Evidence of overfishing in the Eastern Mediterranean

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ORIGINAL ARTICLE

Phenological shift in swarming patterns of *Rhopilema nomadica* in the Eastern Mediterranean Sea

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Jellyfish (JF) swarms impact human wellbeing and marine ecosystems. Their global proliferation is a matter of concern and scientific debate, and the multitude of factors affecting (and affected by) their density and distribution merits long-term monitoring of their populations. Here we present an eight-year time series for *Rhopilema nomadica*, the most prominent JF species swarming the Eastern Mediterranean Sea. Reports were submitted by the public and within it a group of trained participants via an internet website between June 2011 and June 2019. Data collected included species, size, location, ranked amount and stinging. Swarms of *R. nomadica* prevailed in July and ended in August but were also prominent in winter from January to March. Both observations deviate from past swarming patterns described in the late 1980s, when summer swarms persevered until October and winter swarms were not documented. Climate change (increasing water temperature) and the westwards up-current spread of *R. nomadica* are discussed as possible explanations for this phenological shift. We further demonstrate how data obtained by Citizen Science is used to develop a swarming indicator and monitor JF in time and space, and propose a forecast based on these observations.

KEYWORDS: jellyfish; citizen science; climate change; Eastern Mediterranean; *Rhopilema nomadica*

INTRODUCTION

Jellyfish proliferation

Jellyfish (JF) are gelatinous zooplankton that may form massive swarms with far reaching implications for human health and well-being and may indicate changes in the regional ecosystem functioning (Purcell, 2005; Brotz *et al.*, 2012; Schnedler-Meyer *et al.*, 2018). JF are a key part of the food web and in many cases, they serve as important grazers and predators that keep lower trophic levels in

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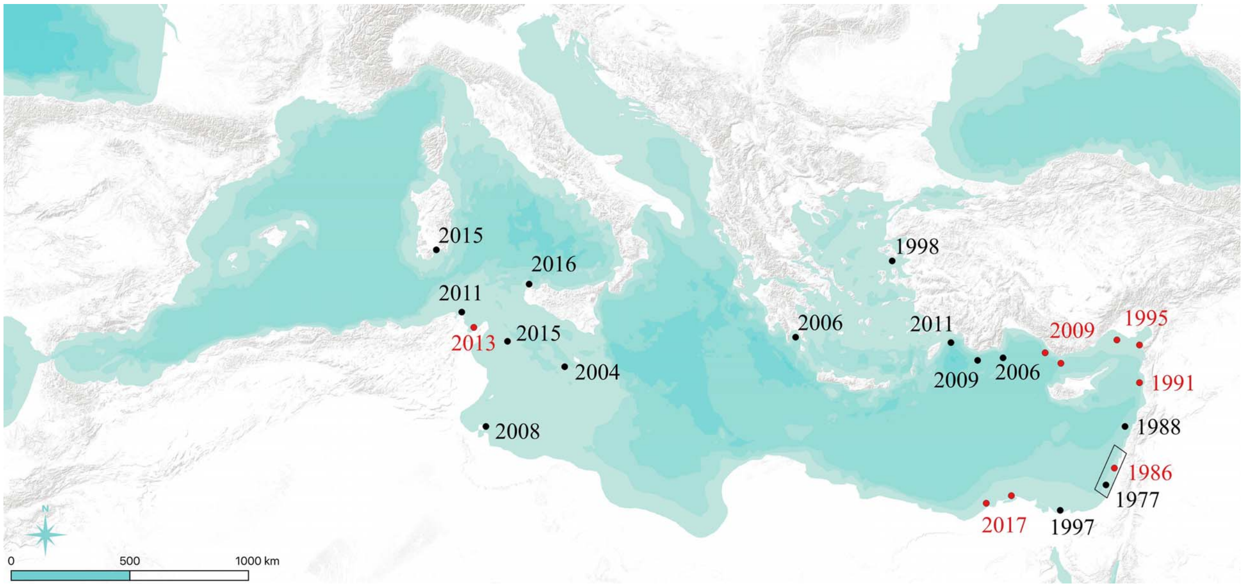

Fig. 1. Distribution and swarming of *R. nomadica* in the Mediterranean Sea. Extended from Yahia *et al*. (Yahia *et al*., 2013) and Balistreri *et al*. (Balistreri *et al*., 2017). = Study area. = First record, = First reported swarm.

check. They may also provide a habitat and serve as a food source to many species (Tilves *et al*., 2018). JF also negatively impact several human ecosystem services. They affect provisioning services through competition and predation on juvenile fishes. Provision of electricity and desalinated water may be hampered by JF blocking of seawater intake pipes (Galil, 2012; Angel *et al*., 2016). JF affect regulating services through top-down control and trophic cascade changes in marine food webs (Pitt *et al*., 2007). Most importantly, they impact cultural services and human health by stinging bathers, which is detrimental to coastal recreation and tourism (Brotz *et al*., 2012; Ghermandi *et al*., 2015). Marine bio-invasions, fishing pressure, increased pollution and climate change have all been postulated to contribute to the rise of JF (Richardson *et al*., 2009; Boero, 2013; Boero *et al*., 2016), but without baselines, time series and long-term monitoring, they remain mere speculations (Gibbons and Richardson, 2013). Furthermore, the limited scientific understanding of factors underlying swarms and the scales of temporal and spatial variability in proliferations still curtail our capacity to devise successful management strategies (Richardson *et al*., 2009; Boero, 2013; Prieto, 2018).

