Tracking Jellyfish Swarm Origins Using a Combined Oceanographic-Genetic-Citizen Science Approach

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Biological invasions of jellyfish may critically affect ecosystems and ecosystem services, yet their complex life cycle makes tracking their origins and dispersal vectors a challenging task. Here we combine citizen science observations, oceanographic modeling, and population genetics to track swarms of the invasive nomad jellyfish, *Rhopilema nomadica*, across the Eastern Mediterranean Sea. Jellyfish observations were recorded by citizens from two Israeli beaches in two consecutive years. A Lagrangian model coupled with a high-resolution 3D hydrodynamic model (SINMOD) was then used to simulate drift of ephyrae from probable polyp bed locations. Finally, mitochondrial DNA (mtDNA) sequence was constructed to examine swarm connectivity. Temporal (both seasonal and interannual) variation in observed swarms generally exceeded spatial differences between the two surveyed beaches. Early detection of swarms by citizens in offshore waters and the higher offshore particle distribution shown by the drift model, point to considerable offshore transport of the swarms. However, a higher probability was found for a nearshore location of the polyp beds, as nearshore origins were more closely correlated to hits on target beaches. *R. nomadica* released as ephyrae in early spring were likely to reach target beaches 200-300 km down current within two to three months as swarms of young adults in the early summer bathing season. *R. nomadica* populations exhibited little temporal or spatial genetic differentiation, a typical feature of a species that has recently undergone rapid population expansion. The offshore transport, the lack of genetic structure, and the interannual differences in both hydrodynamics and citizen scientist observations, all indicate decentralized swarm origins. This type of interdisciplinary approach can thus provide viable tools to track bloom formations. Understanding the complexity of jellyfish swarm dynamics supports future management strategies such as forecasting, preparedness and public education.

Keywords: biological invasion, jellyfish tracking, citizen science (CS), oceanographic modeling, Mediterranean Sea-Eastern, population genetics-empirical

INTRODUCTION

Jellyfish blooms are a global natural phenomenon that is sometimes considered to be exacerbated by human activities (Purcell et al., 2007). Jellyfish are typically perceived as a nuisance, negatively affecting human interests such as coastal leisure, tourism, fisheries, aquaculture, power, and desalination plants (Purcell et al., 2007; Edelist et al., 2021). They also play an important role in marine ecosystems and can be considered as a boon for fishers, a valuable source of food and other products when harvested sustainably (Edelist et al., 2021). For all these reasons, understanding jellyfish swarm dynamics and tracking their origins are important. *Rhopilema nomadica* is the largest, most venomous, and most prominent jellyfish species in the Eastern Mediterranean (Galil et al., 1990; Edelist et al., 2020). This species may have entered the Mediterranean Sea *via* the Suez Canal (Lessepsian migration), though it was rarely recorded outside the Mediterranean. *R. nomadica* was first recorded in the Mediterranean Sea in 1977 (Lotan et al., 1994), and its population has increased considerably since the early 1980s. Appearing in Israel first (Galil et al., 1990), and to date Israeli beaches are the only ones where polyps of *R. nomadica* were found *in situ* (albeit only on settlement plates, see Nakar, 2011; Dror, unpublished), large swarms were then recorded in Lebanon and Syria (Lotan et al., 1994), Turkey, Greece, Malta (Brotz et al., 2012) Egypt (Abu El-Regal and Temraz, 2016; Madkour et al., 2019) and most recently Tunisia, Sardinia and Sicily (Balistreri et al., 2017). *R. nomadica* swarms affect tourism by stinging bathers, thwart fishing operations by clogging nets and power and desalination plants by blocking seawater intake gear (Edelist et al., 2020). This species is therefore regarded as one of the worst invasive species in the Mediterranean Sea (Streftaris and Zenetos, 2006).

Like most coastal scyphozoan jellyfish species, *R. nomadica* has a metagenic life cycle, alternating between a free-swimming, sexually reproducing medusa stage, and an asexual benthic polyp stage. Jellyfish polyps may survive over many years (Purcell et al., 2007) and it is thus plausible that swarms will display some degree of spatial consistency (Fleming et al., 2013). *R. nomadica* polyps were shown to strobilate mostly in mild temperatures of 20-26°C when reared in laboratory conditions (Lotan et al., 1994), they may produce ephyrae almost year-round, and their activity in nature remains unknown. The life cycle of medusae from sessile polyps to sexually mature jellyfish and on to new polyps relies on circulation patterns that provide them with a suitable environment and disperses them over vast expanses of ocean (Johnson et al., 2001; Moon et al., 2010). However, our knowledge of polyp bed locations and the distances travelled by adult medusae are still very limited (Schnedler-Meyer et al., 2018).

Oceanographic models have played a key role in facilitating our understanding of oceanic processes, including jellyfish swarms (e.g. Kawahara et al., 2006; Moon et al., 2010). Shelf currents were among the main factors determining jellyfish distribution and swarm dynamics in the case of *Nemopilema nomurai* in the East China Sea and East/Japan Sea (Moon et al., 2010). In the eastern Mediterranean the Libyo-Egyptian Current

is a major vector spreading jellyfish from the North African coast toward Turkey, *via* Israeli coastal waters (Edelist et al., 2020). Anticyclonic eddies may develop along this route, to the west of the Israeli coast (Rosentraub and Brenner, 2007), impacting the along and cross-slope transport routes. South of Cyprus, an anticyclonic eddy (Cyprus Eddy, **Figure 1**) is a fairly persistent feature that significantly impacts Levantine water transport (Mauri et al., 2019). In addition, the surface currents outside the Israeli coastal zone include cyclonic and anticyclonic eddies associated with the Shikmona Gyre system (**Figure 1**). South-East of Cyprus, there is an eddy system (Latakya Eddy) that can be either cyclonic or anticyclonic. Offshore transport by eddies may thus help explain the large seasonal and interannual fluctuations and complex dynamics in *R. nomadica* swarming (Edelist et al., 2020).

In the absence of frequent oceanographic surveys of gelatinous zooplankton in both coastal and offshore waters, our ability to follow the jellyfish swarm dynamics *in situ* is often highly limited. Here, reports by the public are essential to complement scientific knowledge. Citizen science initiatives are flourishing in recent years (Guerrini et al., 2018; Johansen et al., 2021). Today, smartphone apps and social networks facilitate collection of local ecological knowledge from the public in unprecedented quantity and quality (Newman et al., 2012). Such endeavors have been in use for observing species distribution and invasive species in general (Giovos et al., 2019) and jellyfish swarms particularly in the Mediterranean for more than a decade (Fleming et al., 2013; Edelist et al., 2020; Marambio et al., 2021).

