Hydrobiologia (2010) 645:23–37
DOI 10.1007/s10750-010-0205-z

Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, span the Mediterranean Sea in 2009

**Verónica L. Fuentes · Dror L. Angel · Keith M. Bayha ·
Dacha Atienza · Dor Edelist · Cesar Bordehore ·
Josep-Maria Gili · Jennifer E. Purcell**

Abstract Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, occurred in 2009 along the Mediterranean Sea coasts of Spain and Israel. This voracious zooplanktivore spread throughout the Black Sea basin after its introduction in the early 1980s, throughout northern European coastal waters, and now occurs throughout the Mediterranean Sea. *M. leidyi* occurred throughout the summer along the entire Catalan Spanish and Israeli coasts in 2009. Those locations had high temperatures (18–26°C) and salinities (37–38) during the blooms. The patterns of abundance of large jellyfish along the Catalan coast were unusual in 2009, with low numbers during July, August, and September when ctenophores were abundant. Small populations of those potential predators and food competitors of *M. leidyi* could have contributed to the ctenophore bloom. The identity of the ctenophores from Spain and Israel was confirmed as *M. leidyi* by molecular analysis based on DNA sequencing of the nuclear internal transcribed spacer (ITS) regions. This is the first molecular confirmation of *M. leidyi* in the Mediterranean Sea. Most ctenophores had an ITS genotype previously found in *M. leidyi* from other invaded regions (the Black, Azov, and Mediterranean seas), as well as native regions in the United States,

---

Guest editors: J. E. Purcell & Dror Angel / Jellyfish Blooms: New Problems and Solutions

---

V. L. Fuentes (✉) · D. Atienza · J.-M. Gili
Institut de Ciencies del Mar, CSIC, P. Marítim de la
Barceloneta 37-49, 08003 Barcelona, Spain
e-mail: vfuentes@icm.csic.es

D. L. Angel · D. Edelist
Department of Maritime Civilizations, Leon Recanati
Institute of Maritime Studies, University of Haifa,
Mt Carmel, 31905 Haifa, Israel

K. M. Bayha
University of California Merced, School of Natural
Sciences, 5200 North Lake Rd, Merced, CA 95343, USA

Present Address:
K. M. Bayha
Dauphin Island Sea Lab, 101 Bienville Blvd., Dauphin
Island, AL 36528, USA

C. Bordehore
Departamento de Ecología, Universidad de Alicante,
Ap. 9903080 Alicante, Spain

J. E. Purcell
Western Washington University, Shannon Point Marine
Center, 1900 Shannon Point Rd, Anacortes, WA 98221,
USA

J. E. Purcell
Coastal and Marine Resources Centre, University College
Cork, Naval Base, Haulbowline Island, Cobh, Co. Cork,
Ireland

suggesting common ancestry. Based on the circulation patterns of Mediterranean surface waters and shipping activities, we conclude that the spread of *M. leidyi* in the Mediterranean probably resulted from re-introductions by ballast water transport and subsequent distribution by currents. We also conclude that the near-simultaneous blooms in opposite ends of both the Mediterranean basins indicate that *M. leidyi* is resident around the Mediterranean. We discuss environmental conditions, food, and predators of *M. leidyi* in both regions that would influence the future effects of this voracious consumer on the pelagic food web of the Mediterranean Sea.

Keywords Jellyfish · Zooplankton · Climate · Israel · Spain

Introduction

Several years after its accidental introduction into the Black Sea in the early 1980s, the ctenophore, *Mnemiopsis leidyi* A. Agassiz, formed massive blooms that coincided with abrupt decreases in zooplankton, ichthyoplankton, and fisheries (Vinogradov et al., 1989; Vinogradov & Shushkina, 1992; GESAMP, 1997). Since the 1980s, the introduced distribution of *M. leidyi* spread to the Sea of Azov (1988), the Sea of Marmara (1989–1990), and the northern Aegean Sea (1990) (Shiganova et al., 2001). Additional introductions have transported the ctenophore to the Caspian Sea (1999) (Ivanov et al., 2000; Shiganova et al., 2001) and the North and Baltic seas (first observations 2006) (Faasse & Bayha, 2006; Javidpour et al., 2006). Within the Mediterranean Sea, *M. leidyi* rapidly spread from the Aegean Sea to adjacent waters of Turkey and Syria (Kideys & Niermann, 1994). More recently, *M. leidyi* was reported from the Northern Adriatic Sea and France (Shiganova & Malej, 2009), Israel (Galil et al., 2009), and Italy (Boero et al., 2009).

Mnemiopsis leidyi is a very versatile species native to estuaries and coastal regions along the eastern coasts of North and South America (GESAMP, 1997). Within its native range it occurs in coastal waters with temperatures ranging between 2 and 32°C and salinities of <2–38 (Purcell et al., 2001). It has flourished in non-native waters with winter temperatures above 4°C, estuarine salinity, and high productivity (e.g., Shiganova et al., 2001). The extraordinary success of *M. leidyi* in the Black, Azov, and Caspian seas has been attributed to the lack of predators in combination with the deteriorated conditions for fish populations in those waters due to eutrophication, pollution, and over fishing (e.g., Purcell et al., 2001; Oguz, 2005). The northern European coastal waters, where *M. leidyi* is considered to be established (Javidpour et al., 2008), share the above characteristics.

The first report of *M. leidyi* in the Mediterranean Sea was in the Aegean Sea, where gelatinous predators (e.g., *Beroe* spp. ctenophores) occur, and temperatures and salinities are much higher than in other non-native locations; *M. leidyi* appeared to have limited success there, and the establishment of persistent populations was uncertain (Kideys & Niermann, 1993; Shiganova & Malej, 2009). Short-term occurrences in Mediterranean ports were attributed to ballast-water transfers from the Black Sea to those ports (summarized in Galil et al., 2009).

Siapatis et al. (2008) developed a predictive model to identify the potential habitat of *M. leidyi* in the Mediterranean basin. Their model shows potential habitat around the entire Mediterranean coast. In each of 3 years modeled from environmental conditions (2004–2006), the Catalan and Levantine coast of Spain and the Levant (eastern Mediterranean) areas including Israel showed high probabilities of *M. leidyi* occurrence. In 2009 shortly after publication of that prophetic paper, *M. leidyi* was reported along Israeli shores (Galil et al., 2009), in the Adriatic Sea (Faris, 2009), and from the Catalan and Levantine coast in Spain (Fuentes et al., 2009).

