table 1), suggesting that it can significantly impact polyp
223 populations *in situ* through predation, potentially affecting the size of jellyfish blooms[2,28,33].
224 However, similarly to other nudibranch species, *C. militaris* did not consume the podocysts of *R.*
225 *nomadica*[36,41,46,49]. Thus, podocysts may serve as a protective stage, enabling polyp population
226 replenishment even after grazers have reduced the abundances of polyps[50]. *C. militaris* has only
227 recently been introduced into the eastern Mediterranean[23]. Therefore, the predation
228 preferences and long-term ecological effects of this species on jellyfish polyp populations need
229 to be further studied. Given the role of scyphopolyps as pivot contributors to jellyfish blooms[32],
230 documenting these predator-prey interactions between nudibranchs and scyphopolyps is
231 essential to understand medusan population dynamics.

232 Ingestive conditioning has been known to affect prey selection in some aeolid nudibranchs,
233 such that they will preferentially prey upon species they have been feeding upon recently[51,52].
234 *C. militaris* showed no evidence of ingestive conditioning in a similar manner to the behavior
235 observed in *H. crassicornis*[34]. Although the specific prey of the nudibranchs pre-capture is
236 uncertain, when scyphozoan polyps were offered to freshly-caught nudibranchs, they began
237 feeding on these almost immediately, without an adjustment period. Analysis of cerata from
238 freshly-collected nudibranchs revealed that *C. militaris* exhibits a generalist predatory behavior,
239 such that, in addition to a nematocyst complement consistent with that of the hydrozoans *P.*
240 *disticha* and *E. merulum,*[47,48] multiple nematocyst types and sizes were observed.

241 Nudibranchs that prey on Cnidaria are not immune to nematocyst discharge of the prey, and
242 their response to the sting may vary depending on the prey's cnidome, size, and the number of
243 nematocysts discharged during the attack. While *C. militaris* was unaffected by hydrozoan
244 nematocysts, the discharge of nematocysts from scyphopolyps led to the retraction of the
245 nudibranch, but did not prevent predation, and nematocyst discharge from the anemone
246 prompted the nudibranchs to retreat. *C. pilata*, a known predator of *Chrysaora quinquecirrha*

247 (Desor, 1848) polyps in Chesapeake Bay, was recorded recoiling upon contact with the polyps'
248 tentacles[41]. Although stung by the jellyfish polyps, *C. militaris* minimized injury during feeding
249 by approaching the polyps from above, raising the anterior of its body, and engulfing the polyp
250 as a whole (supp. video S2-S4).

251 Aeolid nudibranchs are known to maintain nematocysts sequestered from their cnidarian prey
252 for defense against predators[1,10,12]. Incorporation of nematocysts is selective and is a function
253 of species, prey choice, and predation pressure[16,18,19,40,53–55]. Our experiments demonstrate that
254 *C. militaris* selectively incorporates nematocysts into its cerata. When provided with
255 scyphozoan polyps and with the hydrozoan *A. pluma*, the nudibranch did not sequester any of
256 the prey nematocysts. In contrast, when provided with the hydrozoan *P. disticha*, nematocysts
257 were detected in the cerata within a few days. This is the first study to report long-term feeding
258 on cnidarian polyps including the ability to feed without incorporation of prey nematocysts.
259 Typically, selectivity in nematocyst incorporation is manifested as a shift in the relative
260 abundance of nematocyst types between the prey and the cerata[14,53,56]. For instance, *C.*
261 *verrucosa* preying on *Aurelia* sp. polyps, incorporated a much higher ratio of rhopaloids to a-
262 isorhizas, compared to that present in the polyps[40] and preferentially retained scyphozoan
263 nematocysts over those from other prey species[19]. *C. militaris* displayed a selective avoidance
264 of scyphopolyp nematocysts, and did not retain these nematocysts in its cerata altogether.