To be able to understand jellyfish swarm dynamics, it is crucial to focus on the origin of the bloom and the connectivity of the populations in time and space; whether the individuals we observe in a swarm are from common local origins, have drifted from another region, or have accumulated in a specific region from multiple sources (Dawson & Hamner, 2008). *R. nomadica* adults were recently shown to have a considerable swimming ability (Malul et al., 2019). Adult jellyfish do not only passively drift (horizontally) but may travel up and down in the water column or, to a limited extent, with or even against the current (Fossette et al., 2015), while juvenile stages exhibit a more passive drift behavior. Therefore, oceanographic current models can be useful in studying swarms especially for ephyrae and juvenile stages, even though they predominately assume a passive drift. Similarly, when locations of the polyp populations are not known, as is the case with *R. nomadica* in the Mediterranean, the population genetic approach using adult specimens forming the swarm can provide valuable information on the scale and origin of the swarm. Population genetics, using either mitochondrial DNA cytochrome oxidase I (mtCOI) as a marker or a microsatellite approach, have been used to clarify the connectivity or distinctness of jellyfish aggregations for several jellyfish taxa (e.g., Stopar et al., 2010; Lee et al., 2013). For some taxa, the population genetic approach enabled clear population subdivisions defining locations where swarms occur among geographically isolated populations (Lee et al., 2013). Conversely, some taxa have shown low genetic diversity and lack of genetic structure (Stopar et al., 2010). For *R. nomadica*, several
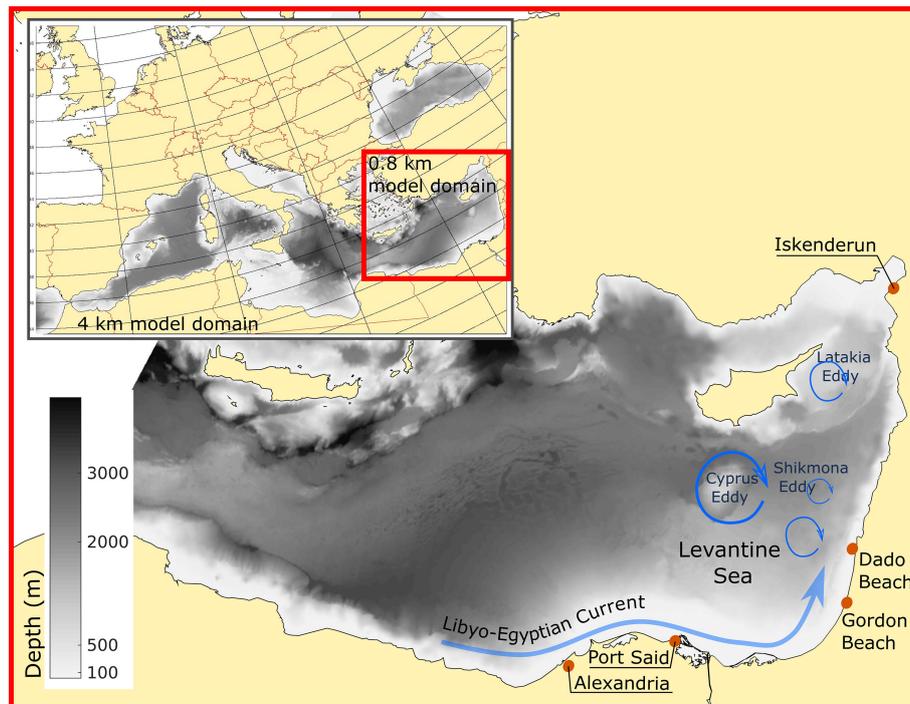
FIGURE 1 | Study area: Bathymetric map of the Mediterranean Sea, with main circulation patterns (blue arrows) and release and target beaches explored in the study (red circles).

microsatellite loci have been identified by a whole genome sequencing approach (Douek et al., 2020). Long-term changes in population genetic features of *R. nomadica* were recently studied by looking at the mtCOI haplotype diversity in the Eastern Mediterranean (Giallongo et al., 2021). The Giallongo et al. (2021) dataset concluded that all specimens of *R. nomadica* collected in the area belong to a single population, lacking clear genetic structure and there was no significant difference in the four seasons along a 12-year sampling period.

In the present study, we applied a high-resolution numerical model of Eastern Mediterranean current vectors to estimate distribution time and track distance scales from probable polyp habitats to areas in which mature *R. nomadica* swarms were observed by a citizen science project. In addition, we used a complementary population genetic approach, to determine the homogeneity of these *R. nomadica* swarms observed in the coast of Israel.

METHODS

In the following we describe methodology for: a) distribution of jellyfish using data from the Israeli citizen science project *Meduzot Ba'am* ("Jellyfish Inc."), b) hydrodynamic tracking used to simulate dispersal from ephyra release to adult swarming along the Levantine coast and c) population genetics of medusae collected along the coast.

Jellyfish Sightings Based on Observations From the Citizen Science Project, *Meduzot Ba'am*

Jellyfish sightings have been recorded by volunteer reporters (citizens) along the entire Israeli coastline since 2011, highlighting massive swarms in the June-July bathing season (Edelist et al., 2020). A subset of *R. nomadica* observations was thus extracted to focus on the two popular urban bathing beaches of Dado (Haifa) and Gordon (Tel Aviv) for the bathing season (calendar weeks 18-40) of 2017 and 2018. Observations were recorded *via* a dedicated internet website (www.meduzot.co.il) and the subset was extracted from Pangaea - an Open Access data archiving and publication repository (https://doi.pangaea.de/10.1594/PANGAEA.897389). For the present study, *R. nomadica* was chosen since it is the most common, conspicuous, stinging, and recognizable species in the Levant. Across the entire eight-year database, out of 6,033 sightings of eight scyphozoan jellyfish species, *R. nomadica* was by far the most common with 4,031 sightings (66.8%). Moreover, other scyphomedusa species in the region, mainly *Rhizostoma pulmo, Phyllorhiza punctata, Aurelia* sp*., Marivagia stellata* and *Cotylorhiza* spp., typically co-occur and intermix with *R. nomadica* during summer swarms (Edelist et al., 2020). The locations were chosen to represent main urban bathing beaches with sufficient spatial and temporal reporting coverage. Detailed information facilitating species identification was provided on the website. The distance from shore, type of activity, jellyfish species encountered, their quantity and size, whether stranded jellyfish were observed on the

beach and if volunteer reporters were stung by jellyfish were also recorded (See Edelist et al., 2020).

The relative abundances of jellyfish observed by volunteers was ranked according to categorical values of "0", "2", "10" and "50", denoting "zero", "few", "medium" and "swarm" situations respectively. The average number of jellyfish per report per week [Eq. (1)] was used to create JSI - a Jellyfish Swarm Index (Edelist et al., 2020), defined as:

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

where A_i is the binned quantity (0, 2, 10 or 50) of *R. nomadica* per report i, and n is the number of reports per week. The main modification in the JSI calculated here (in comparison to the JSI defined in Edelist et al., 2020) was that the JSI was calculated per week rather than per month, in order to match the higher resolution of the oceanographic model. Differences between mean ranked abundances were further tested by Kruskal-Wallis test – a nonparametric one-way ANOVA on ranks.

Hydrodynamic Model for Jellyfish Swarm Tracking

The present study examines how currents along nearshore areas in the Eastern Mediterranean Sea can affect horizontal drift of particles with a 40 m depth threshold, targeting beaches located down current from the release sites (**Figure 1**).

Jellyfish may modulate their swimming behavior in relation to currents, thereby increasing swarm formation or reducing the probability of stranding (Fossette et al., 2015). Despite the fact that large scyphozoan jellyfish like *R. nomadica* show a certain degree of active mobility (Malul et al., 2019), a passive drift in relation to Levantine currents was assumed here, as summer swarms of *R. nomadica* are comprised of more juvenile stages than winter swarms (Edelist et al., 2020). Using passive drifting as a proxy to track jellyfish blooms is a likely assumption especially for ephyrae and young medusae, since drift is the principal dispersal mechanism for early medusae life stages (Moon et al., 2010).

Ocean Model Configuration

In the present study, the SINMOD model framework has been used to track the movement of passive tracers to the Israeli shores. SINMOD is a coupled 3D model developed over the past 30 years to simulate physical (hydrodynamic) and biological processes (see Wassmann et al., 2010). The model's hydrodynamic component is based on the primitive equations that are solved using a z*-coordinate regular grid with square cells.

A model domain covering the Mediterranean Sea with 4 km horizontal resolution and 43 vertical layers was run from 2010 to 2018. Tides from TPXO (www.txpo.net/global), freshwater supply from various sources and atmospheric forcing (ERA5 from European Centre for Medium-Range Weather Forecasts, ECMWF) were applied. A high-resolution model with 0.8 km resolution was nested in the 4 km model and run for 2017 and 2018. The high-resolution model is computationally expensive to run but gives a good representation of ocean dynamics including gyres, coastal currents, and eddies. The spatial scale of the dynamic mesoscale field can be calculated from the internal

Rossby radius of deformation and was previously found to be 5-12 km in the Mediterranean Sea (Pinardi and Masetti, 2000), hence the high resolution model will significantly improve representation of mesoscale variability.

