Aquatic Invasions (2022) Volume 17, Issue 2: 174–185

Research Article

Here today, gone tomorrow – the Levantine population of the Brown mussel *Perna perna* obliterated by unprecedented heatwave

Bella S. Galil[1,*], Henk K. Mienis[1,2], Moti Mendelson[3], Kfir Gayer[4] and Menachem Goren[1,5]

[1]*The Steinhardt Museum of Natural History and Israel National Center for Biodiversity Studies, Tel Aviv University, IL-6997801 Tel Aviv, Israel*
[2]*National Natural History Collections, Hebrew University of Jerusalem, IL-9190401 Jerusalem. Israel*
[3]*3/A HaNoter St., Kiryat Hayim IL-26307, Israel*
[4]*Derech Hapark 59-b Netania, Israel*
[5]*School of Zoology, The George S. Wise Faculty of Life Sciences, Tel Aviv University, IL-6997801 Tel Aviv, Israel*

**Corresponding author*
E-mail: *bgalil@tauex.tau.ac.il*

Citation: Galil BS, Mienis HK, Mendelson M, Gayer K, Goren M (2022) Here today, gone tomorrow – the Levantine population of the Brown mussel *Perna perna* obliterated by unprecedented heatwave. *Aquatic Invasions* 17(2): 174–185, https://doi.org/10.3391/ai.2022.17.2.03

Received: 17 February 2022
Accepted: 17 April 2022
Published: 12 May 2022

Thematic editor: Charles Martin

Abstract

The newly established population of *Perna perna* surveyed at four sites along the Israeli Mediterranean coast averaged between 2155 and 8022 specimens/m² in June 2021. Three sites displayed unimodal size–frequency distributions, whereas the site adjacent to Haifa port – a bimodal distribution. The population suffered catastrophic mortality following a succession of heatwaves culminating in a prolonged heatwave in August (ambient temperature 36 to 38 °C, sea surface 32 °C), with diurnal low tides occurring midday. With the projected rise in both mean temperature, and prevalence, duration, and severity of extreme high temperature events, it is likely that even if a *P. perna* reoccurs, it will be of brief duration.

Key words: invasion, Mediterranean Sea, marine heat wave, mortality, population size-frequency, *Brachidontes pharaonis*

Introduction

The brown mussel *Perna perna* (Linnaeus, 1758), a widely invasive mytilid mussel, was first reported from the Mediterranean coast of Israel in 1965, when live and freshly dead specimens were collected near Tel Aviv; listings from Akko and Kiryat Haim, Israel, and Bardawil, Egypt (Barash and Danin 1992) remain unconfirmed (Mienis 2019). No living specimens of *P. perna* were documented in Israel in the next 55 years. The first documented evidence of the reappearance of *P. perna* along the Israeli coast following the long hiatus consisted of photographs of small densely-packed mussel patches north of Haifa port taken in May 2020, followed by a handful of scattered shells on a popular bathing beach, initially considered the remains of a seaside repast. Subsequent surveys conducted along the shore from Rosh HaNikra (33°05′21″N; 35°06′10″E) to Zikim (31°36′45″N; 34°30′16″E) in summer 2020 revealed patchy but dense aggregations were reported, photographed and sampled in Haifa Bay (32°49′27″N; 35°2′12″E), Neurim (32°21′57″N; 34°51′26″E), Havazelet HaSharon (32°21′39″N;

34°51′17″E), and Ashdod port (31°48′5″N; 34°38′36.58″E). Four molecular markers, the mitochondrial cytochrome *c* oxidase subunit I (COI), ribosomal 18S, 28S subunits (18S rRNA, 28S rRNA) and histone H3, were used to validate samples' taxonomic identities. COI haplotype diversity suggested that the Israeli population was highly polymorphic (Douek et al. 2021). The specimens of the earlier ephemeral introduction were collected near the anchorage for fuel tankers that supplied heavy fuel oil imported from Venezuela, South America, for the operation of the Reading power station (Douek et al. 2021). The presence of *P. perna* in 2020 adjacent to Haifa and Ashdod ports, fits the pattern of a vessel-transported introduction.

Perna perna is considered indigenous to the western Indian Ocean and the west coast of Africa and non-indigenous to the Gulf of Mexico and the Atlantic coast of South America. Its populations in the western Mediterranean and the adjacent Atlantic coast are considered cryptogenic (Cunha et al. 2014; Gardner et al. 2016; de Oliveira et al. 2017; Lourenço et al. 2017; Fofonoff et al. 2018; Silva et al. 2018). Population dynamics have been described for *P. perna* in the western Mediterranean (Abada-Boudjema et al. 1984; Abada-Boudjema and Dauvin 1995), the Atlantic coast of north Africa (Shafee 1992), South Africa (Crawford and Bower 1983; Lasiak and Dye 1989; Lasiak and Barnard 1995; McQuaid et al. 2000; McQuaid and Lindsay 2007), India (Appukuttan et al. 1980), Brazil (Marques et al. 1991, 1998, 2018; Suplicy 2004; Bordon et al. 2014) and Venezuela (Acosta et al. 2009), with highly disparate growth rates documented even among adjacent populations (McQuaid and Lindsay 2007).

An opportunistic species, ecosystem engineer, and important fouling threat with high recruit densities and rapid growth rate over a range of water temperatures (Rajagopal et al. 1995; McQuaid et al. 2000; Hicks and McMahon 2002; de Souza et al. 2003), the presence of *P. perna* on the Israeli coast raised the possibility of major ramifications for intertidal community structure, and warranted investigation. The main objectives of the study were to document and compare the status of *P. perna* population at four intertidal sites along the Mediterranean coast of Israel, comprising basic data on population density, size structure, growth rate, and epibiota within one year of their initial detection. The study plan was upended by an unprecedented heatwave that annihilated the entire population at the sampled sites and throughout the coastline. The preliminary data are presented and discussed in relation to ecological impacts of increasingly frequent extreme heatwaves in the region.

