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

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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).

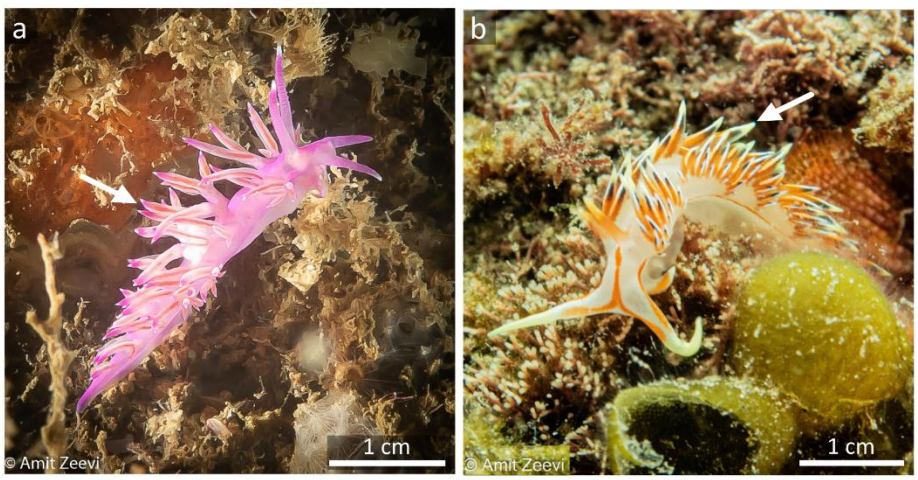

Fig. 1: The aeolid nudibranchs (a) *F. affinis* and (b) *C. militaris*. Arrows mark the tips of the cerata. Photos: Amit Zeevi.

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 scyphozoan polyps,

we scanned the literature for nudibranch species known to feed on scyphozoan polyps (Table 1), and found that *C. militaris* predation rate is within the range of predation rates reported for other nudibranch species. These results indicate that *C. militaris* may be a prominent predator of scyphozoan polyps.

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

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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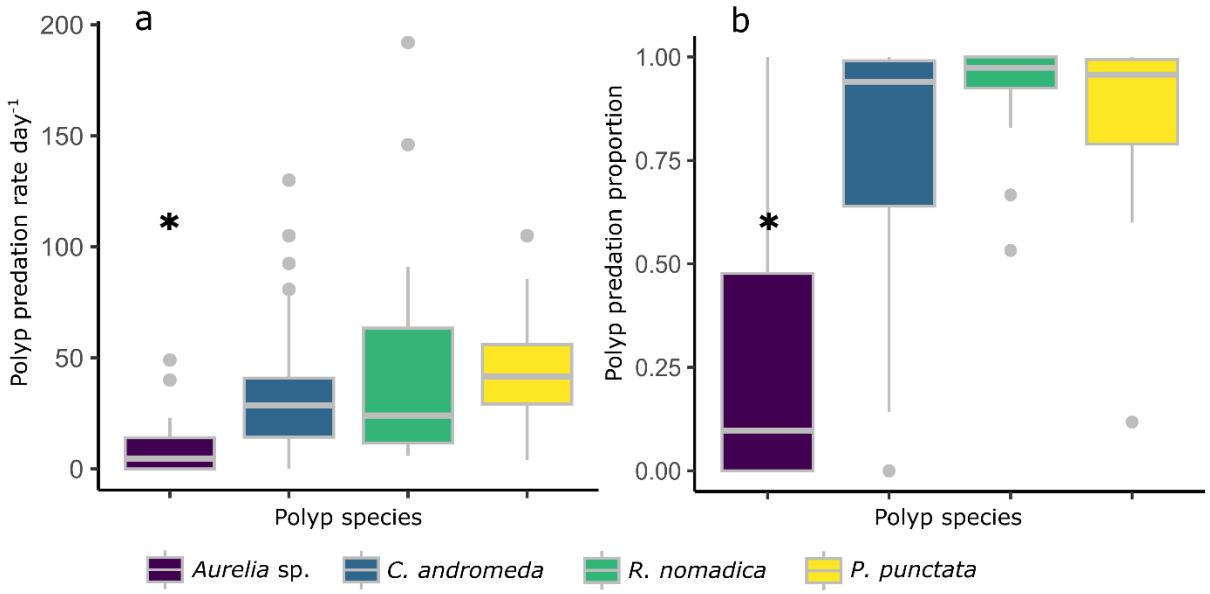