Jellyfish Tracking Module

A Lagrangian particle tracking approach allows examination of multiple release points for simulated *R. nomadica* ephyrae. The particles (ephyrae) drift passively with currents horizontally but are allowed to migrate upwards if they were mixed or advected below 40 m depth. Particles were released at both 8 m and 15 m depths at 269 positions (in total 538 positions) along the Egyptian coast between Alexandria and Port Said. The position of the particles was updated every timestep (80 s) and saved every hour for later analysis. It has been shown that *R. nomadica* accelerates strobilation rates when Levantine waters begin to warm, generally around mid-April (Lotan et al., 1994). We therefore chose April 18th as the start date for release of the particles both in 2017 and 2018, and the simulation was allowed to run until August 31st. The simulations were run for 2017 and 2018, releasing 538 new particles every hour. The particles were not allowed to grow or die during the simulations and were tracked from release to the end of the simulations.

To date Israeli beaches are the only ones where polyps of *R. nomadica* were found *in situ* (Nakar, 2011; Dror, unpublished). We therefore ran a second release from Israel. Particles were released from 55 locations (at 8m and at 15m for each, in total 110 particles released per hour) near the coast off Dado beach in Israel starting on April 18th to the end of August. The aim was to test further spread of the particles to Eastern Turkey - an area where *R. nomadica* is long known to swarm (Avsar et al., 1996). In addition, we calculated the drift time from the Dado release sites, until the particles return to Dado by recirculation in an eddy offshore Dado. While Iskenderun Bay only receives a fraction of the longshore counterclockwise current, *R. nomadica* has long been known to swarm beaches in this region (Avsar et al., 1996; Duysak et al., 2013).

Molecular Analysis for Jellyfish Swarm Identification

Rhopilema nomadica were sampled in the Eastern Mediterranean Sea in different seasons in 2020-2021 and from three locations along the Israeli coast. For the analysis we defined those areas as South and Centre (relating to the Tel-Aviv region), and North (relating to the Haifa region). We focus on two time periods: summer (June-July 2020) and winter (January-March 2021 (for details see **Supplementary Material**). Most medusae were hand-collected from a small boat, 0.5-1.5 nautical miles offshore where bottom depth ranged between 5 to 35m by means of a dip net and 20 L buckets. Tissue samples were also taken from several freshly stranded medusae that had washed to shore. Whenever possible, bell diameter, weight, sex and sea surface temperature were documented. Pieces of gonads or oral arms were removed and immediately fixed in 70% ethanol. DNA from specimens was extracted using a modified Chelex rapid-boiling procedure as explained in Granhag et al. (2012). The mtCOI gene was amplified using primers FFDL and FRDL (Armani et al., 2013). The polymerase chain reaction (PCR) was conducted in a total

volume of 20 μl, containing 1.0 μl of DNA template, 0.4 μL Phire® Hot Start DNA polymerase, 4 μL of Phire ® reaction buffer, 1μL of each primer (final concentration 0.2 mmol), 0.4 μL of DNTP, 0.6 μL of 3% DMSO, and 1.6 μL nuclease-free water. PCR conditions consisted of an initial cycle at 95°C for 5 min, 40 cycles of 94°C for 30 sec, 50°C for 30 sec, 72°C for 90, and a final extension at 72°C for 10 min. PCR products that yielded a clear band on 1.5% agarose gel by electrophoresis were sent to Macrogen Europe for purification and sequencing. All samples were sequenced in the forward and reverse direction to assure the accuracy of description for each polymorphic site and nucleotide haplotype. The resulting nucleotide sequence electropherograms were checked by eye for poor base calls using Chromas Lite 2.1 (Technelysium Pty Ltd). During the process misreads were corrected, and poorly resolved terminal portions of sequences were discarded. High-quality sequences were assembled using BioEdit software (Hall, 1999), and identities of sequences were confirmed by BLAST search in GenBank (>98% identity). Individual sequences were aligned with the MAFFT online service (Katoh et al., 2019). Genetic diversity within populations was estimated by computing haplotype diversity (H) and nucleotide diversity (π) (Nei, 1987) using DnaSP v5 (Librado and Rozas, 2009). A median-joining network showing the relationships between the mtDNA haplotypes was constructed using the PopART (http://popart.otago.ac.nz/howtocite.shtml; Bandelt et al., 2000). Genetic differentiation was calculated by means of pairwise FST values using 10,000 permutations in ARLEQUIN 3.1 (Excoffier et al., 1992) within the analysis of molecular variance (AMOVA) framework (Excoffier et al., 1992). The neutrality statistics Tajima's D and Fu's FS were used to test constant population size versus population growth (Ramos-Onsins and Rozas, 2002) using DnaSP v5. Also, mismatch distributions (Rogers and Harpending, 1992) were generated in DnaSP. Although there is a mismatch between the years used for the simulation of jellyfish distribution (2017-2018) and the years when jellyfish were collected for genetic analyses (2020-2021), we assume the current regimes do not change on an annual basis and that the genetic makeup of *R. nomadica* in this region is stable and does not change rapidly, as also noted in Giallongo et al. (2021). The sequences reported in the study have been deposited in the European Nucleotide Archive repository with accession numbers: OW055719-OW055735.

RESULTS

Jellyfish Observations

Jellyfish reports in the two study beaches for the study period yielded 701 observations of either "*R. nomadica*" (n=198) or "zero jellyfish" (n=503). Most reports were submitted for the inshore zone, from the coastline to a distance of 200 m from shore, with Haifa beaches characterized by a higher quantity and proportion of offshore reports in both study years (**Table 1**).

Both Haifa and Tel Aviv beaches were impacted by jellyfish swarms in both study years. However, a longer and more intense early summer swarm was recorded in 2017; while 2018 was characterized by a shorter early summer swarm followed by a later autumn swarm in mid-September (**Figure 2**). Juveniles (0-10 cm) were only observed in the late summer 2018 swarm and jellyfish typically arrived as young adults (11-30cm) to full adult (30-60) sizes, with a few rare observations of larger specimens in 2017 (**Figure 2**, although large specimens >60 were viewed in the summer and other seasons as well – see Edelist et al., 2020).

Swarms were detected at the northern Dado Beach (Haifa) before they were observed in the southern (Tel Aviv) Gordon Beach (**Figure 2A**). In 2017, swarms arrived earlier and were larger and more diverse in size composition, including extra-large specimens >60cm, while the 2018 autumn swarm consisted of predominately smaller individuals (**Figure 2B**). On average, more *R. nomadica* individuals per report were sighted offshore (>200 m from the beach) than inshore at both beaches, in both study years (**Figure 3**), and distance from shore was found to be a statistically significant factor in determining swarm probability (Kruskal-Wallis H(2) = 70.46, P = 5.551e-16).

Ocean Model Results

Over the two study periods, significant differences in current patterns were simulated. The dynamic structure of Levantine eddies/gyres and currents are known to vary seasonally and interannually (Özsoy et al., 1993). The weak longshore current recorded in May from Egypt towards Israel intensified considerably in June in 2018 and less so in 2017 (**Figure 4**).

The Levantine longshore currents either entered the Shikmona eddy, meandering clockwise south of Cyprus, or flowed northwards closer to shore carrying particles (and jellyfish) towards Turkey (**Figure 4**). Looking into current maps for surface, 8m and 15m depth from May to August, we generally found that the current is a bit weaker at 15m than at shallower depths for the release area and eastwards. This is mainly valid for the shallow shelf and less so for deeper parts of the study area. When we compared the particle drift patterns for particles released at 8m and 15m, only few differences were discernible in the model results, and we used an averaging of results from both depths in further analysis.

Release From the Egyptian Coast

A hindcasting approach was used here, based on citizen reports of adult medusae. These led to postulated ephyra release

TABLE 1 | Number of inshore and offshore observations of *R. nomadica* in 2017 and 2018 in weeks 18-40 (May to September) in Haifa and Tel Aviv beaches.