Materials and methods

Study area

The Israeli coastline, 180 km long, at the southeastern corner of the Mediterranean, describes a slightly curved line with Haifa Bay the sole embayment (Figure 1). Beaches, for the most part are sandy, outcrops of

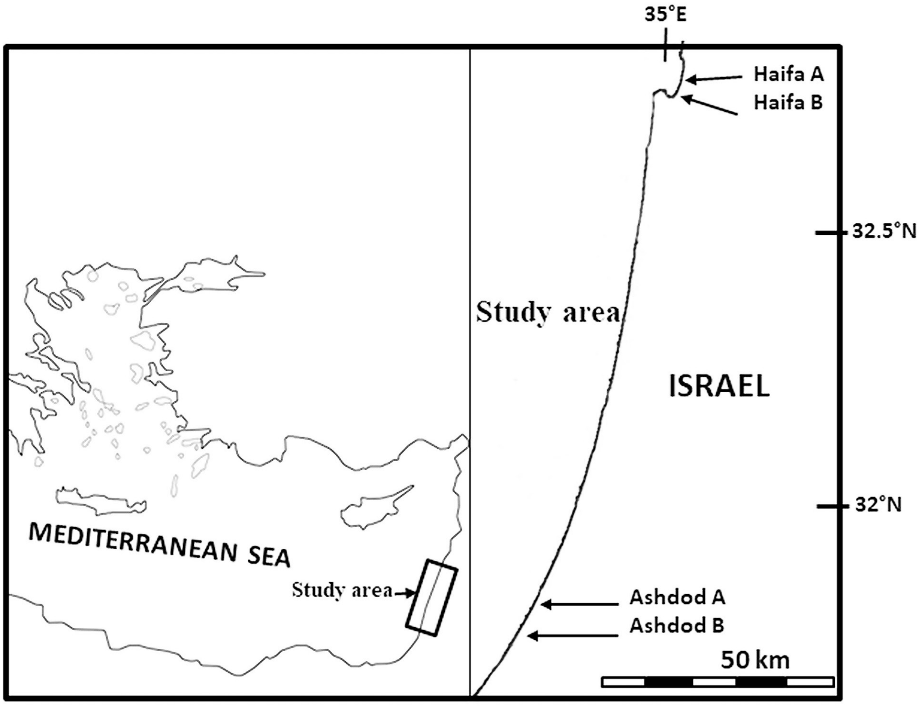

Figure 1. Sites along the Israeli Mediterranean coast where *Perna perna* specimens were collected in 2021.

intertidal beach rock occur intermittently along the coast, though continuous strips of beach rock are rare (Schattner 1967). The tide is semidiurnal with a low-tidal range (0.3–0.6 m). The wave climate is seasonal, characterized by low waves in spring and autumn (significant wave height (Hs < 1 m), medium-sized waves in summer (Hs < 2 m). The most common height is 0.5–1.0 m (54%), twice as common as 0–0.5 m waves; 1.5–3.0 m waves occur 9% of the time. Higher waves are rare, but during winter storms significant waves attain 5 m, very seldom 8 m (Goldsmith and Sofer 1983; Klein 2013). Analysis of a 40-year time series of summer temperature of the Levantine Surface Water reveal a significant long-term increasing trend of 0.13 °C year^{-1} (Herut et al. 2018), a rate much higher than the deseasonalized sea surface temperature for the whole Mediterranean Sea or the entire Levantine–Aegean basin, 0.041 ± 0.006 °C/year and 0.048 ± 0.006 °C/year, respectively (Pisano et al. 2020).

The frequency of summertime heatwaves has increased in the past decade (https://ims.gov.il/he/node/1392).

Sampling

The status of intertidal *Perna perna* along the Israeli coast was determined from analyses of population size structure carried out at four sites, spanning approximately 140 km of coastline. Samples from Haifa A (32°49′59.4″N; 35°03′04.2″E) and Ashdod B (31°44′49.5″N; 34°36′03.6″E) (Figure 2A) were collected from semi-isolated small rocky outcrops separated by shallow troughs from public bathing beaches; from Ashdod A, a stretch