JF proliferation has been described in many parts of the world in recent decades (Richardson *et al*., 2009; Brotz, 2016) and specifically in the Mediterranean Sea (Brotz *et al*., 2012; Angel *et al*., 2016). Ocean currents, storms, light, moon phase, substrate availability, ocean productivity, salinity and temperature are some of the environmental variables that are thought to affect/initiate JF swarms (Lotan *et al*., 1994; Ceh *et al*., 2015; Gibbons *et al*., 2016; Schnedler-Meyer *et al*., 2018). The erratic and often unpredictable nature of swarms suggests that some of these factors may be inter-correlated and act synergistically (Boero, 2013; Gibbons *et al*., 2016). On top of these, swarm seasonality of medusae with an alternating benthic-pelagic (metagenic) life cycle strategy further complicates our understanding of swarm dynamics (e.g. Schnedler-Meyer *et al*., 2018).

Rhopilema nomadica in the Mediterranean Sea

The origin of *Rhopilema nomadica* was postulated to be in the Indian Ocean (Galil *et al*., 1990), but its reports outside of the Mediterranean are rare, far apart (Berggren, 1994; Tahera and Kazmi, 2015) and may also be misidentifications (e.g. Morandini and Gul, 2016). *R. nomadica*, that probably entered the Mediterranean via the Suez Canal (Lessepsian migration), was first recorded in the Mediterranean in 1977 (Lotan *et al*., 1994), and its population exploded in the 1980s. Appearing in Israel first (Galil *et al*., 1990), then Lebanon and Syria (Lotan *et al*., 1994), Turkey, Greece, Malta, Tunisia (Brotz *et al*., 2012, Yahia *et al*., 2013) Egypt (Abu El-Regal and Temraz, 2016; Madkour *et al*., 2019) and most recently Sardinia and Sicily (Fig. 1).

Scyphomedusae have been described in the Mediterranean as far back as the days of Aristotle (Ogle, 1882). Among them, the recent establishment and rapid spread

Table I: Reporting fields in version 1.0 (2011–6) and version 2.0 (2016–9) for the www.meduzot.co.il website

Field	Version 1.0	Version 2.0
Report type*	Inshore\Offshore	Inshore\Offshore
Details	Name*, Email, Phone	Name*, Email, Phone
Latitude*	20 beaches	33 beaches (+Auto GPS option)
Longitude* (dist. from shore)	0, 0-200 m, 200 m-1 nm, 1-6 nm, > 6 nm	0, 0-200 m, 200 m-1 nm, 1-6 nm, > 6 nm
Time/date*	V	V (+auto time option)
Activity types*	6 offshore, 7 inshore	10 offshore, 11 inshore
JF species	7*	12
JF quantity*	Zero, Few (0–5), Medium (5–50), Many (>50)	Zero, Few (0–5), Medium (5–50), Many (>50)
Size (diameter in cm)	0–10, 10–30, 30–60, > 60	0–10, 10–30, 30–60, > 60, 0–30, 0–60, 10–60, > 0, > 10, > 30
Stinging	V	V
JF on the beach	V	V
Photo upload	V	V
Mobile phone option		V
Comment section	V	V

* = obligatory fields, V = viable reporting option.

of *R. nomadica* stands out as a remarkable change in the gelatinous zooplankton community by severely impacting both ecosystems and humans (Galil, 2012; Angel *et al.*, 2016). *R. nomadica* is by far the most prominent medusa in the Levant today. Its swarms have attracted widespread attention and its life cycle, distribution and impacts have been described in detail (Lotan *et al.*, 1992; Lotan *et al.*, 1994; Nakar, 2011; Galil, 2012; Ghermandi *et al.*, 2015; Angel *et al.*, 2016). Lotan *et al.* (Lotan *et al.*, 1994) tracked *R. nomadica* swarms in Israel in 1989–1992 and recorded a long summer-autumn swarm, but no large winter swarms. A 500 km long Levantine coastal zone was reportedly inhabited by *R. nomadica* in the 1990s (Lotan *et al.*, 1994), whereas today its distribution has increased tenfold, and it covers > 5000 km of Mediterranean coasts (Fig. 1).

Citizen science as a tool for JF study

In recent years, citizen science (CS) has become a powerful tool for collecting environmental/ecological data at large spatial or temporal scales (Newman *et al.*, 2012; Tweddle *et al.*, 2012). Enhancement of scientific data collection by volunteers is particularly common in large-scale long-term ecological studies, making JF reporting especially fit for CS (Zenetos *et al.*, 2013; Deidun and Sciberras, 2017; Pires *et al.*, 2018; Nordstrom *et al.*, 2019). Involvement of citizens in environmental science also increases public awareness and connection with nature and can help promote better policy and management of the marine environment (Tweddle *et al.*, 2012).

In the present study, we bring forth biological, ecological and spatiotemporal findings concerning *R. nomadica* swarming as reported by a CS initiative along the Mediterranean shores of Israel over 8 years (2011–2019). We use the data to document changes in swarming trends in the Levant for the first time, observe the species' spatial and temporal distribution and discuss how climate change and range expansion may have contributed to a shift in JF swarm dynamics.