Location	Distance from shore	2017	2018	Total
Dado Beach – Haifa	Inshore (<200 m)	192	105	297
	Offshore (>200 m)	34	28	62
Gordon Beach – Tel Aviv	Inshore (<200 m)	126	189	315
	Offshore (>200 m)	13	14	27
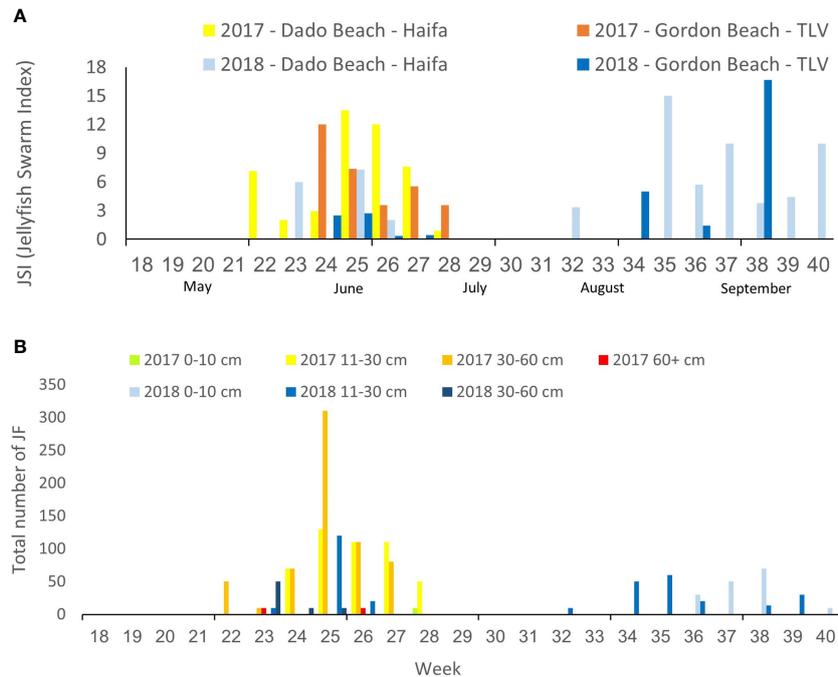
FIGURE 2 | Weekly Jellyfish Swarm Index (JSI) in Tel Aviv and Haifa beaches in the summers of 2017 and 2018 **(A)**, and total number of *R. nomadica* reported per week, ranked by size (bell diameter) distribution **(B)**.
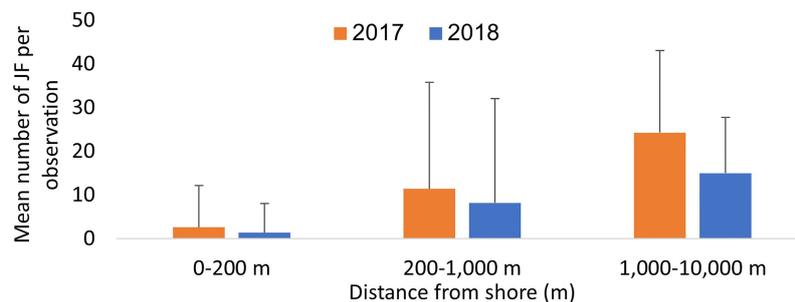
FIGURE 3 | Mean number of jellyfish per observation (JSI) in inshore (0-200 m, n=612) mid-range (200 m – 1,000 m, n=71) and offshore (1,000 m – 10,000 m, n=17) observations in the two study years.

locations, from which the drift of particles was simulated to produce "hits" on the target beaches. Nearshore particle released from the continental shelf (<200m depth) in the Eastern region of Bardawil and Port-Said to Damietta (Egypt) were shown to have the highest correlation with hits on both target beaches in both study years (**Figure 5**).

Interannual differences in the current regime may affect results somewhat (in 2018 stronger currents could have widened hindcasting range westwards), but overall offshore release points and release from points further west in the Baltim-Alexandria region west of the Nile delta showed a

significantly lower hit correlation with the two target beaches than the Bardawil-Port Said-Damietta area, (**Figure 5**).

The final (August 18th) distribution of released particles is shown in **Figure 6**. The highest number of hits was found in the shelf area along the coasts of Egypt and Israel, while some particles meandered offshore and into the gyres. Fewer particles drifted with the longshore currents to the coasts of Lebanon, Syria and Turkey (**Figure 6**).

Overall, the inshore areas east of Alexandria, including the nutrient rich Nile delta were tracked as the probable origins of Israeli summer swarms (**Figure 5**). The early summer swarms

FIGURE 4 | Monthly average surface current velocity and direction used in the particle model for May (left) and June (right) in 2017 (top) and 2018 (bottom).
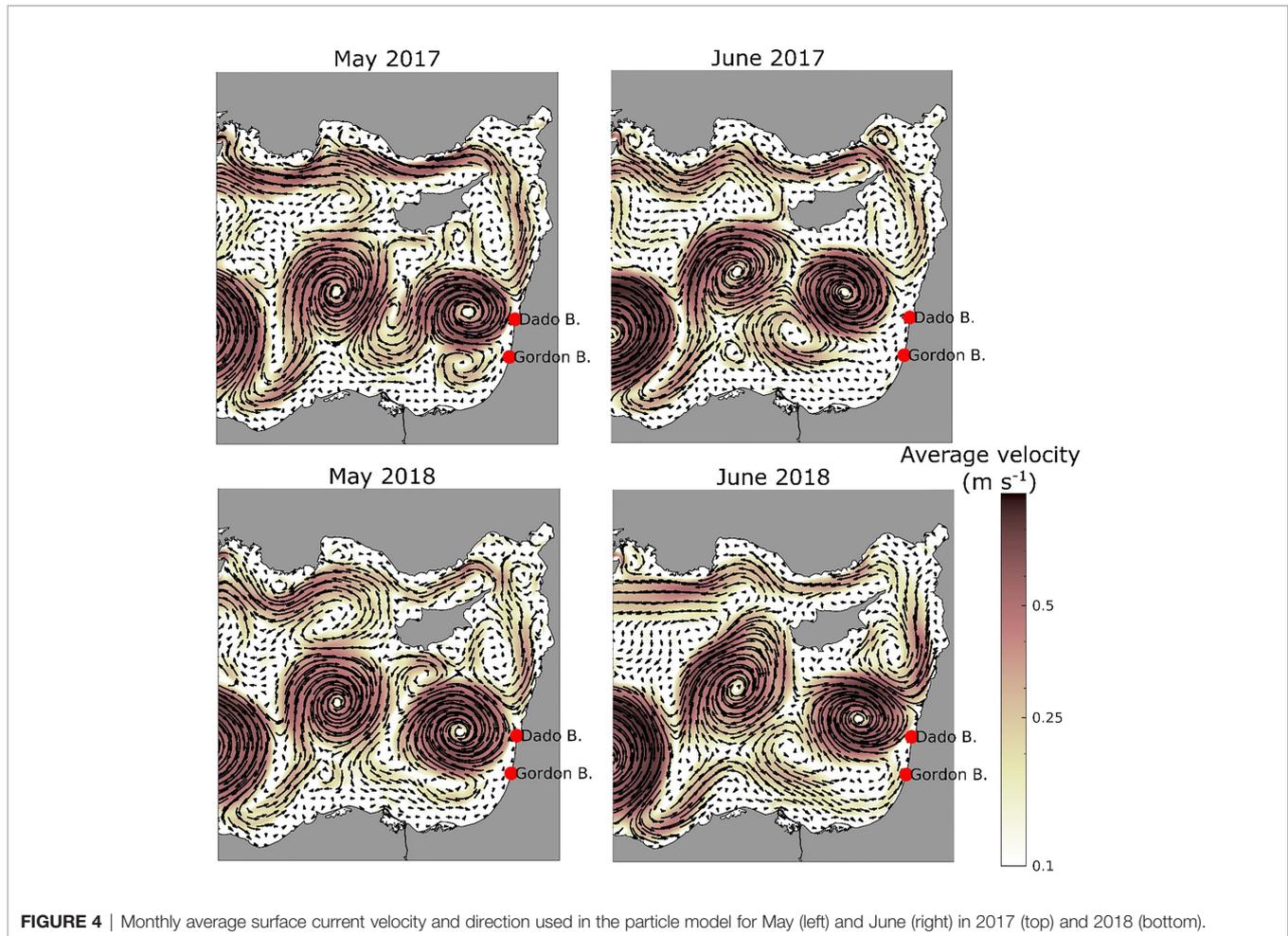
probably emanate from enhanced strobilation and release as water begins to warm in April, reaching Tel Aviv and Haifa in 47.1 and 58.3 days respectively (**Figure 7**).