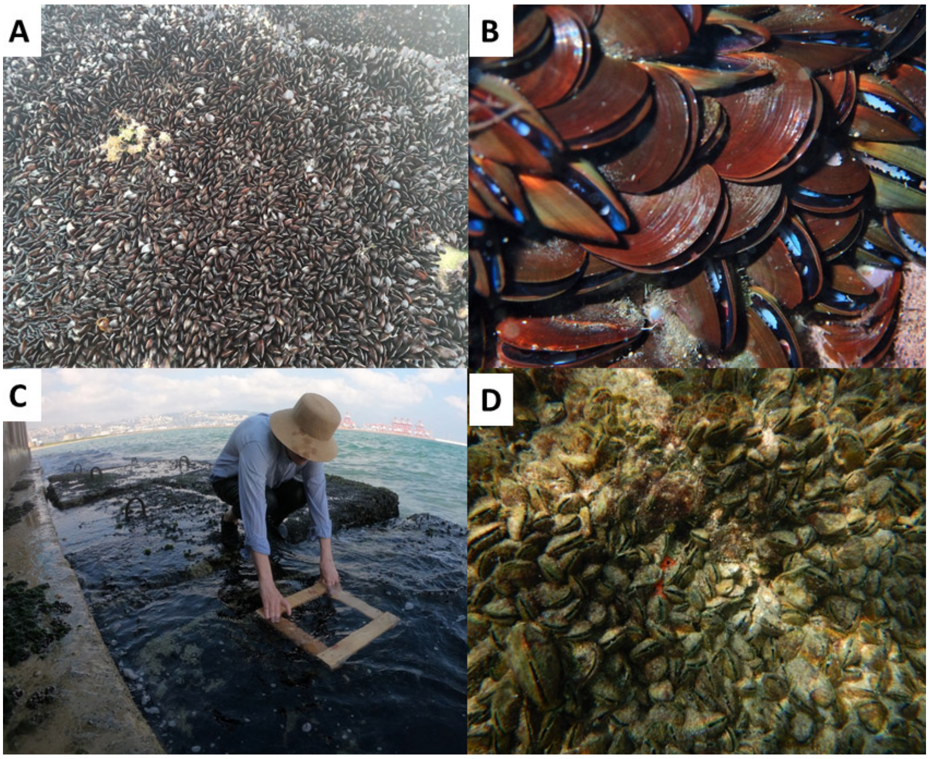

Figure 2. *Perna perna* collected along the Israeli Mediterranean coast in 2021. A. Ashdod B (31°44′49.5″N; 34°36′03.6″E), semi-isolated small rocky outcrops, 25 June 2021; B. Ashdod A (31°51′16.5″N; 34°39′39.3″E), exposed beach rock north of Ashdod Port, 25 June 2021; C. Haifa B (32°49′35.1″N; 35°02′42.8″E), concrete barrier blocks of the seaward fence of Petroleum and Energy Infrastructures (PEI) facility, adjacent to Haifa port, 24 June 2021; D. same location, 27 August 2021, dead shells. Photographs A, B by K. Gayer; C, D by M. Mendelson.

of beach rock situated north of Ashdod Port (31°51′16.5″N; 34°39′39.3″E) (Figure 2B) and from Haifa B, concrete barrier blocks protecting the seaward fence of the Petroleum and Energy Infrastructures (PEI) facility, adjacent to Haifa port (32°49′35.1″N; 35°02′42.8″E) (Figures 1, 2C). *Perna perna* were the space occupiers to the exclusion of all, but a handful of *Brachidontes pharaonis* (P. Fischer, 1870), a long established invasive alien mytilid. During low tide on 24 and 25 June 2021, mussels in mono-layered mussel beds were scraped from within three randomly placed replicate 30 × 30 cm quadrates with a sturdy paint scraper and chisel. The samples were bagged, labelled and frozen. We failed to recover one of the frozen samples collected at the Haifa B site. Sampling was to continue seasonally, however, an extraordinary heatwave in August 2021 eradicated the entire *Perna* population along the Israeli coast. The sampling sites were denuded, with empty shells washed ashore at all sites visited following the heatwave, with the exception of the Haifa B site, where dead shells were collected *in-situ*, still attached by their byssus to the concrete surface (Figure 2D). A sample of the still attached *Perna* shells was collected. The specimens were counted, measured (umbo to ventral margin of the left valve) with calipers to the nearest 0.01 cm. All specimens were preserved in 70% EtOH and deposited at Steinhardt Museum of Natural History, Tel Aviv University (SMNH – MO 100507–100511).

Daily ambient temperatures at Haifa and Ashdod were obtained from the Israeli Meteorological Service website (https://ims.gov.il/en), and the tidal forecast for the Israeli Mediterranean coastline from the Israel Oceanographic Institute website (https://isramar.ocean.org.il/isramar2009/tidehadera/default.aspx).

Statistical analysis

Statistical analysis carried out by employing the Statistic package: IBM SPSS statistic 27. Sites (e.g. Ashdod A, Haifa A) and samples (e.g Ashdod A 1, Ashdod A 2, Ashdod A 3) were compared for the size of the shells using "hierarchical ANOVA" analysis. The null hypothesis of equality of variances was rejected by a significance level of $\alpha < 0.00$.

Results

Population size structure

A total of 5691 live *Perna perna* were collected. The number of individuals and population size structure reveal considerable differences among the four sites, abundance ranging from 4292 to 8022 per m^2 among Ashdod A and B and in Haifa A. In Haifa B their number was considerably lower – 2155 per m^2. Whereas samples collected in Ashdod A and Haifa B displayed the least in-site variability in the number of individuals, those collected in Ashdod B were least uniform. Average shell size was greater for individuals collected in Haifa sites than in the southern sites.

The size–frequency distributions represent mussels measuring ≥ 10 mm, as there are few seeds (< 10 mm), no measurement was made of these mussel seeds (Figure 3). The Ashdod A samples were steeply unimodal, and nearly uniform, the largest size cohort (≥ 25%) measuring 17.6–20.0 mm. The Ashdod B samples differed. Whereas sample 2 resemble the Ashdod A samples, with the largest size cohort at 17.6–20.0 mm. Samples 1 and 3, while still unimodal, had larger sized specimens and a wider size amplitude, the largest size cohorts (≥ 15%) measuring 22.6–25.0 and 37.6–40.0 mm. Haifa A1–3 samples were unimodal too, but differed in size and amplitude, the largest size cohort measured 32.6–35.0, 25.1–27.5 and 27.6–30.0 mm, respectively.

Alone among the sample sites, Haifa B samples 1 and 2 were clearly bi-modal, the largest size cohorts measuring 22.6–25.0, 57.1–60.0 mm and 27.6–30.0, 67.6–70.0 mm, respectively. Mussels of > 50 mm shell length were extremely rare in Ashdod A, B and Haifa A sites (7 of 5303 specimens), but were well represented at Haifa B samples, where a third of the mussels attained this size. The size distribution of mussels in Haifa B samples was skewed to the left, the peak size cohort was followed by steeply reduced numbers of large shells, the second peak distinctly smaller than the first.