Here, we report high abundances of *M. leidyi* in coastal waters of Israel and Spain in winter–summer 2009, in conjunction with hydrographic conditions and the abundances of zooplankton and scyphomedusan species. We compare these factors in 2009 with those in 2008 when *M. leidyi* was not widely reported. We also present the first molecular confirmation of the identity of *M. leidyi* in the Mediterranean Sea, along with possible source region(s).

Materials and methods

Field sampling

Spain

Beginning in 2000, semi-quantitative data were compiled on the occurrences of large gelatinous plankton, predominantly the scyphomedusae, *Pelagia noctiluca* (Forskal), *Rhizostoma pulmo* (Macri), and *Cotylorhiza tuberculata* (Macri), along the Catalan coast. The abundances of jellyfish on the beaches (without distinguishing among species) were classified in three categories: 1 (few, <10 animals per beach), 2 (many, <1 medusa m^{-2}), and 3 (a lot, >1 medusa m^{-2}) (Gili et al., 2007, 2008). This classification system was retained for observations that began in 2007 when the "Medusa Project" began monitoring the presence of individual jellyfish species along the Catalan coast.

The "Medusa Project" monitoring comprised a network of organizations covering the entire Catalan coastline. The Medusa Project is financed by the Catalan Water Agency (ACA) with the main goals of studying and monitoring the jellyfish proliferations along the Catalan coast of the NW Mediterranean Sea. The ACA records the relative abundance (few, many, a lot) of jellyfish daily at more than 300 beaches covering the 69 municipalities of Catalonia. Data are recorded by beach inspectors who observe what is on the sand and in the near-shore water at fixed locations and by inspectors in boats 200-m offshore beyond the swimming area. The project also involves participation of the Emergency Services from 26 of the 69 municipalities that each completes a form daily to report the relative abundance of jellyfish at the beaches (ACA, 2009). The Fisherman Associations of Catalonia also report to the Medusa Project. All the collected information, including daily observations of jellyfish from ACA boats, beach inspectors, and emergency services, are summarized on the ACA web page and are available to the public (ACA, 2009). As part of the observation and monitoring protocol, data on water temperature, transparency, salinity, chlorophyll *a*, and nutrients have been recorded since 2000 along the coast.

As part of a cooperative project, information about jellyfish presence in other parts of Spain is also available. In Denia (Levantine coast of Spain, south of Catalonia), daily visual inspection of the beaches has been conducted by the local Administration (Environmental Department) and by its summer beach emergency services (Red Cross) since summer 2001. The presence of jellyfish is recorded daily as part of this monitoring procedure. Water samples have been collected monthly since 2001 at four locations, separated by 3–5 km, along the coast at 4–5 m depth and 300–700 m from shore. Data on water temperature, O_2, pH, and nutrients were recorded in those samples.

Israel

Jellyfish occurrences in coastal or offshore waters of Israel have been recorded on an ad hoc basis; many of the observations were made by fishermen. Data on the occurrences and abundances of medusae and ctenophores in 2009 were compiled during trawling (fishing) cruises and from interviews with trawl, seine, and inshore fishermen at the ports of Jaffa and the Kishon River (Haifa). Trawlers used 40–48-mm stretched diamond mesh nets with a vertical opening of 2–3 m, trawling at depths of 15–100 m. Inshore and purse-seine fishermen trawled at 0–50 m depth with 22–120-mm (mostly 50–60 mm) mesh gill- and trammel-nets with a 12-m vertical opening in shallow waters and up to 24 m in deep waters. Purse-seiners used 18–24-mm mesh nets.

Presence/absence and the relative abundances of gelatinous animals were recorded. The abundances of gelatinous zooplankton reported were "none," "occasional" (sporadic sightings in surface waters or 1–5 specimens in each trawl), or "abundant" (either swarms in surface waters or >5 specimens in each trawl). Zooplankton abundances in coastal waters were determined between March and May 2009 by means of horizontal net tows at 5-m depth for 3 min at $1\ m\ s^{-1}$ and vertical tows from the seafloor to the surface at $1\ m\ s^{-1}$ with 64- and 303-μm plankton nets. Surface seawater temperatures were recorded at Ashdod Port during the past 12 years (CAMERI, 2008) and both surface seawater temperatures and salinities were recorded near Ashkelon (IEC, 2009) during 2009.

Molecular analysis

Ctenophores collected in the field were provisionally identified morphologically as *M. leidyi* based on a typical morphotype, namely that the lobes extended to the region of the statocyst (see Faasse & Bayha, 2006). In order to confirm field identification, a few specimens of this consistent morphotype were collected, preserved, and identified molecularly. Molecular species identification was performed making use of the DNA sequence from the nuclear internal transcribed spacer (ITS) region (ITS-1, 5.8S, ITS-2), a region that has been useful for ctenophore identification in the past (Podar et al., 2001; Bayha et al., 2004; Faasse & Bayha, 2006). A total of three ctenophores were collected and preserved in 75–100% ethanol, including one from the vicinity of Haifa, Israel (HAF-1) and two from the vicinity of Salou, Spain (SAL-1 and SAL-2). DNA extraction was performed using a standard CTAB protocol (Dawson et al., 1998), and polymerase chain reaction (PCR) amplifications were performed using an Applied Biosystems 2720 Thermal Cycler. The entire ITS region was PCR amplified using primers KN-8 (ATTACGTCCCTGCCCTTTGTA) and KN-9 (GCAATCCCAAACAGTCCGACTCTTC) in conditions consisting of 95°C for 3 min, followed by 38 cycles of 95°C for 45 s, 52°C for 1 min, 72°C for 1.5 h, and a single cycle of 72°C for 10 min (then 4°C). Successful PCR products were treated with Exonuclease I and Shrimp Alkaline Phosphatase (USB Corp.) to prevent interference by unused primers and dNTPs in sequencing reactions. PCR products were then directly cycle sequenced by Northwoods DNA, Inc. (Solway, MN) using primers KN-8 and KN-11 (ATTTGAGCTGTTCCCTGTTCGT) (Bayha, 2005). All sequences were deposited into GenBank. All DNA sequences were assembled using Seqman II (DNAStar, Inc.), and electropherograms were amended by eye for bad sequence calls. Loci that showed clear peaks of two different bases were coded as degenerate (i.e., Y = C and T). Sequence identity was evaluated by performing BLASTN searches against GenBank (Altschul et al., 1997).