METHOD

Data collection

JF sightings were recorded by volunteer reporters (citizens) along the Mediterranean coast of Israel between latitudes 31.593541 N and 33.094052 N, between 30 June 2011 and 30 June 2019 via a dedicated internet website (www.meduzot.co.il) in Hebrew. Photographs of 11 JF species (9 scyphozoans and 2 ctenophores) and detailed information facilitating identification of these species were provided in the website. Citizen scientists were asked to report the longitude (binned into 4 zones) and latitude (20 zones) of the observation, the type of activity they were engaged in (bathing, swimming, surfing, kayaking, diving, walking on the beach, yachting and fishing), JF species encountered, their quantity and size, whether stranded JF were observed on the beach and if they were stung by JF (Table I). The first version of the website was released in June 2011, and in July 2016 a newer version of the website was debuted. In the new version, some cosmetic changes were made, a smartphone reporting option was added (which substantially boosted reporting) and some reporting fields were revised (Table I).

As five out of eight years surveyed relied on version 1.0, we refer to the first version for both periods in the analysis. For example, JF size was estimated as bell diameter in cm ranked in four size groups: 0–10, 10–30, 30–60 and >60 cm.

Table II: Parameters and scoring used in the screening algorithm

Parameter	EO Conflict with expert opinion	*S* Excessive size for species	FL Menacing comments and foul language	*M* Multiple (>4) species	*R* Rare species
Score	2	1	1	1	1

A value of 0, 1 or 2 points was assigned to five reasons for deleting a report: Conflict with Expert Opinion (EO) received extra weight (2 points), while unusually large size for small jellyfish species (*S*), Menacing comments and foul language in the comments section (FL), More than four species are reported simultaneously (*M*) and Rare species reported in unusual large amounts (*R*) all received 1 point. RD is Report Deletion. If RD was ≥4, the report was deleted and omitted from the database. RD = (EO X 2) + S + FL + M + R

DATA ANALYSIS

Quality assurance and weighing

Taxonomic identification was facilitated by technological aids such as photos and short descriptions for the JF species in the website. A ranking system was established for volunteers (see Freitag *et al.*, 2016), as follows. The observations of 101 trained observers were allocated twice the weight of the "regular" reports in the database. The trained observers included 85 marine scientists (71 of them marine biologists) and 16 trained divers/swimmers/fishers trained by us to identify JF.

A daily screening of reports was performed, during which reports that seemed false (e.g. accidental double-sending) or suspected as intentionally false (troll reports) were removed. Troll reports typically contained multiple species (a quarter of the removed reports indicated presence of all 9 species at once) in which large numbers (>50) of large JF specimens (>60 cm) were reported, at times when no JF were reported in the water by any other user. Foul language and menacing threats typically accompanied troll reports in the "comments" section, and we used these comments to identify and remove troll reports.

All removed reports were screened retroactively based on a simple algorithm, using the parameters listed in Table II. In total, 845 (6.6%) of all reports were removed as false or troll.

Jellyfish swarm indicator (JSI)

A large variety of activities (e.g. swimming, diving, sailing and walking on the beach), sea conditions (rough, calm), area covered (meters to kilometers), duration of the visit (few minutes to many hours) and differences in reporting frequency contribute to the ultimate observations (or absence) of JF. The relative abundances of JF observed by volunteers can be reported by means of a ranking system (Bernard *et al.*, 2011). In the website reporting form, participants were offered a categorical value of "0", "1–5", "5–50" and ">50" for abundances (similar to that applied by Fuentes *et al.*, 2010), which was in addition literally denoted as "zero", "few", "medium" and "many" JF observed. We subsequently used values of "0","2","10" and "50", respectively, to account for JF abundance, and the average number of JF per report per month [Eq. (1)] was used to create a Jellyfish Swarm Indicator (JSI), defined as:

$$JSI = \frac{\sum_{i=1}^{n} A_i}{n} \quad (1)$$

where *Ai* is the binned quantity (0, 2, 10 or 50) of *R. nomadica* per report *i* and *n* is the number of reports per month.

What constitutes a swarm may change markedly over different periods, locations and JF species, and arbitrary values may be used to help determine cutoff points for this definition (Bernard *et al.*, 2011). Here we use an average JSI value of 5 as cutoff to indicate a swarm in each month, as it successfully separated months with large conspicuous swarms from months with no swarms according to our own observations throughout the study period. A value of JSI >5 also literally means that on average, more than a few JF were observed in the water for this month.

High spatial resolution may present considerable challenges due to uneven reporting of JF in different zones (e.g. Bernard *et al.*, 2011). Considering *R. nomadica* swarms may stretch for hundreds of km (Lotan *et al.*, 1994), we grouped the 20 reporting zones given in the website reporting form into three 60 km long areas (North, Center and South), each including both large urban beaches and less frequented beach zones. A total of 5294 reports were submitted in the northern area, 3930 in the Center and 3396 in the South. Within these areas, 23, 20 and 15.5%, respectively, were offshore reports (>200 m from the beach).