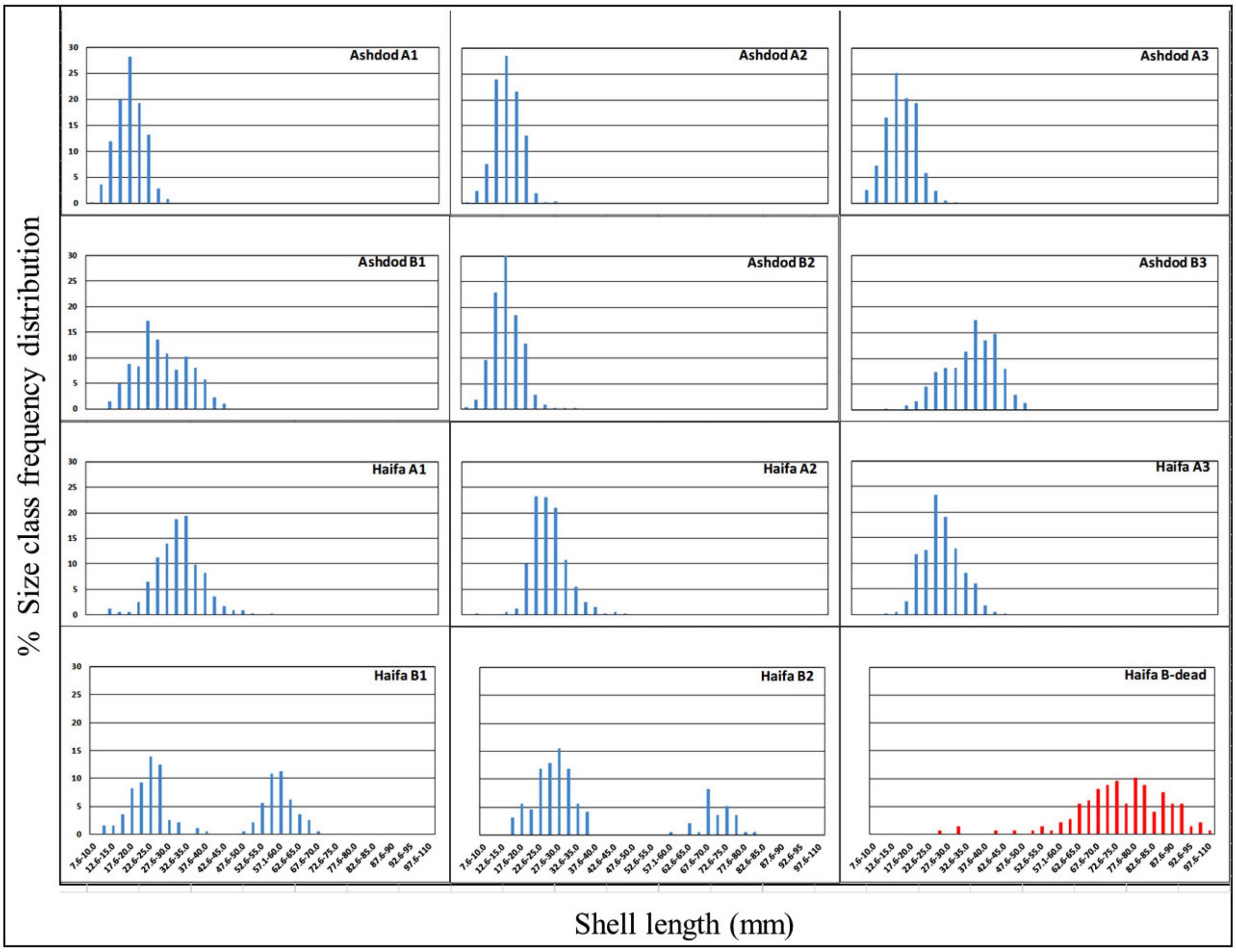

Figure 3. Size frequency distributions of live *Perna perna* shells sampled in Ashdod A,B and Haifa A, B sites in June 2021, and of dead *P. perna* shells sampled in Haifa B site in August 2021.

A total of 147 dead shells were collected off the concrete slabs at Haifa B following the August 2021 heatwave. The sample size–frequency distribution was unimodal with the largest size cohort (≥ 10%) 77.6–80.0 mm, and largest shell length 101.8 mm. Shell sizes differed greatly between June and August in Haifa B site: in June 66% of the shells wee < 50 mm (average size 38 mm, ± 19.7 SD, n = 194), while in August only 3% were < 50 (average size 75 mm, ± 12.5 SD, n = 174) suggesting that smaller shells had been swept away by wave surge. The average shell sizes of the larger shells (> 50 mm) in the June and August samples were 71.5 mm (± 4.7 SD, n = 48) and 97.5 mm (± 9.4 SD, n = 142), respectively.

Discussion

Population size structure

Annual growth rates of *P. perna* differ greatly among sites and continents, and may range from 25 to 78 mm in the first year (Hicks et al. 2001). The annihilation of the Israeli population within 2.5 months of its first and only live-sampled specimens left us with fragmentary but tantalizing data. The great majority of small-sized dead shells were swept away, but those remaining *in-situ* were significantly larger than those collected in June – the largest specimens being 101.8 in shell length compared to 82.7 mm shell length in the earlier sample. The average size of large shells (> 50 mm) was 71.5 and 97.5 mm in June and August respectively. The postulated growth rate is high but aligns with figures from other warm water locales—off the Republic of the Congo the mussel grows rapidly under natural conditions (40 mm in just over 4.5 months) (Cayré 1978), the Texas Gulf of Mexico populations achieved in the first year 42 to 53 mm growth, with estimated maximum shell length values 96.8 to 101.2 mm (Hicks et al. 2001)—similar in size to the largest specimens sampled in Haifa Bay.