265 Selective incorporation of nematocysts by *C. militaris* was also apparent through the difference
266 in the relative abundance of nematocyst types. As opposed to the nudibranch *C. pilata* (as
267 *Aeolis pilata*), which incorporated only microbasic mastigophores from the hydrozoan *P.*
268 *disticha* (as *Pennaria tiarella*)[53], *C. militaris,* retained all nematocyst types of this hydrozoan in
269 the cerata[47]. However, the relative abundance of the various nematocyst types in the predator
270 was significantly different than that of the prey. This type of selectivity in nematocyst
271 incorporation was reported for many other nudibranchs[14,16,18,19,40,53,56,57], although in *Berghia*
272 *stephanieae* (Valdés, 2005) and *Cratena peregrina* (Gmelin, 1791), no direct evidence of
273 selectivity was observed[11,58].

Variation across nudibranch species in kleptocnidae processes include the types of nematocysts retained, the level of selectivity, nematocyst transfer time, turnover rate, and the quantity of nematocysts stored within each cnidosac[55,59]. For instance, in the nudibranch *B. stephanieae*, new nematocysts appeared in the cerata within 2-4 days of feeding[58], while in *C. peregrina*, this process took only 2 hours[60]. In our experiments, the first nematocysts appeared in the cerata of *C. militaris* after 3 days. A turnover of nematocyst complement has been documented in *Spurilla neapolitana* (Delle Chiaje, 1841) within six days[14], while in *H. crassicornis*, it extended over a month[61]. In *C. militaris*, the cerata retained previously acquired nematocysts for over a month when scyphozoan polyps were the exclusive food source.

Intraspecific variation is also substantial: differences in nematocyst composition have been observed in the cerata of individuals from the same species when fed the same diet[54] and even within different cerata of a single nudibranch[1,60,61]. During our experiments, some cerata contained hundreds of new nematocysts, while others had only just begun to accumulate them. This level of variation raises questions regarding the process and mechanism of nematocyst selection and transport.

Jellyfish blooms have significant ecological, economic, and social impacts worldwide[62] with scyphopolyps playing a key role in driving these blooms[28,32,63]. However, the location of the polyps of most scyphozoan species *in situ* is unknown. Since this is a major challenge with respect to understanding polyp ecology, many methods (mainly molecular approaches) have been employed to address this problem[21,64–66]. Mills & Miller[67] were able to identify the prey of the ctenophore *Haeckelia rubra* (Kölliker, 1853) from analysis of nematocysts. Although *C. militaris* does not sequester scyphopolyp nematocysts, the method described here can be used to locate cryptic scyphopolyps *in situ* using other nudibranch species.

Nudibranchs are generally considered specialized feeders, relying on a narrow range of prey species[2]. While *C. militaris* is known to feed on certain hydrozoan species, our findings reveal that it also preys on a variety of scyphozoan polyps, and can use these as a long-term food source. Nudibranchs utilize their cnidarian prey both for nourishment and as a source of nematocysts. Our study shows that *C. militaris* consumes both hydrozoan and scyphozoan

302 polyps, but relies on scyphozoan tissue exclusively for nutrition, selectively incorporating
303 hydrozoan nematocysts for defense. Some nudibranchs have been shown to preferably
304 incorporate scyphozoan nematocysts over the nematocysts of other prey[19], meaning that these
305 provide adequate protection for nudibranchs against predators. Other nudibranchs rely on
306 cnidarian and non-cnidarian prey for different biological needs: the non-cnidarian supports
307 nourishment and the cnidarian, a source for nematocysts[34]. However, no nudibranch has been
308 reported to utilize Cnidaria only as a food source, discarding its defensive qualities. This type of
309 diversified prey consumption, yet complete selectivity in nematocyst incorporation is unique.
310 Future research exploring the mechanisms underlying nematocyst selection and the ecological
311 consequences of *C. militaris* predation on scyphozoan polyps in the eastern Mediterranean will
312 provide further insights into the role of aeolid nudibranchs in regulating cnidarian populations.