Release From the Israeli Coast

Most particles released from the Israeli coast hit the beaches of Lebanon and Syria, and lower numbers reached Turkey. There was also considerable meandering of particles westwards towards the gyres and the Cypriot coast (**Figure 8**).

In 2018, there was a significantly lower hit correlation to Iskenderun than in 2017, and a longer mean duration of 93.6 days of particle drift time from Haifa to Iskenderun (**Figure 9** and **Table 2**).

In the simulation from April 2017 and 2018, particles were released from 55 points in northern Israel (**Figure 8**). In 2017, there were high hit rates of particles reaching Iskenderun (**Figure 8**) and the mean transportation time was 69.1 days (**Table 2** and **Figure 9**).

Some particles released near Haifa did not follow the coast northwards as **Figure 8** indicates, but instead went into the Shikmona eddy or southwestwards before returning to Haifa. Counting returned particles older than average drifttime from

offshore Egypt (57 days), gave mean/standard deviation of 69.4 d/14.4 d drift time for 2017 and 72.1 d/16.9 d for 2018, indicating the probability of cyclic swarming dynamics. In 2017 the number of paticles from Haifa to Iskenderun was higher than particles from Haifa to Haifa, but for 2018 the situation was reversed.

Sequence Diversity and Population Structure

To assess the genetic diversity of *R. nomadica*, a sequence length of 433 bp of the mtCOI gene was analysed from a total of 42 *R. nomadica* individuals sampled from the three areas during the summer of 2020 and winter of 2021). Over the whole data set collected in this study, 22 polymorphic sites, of which 9 were parsimony informative, were identified leading to the definition of 18 haplotypes. Haplotype richness was high (h = 0.90 ± 0.03 on average), but differentiation among haplotypes was modest (π (%) = 0.49 ± 0.5). All geographical regions showed similar haplotype and nucleotide diversity (**Table 3**).

A haplotype network based on mtCOI supports the non-differentiation of *R. nomadica* in the various regions along the Mediterranean coast of Israel. Analysis of molecular variance

FIGURE 5 | Colour-coded release points off the Egyptian coast according to particle hit distribution on Israeli target beaches in 2017 and 2018, averaged across both release depths of 8 m and 15 m. The numbers refer to hits at Gordon (Tel Aviv) and Dado (Haifa) for every release point.
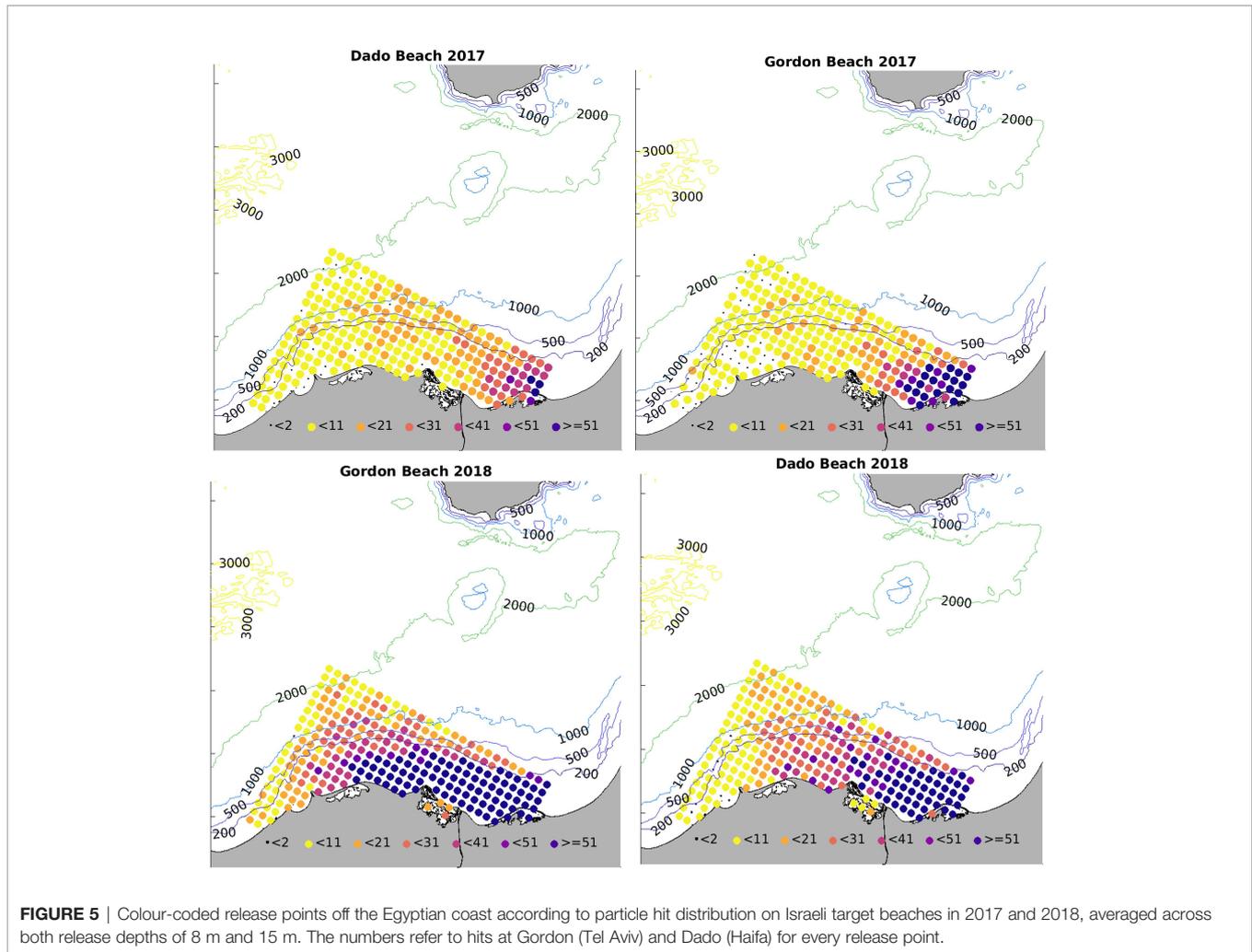
(AMOVA) showed that maximum variance was obtained within geographic regions (100%) while the variation among populations displayed negligible variance. This picture was concordant with pairwise F_{ST} values (**Table 4**).

Similarly, when comparing specimens collected from the coast of Israel in summer 2020 and the same region in winter 2021 (n=39), 22 polymorphic sites, of which 8 were parsimony informative, were identified leading to the definition of 18 haplotypes (**Figure 10**) and no significant inter-population genetic divergence was observed (F_{ST}=-0.01, p> 0.05). Moreover, all measures of genetic diversity and population structure calculated across populations pointed to low genetic structure regarding seasonal variations.

Despite the low sample number, the overall mismatch distributions of mtCOI haplotypes from the coast of Israel displayed unimodal distributions similar to the curve expected when a population has undergone rapid population growth in the past (Roman and Darling, 2007). Moreover, tests of neutrality also showed low and significant values of Fu's FS (−11.93, p < 0.05) and Tajima's D (−1.099, p < 0.05), further pointing to a recent demographic expansion. The low

subdivision observed across space and time was also recorded across sizes, further strengthening the notion of a single unstructured population.