Temperature

2021 was the fourth warmest year measured in Israel since temperature measurements began in the 1950s. The first half of 2021 ranked the sixth warmest since the early 1950s. A prolonged heatwave in late June (June 27–30) extended into early July (July 1–3) with coastal temperatures reaching 33 to 34 °C, followed by another heatwave (July 17–19) with temperatures 31–32 °C. August was considerably warmer than average, ranking as fourth warmest in the past 70 years, a prolonged heatwave prevailed during its first week, with 36 to 38 °C measured in the coastal plain, sea surface temperature around 32 °C, and diurnal low tides occurring between the hours of 12:00 and 16:00 (https://www.israelweather.co.il/news-weatherview.asp?id=21934, https://isramar.ocean.org.il/isramar2009/tidehadera/default.aspx). Though cooling later, temperatures remained 2 to 2.5 °C above average (https://ims.gov.il/he/ClimateReports). Summer heatwaves in the coastal plain occurred in the past once every 5 to 10 years, and lasted one or two days. The 2021 August heat wave was unprecedented in its duration.

Mass mortality

The four *P. perna* sites held thriving mussel aggregations from May through the end of July 2021, through an unusually hot weather and heatwaves in both June and July. The unprecedented prolonged heatwave in early August laid waste to the entire mussel population. Noticeably, larger-sized mussels remained tethered to the substrate by their byssal threads whereas smaller ones were swept away. The weaker byssal attachment strength in small-sized mussels (Babarro et al. 2008; Macala and McQuaid 2017), and byssus thread production decline at 32.5 °C (Rajagopal et al. 1995), may point to a possible explanation.

Marine heatwaves (MHWs) in the Mediterranean Sea have been linked to extirpations of hard substrate macroinvertebrates, including octocorals, sponges, bryozoans, ascidians and bivalves (Garrabou et al. 2009; Galli et al. 2017). Intertidal sessile biota in particular are vulnerable to heatwaves, unable to relocate in search of thermal refugia. Mussels, sessile inhabitants of rocky intertidal shores, are obliged to contend with exposure to the marine and aerial environments, requiring ample thermal tolerance. Mortalities of marine intertidal mussels have led to studies on thermal exposure. While some concerned native species—*Mytilus californianus* Conrad, 1837 in California (Harley 2008), *M. edulis* on the French Atlantic coast (Seuront et al. 2019)—few have documented heatwave-induced mortalities in introduced mussels. *Mytilus edulis* (*M. galloprovincialis* Lamarck, 1819, *fide* Inoue et al. 1997) established in Mutsu Bay, northern Japan, since the late 1940s, suffered repeated high mortalities of specimens inhabiting the upper intertidal in the abnormally hot summers of 1960, 1967/1968 and 1981, but not at the lower tidal level (Tsuchiya 1983). The sole documented case of heat-induced mortality in introduced *P. perna* concerns the population introduced to Texas, USA (Fofonoff et al. 2018). The upper long-term (chronic) thermal limit for *P. perna* is 31 °C (Hicks and McMahon 2002). Mortality of 44 mm long specimens originating from the Texan coast of the Gulf of Mexico and acclimated to 15 °C, 25 °C and 30 °C, occurred after 96, 160 and 160 h at 32 °C, respectively (Hicks and McMahon 2002) – congruent with our observations. The Gulf populations, settled in thermally marginal habitats, collapsed when mean summer seawater temperature rose in 1997, but reappeared in 2000 when the average summer surface-water temperature was 28.5 °C (Hicks and McMahon 2002).

Experimental heatwave simulations revealed that sequential exposures to sublethal temperatures reduce thermal tolerance, affecting population demographics and survival (Pansch et al. 2018; Siegle et al. 2018). In the two months prior to the mass mortality of *M. edulis* along the French Atlantic coast in 2018, biomimetic loggers registered four periods of 5 to 6 consecutive days each when mussel body temperatures of more than 30 °C, and occasionally more than 35 °C were recorded. Subsequent experimental treatment revealed that survival consistently decreased with increasing exposure events (Seuront et al. 2019). We suggest the annihilation of the Israeli population of *P. perna* was brought about by concurrent exposure to unprecedented high seawater and aerial temperatures, midday low tide, and previous intermittent exposure to sublethal temperatures (Helmuth et al. 2002; Hicks and McMahon 2002; Tagliarolo and McQuaid 2015; Barker et al. 2021). With the projected rise in both mean temperature, and prevalence, duration, and severity of MHWs in the Eastern Mediterranean (Pastor et al. 2020; Pisano et al. 2020), it is likely that even if a *P. perna* outbreak reoccurs, it will be of brief duration.

The Erythraean mytilid *Brachidontes pharaonis*, introduced through the Suez Canal, is the most abundant intertidal bivalve along the Israeli coast. Its populations were reported to have undergone heatwave-induced massive mortality in August 2016 and failed to recover (Rilov 2017, 2018). However, contemporaneous documentation (Barnea and Zemel 2017), backed by material preserved at the Steinhardt Museum of Natural History, Tel Aviv

Figure 4. *Brachidontes pharaonis*, Tel Aviv, summer 2021, mussel beds cover intertidal rocky ledges, low tide. Photograph by B. Galil.