Statistical analyses

JSI datasets (Month X Year, Week X Year, Distance X Area) were tested for homogeneity of variance using Bartlett's test. Two-way analysis of variance (ANOVA) was conducted to compare the main and interactive effects of: (1) year and month on JF swarming (JSI), and (2) area (north, center, south) and distance (onshore, offshore)

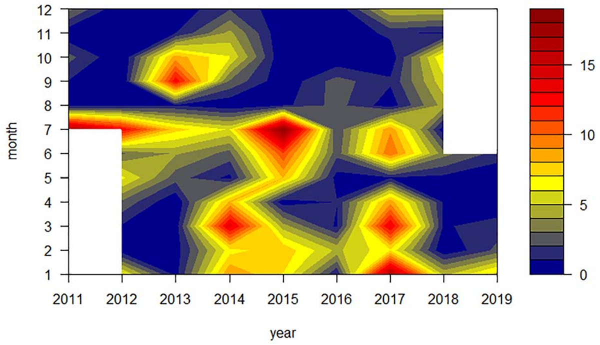

Fig. 2. Eight year time series of the monthly JSI, as a proxy for *R. nomadica* swarming. Hot (red) colors indicate high JSI values (i.e. high swarming intensity).

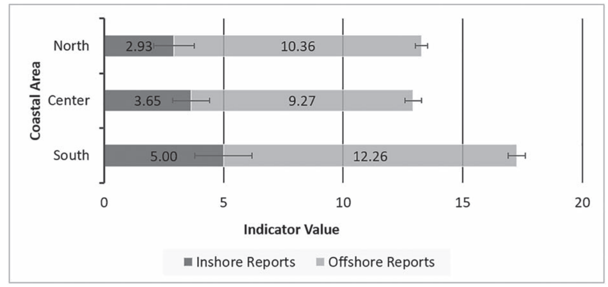

Fig. 3. Average numbers of *R. nomadica* per inshore and offshore report (JSI) for the three latitudinal areas over the eight-year study period ±SE.

on number of reports, and followed by Tukey HSD post hoc tests. Significance was determined at $\alpha \leq 0.05$. All statistical analyses were conducted using R version 3.5.1 (R Core Development Team, 2018).

RESULTS

Reporting trends

From June 2011 to June 2019, 2798 individual users logged 12620 reports in the website. There were 4032 reports of *R. nomadica* and 5963 reports of "zero jellyfish"—both were used for calculating the JSI. Additionally, there were 2625 reports of other JF species that were not analyzed here but will be presented in future publications. A total of 10 147 of the reports (80%) were inshore (<200 m from the coast) and 2473 offshore; 6161 of the reports were submitted in the early summer months of June and July and varied between 393 (December) to 907 (September) in other months. Stinging by JF was indicated in 2978 reports; 1210 (40%) of these were directly associated with *R. nomadica* and an additional 950 (32%) stingings with no JF sighted. A total of 81% of the *R. nomadica*-associated stinging events occurred during the summer months of June and July. Beached *R. nomadica* specimens were also reported in larger numbers in June and July, with 84% of the stranding reports of >50 specimens occurring in these months.

Temporal trends in *R. nomadica* distribution

The monthly JSI displayed high variance over the 96-months of the study (Fig. 2). *R. nomadica* was found to swarm annually in July, but sometimes two (e.g. 2015) or even three (2014 and 2017) swarming episodes were recorded in a single year, and in 2016 and 2018, there were no swarms in July (Fig. 2).

There were 27 months with a JSI value higher than five. Of these, 18 were in 2014, 2015 and 2017—years that included long winter swarms. JSI data were normally distributed (Bartlett's test, $P < 0.01$). Two-way ANOVA showed that "month" was an important factor contributing to the JSI ($F = 5.419$, $P = 0.022$), but not "year" ($F = 0.023$, $P = 0.878$) or their interaction. Swarms were particularly prominent in the month of July appearing in all years except for 2016 and 2018. Tukey HSD post hoc tests showed that the pairs of months differing significantly from each other with respect to swarm occurrence (using JSI) are July–May, July–August, July–November and July–December.

Spatial trends in *R. nomadica* distribution

A total of 176–1190 reports per zone were submitted in the 20 designated zones over the 190 km long Israeli Mediterranean coast. Many reports were submitted in the bathing beaches of the cities of Tel-Aviv, Ashdod and Haifa. These urban cells were characterized by many inshore reports, mostly in the bathing season. After grouping of the zones into three areas, the number of inshore reports submitted totaled 3682 (North), 2367 (Center) and 2180 (South) and offshore reports totaled 789 (North), 638 (Center) and 338 (South). The average number of *R. nomadica* per report (JSI value) was significantly higher in the South and significantly higher offshore (Fig. 3).

Two-way ANOVA on JSI showed that both area ($F = 51.6$, $P < 0.01$) and distance from shore ($F = 502.8$, $P < 0.01$) were significant as well as their interaction ($F = 12.4$, $P < 0.01$). Tukey HSD post hoc test showed that all areas differed significantly.

Size distribution of *R. nomadica*

Among the reports on JF, 3257 entries included information on bell diameter, but 775 entries failed to report JF size. The mixed size groups (0–30, 0–60 and 10–60 cm) were seldom used by citizen scientists (only 3% of all

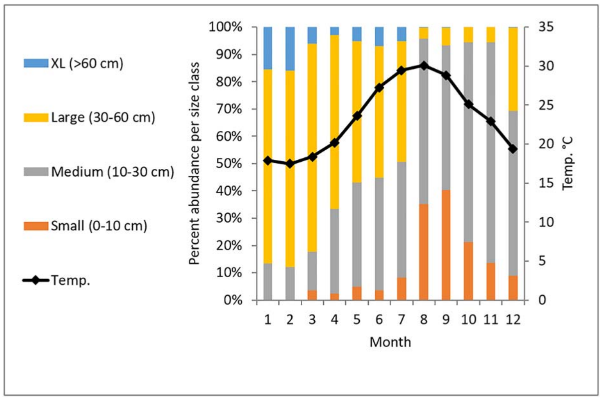

Fig. 4. Monthly weighted proportion of *R. nomadica* size classes (bell diameters in cm) in 2011–2019 and mean monthly Sea Surface Temperatures (black line. Source: daily mean temperature in Haifa at a depth of 3 m in January–December 2013 by Guy-Haim *et al*., 2016).