Fig. 2: Predation of *C. militaris* on *Aurelia* sp., *C. andromeda*, *R. nomadica,* and *P. punctata* polyps. (a) Predation rate presented as polyps day^{-1} (b) Predation proportion. Asterisk (*) indicates significant difference between prey species at $P < 0.0001$. Number of nudibranchs tested for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

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

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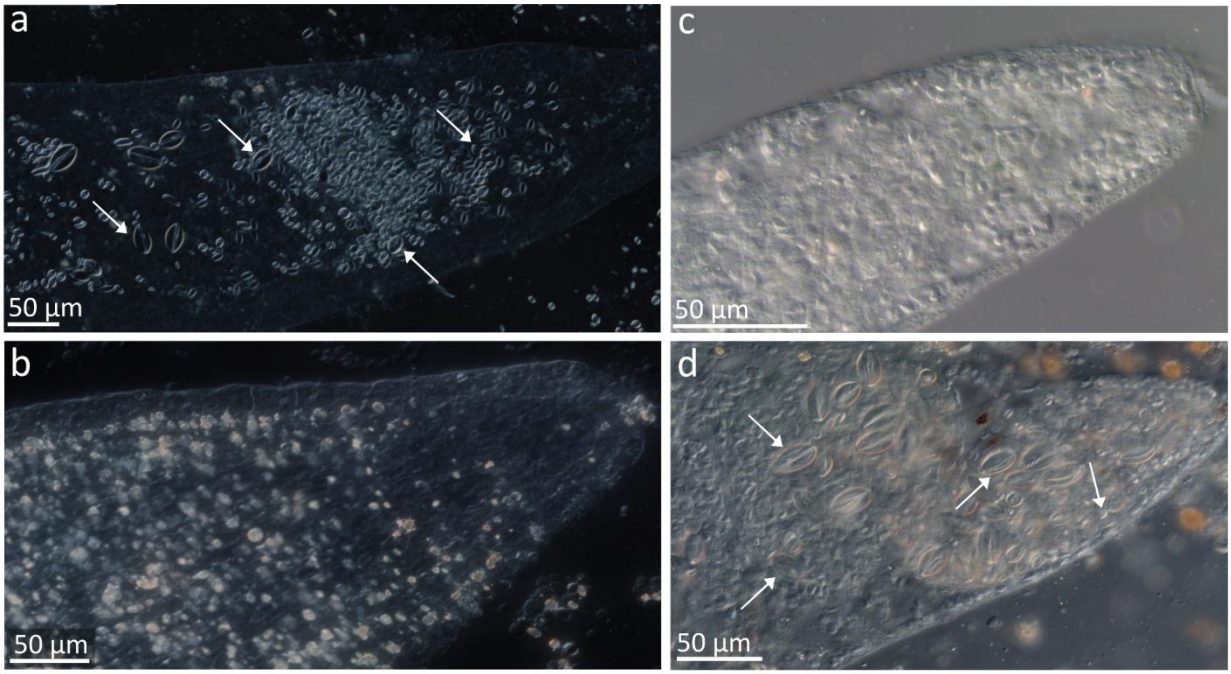