University, prove beyond doubt the continuous profuse presence of *B. pharaonis* along the coast. Surveys of intertidal rocky ledges and maritime infrastructure, including the newly inaugurated Haifa Bayport breakwater, reveal dense beds of live *B. pharaonis* despite the unparalleled sequence of MHWs in 2021 (Figure 4).

Over the past two decades, concurrent with long-term persistent warming, the mean MHW frequency and duration in the Eastern Mediterranean increased by 40% and 15%, respectively (Ibrahim et al. 2021). Climate change projections suggest increased frequency and duration of MHWs in the Mediterranean Sea. It is predicted that by 2100, at least one MHW will occur every year, be up to three months longer, about 4 times more intense and 42 times more severe than present-day MHW events, affecting at peak the entire basin (Darmaraki et al. 2019; Oliver et al. 2019). The southern Levant is the world's most invaded marine ecosystem, with nearly 90% of the alien species considered to have been introduced through the Suez Canal. The warming trend, boosted by ever more frequent MHWs, favors thermally-tolerant species and those adapted to warmer waters. It is likely that native stenothermal biota unable to shift their range to deeper and/or colder water may endure increasing stress and demographic attrition, and replacement by warm water invasives, likely introduced through the Suez Canal.

Acknowledgements

We thank Christopher McQuaid, Rhodes University, Grahamstown, South Africa, for his comments. We thank both anonymous reviewers for their careful reading of our manuscript and their helpful comments.

Authors' contributions

BSG – research conceptualization, investigation and data collection, data analysis and interpretation, writing, HKM – species identification, MM and KG – data collection, photography, MG – data analysis and interpretation, writing, editing.

References

Abada-Boudjema Y, Dauvin J (1995) Recruitment and life span of two natural mussel populations *Perna perna* (Linneaus) and *Mytilus galloprovincialis* (Lamarck) from the Algerian Coast. *Journal of Molluscan Studies* 61: 467–481, https://doi.org/10.1093/mollus/61.4.467

Abada-Boudjema Y, Altes J, Moueza M (1984) Croissance comparée de deux espéces de moules *Mytilus galloprovincialis* (Lmk.) et *Perna perna* (L.) dans une moulié naturelle de la baie d'Alger. *Haliotis* 14: 33–38

Acosta V, Glem ME, Natera Y, Urbano T, Himmelman JH, Rey-Méndez M, Lodeiros C (2009) Differential growth of the mussels *Perna perna* and *Perna viridis* (Bivalvia: Mytilidae) in suspended culture in the Golfo de Cariaco, Venezuela. *Journal of the World Aquaculture Society* 40: 226–235, https://doi.org/10.1111/j.1749-7345.2009.00245.x

Appukuttan KK, Nair TP, Joseph M, Thomas KT (1980) Culture of brown mussel at Vizhinjam. *Central Marine Fisheries Research Institute Bulletin* 29: 30–32

Barash A, Danin, Z (1992) Fauna Palaestina: Mollusca I. Annotated list of Mediterranean molluscs of Israel and Sinai. The Israel Academy of Sciences and Humanities, Jerusalem, 372 pp

Babarro J, Fernández Reiriz M, Labarta U (2008) Secretion of byssal threads and attachment strength of *Mytilus galloprovincialis*: The influence of size and food availability. *Journal of the Marine Biological Association of the United Kingdom* 88: 783–791, https://doi.org/10.1017/S0025315408001367

Barnea O, Zemel A (2017) Summary of biological survey on vermetid platforms along the coast of Acre. 22 pp, https://www.parks.org.il/article/aco/ [in Hebrew]

Barker C, Monaco CJ, McQuaid CD (2021) Exposure to fluctuating temperature increases thermal sensitivity in two lineages of the intertidal mussel *Perna perna*. *Marine Ecology Progress Series* 668: 85–95, https://doi.org/10.3354/meps13713

Bordon IC, Marques HL, Alves JL, Rossi A, Pecora IL (2014) Influence of densities on the growth of brown mussel *Perna perna* L. cultivated in suspended socks at Caraguatatuba, southeastern Brazil. *Aquaculture International* 22: 41–549, https://doi.org/10.1007/s10499-013-9662-5

Cayré P (1978) Étude de la moule *Perna perna* L. et des possibility de mytiliculture en République Populaire du Congo. *Cahiers de l'ORSTOM, Série Oceanographie* 16: 9–17

Crawford RM, Bower DF (1983) Aspects of growth, recruitment and conservation of the brown mussel *Perna perna* along the Tsitsikamma coast. *Koedoe* 26: 123–133, https://doi.org/10.4102/koedoe.v26i1.592

Cunha RL, Nicastro KR, Costa J, McQuaid CD, Serrao EA, Zardi GI (2014) Wider sampling reveals a non-sister relationship for geographically contiguous lineages of a marine mussel. *Ecology and Evolution* 4: 2070–2081, https://doi.org/10.1002/ece3.1033

Darmaraki S, Somot S, Sevault F, Nabat P, Cabos W, Cavicchia L, Cabos Narvaez WD, Djurdjevic V, Li L, Sannino G, Sein DV (2019) Future evolution of marine heatwaves in the Mediterranean Sea. *Climate Dynamics* 53: 1371–1392, https://doi.org/10.1007/s00382-019-04661-z

de Oliveira MJS, Beasley CR, Barros NGV, do Socorro Marques-Silva N, de Simone LRL, Lima ES, Tagliaro CH (2017) Two African origins of naturalized brown mussel (*Perna perna*) in Brazil: past and present bioinvasions. *Hydrobiologia* 794: 59–72, https://doi.org/10.1007/s10750-016-3082-2