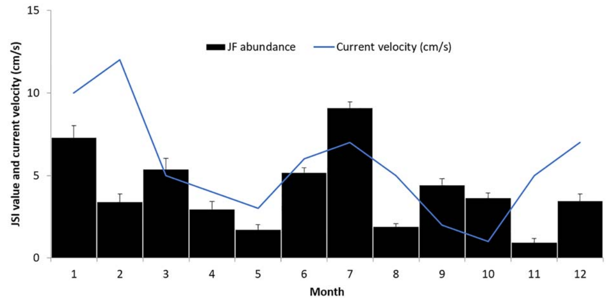

Fig. 5. Average number of *R. nomadica* per report per month (JSI value), with overlaid northward current velocity (blue line, source: monthly mean surface currents in Ashdod in 1990–5 by Rosentraub and Brenner, 2007).

reports) and these were therefore omitted from the size analysis; however, it should be recognized that mixed size classes in a swarm are quite common and could have been under-reported. We observed a marked seasonal pattern in the size of *R. nomadica* individuals (Fig. 4). The proportion of small JF (<10 cm bell diameter) increased from March and peaked in September, then disappeared in January. Medium size class (10–30 cm) proportion increased as the year progressed and declined in January as larger JF moved in. Large (30–60 cm) and extra-large (>60 cm) specimens were consistently observed in the winter months as the water cooled and then decreased in proportion and disappeared altogether as the water warmed (Fig. 4).

DISCUSSION

Spatial and temporal trends

Since its first observations in the Mediterranean in the 1970s, *R. nomadica* has spread throughout the Levant and beyond (Fig. 1). In our 8-year study, no multiannual trend of increase or decrease in *R. nomadica* swarming was observed on the Mediterranean coast of Israel. Although there is a clear pattern, whereby *R. nomadica* swarms occur most summers around July, there are additional noteworthy trends that derive from the data. The JF-reporting citizen science website, www.meduzot.co.il, was initially established to enhance the limited spatial and temporal monitoring that a small team of scientists could manage, considering the patchy distribution of this and other JF species. Eventually, a real-time online map of JF occurrence was made available to both alert the public about the occurrence of stinging JF along the beaches and to help recruit citizen scientists to the project. Early summer swarms of *R. nomadica* featured several co-occurring schyphomedusa species—mainly *Rhizostoma pulmo*, *Phyllorhiza punctata*, *Aurelia sp.*, *Marivagia stellata* and *Cotylorhiza* spp., particularly during the 2015 and 2019 summer swarms. These co-occurring species typically intermixed with *R. nomadica*, rather than formed their own separate swarms, supporting the notion that JF ecology across different taxa may be determined by similar processes (Omori and Hammer, 1982).

The larger offshore presence of *R. nomadica* (Fig. 3) points to its preferred pelagic habitat in the prevailing current, away from the swash and shallow wave action. The higher JSI values observed in the south may be a result of the early arrival of swarms to the south (swarm emergence tends to be more dramatic than its more gradual demise) or due to swarm dwindling as it drifts northwards.

R. nomadica swarms with a JSI > 5 may occur in almost every month of the year and in the present study only August and November never exceeded this value (Fig. 2). The extended winter swarms of extra-large specimens appeared in January, typically decreased in April and were followed by shorter yet more frequent and intense early summer swarms of smaller (11–60 cm) individuals (Fig. 4). Summer swarms typically occur in late June but also as early as May (in 2015) and intensify in July. These months are also characterized by a northwards current intensification. From August to December, swarms were found to be rare and generally smaller (Fig. 5).

JSI trends were monthly and seasonal, rather than multiannual. July and January were the months with the highest JSI values (Fig. 5), exceeding five in six and five years out of eight, respectively. Importantly, these months are also characterized by strong currents carrying the JF northwards (Fig. 5). These observations vary considerably from those made by Lotan *et al*. (Lotan *et al*., 1994) who documented longer summer swarms lasting through autumn and much smaller winter swarms. This change may either be due to the extended duration of the present study which covered more years, different methods for assessing JF densities or due to an actual phenological change in swarming patterns and the conditions and mechanisms underlying them, as discussed below. Based on these trends, we forecast that large Levantine *R. nomadica* swarms will persist in July, often arrive earlier and vanish in early August. Winter swarms may intensify with warming waters, while lower swarming is expected in the autumn and spring as the currents decrease.

Factors involved in the observed shift in *R. nomadica* swarming

Phenological shifts in JF populations are common (Schnedler-Meyer *et al.*, 2018) and may be decoupled from certain ecosystem factors while corresponding to others (van Walraven *et al.*, 2015). Here we discuss warming Mediterranean water and range expansion of *R. nomadica* as factors that exhibited marked changes in the past three decades and are likely to contribute to the observed shift in swarming patterns.