Results

Field sampling

Spain

During the summer of 2009, we received many reports from the entire length of the Catalan coast describing the presence of an unusual jellyfish species, which we identified as *M. leidyi* (Fig. 1). Only the observations for which we visually confirmed that the reported jellyfish species was *M. leidyi* are given in Table 1. Many other similar reports were received from several additional locations along the Catalan coast, but we were not always available to make identifications; therefore, *M. leidyi* may have been even more commonly distributed than reported here. The confirmed reports show that large swarms of *M. leidyi* were observed from the

Fig. 1 Reports of blooms of *Mnemiopsis leidyi* in the Mediterranean Sea in 2009 in Spain, Israel, and Italy

Table 1 Records of *Mnemiopsis leidyi* along the Spanish NW Mediterranean coast during summer 2009

Location	Geographic coordinates		Survey date 2009 and (No. of reports)	Source	Water conditions	
	Latitude, N	Longitude, E			Temp. (°C)	Salinity
Catalan coast						
Cap de Creus	42°19′5.78	3°19′31.40	July (2 reports)	ACA, Fishermen	22.7	37.7
Arenys de Mar	41°34′44.6	2°33′10.62	August (1 report)	ACA	23.9	37.6
Mataro port	41°32′1.70	2°27′1.62	August (1 report)	ACA	24.7	37.7
Salou La Pineda beach	41°3′12.28	1°10′8.52	August (reported daily for 1 week)	ACA–Red Cross	23.3	37.9
Cambrils	41°3′46.60	1°10′20.63	August (reported daily for 1 week)	ACA–Red Cross	20.8	37.8
Les Cases d'Alcanar beach	40°33′2.22	0°31′49.37	July–August (several reports)	ACA	25.3	37
Alcanar Del Marjal beach	40°33′15.13	0°32′4.41	July–August (several reports)	ACA	25.3	37
Other Spanish coastal areas						
Cabrera port (Balearic Islands)	39°8′43.13	2°55′49.70	August (1 report)	Red Cross	23	ND
Denia (Alicante) Big port	38°50′57.18	0°6′34.25	July–August (observed frequently)	Red Cross	27.5	ND

ACA Catalan Water Agency, *ND* no data

The temperature and salinity data correspond to the period when *M. leidyi* were observed

beginning of July to the end of September along the entire coast from Cap de Creus in the northern Catalan coast to Alcanar in the south. The presence of *M. leidyi* also was confirmed in the south of Catalonia in Denia (Valencia, Levantine coast of Spain) and Cabrera (Balearic Islands) (Table 1; Fig. 1). Most of the *M. leidyi* observations made by ACA during summer 2009 were in the highest abundance category 3.

The surface coastal waters of the Catalan Sea (NW Mediterranean) during the summer months of 2009, when the presence of *M. leidyi* was confirmed (from July to September), were characterized by salinities between 30.5 in the south, where the delta of the Ebro River is located, and 38.2, and temperatures between 21.5 and 25.8°C. Temperature and salinity (S) of the waters where *M. leidyi* was present ranged from 22.7 to 25.3°C and 37–37.9 S (Table 1).

Along the coast of Denia, a high-density area of *M. leidyi* was detected from 16 to 18 July 2009, with densities ranging from 5 to 100 ind. m^{-2}. The ctenophores were seen only on those days in an area of about 2,500 m^2 at depths of 0–4 m (Table 1). The high-density patch dispersed after 18 July; however, low densities of *M. leidyi* were observed by SCUBA divers between June and August in that area. Temperatures of coastal waters in Denia (2 m depth) ranged from 12.5°C in March to 27.5°C in July. In this area, the effects of river runoff are very important; for example, nitrate values are normally very high, reaching a maximum of 361 $\mu g\ l^{-1}$ in November 2006.

The observations of large jellyfish (scyphomedusae and hydromedusae) were atypical along the Catalan coast during the spring and summer months of 2009. The typical pattern in 2000–2008 showed that the greatest jellyfish abundances occurred during July and August (Gili et al., 2007, 2008); however, in 2009, most jellyfish occurred during May and June (Fig. 2). In July, most of the jellyfish species usually seen then (*P. noctiluca*, *Aequorea forskalea* Péron & Lesueur, and *R. pulmo*) nearly disappeared, which coincided with the period when *M. leidyi* was most abundant and frequently observed (Fig. 2).

Israel

Observations, including relative abundances, of gelatinous zooplankton in Israeli coastal waters were recorded from January to July 2009 with an emphasis