DISCUSSION

Currents are an important factor that can alter the formation of jellyfish swarms, in addition to productivity, storms, light, moon phase, substrate availability, salinity, and temperature (Gibbons et al., 2016). It was suggested that in the Levant, swarming synchronicity of *R. nomadica* is triggered by temperature (Lotan et al., 1994). However, the presence of large swarms both in winter (Edelist et al., 2020) and/or autumn, as shown in this study (**Figure 2**), suggests that the process is more complex. Here, our model suggests that timing of *R. nomadica* swarm arrival is congruent with ephyrae releases hundreds of km up current, and our observations suggest that the typical expected drifting period of early life-stages of *R. nomadica* is two to three months, before swarming is recorded at the target beaches. The growth rates of *R. nomadica* in the wild are unknown, and as
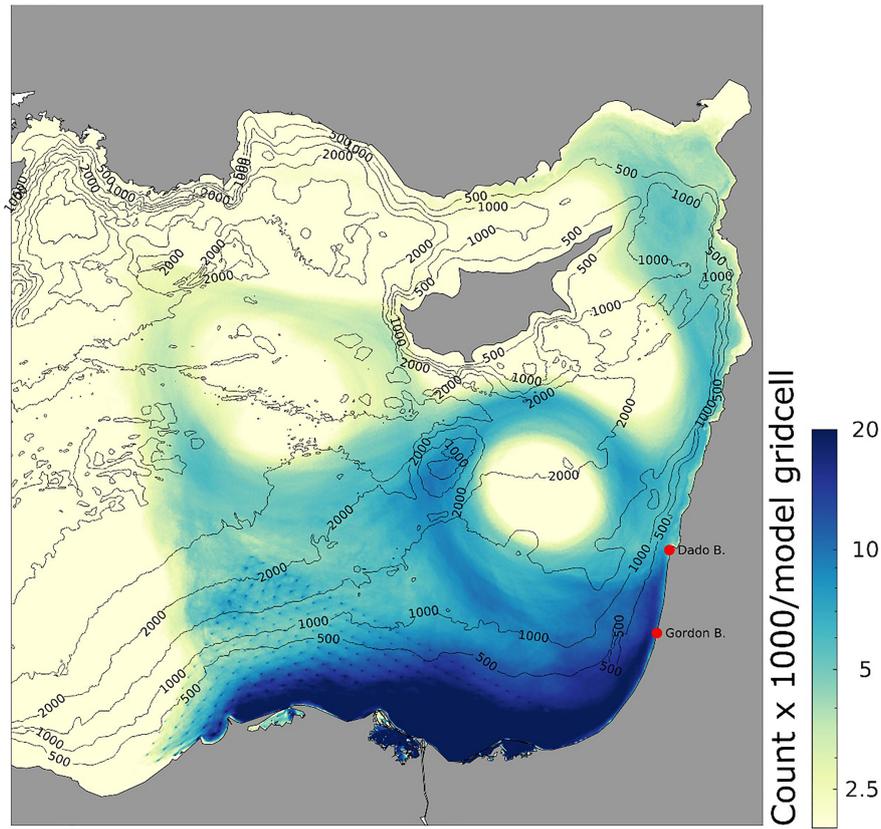
FIGURE 6 | Total number of particle hits within each model gridpoint, released from April 18th to August 31st 2018. Release locations along the Egyptian coast are shown in **Figure 5**.

ephyrae of metagenic jellyfish species may spend their early life period below the benthic boundary layer (Higgins et al., 2008), an earlier release and delayed transport may also occur. In the 2017 bathing season, a long, dense swarm of *R. nomadica* of mixed sized specimens was recorded in both Israeli beaches from mid-June to late July, while in 2018 a low-density swarm was recorded in early July followed by another low-density autumn swarm in September (**Figure 2**). Such autumn swarms are relatively rare and have only been recorded twice (2013 and 2018) over the past decade, while winter swarms comprised of large adult specimens are much more common (Edelist et al., 2020). In 2017, currents were strong in April and May and weakened in June while 2018 showed an opposite trend. In this study, we tackled the question - did the weaker longshore current in May 2018 lead to a smaller and later swarm? Temperatures in the Levant were relatively high throughout the winter of 2018 (Herut et al., 2019), so is there a logical explanation for the smaller, later swarm? Usually, a single factor is too simplistic to explain interannual variations in jellyfish phenology and swarming, and other factors like productivity, salinity, and storm conditions need to be taken into consideration to understand the full complexity of bloom dynamics (Boero et al., 2008). Here, we propose that such complexity may

involve the entry of the jellyfish into offshore eddies (**Figures 6**, **8**) or alternative factors affecting strobilation in the polyp beds. While no observations of *R. nomadica* in the offshore Levantine gyres are known from literature, their presence in offshore pelagic and mesopelagic realms should not be excluded *a priori* and further studies investigating the presence of *R. nomadica* in open offshore waters are needed.

The present study suggests that ephyrae of *R. nomadica* travel hundreds of kilometers over a period of 2-3 months to reach beaches down-current as young adults during the bathing season. The simulations of current-induced particle drift provide scenarios for the nearshore jellyfish observations in the Eastern Mediterranean Sea, as well as some offshore meandering, triggered by a complex system of eddies and gyres (**Figures 4**, **6** and **8**). A recent study (Kuplik et al., 2021) has shown that *R. nomadica* is able to successfully utilize scarce resources found in hyper-oligotrophic environments, such as the Levantine offshore waters. This property of *R. nomadica* may allow survival during extended offshore migrations, e.g. in the Shikmona-Cyprus eddies, or the counterclockwise transport from the Levant longshore to Turkey and then back through the gyre system. The arrival of large specimens in winter (Edelist et al., 2020) and the genetic connectivity between summer and winter specimens
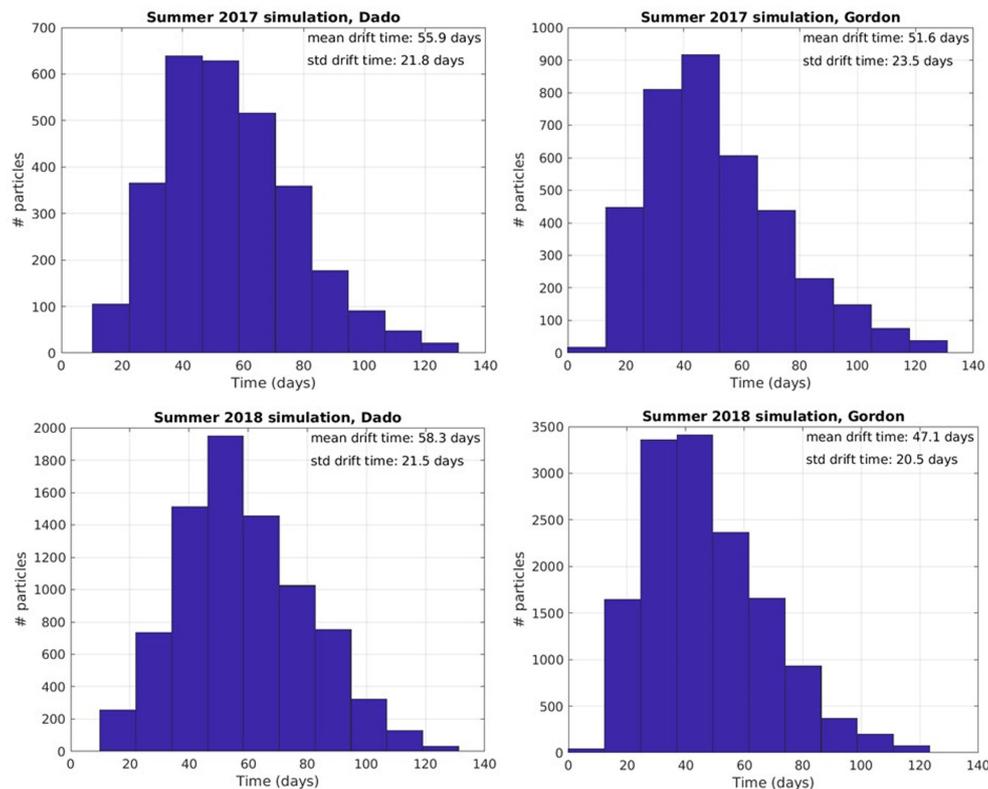
FIGURE 7 | Particle hit distribution on target beaches and mean drift time in days from release locations along the Egyptian coast (Between Alexandria and Bardawil) to Gordon (Tel Aviv) and Dado (Haifa) beaches in 2017 and 2018.