313 **4. Methods**

314 **4.1. Stock cultures of scyphozoan polyps**

315 Stock cultures of *R. nomadica* polyps were produced by laboratory fertilizations of several (4-8)
316 sexually mature male and female jellyfish collected near Mikhmoret, eastern Mediterranean
317 Sea (32°24′23″N 34°52′24″E). To enable planula settlement, glass slides were placed in a
318 fertilization tank with the adult medusae following the protocol described in Dror & Angel [68](in
319 press). Polyps of *C. andromeda* have been maintained in the laboratory since their discovery on
320 a rock collected near Jisr az-Zarqa, eastern Mediterranean (32°53’32″N, 34°90’10″E). Polyps of
321 *P. punctata* were produced after collecting planulae from the oral arms of a gravid female
322 medusa collected near Mikhmoret and allowing them to settle onto glass slides. Polyps of an as
323 yet unidentified *Aurelia* sp. were cultivated and maintained in the laboratory from three polyps
324 that appeared in our flowing seawater aquaria. Each species' polyps were kept in separate
325 containers in a 50 µm filtered flowing seawater aquarium system, maintained at sea surface
326 temperature (SST) ranging annually from 17 to 29 °C. The polyps were fed daily with newly
327 hatched *Artemia salina* nauplii and subjected to a 12-h illumination cycle.

328 **4.2. Nudibranch sampling and maintenance**

329 Nudibranchs were collected between 2020-2024 by SCUBA diving near Mikhmoret. The
330 nudibranchs were found on natural rocky (kurkar) reefs at depths of 6-12 m during winter and
331 spring (SST 17-23 °C). Each nudibranch was carefully hand-collected into a 50 ml centrifuge tube
332 and brought to the laboratory for handling. The nudibranchs were kept in 1 L containers of 50
333 µm filtered flowing seawater, aerated and maintained at SST, subjected to a 12-h illumination
334 cycle.

335 **4.3. Short-term predation of nudibranchs on various cnidarian**

336 The short-term feeding experiments were conducted in 200 ml glass bowls of 50 µm filtered
337 seawater with a glass slide (7.5 X 2.6 $cm^2$) holding the prey items. Each set of nudibranchs were
338 starved for 24-72 h prior to the experiment to standardize feeding conditions.

339 Four *C. militaris* (size 1.5-2.5 cm) and four *F. affinis* (size 1-1.5 cm) individuals were each
340 provided with 13-28 *R. nomadica* (Scyphozoa) polyps. In addition, four *C. militaris* individuals
341 (size 1.5-2.5 cm) were each provided with a different cnidarian prey – seven *Exaiptasia*
342 *diaphana* (Rapp, 1829) (anemone), 14 polyps of *Oculina patagonica* (de Angelis D'Ossat, 1908)
343 (coral), seven polyps of *C. andromeda* (Scyphozoa), six branches of *P. disticha* (Hydrozoa) (Supp.
344 Fig. S8). Another set of three *C. militaris* (size 2-3 cm) were individually introduced into bowls
345 containing three to five 10 cm long tentacles removed from an adult *R. nomadica* medusa (40
346 cm bell diameter).

347 The nudibranchs were observed under a dissecting microscope for three hours to study their
348 feeding behavior. The time to the first encounter with a polyp, response to the encounter, and
349 the manner of feeding were recorded. Following this initial close-up examination, the
350 nudibranchs were each placed in an aerated flowing seawater container, maintained at SST,
351 and were allowed to feed for an additional 21 hours (overall 24 h) to record predation rate
352 (number polyps consumed $day^{-1}$), and the predation proportion (number polyps consumed /
353 number polyps provided).

354 **4.4. Long-term predation of *C. militaris* on scyphozoan polyps**

355 *C. militaris* nudibranchs were each placed in a 1 L container with flowing 50 µm filtered
356 seawater and with polyps of different scyphozoan species on glass slides. The provided prey
357 polyps included *R. nomadica*, *C. andromeda*, *P. punctata*, and *Aurelia* sp. The polyps were
358 replenished twice weekly, and the predation rate, predation proportion and survival period of
359 *C. militaris* on each species was documented. The experiment lasted for 50 d for the *Aurelia* sp.
360 polyps, and until the nudibranchs died in the other treatments (polyp species). All nudibranchs
361 appeared in good condition during the experiment: feeding continuously, growing, and moving.