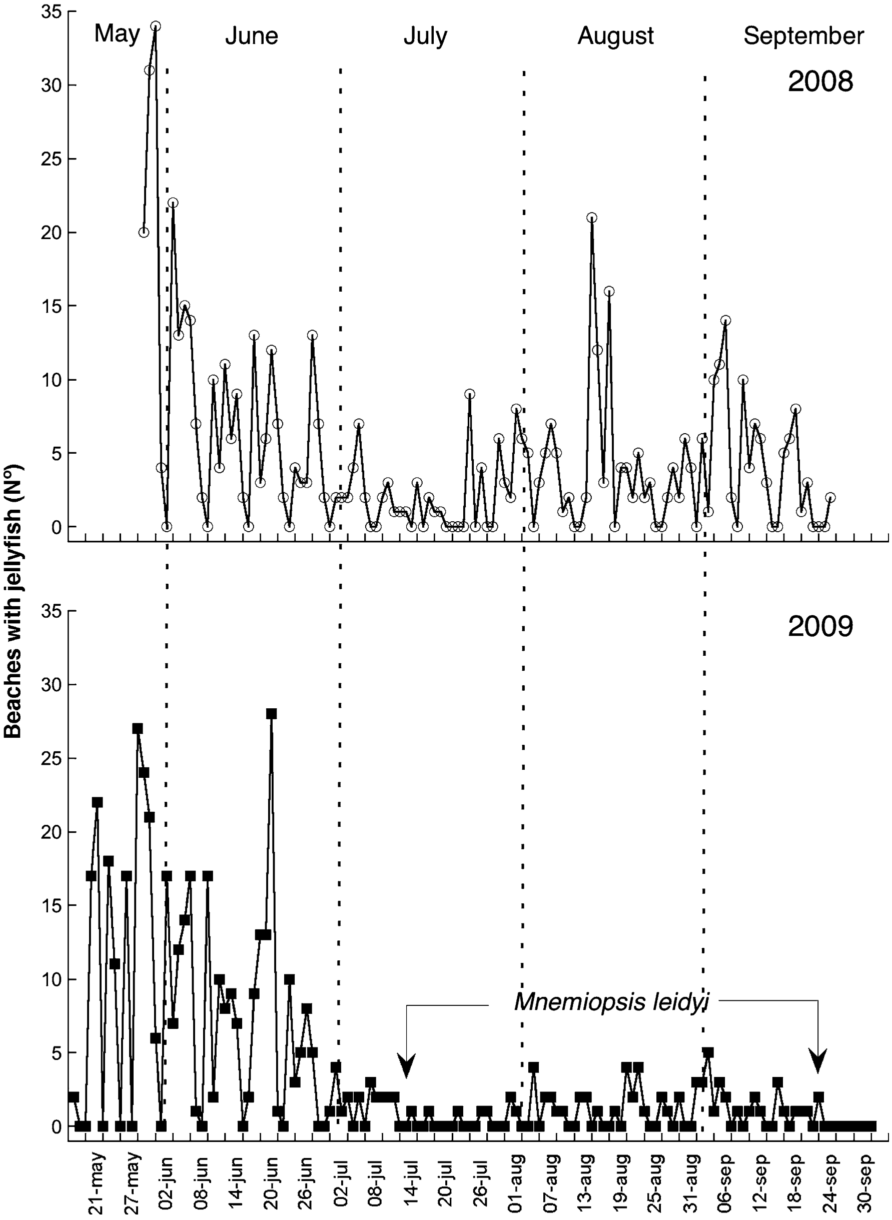

Fig. 2 The numbers of beaches with scyphozoan and hydrozoan jellyfish during the beach season 18 May to 30 September 2008 (*circles*) and 2009 (*squares*). The *arrows* mark the period of time when high numbers of *Mnemiopsis leidyi* ctenophores were observed in 2009 in the Catalan Sea, Spain

on medusae (mainly *Rhopilema nomadica* Galil, Spanier & Ferguson and *R. pulmo*) and ctenophores (Table 2). This record-keeping was stimulated by the appearance in January of a massive bloom of *M. leidyi*, which had not been observed prior to this year in such abundances in these coastal waters. The earliest reports of the ctenophore swarms were from purse seine and trawl fishermen, describing "marmalade" or "medusa jelly" that made it difficult to lift the fishing gear. Continuous onboard observations of the ctenophores led to subsequent visual confirmation during a SCUBA diving expedition to 32°51′02″N–034°56′33″E. All of the ctenophore swarms were observed within 5 nautical miles of shore. Ctenophores were reported to occur either sporadically or abundantly from January to mid-June (Table 2). Most of the medusae observed in 2009 were *R. pulmo*, which was often abundant in January through March, and several patches of *R. nomadica* that occurred in June (Table 2). Routine coastal monitoring did not

Table 2 Observations of ctenophores in coastal waters of Israel during 2009

Location	Month/week	Ctenophore abundance	Medusa abundance	Source	Temp. (°C)
Jaffa Port	January/3rd	Abundant	Abundant	Trawl	18
Jaffa Port	March/1st	Occasional	Occasional	Fishermen	NR
Jaffa Port	March/2nd	Abundant	Abundant	Fishermen	NR
Jaffa Port	March/4th	Abundant	Absent	Trawl + Fishermen	18
Jaffa Port	April/1st	Occasional	Absent	Fishermen	NR
Jaffa Port	April/2nd	Occasional	Absent	Fishermen	NR
Jaffa Port	April/3rd	Abundant	Occasional	Trawl + Fishermen	19
Jaffa Port	April/4th	Abundant	Occasional	Trawl + Fishermen	19
Jaffa Port	May/1st	Abundant	Absent	Fishermen	NR
Jaffa Port	May/2nd	Occasional	Absent	Trawl + Fishermen	21
Jaffa Port	May/4th	Occasional	Absent	Fishermen	NR
Jaffa Port	June/1st	Abundant	Occasional	Fishermen	NR
Jaffa Port	June/2nd	Abundant	Occasional	Fishermen	NR
Jaffa Port	June/3rd	Absent	Occasional	Trawl + Fishermen	26
Haifa Bay	January/3rd	Abundant	NR	Trawl	NR
Haifa Bay	March/4th	Occasional	NR	Trawl	NR
Haifa Bay	April/4th	Abundant	NR	Trawl	NR
Haifa Bay	May/2nd	Occasional	NR	Trawl	NR
Haifa Bay	June/3rd	Absent	NR	Trawl	NR

Observations were made by inshore and purse-seine fishermen and recorded during and following trawl fishing at two fishing ports in Israel. Jaffa (32°03′21.1N and 034°43′53.4E) and Kishon (Haifa: 32°52′44.8N and 034°56′04.4E). Abundance categories were "Occasional" = sporadic sightings of jellyfish (no swarms) or 1–5 specimens in each trawl. "Abundant" = consistent reports of jellyfish in swarms or >5 specimens in each trawl. Ctenophores were not observed or caught by fishermen from either port from the third week of June through July 2009

NR not recorded

reveal unusual patterns in seawater temperatures, salinities (39.1–39.8), or chemistry during spring and early summer 2009 as compared with other years (Herut et al., 2005, 2006, 2008); however, winter 2008/2009 temperatures were higher than average winter temperatures (Fig. 3).

Molecular species identification

The sequences for the nuclear ITS region (ITS-1, 5.8S, and ITS-2) from all three ctenophores sequenced were identical in length (638 base pairs) and nearly identical in sequence to published *M. leidyi* sequences, indicating positive identification as *M. leidyi*. Sequences for the three ctenophores analyzed differed by at most a single degenerate base (T in SAL-1 and HAF-1 and Y [C and T] in SAL-2). All sequences were extremely similar to published *M. leidyi* sequence for ITS (NCBI Accession #AF293700), all being the same length and differing by 3 (SAL-1 and HAF-1) or 4 (SAL-2) bases out of 638 (all degenerate changes, i.e., T vs. Y, etc.), indicative of within-species differentiation. In comparison, the three ctenophores differed markedly from the next closest match (*Bolinopsis* sp.—Accession #BSU65480) in being 2 bp shorter and diverging by 19–20 bp.