Douek J, Paz G, Gayer K, Mendelson M, Rinkevich B, Galil BS (2021) An outbreak of *Perna perna* (Linnaeus, 1758) (Mollusca, Bivalvia, Mytilidae) in the Eastern Mediterranean. *BioInvasions Records* 10: 136–148, https://doi.org/10.3391/bir.2021.10.1.15

Fofonoff PW, Ruiz GM, Steves B, Simkanin C, Carlton JT (2018) National Exotic Marine and Estuarine Species Information System, http://invasions.si.edu/nemesis/ (accessed 22 December 2021)

Galli G, Solidoro C, Lovato T (2017) Marine heat waves hazard 3D maps and the risk for low motility organisms in a warming Mediterranean Sea. *Frontiers in Marine Science* 4: 136, https://doi.org/10.3389/fmars.2017.00136

Gardner JP, Patterson J, George S, Edward JP (2016) Combined evidence indicates that *Perna indica* Kuriakose and Nair 1976 is *Perna perna* (Linnaeus, 1758) from the Oman region introduced into southern India more than 100 years ago. *Biological Invasions* 18: 1375–1390, https://doi.org/10.1007/s10530-016-1074-9
Garrabou J, Coma R, Bensoussan N, Bally M, Chevaldonné P, Cigliano M, Diaz D, Harmelin JG, Gambi MC, Kersting DK, Ledoux JB, Lejeusne C, Linares C, Marschal C, Pérez T, Ribes M, Romano JC, Serrano E, Teixido N, Torrents O, Zabala M, Zuberer F, Cerrano C (2009) Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Global Change Biology* 15: 1090–1103, https://doi.org/10.1111/j.1365-2486.2008.01823.x
Goldsmith V, Sofer S (1983) Wave climatology of the southeastern Mediterranean. *Israel Journal of Earth Sciences Jerusalem* 32: 1–51
Harley CDG (2008) Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. *Marine Ecology Progress Series* 371: 37–46, https://doi.org/10.3354/meps07711
Helmuth BS, Harley CDG, Halpin P, O'Donnell M, Hofmann GE, Blanchette C (2002) Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298: 1015–1017, https://doi.org/10.1126/science.1076814
Herut B, Segal Y, Gertner Y, IOLR group (2018) The National Monitoring Program of Israel's Mediterranean waters - Scientific Report on Marine Pollution for 2017, Israel Oceanographic and Limnological Research, IOLR Report H50/2018 [in Hebrew]
Hicks DW, McMahon RF (2002) Temperature acclimation of upper and lower thermal limits and freeze resistance in the nonindigenous brown mussel, *Pern perna* (L.), from the Gulf of Mexico. *Marine Biology* 140: 1167–1179, https://doi.org/10.1007/s00227-002-0787-8
Hicks DW, Tunnell Jr JW, McMahon RF (2001) Population dynamics of the nonindigenous brown mussel *Perna perna* in the Gulf of Mexico compared to other world-wide populations. *Marine Ecology Progress Series* 211: 181–192, https://doi.org/10.3354/meps211181
Ibrahim O, Mohamed B, Nagy H (2021) Spatial variability and trends of marine heat waves in the Eastern Mediterranean sea over 39 years. *Journal of Marine Science and Engineering* 9: 643, https://doi.org/10.3390/jmse9060643
Inoue K, Odo S, Noda T, Nakao S, Takeyama S, Yamaha E, Yamazaki F, Harayama S (1997) A possible hybrid zone in the *Mytilus edulis* complex in Japan revealed by PCR markers. *Marine Biology* 128: 91–95, https://doi.org/10.1007/s002270050072
Klein M (2013) The Nile littoral Cell and Recent Shoreline Change: A Review. In: Stambler N (ed), Life in the Mediterranean Sea: A look at habitat changes. Nova Science Publishers, Hauppauge, New York, USA, pp 32–43
Lasiak TA, Barnard TCE (1995) Recruitment of the brown mussel *Perna perna* onto natural substrata: a refutation of the primary/secondary settlement hypothesis. *Marine Ecology Progress Series* 120: 147–153, https://doi.org/10.3354/meps120147
Lasiak T, Dye A (1989) The ecology of the brown mussel *Perna perna* in Transkei, southern Africa: implications for the management of a traditional food resource. *Biological Conservation* 47: 245–257, https://doi.org/10.1016/0006-3207(89)90068-2
Lourenço CR, Nicastro KR, Serrão EA, Zardi GI (2012) First record of the brown mussel (*Perna perna*) from the European Atlantic coast. *Marine Biodiversity Records* 5: e39, https://doi.org/10.1017/S1755267212000280
Lourenço CR, Nicastro KR, McQuaid CD, Chefaoui RM, Assis, J, Taleb MZ, Zardi GI (2017) Evidence for rangewide panmixia despite multiple barriers to dispersal in a marine mussel. *Scientific Reports* 7: 1–16, https://doi.org/10.1038/s41598-017-10753-9
Macala L, McQuaid CD (2017) Effects of size-dependent allocation of energy to maintenance, growth, and reproduction on rehabilitation success in overexploited intertidal mussels *Perna perna* (L.). *Journal of Shellfish Research* 36: 9–16, https://doi.org/10.2983/035.036.0103
Marques HLA, Pereira RTL, Correa BC (1991) Crescimento de Mexilhões *Perna perna* (Linnaeus, 1758) em populações naturais no litoral de Ubatuba (SP) Brazil. *Boletim do Instituto de Pesca San Paulo* 18: 61–72
Marques HLA, Pereira RTL, Correa BC (1998) Seasonal variation in growth and yield of the brown mussel *Perna perna* (L.) cultured in Ubatuba, Brazil. *Aquaculture* 169: 263–273, https://doi.org/10.1016/S0044-8486(98)00372-X
Marques HLA, Pereira RTL, Correa BC (2018) Growth of mussels *Perna perna* [Linnaeus, 1758] in natural populations from Ubatuba shore, São Paulo State, Brazil. *Boletim do Instituto de Pesca* 18: 61–72
McQuaid CD, Lindsay TL (2007) Wave exposure effects on population structure and recruitment in the mussel *Perna perna* suggest regulation primarily through availability of recruits and food, not space. *Marine Biology* 151: 2123–2131, https://doi.org/10.1007/s00227-007-0645-9
McQuaid CD, Lindsay JR, Lindsay TL (2000) Interactive effects of wave exposure and tidal height on population structure of the mussel *Perna perna*. *Marine Biology* 137: 925–932, https://doi.org/10.1007/s002270000398