362 **4.5. Prey nematocysts in nudibranch cerata**

363 **4.5.1. Microscopy and photography**

364 Examination of cerata and nematocyst samples was performed by means of Differential
365 Interference Contrast (DIC) microscopy using a Zeiss AXIO Imager.M2 microscope (20X or 40x
366 magnification) and photographed using a digital Axiocam 503 color camera. Measurements of
367 nematocysts were conducted using a Zeiss Zen-Pro 2.5 program.

368 **4.5.2. Induced ejection of nematocysts from *C. militaris* cerata**

369 To remove all the nematocysts from the cerata, nudibranchs were immersed in 5% KCl for 30 s
370 followed, immediately, by three washes in seawater[69]. Two cerata located at the front, and two
371 at the rear of each nudibranch, were carefully removed using a sterile scalpel before and after
372 the treatment. To determine the presence of nematocysts, squash preparations of pre- and
373 post-treatment cerata were examined under a microscope.

374 **4.5.3. Identification of nematocysts in the cerata of *C. militaris***

375 Cerata (3-5) from each of freshly collected *C. militaris* nudibranchs were removed and stored at
376 -20 °C for identification of nematocysts in naturally feeding nudibranchs. To identify prey
377 nematocysts, the nudibranchs were starved for 96 h, then treated with 5% KCl, and cerata from
378 three nudibranchs were inspected under a microscope to check that all nematocysts were
379 ejected. The experiment was conducted over 12 days, during which the nudibranchs were
380 provided with an excess amount of polyps of the scyphozoan and hydrozoan species as prey,
381 including *R. nomadica* (Scyphozoa, n = 6), *C. andromeda* (Scyphozoa, n = 5), *Aurelia* sp.

382 (Scyphozoa, n = 5), *P. disticha* (Hydrozoa, n = 2), and *Aglaophenia pluma* (Linnaeus, 1758)
383 (Hydrozoa, n = 2). Two-three cerata were removed from each nudibranch on the last day of the
384 experiment (day 12) and stored at -20 °C. In addition, for nudibranchs feeding on *C.*
385 *andromeda*, *Aurelia* sp. and *P. disticha,* cerata were removed from two nudibranchs on day 3, 6,
386 and 9 of the experiment to determine when the nematocysts appear in the cerata (see supp.
387 Table S9 for sample details). The number of polyps consumed by each nudibranch were
388 counted each time food items were replaced to check that the nudibranchs were actively
389 feeding (supp. Table S6). Squash preparations of the cerata were examined and photographed
390 to check for the incorporation of nematocysts of the various food items in the nudibranch's
391 cerata. Nematocysts were identified based on Östman[20] , and the relative abundances of the
392 various nematocyst types in the cerata were documented . For each nematocyst type, width
393 and length of undischarged capsules (n = 10) were measured.

394 **4.5.4. Nematocyst isolation and characterization from the hydrozoan *P. disticha***

395 Colonies of *P. disticha* were sampled from the sides of the pier in Jaffa port, Israel (32°03′09″N
396 34°44′57″E). Nematocysts were isolated from 3-5 branches (2-3 cm long) of *P. disticha* (n = 7)
397 by centrifugation of the Hydrozoa in 50% Percoll (Sigma-Aldrich, USA) at 1000 g for 10 min at 4
398 °C. The resulting pellet was re-suspended in DDW and stored at -20 °C. The discharge of
399 nematocysts was achieved by addition of 1 µl of 0.1M NaOH to 3 µl nematocyst suspensions
400 placed on glass slides. For each sample, the relative abundances of the various nematocysts
401 were documented. The description of each nematocyst type included measurements of capsule
402 width and length of discharged and undischarged capsules (n = 10).