Discussion

Arrival and transport of *Mnemiopsis leidyi* in the Mediterranean Sea

Although May 2009 was the first confirmed report of *M. leidyi* on the Spanish coast, this species was present before but remained unrecorded until its populations increased. We located unpublished information about the presence of *M. leidyi* in Cabrera

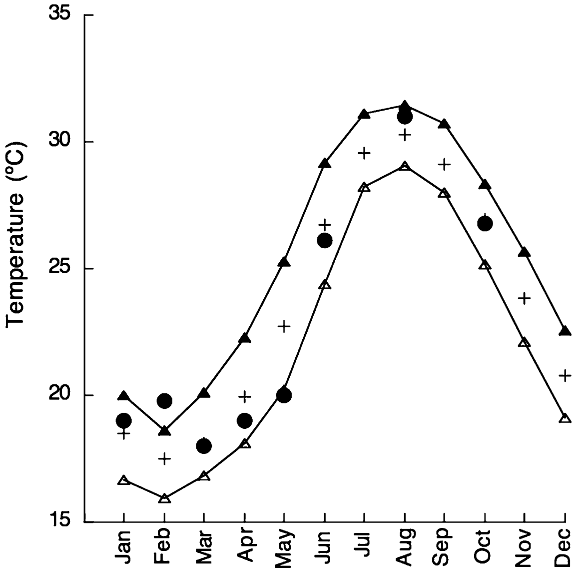

Fig. 3 Sea water temperature (°C) of last 12 years from Palmachim, Israel. *Solid triangles* maxima, *open triangles* minima, *crosses* means. *Solid circles* mark the 2008–2009 winter–spring water temperatures

(Balearic Islands) (OCEANA, 2008); we confirmed its presence there in 2009 (Fig. 1). Earlier occurrences of *M. leidyi* in other Mediterranean areas may be established by examination of formalin-preserved plankton samples, as in Purcell (1988). High numbers of *M. leidyi* along the Mediterranean coastlines of Israel (Galil et al., 2009), Italy (Boero et al., 2009), and Spain during summer 2009, plus the fact that the species was also present in Spanish waters in 2008, strongly suggest that its population is established in the Mediterranean.

Molecular species identification confirmed representative ctenophores as *M. leidyi* through the use of DNA sequence from the nuclear ITS region. Some previous articles on invasive ctenophores in the Baltic Sea apparently have misidentified the ctenophores to the genus *Mnemiopsis* (Kube et al., 2007; Lehtiniemi et al., 2007); the errors only were recognized upon the use of molecular identification tools (Gorokhova et al., 2009).

Although the molecular dataset is small ($n = 3$), it may also give some preliminary indication of the original source region(s) of some of the ctenophores. Two of the sequenced ctenophores (SAL-1 and HAF-1) contained an ITS composite genotype that was previously found in invasive *M. leidyi* from the Black Sea (southwestern Black Sea and Gelendzhik Bay, Russia) and the Sea of Azov (various locations), as well as in native ctenophores from the United States (only from the Gulf of Mexico at Mobile, Alabama and Atlantic Ocean at Miami, Florida) (Bayha, 2005), possibly indicating common recent ancestry for these animals. The third ctenophore (SAL-2) contained an ITS composite genotype not previously found in any geographic region (Bayha, 2005). These results must be interpreted cautiously, however. First, the dataset is extremely small, so the findings are specific only to these individuals and do not reflect anything regarding the greater Mediterranean population (i.e., others may have originated elsewhere). Description of the entire population would require the examination of significantly more Mediterranean individuals. Secondly, while the ITS region historically has been useful at the species level, the ITS genetic region occurs in multiple copies (Arnheim et al., 1980) and its use in population-level studies can be problematic (Vollmer & Palumbi, 2004). Therefore, ITS data ideally should be corroborated with data from additional single-copy genetic marker(s). Nevertheless, our preliminary data are consistent with two of our specimens having a common source with Black and Azov sea invaders, as well as ctenophores from the Gulf of Mexico (Mobile, Alabama) and/or Miami (Florida) in the native range.

The introduction of *M. leidyi* and its distribution throughout the Mediterranean Sea probably resulted from transport by both ballast waters from the Black Sea region and currents. *M. leidyi* was first reported in the Mediterranean Sea in 1990, transported into the Aegean Sea by water flow through the Dardanelles from the Sea of Marmara or by ballast water from ships. The ctenophore was reported in Turkey and Syria soon thereafter (1992 and 1993; Table 3). No other reports were made in the Mediterranean until 2005, when *M. leidyi* appeared in France and 2006 in the Gulf of Trieste (Table 3). The simultaneous blooms of *M. leidyi* all along the Mediterranean coasts of Israel, Spain, and Italy in 2009 (Fig. 1; Boero et al., 2009; Fuentes et al., 2009; Galil et al., 2009) suggest that such wide-spread, abundant ctenophores could not have been distributed by either currents or shipping in 2009, but that the ctenophores already were present and were stimulated to bloom in favorable conditions in 2009.

Table 3 Hydrological characteristics and mesozooplankton biomass (μg C) or abundance (number m^{-3}) of the seas of the Mediterranean basin, and the year when *Mnemiopsis leidyi* was first reported and the seasons when it is known to be active in each location

Location	Temperature (°C)		Salinity	Mesozoo (μg C or # m^{-3})	First report	Active Season
	Winter	Summer				
Black Sea[a]	0–8	24–27	18–22.3	33,000C*	1982	Spr–Aut
Sea of Azov[b]	−0.8 to +1.2	24–30	0–14		1988	Spr–Aut
Sea of Marmara[b]	8–15	24–29	18–29		1989–1990	All year
Caspian Sea[b]	0–11	24–28	0.1–11		1999	Spr–Aut
Aegean Sea[c]	13.3–14.1	24–29	38.7–39.1	450–10,940#	1990	All year
Turkey[d]		~25–26.5	~32.6–33.8		1992	ND
Syria					1993	ND
Gulf of Trieste[e]	<10	20 to >26	32–38	3.6–9C	2005	ND
France[e]		31.5	39.5		2006	ND
Catalan Sea[f]	12–13	25–26	37–39.2	500–8000#*	2008	ND
Italy[g]	13–14	23–26	37.5–37.9	500–4000#*	2009	ND
Israel	16–20	29–32	39.1–39.8	0–2598#	2009	ND