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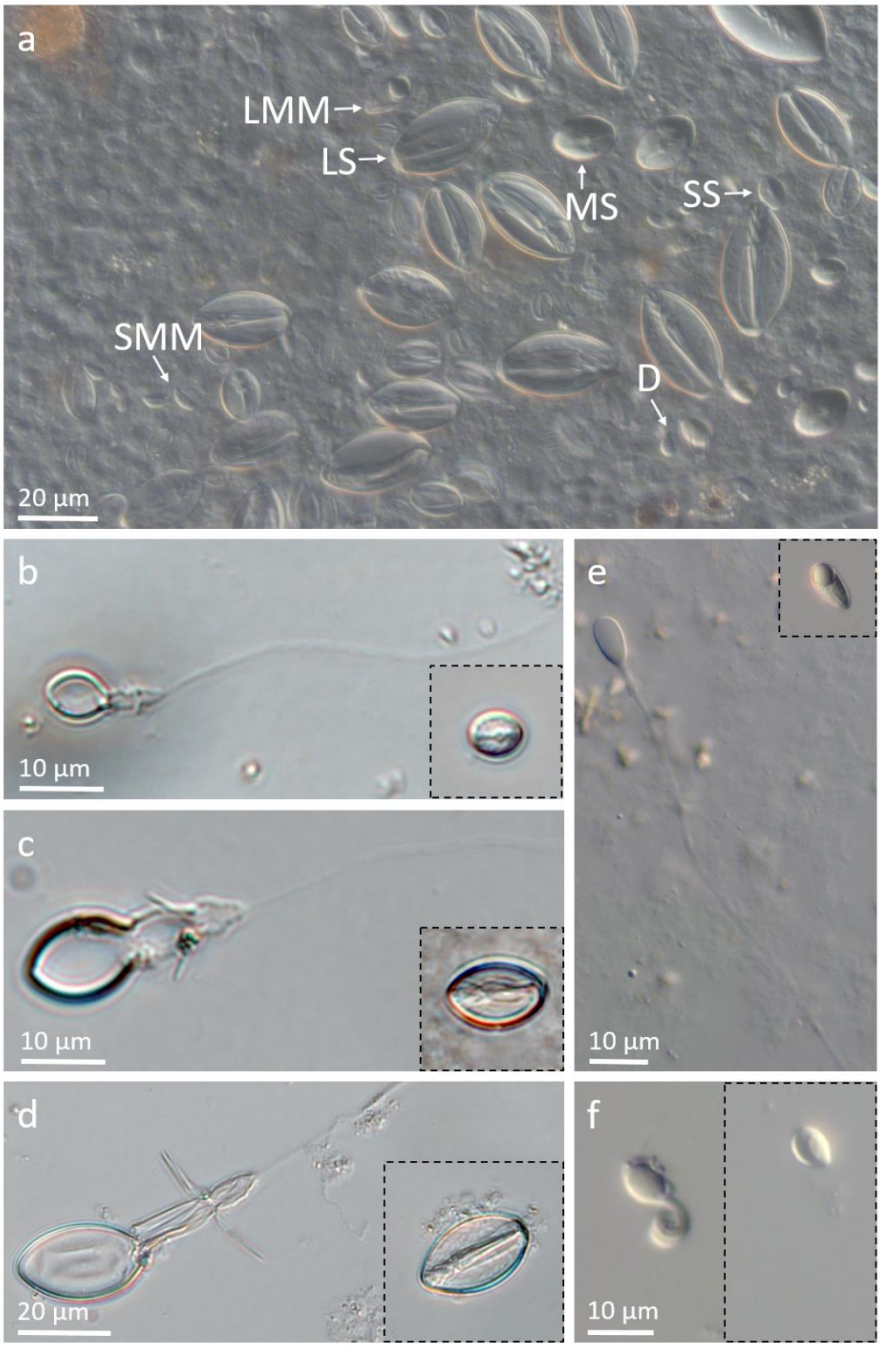
163 Fig. 3: Cerata of *C. militaris* nudibranchs. (a) Naturally feeding (b) After treatment with 5% KCl.
164 (c) Fed with polyps of the scyphozoan, *R. nomadica* on day 12. (d) Fed with the hydrozoan *P.*
165 *disticha* on day 9.

166

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

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



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

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

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

206

207

208 ## 3. Discussion

209 The aeolid nudibranch, *C. militaris,* is known to feed on several hydrozoan species[3,25]. Our study
210 examined whether this nudibranch can also prey on scyphozoan polyps and use these as a food
211 source. We show that *C. militaris* preys on various scyphozoan polyps of common eastern
212 Mediterranean species, and that these may serve as an exclusive food source for prolonged
213 periods of time. *C. militaris* exhibited broad predatory behavior, consuming all hydrozoan and
214 scyphozoan polyp species offered, with a maximum intake of 192 *R. nomadica* polyps d^{-1}. Feeding
215 on *C. andromeda* polyps facilitated the longest survival period (255 d), whereas nudibranchs
216 feeding on *P. punctata* survived only 40 d. *Aurelia* sp. was the least favorable prey type, showing
217 the lowest predation rate and proportion of polyps consumed (8 ± 10.2 and 27% ± 34%,
218 respectively), while *R. nomadica* was the preferred scyphozoan prey type (44 ± 45.3 and 92.8% ±
219 11.2% predation rate and proportion of polyps consumed, respectively).