may support this notion. However, for the early summer bathing season during which the large dense mixed-size swarms are recorded, nearshore releases were shown to have a higher hit probability on target beaches than offshore releases (**Figure 5**). Ephyrae released from the Bardawil-Damietta area will typically reach Israeli beaches located 200-300 km down current in 20-40 days, while release from the Alexandria-Baltim area located 300-600 km up current from target beaches will take up to 90 days. This may of course change with variation in current velocities, but an overall mean arrival time of 55-60 days (**Figure 8** and **Table 2**) was found for the study duration in the spring. Similar results are attained when particles are released from Israeli beaches, reaching areas 200 km down current within a month and 400 km (Iskenderun) within three months (**Figure 8** and **Table 2**).

Surprisingly, jellyfish were occasionally spotted in the north (Haifa) before they were reported 100km up current in Tel Aviv (**Figure 2**). When observing the Meduzot Citizen Science database we find that the reason for this may be that at Dado Beach in Haifa, many of the reporters are long-distance swimmers that spotted the jellyfish offshore (twice that of Tel Aviv – **Table 1**) while most Tel Aviv Beach observations were submitted by inshore bathers. This pattern of an offshore positioning of the swarm (>1km from shore) before actually hitting the beaches is also in line with the oceanographic data

that predicted a larger number of hits in offshore locations (**Figure 6**).

Where jellyfish swarm, they are likely to leave polyps on the seabed if the right conditions and suitable habitat exist. The present study only models about a quarter of the Mediterranean distribution area of *R. nomadica* (see Balistreri et al., 2017; Edelist et al., 2020), and while polyp beds located in Egypt may lead to outbreaks on Israeli beaches, Tunisian polyp beds could cause swarms along the Libyan or Egyptian coasts. In 2017, *R. nomadica* swarms were reported from the Israeli coast from June to July while they occurred along the Egyptian coast in mid-June at Port Said (Madkour et al., 2019) and at Baltim and Alexandria from late June to early July (http://www.egyptindependent.com/sea-turtlesto-counter-jellyfish-on-shores/). A swarm covering the entire South-Eastern Mediterranean simultaneous basin thus remains a viable possibility. The availability of observations in the present study was limited to Israeli beaches, and the oceanographic model that tracked them up-current inevitably pointed at potential polyps located in Northern Sinai and the Nile delta region. Similarly, particles released from the Israeli coast showed how Israeli polyp beds may support swarm formation impacting beaches in East Turkey, or even returning (**Figure 8**).

One of the outstanding features of *R. nomadica* in the winter months is their exceptionally large size, up to 90 cm bell diameter
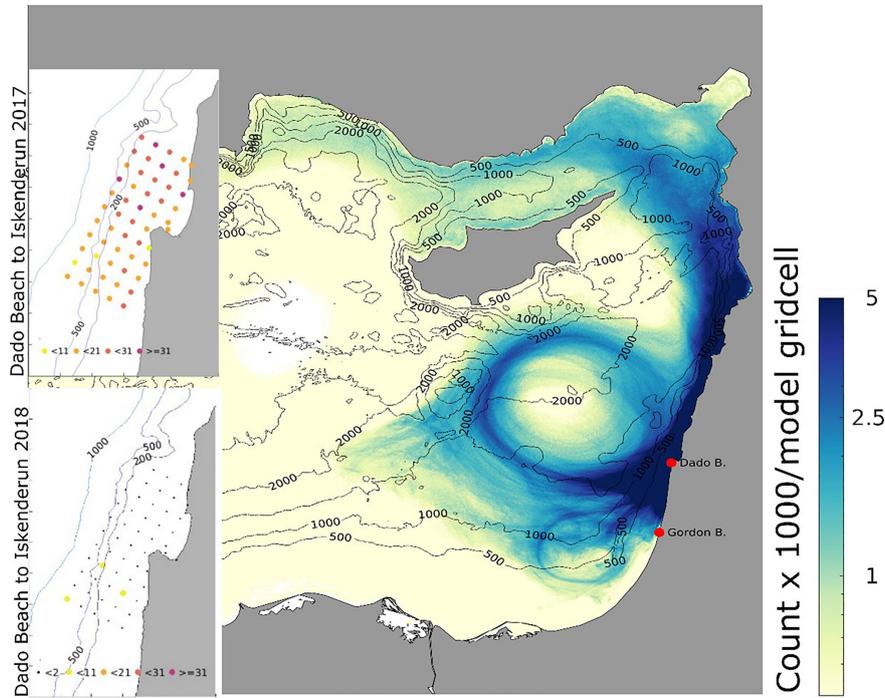
FIGURE 8 | Total number of particle visits within each model gridpoint, released from Dado beach (Haifa) from April 18th to August 31st of 2018. Insets: colour-coded release points off the coast of Haifa according to particle hit distribution on target beaches in 2017 (upper, left) and 2018 (lower, left), averaged across both release depths of 8m and 15m. Inset numbers refer to hits at Iskenderum from the release points, so the red points are connected to the target beach with more than 31 particles (2017) and small black points less than two particles (2018).
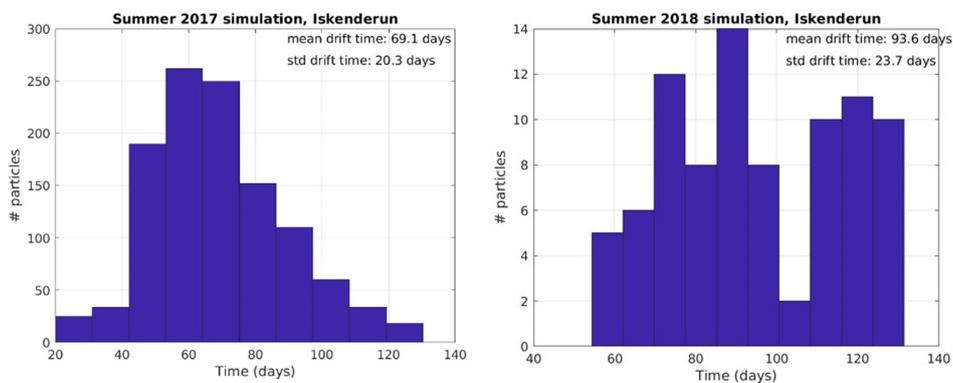
FIGURE 9 | Particle hit distribution on target beaches and mean drift time in days from release locations in Haifa region from April 18th to August 31st to Iskenderun, Turkey.

TABLE 2 | Mean and standard deviation of drift times to and from Haifa from simulations.

Period	Alexandria-Port Said to Haifa Mean/standard dev.	Haifa to Iskenderun Mean/standard dev.
Summer 2017	55.9 d/21.8 d	69.1 d/20.3 d
Summer 2018	58.3 d/21.5 d	93.6 d/23.7 d

TABLE 3 | Sample sizes and standard diversity indices for partial mtCOI sequences of *Rhopilema nomadica* sampled at three locations (North, Centre and South) and two seasons (summer 2020 and winter 2021).

Population	N	h	H	π (%)
North	9	8	0,97 ± 0,06	0,63 ± 0,18
Centre	19	11	0,90 ± 0,06	0,33 ± 0,23
South	14	9	0,91 ± 0,06	0,47 ± 0,48
Summer 2020	18	12	0,95 ± 0,03	0,62 ± 0,12
Winter 2021	21	11	0,88 ± 0,06	0,43 ± 0,43

Summer 2020 and winter 2021 samples were collected from Centre and Centre North area, as no specimens from South were recovered (N, number of specimens; h, number of haplotypes; H, haplotype diversity and π nucleotide diversity).