Climate change

Climate may (Purcell, 2005; Boero *et al.*, 2016) or may not (van Walraven *et al.*, 2015) play a role in phenological shifts in JF swarming. Lotan *et al*. (Lotan *et al.*, 1994) proposed that temperature synchronizes population dynamics of *R. nomadica*, relating to summer Levantine maxima of 28.5°C in the late 1980s. Nevertheless, over the past 3 decades, Levantine Surface Waters have warmed by an average of 0.12°C per year (Ozer *et al.*, 2017), and nowadays, temperatures as high as 30.5–31.5°C prevail over the Israeli continental shelf in August (Yeruham *et al.*, 2015; Guy-Haim *et al.*, 2016). Our results show that rather than lasting from July through autumn (Lotan *et al.*, 1994), summer swarms now vanish in August (Figs 2 and 5). Warmer summers may accelerate adult JF mortality, as even invasive opportunistic marine organisms may be pushed beyond their thresholds by excess warming (Belmaker *et al.*, 2013). Lotan *et al*. (Lotan *et al.*, 1994) attributed the synchronous summer swarms of *R. nomadica* to rising temperatures in the spring. This periodicity resembles spring vernalization processes in plants and seasonal heterotrichy in algae (Guy-Haim *et al.*, 2016). Earlier warming of the waters in recent years matches the earlier arrival of *R. nomadica* swarms, and warming waters may now allow JF to survive and even flourish in winter.

Range expansion

Changes in temperature alone are probably not the single explanatory variable leading to JF swarming (Boero *et al.*, 2016), and it is likely that current regime, predation, marine productivity and life history are also involved (Gibbons *et al.*, 2016; Schnedler-Meyer *et al.*, 2018). The appearance of extra-large *R. nomadica* in winter (Fig. 4) suggests either the return or arrival of an older JF cohort. In the past, the westward spread of *R. nomadica* was thought to be limited by low winter temperatures west of Greece, and by lack of rocky substrate for polyp settlement in Egypt (Lotan *et al.*, 1992). Nowadays, *R. nomadica* has been observed as far west as Tunisia and Sardinia (Balistreri *et al.*, 2017; Fig. 1), and recently, numerous swarms were reported off Egyptian coasts (Abu El-Regal and Temraz, 2016). Notably, in July 2017, *R. nomadica* swarms were simultaneously reported in Israel (Fig. 2) and from Baltim and Alexandria in Egypt, 700 km up-current (http://www.egyptindependent.com/sea-turtles-to-counter-jellyfish-on-shores/). A synchronous bloom across the entire SE basin thus cannot be ruled out, and swarms are probably much larger than previous estimates of 100 km (Galil and Zenetos, 2002). As *R. nomadica* distribution expands, it likely spreads additional polyps. The origins of the extra-large *R. nomadica* cohort we observe in the winter months along the Israeli coast may thus be from ephyrae released as far west as Tunisia. We also suggest that while swarming synchronicity is triggered by temperature, growth and feeding of both summer and winter swarms probably occur up-current, possibly in the nutrient rich waters off the Nile Estuary.

Prediction and future recommendations

Based on the present findings, we expect that summer *R. nomadica* swarms will continue to occur in July and possibly earlier and disappear in early August. Winter swarms are expected to persist and may intensify with further warming of the Mediterranean. We suggest that these predictions represent a phenological shift in *R. nomadica* swarming, which is of importance to the public as well as a wide range of maritime stakeholders that are critically affected by JF swarms. As demonstrated in the present study, *R. nomadica* swarming can happen in almost every month of the year, yet sometimes, a whole year may pass with no large swarms at all. In order to fully understand what drives such complex swarming patterns, ecosystem models must be established that incorporate all underlying factors. Importantly, such models should be developed in a regional ecosystem context, to provide a wide enough spatial picture. Standardized protocols to estimate abundances (Gibbons and Richardson, 2013) need to be adopted in future CS initiatives, to allow for comparable population surveys. Finally, the use of citizens was shown by us and by others (Pires *et al.*, 2018; Nordstrom *et al.*, 2019) to be a useful tool for monitoring JF populations, and we advocate its expansion. Its application should be considered with these approaches of ecosystem modelling, regionalization (or even globalization) and standardization in mind.

CONCLUSION

This study observes a shift in swarming patterns of the invasive scyphomedusa, *R. nomadica* in the Eastern Mediterranean Sea. Data provided by citizen science enabled us to find that winter swarms are now longer and more common than previously thought, and that summer swarms, which three decades ago extended to October, today stop in August. This phenological shift may be attributed to warming of Levantine waters over the past three decades or/and to the observed westwards spread of *R. nomadica* in the Mediterranean in this period.

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DATA ARCHIVING

All data were deposited in an Open Access data archiving and publication repository (Pangaea, a member of the ICSU World Data System) and are available at: https://doi.pangaea.de/10.1594/PANGAEA.897389

REFERENCES

Abu El-Regal, M. and Temraz, T. (2016) Blooming of nomad jelly fish *Rhopilema nomadica* along the Egyptian Mediterranean coasts. *Comm. Int. Explor. Sci. Mer Mediterr., Rapp*, **41**, 489–490.

Angel, D., Edelist, D. and Freeman, S. (2016) Local perspectives on regional challenges: jellyfish proliferation along the Israeli Mediterranean coast. *Reg. Environ. Chang.*, **16**, 315–323.