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

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

240 Nudibranchs that prey on Cnidaria are not immune to nematocyst discharge of the prey, and
241 their response to the sting may vary depending on the prey's cnidome, size, and the number of
242 nematocysts discharged during the attack. While *C. militaris* was unaffected by hydrozoan
243 nematocysts, the discharge of nematocysts from scyphopolyps led to the retraction of the
244 nudibranch, but did not prevent predation, and nematocyst discharge from the anemone
245 prompted the nudibranchs to retreat. *C. pilata*, a known predator of *Chrysaora quinquecirrha*
246 (Desor, 1848) polyps in Chesapeake Bay, was recorded recoiling upon contact with the polyps'
247 tentacles[41]. Although stung by the jellyfish polyps, *C. militaris* minimized injury during feeding by

248 approaching the polyps from above, raising the anterior of its body, and engulfing the polyp as a
249 whole (supp. video S2-S4).

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

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

273 Variation across nudibranch species in kleptocnidae processes include the types of nematocysts
274 retained, the level of selectivity, nematocyst transfer time, turnover rate, and the quantity of
275 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 polyps, but relies on scyphozoan tissue exclusively for nutrition, selectively incorporating hydrozoan nematocysts for defense. Some nudibranchs have been shown to preferably incorporate scyphozoan nematocysts over the nematocysts of other prey[19], meaning that these provide adequate protection for

304 nudibranchs against predators. Other nudibranchs rely on cnidarian and non-cnidarian prey for
305 different biological needs: the non-cnidarian supports nourishment and the cnidarian, a source
306 for nematocysts[34]. However, no nudibranch has been reported to utilize Cnidaria only as a food
307 source, discarding its defensive qualities. This type of diversified prey consumption, yet complete
308 selectivity in nematocyst incorporation is unique. Future research exploring the mechanisms
309 underlying nematocyst selection and the ecological consequences of *C. militaris* predation on
310 scyphozoan polyps in the eastern Mediterranean will provide further insights into the role of
311 aeolid nudibranchs in regulating cnidarian populations.

312 **4. Methods**

313 **4.1. Stock cultures of scyphozoan polyps**

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

327 **4.2. Nudibranch sampling and maintenance**

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

332 µm filtered flowing seawater, aerated and maintained at SST, subjected to a 12-h illumination
333 cycle.

334 **4.3. Short-term predation of nudibranchs on various cnidarian**

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

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

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

352 **4.4. Long-term predation of *C. militaris* on scyphozoan polyps**

353 *C. militaris* nudibranchs were each placed in a 1 L container with flowing 50 µm filtered seawater
354 and with polyps of different scyphozoan species on glass slides. The provided prey polyps
355 included *R. nomadica*, *C. andromeda*, *P. punctata*, and *Aurelia* sp. The polyps were replenished
356 twice weekly, and the predation rate, predation proportion and survival period of *C. militaris* on
357 each species was documented. The experiment lasted for 50 d for the *Aurelia* sp. polyps, and

358 until the nudibranchs died in the other treatments (polyp species). All nudibranchs appeared in
359 good condition during the experiment: feeding continuously, growing, and moving.