ND no data

* = Before Mnemiopsis, # = number, C = carbon

[a] Purcell et al. (2001)

[b] Shiganova et al. (2001)

[c] Shiganova et al. (2004)

[d] Isinibilir & Tarkan (2002)

[e] Shiganova & Malej (2009)

[f] Calbet et al. (2001)

[g] Kamburska & Fonda-Umani (2009)

Transport of *M. leidyi* in ballast water to Spain could have been to Barcelona, which was listed as the Mediterranean port with greatest ship traffic in 2006 (REMPEC, 2008). Of the Spanish locations with confirmed *M. leidyi*, only Denia represents an important commercial and passenger port; however, because all ships use the container system to transfer cargo, they do not release ballast water; therefore, it is unlikely that *M. leidyi* arrived in Denia by ship transport. The ctenophores found in the southern Catalan Sea as well as in Denia may be explained by circulation patterns in those areas.

The general circulation pattern in the Catalan Sea is characterized mainly by a current that follows the continental slope, in geostrophic equilibrium with a shelf/slope hydrographic front (Font et al., 1988). This current, the Liguro-Provençal-Current (LPC), is directed from the northeast towards the southwest partially governed by the effect of a permanent cyclonic gyre north of the Balearic Islands at the western side of Gulf of Lyon. This current transports the major outside Mediterranean surface waters to the Catalan Sea from the Gulf of Lyon along with considerable runoff from the Rhone River. This mesoscale circulation pattern persists throughout the year but is most intense in winter and spring (Font et al., 1988). In the southern Catalan Sea, the LPC follows the shelf break, entering the Gulf of Valencia and continuing to the Eivissa Channel (Salat, 1995). Water balances in the region show that the volume of water flowing southward through the Eivissa Channel is always smaller than the transport along the shelf break by the LPC and Atlantic waters that penetrate into the eastern Catalan Sea by the Eivissa Channel (García et al., 1994). The southern penetration of Atlantic waters mainly occurs through the channel between Eivissa and Mallorca all year, but this water mass remains in the eastern sector of the region (Monserrat et al., 2008). In years with mild winters, the flow of Atlantic waters through the Eivissa Channel is more intense especially in late spring and summer. These circulation patterns make intrusion of Atlantic waters into the Catalan Sea from the northeast with surface waters more probable than flow through the eastern Balearic Islands and the Gulf of Lyon. However, after mild winters, the intrusions from the south through the Eivissa Channel could had been of great importance incorporating Atlantic waters flowing around the Iberian Peninsula from the Strait of Gibraltar, being this another possibility for the introduction of *M. leidyi* into the southern Catalan Sea waters.

Hamad et al. (2005) analyzed satellite thermal images of Mediterranean surface waters and proposed a revision to the accepted scheme of large-scale flow in the Mediterranean Sea. Hamad et al.'s analysis indicates that there is a direct link between water flowing from the Aegean Sea, where *M. leidyi* has occurred since 1990, to the Levant. Alternatively, because the swarms of *M. leidyi* were observed mainly in the southern half of Israel, between Ashkelon and Netanya and considering that the predominant current in this region is along shore from south to north (Rosentraub & Brenner, 2007; Zviely et al., 2007), it is possible that *M. leidyi* was released in ballast water from ships traveling toward the southern Israeli port of Ashdod or to Egypt.

Factors affecting the success of *Mnemiopsis leidyi* in the Mediterranean Sea

Environmental conditions

Conditions for *M. leidyi* in the Mediterranean are quite different from the conditions in most native and introduced habitats. *M. leidyi* typically inhabits shallow estuaries and coastal waters in its native American waters (reviewed in Kremer, 1994; Purcell et al., 2001). In its northern temperate habitats (Rhode Island and Maryland), temperatures range from 1°C in the winter to 30°C in the summer and salinities range from ≤ 2 to 32. The annual peak in biomass of northern *M. leidyi* populations is in mid-summer to fall, which have occurred earlier with rising temperatures since 1950 (Sullivan et al., 2001; Costello et al., 2006a). Ctenophore biomass declines in the autumn when temperatures decrease and the ctenophores overwinter in nearshore bottom-water refugia (Costello et al., 2006b). Ctenophores in more southerly native locations (Florida and Texas) experience higher temperatures (winter minima of 7–18°C and summer maxima 31–32°C) and higher salinities (14–45) than in the north. The populations peak in winter when temperatures are lower ($\sim$20°C) than the rest of the year, and the population can display several small peaks (20–30 ml m^{-3} live volume) throughout the year.

These same patterns are seen among the locations where *M. leidyi* was introduced earlier. The Black, Caspian, North, and Baltic seas in the northern range are often estuarine, with a summer bloom of *M. leidyi* that subsides in cool temperatures (reviewed in Purcell et al., 2001; Shiganova et al., 2001). The southern introduced habitats in the Sea of Marmara and Mediterranean Sea are similar to the southern U.S. native habitats, with high salinities and temperatures (Shiganova et al., 2001; Shiganova & Malej, 2009). The only study of osmoregulation in ctenophores showed *M. leidyi* to conform to salinity within the range tested (8–23; Foshtomi et al., 2007). Clearly, the habitats of *M. leidyi* seem unrestricted by most physical conditions, with the exception of temperatures <4°C in high latitudes.

Water conditions along the Catalan coast are suitable for *M. leidyi* throughout the year (Fig. 4), because they would not be limited by cold winter temperatures as in northern latitudes. *M. leidyi* is present all year in the Aegean Sea (Shiganova et al., 2004), but its seasonal distributions in other Mediterranean locations are unknown.