Balistreri, P., Spiga, A., Deidun, A., Gueroun, S. K. M., Nejib, M. and Yahia, D. (2017) Further spread of the venomous jellyfish *Rhopilema nomadica* Galil, Spannier and Ferguson, 1990 (Rhizostomeae, Rhizostomatidae) in the western Mediterranean. *BioInvasions Rec.*, **6**. doi: 10.3391/bir.2017.6.1.04.

Belmaker, J., Parravicini, V. and Kulbicki, M. (2013) Ecological traits and environmental affinity explain Red Sea fish introduction into the Mediterranean. *Glob. Environ. Chang.*, **19**, 1373–1382.

Berggren, M. (1994) *Periclimenes nomadophila* and *Tuleariocaris sarec*, two new species of Pontoniine shrimps (Decapoda:Pontoniinae), from Inhaca Island, Moçambique. *J. Crustac. Biol*, **14**, 782–802.

Bernard, P., Berline, L. and Gorsky, G. (2011) Long term (1981– 2008) monitoring of the jellyfish *Pelagia noctiluca* (Cnidaria, Scyphozoa) on Mediterranean coasts (Principality of Monaco and French Riviera). *Jour. Oceanogr. Res. Data*, **4**, 1–10.

Boero, F. (2013) Review of jellyfish blooms in the Mediterranean and Black Sea. *Gen. Fisheries. Commis. Medit. Stud. Rev.*, **92**, 63.

Boero, F., Brotz, L., Gibbons, M. J., Piraino, S. and Zampardi, S. (2016) Impacts and effects of ocean warming on jellyfish. In Laffoley, D. and Baxter, J. M. (eds.), *Explaining Ocean Warming: Causes, Scale, Effects and Consequences*Full report, Vol. **3.10**, IUCN, Gland, Switzerland, pp. 213–237.

Brotz, L., Cheung, W. W. L., Kleisner, K., Pakhomov, E. and Pauly, D. (2012) Increasing jellyfish populations: trends in large marine ecosystems. *Hydrobiologia*, **690**, 3–20.

Brotz, L. (2016) *Jellyfish fisheries—a global assessment. PhD dissertation*, University of British Columbia, p. 180.

Ceh, J., Gonzalez, J., Pacheco, A. S. and Riascos, J. M. (2015) The elusive life cycle of scyphozoan jellyfish – metagenesis revisited. *Sci. Rep.*, **5**, 12037.

Deidun, A. and Sciberras, A. (2017) Unearthing marine biodiversity through citizen science - the spot the jellyfish and the spot the alien fish campaign case studies from the Maltese islands (Central Mediterranean). *Bull. Entomol. Soc. Malt.*, **9**, 86–87.

Freitag, A., Meyer, R. and Whiteman, L. (2016) Strategies employed by citizen science programs to increase the credibility of their data. *Citiz. Sci. Theory Pract*, **1**, 2. doi: 10.5334/cstp.6.

Fuentes, V. L., Angel, D. L., Bayha, K. M., Atienza, D., Edelist, D., Bordehore, C., Gili, J. M. and Purcell, J. E. (2010) Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, span the Mediterranean Sea in 2009. *Hydrobiologia*, **645**, 23–27.

Galil, B. S., Spanier, E. and Ferguson, W. W. (1990) The scyphomedusae of the Mediterranean coast of Israel, including 2 Lessepsian migrants new to the Mediterranean. *Zool. Med.*, **64**, 95–105.

Galil, B. S. and Zenetos, A. (2002) A sea change – exotics in the Eastern Mediterranean. In Leppäkoski, E., Olenin, S. and Golasch, S. (eds.), *Invasive aquatic species of Europe: Distributions, impacts and management*, Kluwer Academic Publishers, Dordrecht, the Netherlands, pp. 325–336.

Galil, B. S. (2012) Truth and consequences: the bioinvasion of the Mediterranean Sea. *Integr. Zool.*, **7**, 299–311.

Ghermandi, A., Galil, B., Gowdy, J. and Nunes, P.A.L.D. (2015) *Jellyfish outbreak impacts on recreation in the Mediterranean Sea: welfare estimatesfrom a socioeconomic pilot survey in Israel. Ecosystem Services*, doi: 10.1016/j.ecoser.2014.12.004 [accessed 13 June 2018].

Gibbons, M. J. and Richardson, A. J. (2013) Beyond the jellyfish joyride and global oscillations: advancing jellyfish research. *J. Plankton Res.*, **35**, 929–938.

Gibbons, M. J., Boero, F. and Brotz, L. (2016) We should not assume that fishing jellyfish will solve our jellyfish problem. *ICES J. Mar. Sci.*, **73**, 1012–1018.

Guy-Haim, T., Silverman, J., Raddatz, S., Wahl, M., Israel, A. and Rilov, G. (2016) The carbon turnover response to thermal stress of a dominant coralline alga on the fast warming Levant coast. *Limnol. Oceanogr.*, **61**, 1120–1133.

Lotan, A., Ben-Hillel, R. and Loya, Y. (1992) Life cycle of *Rhopilema nomadica*: a new immigrant scyphomedusan in the Mediterranean. *Mar. Biol.*, **112**, 237–242.

Lotan, A., Fine, M. and Ben-Hillel, R. (1994) Synchronization of the life cycle and dispersal pattern of the tropical invader scyphomedusan *Rhopilema nomadica* is temperature dependent. *Mar. Ecol. Prog. Ser.*, **109**, 59–65.