360 **4.5. Prey nematocysts in nudibranch cerata**

361 **4.5.1. Microscopy and photography**

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

366 **4.5.2. Induced ejection of nematocysts from *C. militaris* cerata**

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

372 **4.5.3. Identification of nematocysts in the cerata of *C. militaris***

373 Cerata (3-5) from each of freshly collected *C. militaris* nudibranchs were removed and stored at
374 -20 °C for identification of nematocysts in naturally feeding nudibranchs. To identify prey
375 nematocysts, the nudibranchs were starved for 96 h, then treated with 5% KCl, and cerata from
376 three nudibranchs were inspected under a microscope to check that all nematocysts were
377 ejected. The experiment was conducted over 12 days, during which the nudibranchs were
378 provided with an excess amount of polyps of the scyphozoan and hydrozoan species as prey,
379 including *R. nomadica* (Scyphozoa, n = 6), *C. andromeda* (Scyphozoa, n = 5), *Aurelia* sp.
380 (Scyphozoa, n = 5), *P. disticha* (Hydrozoa, n = 2), and *Aglaophenia pluma* (Linnaeus, 1758)
381 (Hydrozoa, n = 2). Two-three cerata were removed from each nudibranch on the last day of the
382 experiment (day 12) and stored at -20 °C. In addition, for nudibranchs feeding on *C. andromeda*,
383 *Aurelia* sp. and *P. disticha,* cerata were removed from two nudibranchs on day 3, 6, and 9 of the
384 experiment to determine when the nematocysts appear in the cerata (see supp. Table S9 for

385 sample details). The number of polyps consumed by each nudibranch were counted each time
386 food items were replaced to check that the nudibranchs were actively feeding (supp. Table S6).
387 Squash preparations of the cerata were examined and photographed to check for the
388 incorporation of nematocysts of the various food items in the nudibranch's cerata. Nematocysts
389 were identified based on Östman[20] , and the relative abundances of the various nematocyst types
390 in the cerata were documented . For each nematocyst type, width and length of undischarged
391 capsules (n = 10) were measured.

392 **4.5.4. Nematocyst isolation and characterization from the hydrozoan *P. disticha***

393 Colonies of *P. disticha* were sampled from the sides of the pier in Jaffa port, Israel (32°03'09"N
394 34°44'57"E). Nematocysts were isolated from 3-5 branches (2-3 cm long) of *P. disticha* (n = 7) by
395 centrifugation of the Hydrozoa in 50% Percoll (Sigma-Aldrich, USA) at 1000 g for 10 min at 4 °C.
396 The resulting pellet was re-suspended in DDW and stored at -20 °C. The discharge of nematocysts
397 was achieved by addition of 1 µl of 0.1M NaOH to 3 µl nematocyst suspensions placed on glass
398 slides. For each sample, the relative abundances of the various nematocysts were documented.
399 The description of each nematocyst type included measurements of capsule width and length of
400 discharged and undischarged capsules (n = 10).

401 **4.6. Data analysis**

402 Data analysis and graphs were performed using RStudio (version 2023.06.0, R Development Core
403 Team 2023). Analysis of variance (ANOVA) was conducted to check for significant differences in
404 predation rate and proportion of polyps consumed between the various scyphozoan polyps
405 offered as food. All tests were conducted at the $\alpha = 0.05$ significance level. Assumptions for
406 ANOVA were checked using Levene's test for homogeneity of variance and a Shapiro-Wilk test
407 for normality. Tukey's HSD tests were conducted for multiple pairwise post-hoc comparisons of
408 means for the significantly different ANOVA results. Permutational multivariate ANOVA
409 (PERMANOVA) (9999 permutations) were used to test for significant differences in the cnidome
410 of *P. disticha* and the nematocysts found in the cerata of nudibranchs feeding on *P. disticha*.
411 Permutational multivariate analyses of dispersion (PERMDISP) were used to ensure homogeneity
412 of group dispersions and Similarity percentage analyses (SIMPER) were calculated to determine

413 the main contributors to the observed dissimilarity in the cnidomes. Results are presented as %
414 or as mean ± SD.

415

416 **Data availability**

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

419

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599

600 **Figure legends**

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

603 Fig. 2: Predation of *C. militaris* on *Aurelia* sp., *C. andromeda*, *R. nomadica,* and *P. punctata* polyps.
604 (a) Predation rate presented as polyps day^{-1} (b) Predation proportion. Asterisk (*) indicates
605 significance at $P < 0.0001$. Number of nudibranchs tested for each prey species: 5, 4, 2, and 4 for
606 *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 available).
619 * Predation rates are provided as polyps day^{-1}, unless otherwise stated. ** Dependent on body
620 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 feeding 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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634

635 **Author contributions**

636 The research was designed by Hila Dror (HD), Dror Angel (DA), and Tamar Lotan (TL) and executed
637 by HD, DA and various volunteers. Data analyses were conducted by HD. All authors were
638 involved in writing the manuscript and all authors read and approved the final version.
639

640 **Additional information**

641 **Competing interests**

642 The authors declare that they have no conflict of interest.
643