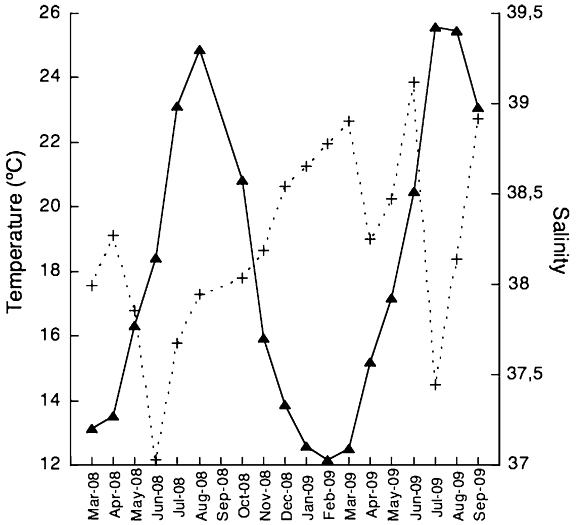

Fig. 4 Monthly measurements of sea temperature (°C) and salinity in the surface waters of the Catalan Sea from March 2008 to September 2009. *Solid triangles* salinity, *crosses* temperature

Food resources

Zooplankton abundance directly affects ctenophore abundance. *M. leidyi* was found in waters with high zooplankton stocks and did not occur where zooplankton biomass was <3 mg C m^{-3} (reviewed by Kremer, 1994; Purcell et al., 2001). In native locations, peak zooplankton biomass (~100 mg C m^{-3}) was higher in northern than in southern latitudes (~25 to 50 mg C m^{-3}).

In contrast to rich environments where *M. leidyi* is found, the north western Mediterranean is considered to be an oligotrophic sea, with low nutrient concentrations but relatively moderate levels of pelagic primary production (100–150 g C m^{-2} y^{-1}; reviewed by Estrada, 1996). In particular, the Catalan Sea is a highly dynamic oligotrophic environment, subjected to important forcing from the alternation of stratification and mixing periods and from the strength of mesoscale singularities (Saiz et al., 2007). Two features of special importance for productivity in the Mediterranean are the deep chlorophyll maximum (DCM) at the base of the pycnocline during most of the stratification period, and the occurrence of two phytoplankton blooms (Estrada, 1996), which are followed by two peaks of zooplankton in late winter–spring and in autumn. During stratification, the DCM is an oasis for zooplankton feeding and accentuates the difference between the poor surface layer (0.2–0.3 μg chl l^{-1}) and richer waters at depth (1–2 μg chl l^{-1}) (Estrada, 1996). During the stratified period, the trophic web based on the microbial loop could assume great importance; microzooplankton is responsible for most of the secondary production in warm waters (Fernández de Puelles et al., 2007; Saiz et al., 2007). In the Mediterranean Sea, there appears to be strong coupling between the microbial food webs and the upper trophic levels (Cushing, 1989). During the warm months, the diverse mesozooplankton community is predominated by filter-feeding organisms that efficiently consume the small fractions of the food web (Calbet et al., 2001).

Mnemiopsis leidyi is very versatile in the types of prey it consumes, which range from microplankton to mesozooplankton and ichthyoplankton; *M. leidyi* larvae ≤5 mm diameter contained diatoms, dinoflagellates, and ciliates, and larger larvae also contained copepod nauplii and copepodites (reviewed in Purcell et al., 2001; see also Sullivan & Gifford, 2004; Rapoza et al., 2005). Several studies report inverse correlations of *M. leidyi* and zooplankton abundances (reviewed in Purcell, 1988); when *M. leidyi* were abundant, clearance rates of the ctenophores were sufficient to reduce zooplankton populations (reviewed in Purcell et al., 2001; Shiganova et al., 2001; see also Purcell & Decker, 2005; Riisgård et al., 2007). In addition, *M. leidyi* had higher clearance rates on copepods than did scyphomedusae of equal biomass (Purcell & Decker, 2005). The wide variety of prey types and high feeding rates could have allowed this species to establish in the oligotrophic conditions of the NW Mediterranean.

Other important food resources for *M. leidyi* are fish eggs and larvae. In the NW Mediterranean, ichthyoplankton has a pronounced seasonal variability because most fishes (neritic, small pelagics, and migratory species) spawn during spring and summer. The most abundant pelagic species are European sardine and anchovy, which have non-overlapping spawning periods, autumn–winter and spring–summer, respectively (Sabatés et al., 2007). Consumption of ichthyoplankton by *M. leidyi* can be very important in native and non-native environments (reviewed in Purcell et al., 2001; Shiganova et al., 2001); however, the importance of *M. leidyi* predation on zooplankton and ichthyoplankton in the recently invaded Mediterranean regions are not yet known.

In addition to the wide spectrum of prey that this ctenophore can exploit, the success of introduced *M. leidyi* also could be attributed to reduced competition from over-fished populations of zooplanktivorous fish (Oguz et al., 2008; Siapatis et al., 2008). In the NW Mediterranean Sea, over-fishing is believed to be one reason that gelatinous zooplankton seem to be increasing in abundance in recent decades (Gili & Pagés, 2005). Two important features of the fishing activity in the Mediterranean Sea are the multi-specificity of catches and the absence of large single stocks, especially in the demersal regime, as compared with those that inhabit other seas (Coll et al., 2006). The development of fishing technologies and over-capitalization, with an increasing demand for marine resources, is placing intensive pressure on marine resources in the western basin, and the general assessment suggests that most demersal stocks are fully exploited, while some pelagic stocks are even overexploited (Bas et al., 2003; Leonard & Maynou, 2003; Coll et al., 2006).

It is not clear what lead to the bloom of this ctenophore in the Levant but it may be related to the dietary similarities of larval fish, zooplanktivorous fish, and *M. leidyi*. The fishing pressure along Israeli coasts continues to be very high (Pisanty & Grofit, 1991) and may have caused an untimely imbalance in favor of the invasive ctenophore, enabling it to flourish, despite the relatively low abundances of micro- and mesozooplankton detected in the coastal waters of Israel during the period that *M. leidyi* was present. Zooplankton abundances in the eastern Mediterranean Sea off the coast of Israel generally are very low, and median values ranged from 256 to 1,261 m^{-3} for microzooplankton and 13–196 m^{-3} for mesozooplankton, as recorded from March to May 2009.