Madkour, F. F., Hanafy, M. H. and Zaghloul, W. S. (2019) Record of aggregation of alien tropical schyphozoan *Rhopilema nomadica* Galil, 1990 in the Mediterranean coast of Egypt. *Int. Mar. Sci. J.*, **2**, 1–7.

Morandini, A. and Gul, S. (2016) Rediscovery of *Sanderia malayensis* and remarks on *Rhopilema nomadica* record in Pakistan (Cnidaria: Scyphozoa). *Pap. Avulsos Zool.*, **56**, 171–175.

Nakar, N. (2011) *Economic evaluation of jellyfish effects on the fishery sector-Case study from the Eastern Mediterranean. M.A. Dissertation*, University of Haifa, pp. 1–95.

Newman, G., Wiggins, A., Crall, A., Graham, E., Newman, S. and Crowston, K. (2012) The future of citizen science: emerging technologies and shifting paradigms. *Front. Ecol. Environ.*, **10**, 298–304.

Nordstrom, B., James, M. C., Martin, K. and Worm, B. (2019) Tracking jellyfish and leatherback sea turtle seasonality through citizen science observers. *Mar. Ecol. Prog. Ser.*, **620**, 15–32.

Ogle, W. (1882) *Aristotle on the Parts of Animals*, Kessinger Publishing, LLC, p. 310.

Omori, M. and Hammer, W. M. (1982) Patchy distribution of zooplankton: behavior, population assessment and sampling problems. *Mar. Biol.*, **72**, 193–200.

Ozer, T., Gertman, I., Kress, N., Silverman, J. and Herut, B. (2017) Interannual thermohaline (1979–2014) and nutrient (2002–2014) dynamics in the Levantine surface and intermediate water masses, SE Mediterranean Sea. *Glob. Planet. Chang*, **151**, 60–67.

Pires, R. F. T., Cordeiro, N., Dubert, J., Marraccini, A., Relvas, P. and DOS Santos, A. (2018) Untangling *Velella velella* (Cnidaria: Anthoathecatae) transport: a citizen science and oceanographic approach. *Mar. Ecol. Prog. Ser.*, **591**, 241–251.

Pitt, K. A., Kingsford, M. J., Rissik, D. and Koop, K. (2007) Jellyfish modify the response of planktonic assemblages to nutrient pulses. *Mar. Ecol. Prog. Ser.*, **351**, 1–13.

Prieto, L. (2018) Diagnosis, Prognosis, and Management of Jellyfish Swarms. In Pascual, A., Tintoré, J., Verron, J. and Chassignet, E. (eds.), New Frontiers in Operational Oceanography, GODAE OceanView, pp. 737–758.

Purcell, J. (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. *J. Mar. Biol. Ass. UK*, **85**, 461–476.

R Core Development Team (2018) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org.

Richardson, A. J., Bakun, A., Hays, G. C. and Gibbons, M. J. (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends Ecol. Evol*, **24**, 312–322.

Rosentraub, Z. and Brenner, S. (2007) Circulation over the Southeastern continental shelf and slope of the Mediterranean Sea: direct current measurements, winds, and numerical model simulations. *J. Geophys. Res.*, **112**, 1–21.

Schnedler-Meyer, N. A., Kiørboe, T. and Mariani, P. (2018) Boom and bust: life history, environmental noise and the (un)predictability of jellyfish blooms. *Front. Mar. Sci.*, **5**, 257.

Tahera, Q. and Kazmi, Q. B. (2015) Occurrence of *Rhopilema nomadica* Galil, 1990 (Cnidaria: Scyphozoa: Rhizosdomatidae) in Pakistani waters. *J. Biol. Res.*, **3**, 49–51.

Tilves, U., Fuentes, V. L., Milisenda, G., Parrish, C. C., Vizzini, S. and Sabatés, A. (2018) Trophic interactions of the jellyfish *Pelagia noctiluca* in the NW Mediterranean: evidence from stable isotope signatures and fatty acid composition. *Mar. Ecol. Prog. Ser.*, **591**, 101–116.

Tweddle, J. C., Robinson, L. D., Pocock, M. J. O. and Roy, H. E. (2012) Guide to citizen science: developing, implementing and evaluating citizen science to study biodiversity and the environment in the UK. *Wallingford, NERC/Centre for Ecology and Hydrology*, 1–29.

VAN Walraven, L., Langenberger, V., Dapper, R., Witte, J. I. J., Zuur, A. F. and VAN DER Veer, H. W. (2015) Long-term patterns in 50 years of scyphomedusae catches in the western Dutch Wadden Sea in relation to climate change and eutrophication. *J. Plankton Res.*, **37**, 151–167.

Yahia, M. N. D., Yahia, O. K. D., Gueroun, S. K. M., 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 Rec.*, **2**, 319–323.

Yeruham, E., Rilov, G., Shpigel, M. and Abelson, A. (2015) Collapse of the echinoid *Paracentrotus lividus* populations in the Eastern Mediterranean - result of climate change? *Sci. Rep.*, **5**, 13479.

Zenetos, A., Koutsogiannopoulos, D., Ovalis, P. and Poursanidis, D. (2013) The role played by citizen scientists in monitoring marine alien species in Greece. *Cah. Biol. Mar.*, **54**, 419–426.