403 **4.6. Data analysis**

404 Data analysis and graphs were performed using RStudio (version 2023.06.0, R Development
405 Core Team 2023). Analysis of variance (ANOVA) was conducted to check for significant
406 differences in predation rate and proportion of polyps consumed between the various
407 scyphozoan polyps offered as food. All tests were conducted at the $\alpha = 0.05$ significance level.
408 Assumptions for ANOVA were checked using Levene's test for homogeneity of variance and a
409 Shapiro-Wilk test for normality. Tukey's HSD tests were conducted for multiple pairwise post-

410 hoc comparisons of means for the significantly different ANOVA results. Permutational
411 multivariate ANOVA (PERMANOVA) (9999 permutations) were used to test for significant
412 differences in the cnidome of *P. disticha* and the nematocysts found in the cerata of
413 nudibranchs feeding on *P. disticha*. Permutational multivariate analyses of dispersion
414 (PERMDISP) were used to ensure homogeneity of group dispersions and Similarity percentage
415 analyses (SIMPER) were calculated to determine the main contributors to the observed
416 dissimilarity in the cnidomes. Results are presented as % or as mean ± SD.

417

418 **Data availability**

419 The datasets generated and analyzed during the current study are available from the authors
420 upon request.

421

422 **References**


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600 **Figure legends**

601 Fig. 1: The aeolid nudibranchs (a) *F. affinis* and (b) *C. militaris*. Arrows mark the tips of the
602 cerata. Photos: Amit Zeevi.

603 Fig. 2: Predation of *C. militaris* on *Aurelia* sp., *C. andromeda, R. nomadica,* and *P. punctata*
604 polyps. (a) Predation rate presented as polyps day$^{-1}$ (b) Predation proportion. Asterisk (*)
605 indicates significance at $P < 0.0001$. Number of nudibranchs tested for each prey species: 5, 4,
606 2, and 4 for *Aurelia* sp., *C. andromeda*, *R. nomadica,* and *P. punctata,* respectively.

607 Fig. 3: Cerata of *C. militaris* nudibranchs. (a) Naturally feeding (b) After treatment with 5% KCl.
608 (c) Fed with polyps of the scyphozoan, *R. nomadica* on day 12. (d) Fed with the hydrozoan *P.*
609 *disticha* on day 9.

610 Fig. 4: Similar nematocyst types observed in the cerata of *C. militaris* feeding on the Hydrozoa *P.*
611 *disticha,* and occurring in *P. disticha* (a) Nematocysts in the cerata of *C. militaris* feeding on *P.*
612 *disticha* (day 9). SS, small stenoteles; MS, medium stenoteles; LS, large stenoteles; LMM, large
613 microbasic mastigophores; SMM, small microbasic mastigophores; D, desmonemes. (b-f)
614 Discharged and intact nematocysts types observed in *P. disticha.* (b-d) Small, medium, and large
615 stenoteles, (e) Microbasic mastigophores, (f) Desmonemes.

616

617 **Table legends**

618 Table 1: Nudibranch species that prey on scyphozoan polyps and predation rate (when
619 available). * Predation rates are provided as polyps day$^{-1}$, unless otherwise stated. **
620 Dependent on body size.

621 Table 2: Measurements and relative abundance of the various intact nematocyst types found in
622 the cerata of *C. militaris* nudibranchs after 9 days of preying on the hydrozoan *P. disticha* and in
623 *P. disticha*. Measurements are presented as mean ± SD (n = 10) and relative abundance is
624 presented as percent of >100 nematocysts counted (n = 7).
625
626

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633

634 **Author contributions**

635 The research was designed by Hila Dror (HD), Dror Angel (DA), and Tamar Lotan (TL) and
636 executed by HD, DA and various volunteers. Data analyses were conducted by HD. All authors
637 were involved in writing the manuscript and all authors read and approved the final version.
638

639 **Additional information**

640 **Competing interests**

641 The authors declare that they have no conflict of interest.

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