Mienis HK (2019) On the sudden appearance and disappearance of *Perna perna* on the Mediterranean coast of Israel (Mollusca, Bivalvia, Mytilidae). *Triton* 38: 1–3

Oliver EC, Burrows MT, Donat MG, Sen Gupta A, Alexander LV, Perkins-Kirkpatrick SE, Benthuysen JA, Hobday AJ, Holbrook NJ, Moore PJ, Thomsen MS (2019) Projected marine heatwaves in the 21st century and the potential for ecological impact. *Frontiers in Marine Science* 6: 734, https://doi.org/10.3389/fmars.2019.00734

Pansch C, Scotti M, Barboza FR, Al-Janabi B, Brake J, Briski E, Bucholz B, Franz M, Ito M, Paiva F, Saha M (2018) Heat waves and their significance for a temperature benthic community: A near-natural experimental approach. *Global Change Biology* 24: 4357–4367, https://doi.org/10.1111/gcb.14282

Pastor F, Valiente JA, Khodayar S (2020) A warming Mediterranean: 38 years of increasing sea surface temperature. *Remote Sensing* 12: 2687, https://doi.org/10.3390/rs12172687

Pisano A, Marullo S, Artale V, Falcini F, Yang C, Leonelli FE, Santoleri R, Nardelli BB (2020) New evidence of Mediterranean climate change and variability from sea surface temperature observations. *Remote Sensing* 12: 132, https://doi.org/10.3390/rs12010132

Rajagopal S, Nair KVK, Azariah A (1995) Response of Brown mussel, *Perna indica*, to elevated temperatures in relation to power-plant biofouling control. *Journal of Thermal Biology* 20: 461–467, https://doi.org/10.1016/0306-4565(95)00006-I

Rilov G (2017) Ch. 5 monitoring ecological communities on rocky shores. In: Rahav E, Herut B (eds), The National Monitoring Program of Israel's Mediterranean waters - Scientific Report on Biodiversity for 2016 (June, 2017). Israel Oceanographic and Limnological Research (IOLR), IOLR Report H48b/2017, pp 79–92 [in Hebrew]

Rilov G (2018) Ch. 5 monitoring ecological communities on rocky shores. In: Rahav E, Herut B (eds), The National Monitoring Program of Israel's Mediterranean waters - Scientific Report on Biodiversity for 2017, (December 2018). Israel Oceanographic and Limnological Research (IOLR), IOLR Report H48/2018, pp 78–90 [in Hebrew]

Schattner I (1967) Geomorphology of the northern coast of Israel. *Geografiska Annaler: Series A, Physical Geography* 49: 310–320, https://doi.org/10.1080/04353676.1967.11879759

Seuront L, Nicastro KR, Zardi GI, Goberville E (2019) Decreased thermal tolerance under recurrent heat stress conditions explains summer mass mortality of the blue mussel *Mytilus edulis*. *Scientific Reports* 9: 17498, https://doi.org/10.1038/s41598-019-53580-w

Shafee MS (1992) Production estimate of a mussel population *Perna picta* (Born) on the Atlantic coast of Morocco. *Journal of Experimental Marine Biology and Ecology* 163: 183–197, https://doi.org/10.1016/0022-0981(92)90048-F

Siegle MR, Taylor EB, O'Connor MI (2018) Prior heat accumulation reduces survival during subsequent experimental heat waves. *Journal of Experimental Marine Biology and Ecology* 501: 109–117, https://doi.org/10.1016/j.jembe.2018.01.012

Silva EP, Souza RC, Lima TA, Fernandes FC, Macario KD, Netto BM, Alves EQ, Carvalho C, Aguilera O, Duarte MR (2018) Zooarchaeological evidence that the brown mussel (*Perna perna*) is a bioinvader of coastal Brazil. *The Holocene* 28: 1771–1780, https://doi.org/10.1177/0959683618788670

de Souza RCCL, da Costa Fernandes F, da Silva EP (2003) A study on the occurrence of the brown mussel *Perna perna* on the sambaquis of the Brazilian coast. *Revista do Museu de Arqueologia e Etnologia* 13: 3–24, https://doi.org/10.11606/issn.2448-1750.revmae.2003.109462

Suplicy FM (2004) Population and ecophysiological modelling of the cultured mussel *Perna perna*: towards the development of a carrying capacity model. PhD Thesis, University of Tasmania, Australia, 195 pp

Tagliarolo M, McQuaid CD (2015) Sub-lethal and sub-specific temperature effects are better predictors of mussel distribution than thermal tolerance. *Marine Ecology Progress Series* 535:145–159, https://doi.org/10.3354/meps11434

Tsuchiya M (1983) Mass mortality in a population of the mussel *Mytilus edulis* L. caused by high temperature on rocky shores. *Journal of Experimental Marine Biology and Ecology* 66: 101–111, https://doi.org/10.3354/meps11434