TABLE 4 | Pairwise FST values among samples of Rhopilema nomadica in three locations the coast of Israel (p>0.05).

	North	Centre
Centre	-0.034	–
South	-0.011	-0.012

as observed in Israeli coastal waters (Edelist et al., 2020). This size disparity may be a result of currents that carry the summer populations into the gyres and return them to the Levantine shores in winter. The population genetic data found in this study supports this possibility since the specimens sampled did not show any strong temporal or spatial genetic differentiation of the populations. Another possibility is that such large specimens (>60cm) could have been released as ephyrae in Western Egypt, Libya or even Tunisia (where autumn *R. nomadica* swarms have been reported in recent years by Balistreri et al., 2017). Peculiarly, *R. nomadica* swarms are seldom reported in Cyprus (www.ciesm.

org/gis/JW/build/JellyBlooms.php) despite currents that may carry them both north and south of the Island (**Figures 4**, **8**). A wider population genetic study with specimens collected from these regions is imperative for the study of both origins and spread of *R. nomadica* in the region.

Kawahara et al. (2006) and Moon et al. (2010) showed that *Nemopilema nomurai* swarms can travel thousands of km in the Tsushima current along Japanese coasts from July to November. *R. nomadica* may similarly traverse the ~2000km distance from Tunisia to Israel, or the ~3000km long Egypt-Israel-Lebanon-Syria-Turkey-Rhodes-Egypt circuit (**Figure 6**). Said et al. (2013) showed that drogue drifters released at 15 m depth near the Rhodes gyre may reach the Egyptian longshore current and drift eastwards at mean velocities of 20-25 cm/s (17.2-21.6 km/day). These values change geographically and throughout the year and the longshore current may at times be an order of magnitude slower. Mean monthly current velocities over the Israeli shelf as measured by Rosentraub and Brenner (2007) were only 0.86 km/
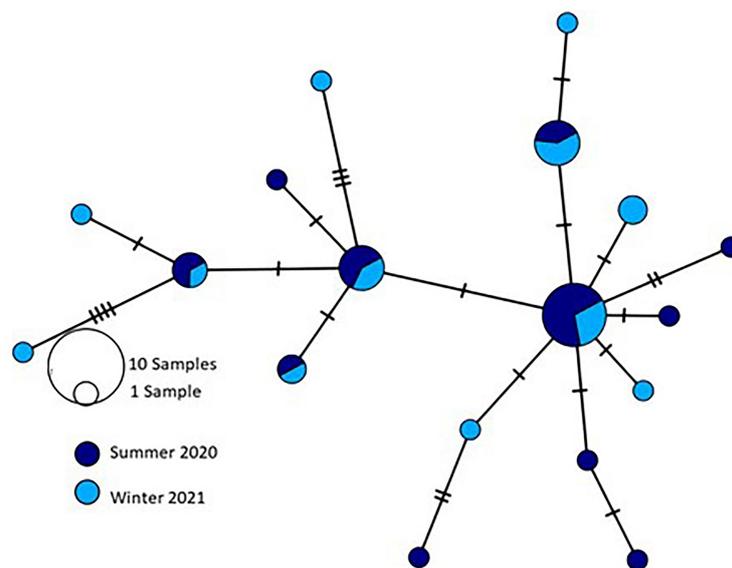
FIGURE 10 | Median-joining network showing the relationships between 18 haplotypes detected by sequencing *R. nomadica* collected from the coast of Israel during summer 2020 and winter 2021 for the partial mitochondrial DNA cytochrome oxidase I (mtCOI) region. Circle sizes are approximately proportional to haplotype frequency: the smallest circle represents a single individual; the largest circle represents 10 individuals. Each connection represents a single mutation, and small open black dots represent missing intermediate haplotypes.

day (July) to 10.36 km/day (February). If jellyfish do travel with the currents at these velocities, it should take a specimen only 18 days in February and 30 days in July to cover a distance of 200 km.

Initially, low winter temperatures were thought to be the main barrier to westward spread of *R. nomadica* beyond Greece in the northern Mediterranean, and an absence of *R. nomadica* from the coastal waters of Egypt was thought to result from lack of sufficient rocky substrates necessary for polyp settlement (Lotan et al., 1992). Since then, however, these supposed barriers proved no match for *R. nomadica*, which is now known to swarm beaches as far west as Sardinia and Tunisia (Balistreri et al., 2017) with numerous recent reports of swarms off Egyptian coasts (Abu El-Regal and Temraz, 2016; Madkour et al., 2019). Swarms may thus be much larger than the 100 km estimated by Galil and Zenetos (2002) as Alexandria and Baltim are located >500 km up current from Israel. Moreover, a synchronous bloom across the entire SE Mediterranean basin also seems reasonable, with numerous polyp beds contributing to these pan-basin blooms. Seascape genetics can potentially align hydrodynamic modelling with population genetic data and help identify population differentiation in swarms over local vs. broader spatial scales. Tools that are more advanced and better suited for populations genetic studies than mtCOI exist today and can be applied. For *R. nomadica*, future studies should also extend to pan-basin and cross-basin swarm dynamics, including reports from more target beaches over longer periods and sampling of specimens from countries across the Mediterranean for a full population genetics study.

A recent genetic study of *R. nomadica* populations indicates that the Israeli medusae are all part of a single Levantine population (Giallongo et al., 2021), with phylogenetic trees showing no geographical or temporal partitioning, but haplotype numbers indicating a small north-south gradient. Our findings agree with these results, and no significant spatial and temporal gradients were found in the medusae analysed. Some scyphozoan species, such as *Pelagia noctiluca* (Stopar et al., 2010), *Nemopilema nomurai* (Dong et al., 2016) and *Periphylla periphylla* (Majaneva pers. comm), have shown similar lack of genetic structure at comparable geographical scales over several hundred kilometres. However, other species have shown a clear geographically structured pattern; for example, *Cyanea capillata* and *Aurelia aurita* (Majaneva et al. In Prep)., particularly when observations cover different bodies of water (e.g. the Baltic and North Sea). The single unstructured Israeli population, and high number of haplotypes and singletons in *R. nomadica* were proposed by Giallongo et al. (2021) to indicate recurring independent introductions, or an open corridor augmenting gene flow. While this may be the case inside the Mediterranean, *R. nomadica* is unique in the sense that large swarms have never been recorded anywhere outside the Mediterranean, and the nearest 'origin' specimens ever recorded were >2,000 km away from the mouth of the supposed invasion vector, the Suez-Canal. The unimodal distribution found here for mtCOI haplotypes resembles that of a population that has experienced a recent

demographic expansion (Roman and Darling, 2007; Giallongo et al., 2021). Therefore, while it is still unknown how (and whether) *R. nomadica* first entered the Mediterranean, ballast water or hull fouling scenarios should be favoured over direct drift\swimming through the canal. Recurring wide scale swarm observations and the oceanographic modelling of the currents driving them from various locations suggest a decentralized, inshore origin for *R. nomadica* swarms in the Mediterranean, rather than a single polyp bed.

The many unresolved questions regarding *R. nomadica*'s successful ongoing colonization of the Mediterranean merit a wide spatial future study, that includes examination of specimens from all Mediterranean areas alongside Indo-Pacific 'origin' populations, if such can be found. As shown here, a combination of citizen-science with oceanographic and molecular approaches can be instrumental in such applications.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: European Nucleotide Archive OW055719-OW055735.

AUTHOR CONTRIBUTIONS

DE and DA drafted the manuscript and oversaw acquisition of jellyfish observation data, ØK and IE carried out oceanographic modelling and spatial analysis, NA, SM and HD carried out genetic sampling and analysis. All authors contributed to manuscript writing and editing.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.869619/full#supplementary-material

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