Predators and competitors

Interannual variation in *M. leidyi* abundance is strongly related to predator abundance in their native waters (reviewed in Purcell et al., 2001; Purcell & Decker, 2005). A variety of predators occur, including the ctenophore, *Beroe ovata* Brugière, the scyphomedusae, *Chrysaora quinquecirrha* Desor and *Cyanea capillata* (Linnaeus), harvestfish, *Peprilus alepidotus* (Linnaeus), and butterfish *P. triacanthus* (Peck), but their effects on *M. leidyi* populations have rarely been studied. Low and high salinity waters can serve as a refuge for *M. leidyi* from predators, as in Chesapeake Bay. Purcell et al. (2001) concluded that the key difference between native U.S. habitats of *M. leidyi* and the Black, Azov, and Caspian seas was the lack of predators there, perhaps enabling the devastating blooms of the ctenophore in those non-native habitats. Subsequently, *B. ovata* arrived in the Black and Azov seas and has limited *M. leidyi* populations since 1999.

The NW Mediterranean Sea has a diversity of potential predators of *M. leidyi*. The ctenophores *Beroe cucumis* Fabricius and *Beroe forskalii* Milne Edwards are common (Shiganova & Malej, 2009); however, *Beroe* spp. normally are abundant only in spring and early summer along the Catalan coast (F. Pagès, pers. com.), suggesting that they were not abundant there when *M. leidyi* occurred in high numbers (July and August 2009). Nevertheless, at the beginning of July 2009, both *M. leidyi* and *P. noctiluca* were present in the coastal waters and *P. noctiluca* ate *M. leidyi* in the laboratory (V. Fuentes, pers. obs.). In late July 2009, *P. noctiluca* almost disappeared from the Catalan coast; their absence coincided with high abundances of *M. leidyi* (Fig. 2). Another abundant potential predator is the hydromedusa, *A. forskalea*; its congeners are voracious predators of gelatinous species (Purcell, 1991).

In addition to the potential predators, many potential competitors for zooplankton foods occur in the NW Mediterranean, including the large jellyfish, *P. noctiluca*, *C. tuberculata*, *R. pulmo*, and *A. forskalea*, and many species of small hydromedusae and siphonophores (Sabatés et al., this volume), as well as several species of zooplanktivorous fishes (Leonard & Maynou, 2003; Sabatés et al., 2007).

Jellyfish observations in Israel indicate that in addition to the persistent swarms of *R. nomadica* and *R. pulmo* that have been documented along the Mediterranean shores since the 1980s (Galil, 2007), there are occasional blooms of novel exotic gelatinous species that had not been previously recorded. A comprehensive list of scyphomedusae of the Mediterranean coast of Israel includes *P. noctiluca*, *Aurelia aurita*, *C. tuberculata*, *Phyllorhiza punctata* von Lendenfeld, *Cassiopea andromeda* (Forsskal), *R. pulmo*, and *R. nomadica* (in Galil et al., 1990). Despite annual outbreaks of stinging jellyfish, few attempts have been made to quantify these swarms (Spanier & Galil, 1991; Lotan et al., 1992) or to follow their spatio-temporal dynamics. As in the NW Mediterranean, all of these species are potential competitors with *M. leidyi* for zooplankton prey, and *P. noctiluca* is a likely predator of *M. leidyi*. The importance of these various species as predators and competitors of *M. leidyi* in Mediterranean waters remains to be investigated.

The lack of basic information on these exotic invasives throughout the Mediterranean led to the 2008 CIESM initiative, “JellyWatch” (http://www.ciesm.org/marine/programs/jellywatch.htm) and the “Medusa Project” (ACA, 2009) created to document the frequency and distribution of jellyfish blooms in the Mediterranean Sea. Those efforts need to be expanded to include other gelatinous groups in addition to large jellyfish. For example, the records for ctenophores in the Mediterranean Sea are scarce; *M. leidyi* may have been resident previously but was not noticed before the spectacular 2009 blooms.

Conclusions

Nearly simultaneous blooms of the invasive ctenophore, *M. leidyi*, occurred throughout the Mediterranean Sea in 2009. This voracious zooplanktivore has caused wide-spread ecosystem disruption and damage to fisheries following its accidental introduction to the Black Sea basin in the early 1980s. It subsequently invaded waters of the North and Baltic seas, where its spread and abundance may be restricted by cold temperatures and native gelatinous predators. Conditions in the Mediterranean Sea are very different (comparatively warm temperatures, high salinities, and low productivity) from those in the northern habitats invaded by *M. leidyi*; therefore, *M. leidyi* is unlikely to be constrained by physical conditions in the Mediterranean Sea. On the other hand, a variety of gelatinous species are potential predators and competitors of *M. leidyi* that may constrain its populations in the Mediterranean. Whether or not *M. leidyi* flourishes, the presence of this species will change the Mediterranean ecosystems and poses a threat to fisheries.

Acknowledgments Thanks are due to the Catalan Water Agency for funding the Medusa Project. We are indebted to all institutions collaborating with the reporting network. We thank the Haifa University Maritime Workshop for their help in collecting *M. leidyi* at sea; G. Yahel and the School of Marine Sciences and Marine Environment, Ruppin Academic Center, Michmoret Israel for provision of zooplankton abundance data; N. Drimmer at CAMERI - Coastal and Marine Engineering Research Institute Ltd. for the Israel Ports Development & Assets Company Ltd. for the sea-surface temperature data, and A. Glazer at the Israel Electric Corporation for sea-surface temperature and salinity data. All molecular work was performed in the lab of Dr. Michael N Dawson at the University of California Merced.

References

ACA, 2009. Catalan water agency “Medusa Project”, http://aca-web.gencat.cat:80/aca/appmanager/aca/aca?_nfpb=true&_pageLabel=P2020096158125077724062 5&_nfls=false.

Altschul, S. F., T. L. Madden, A. A. Schäffer, J. Zhang, Z. Zhang, W. Miller & D. J. Lipman, 1997. Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. Nucleic Acids Research 25: 3389–3402.

Arnheim, N., M. Krystal, R. Schmickel, G. Wilson, O. Ryder & E. Zimmer, 1980. Molecular evidence for genetic exchanges among ribosomal genes on nonhomolohous chromosomes in man and apes. Proceedings of the National Academy of Sciences, USA 77: 7323–7327.

Bas, C., F. Maynou, F. Sardà & J. Leonard, 2003. Variacions demogràfiques a les poblacions d’espècies demersals explotades: es darrers quaranta anys a Blanes i Barcelona. Institut d’Estudis Catalans. Secció de Ciències Biològiques Vol. 135: 202 pp.

Bayha, K. M., 2005. The molecular systematics and population genetics of four coastal ctenophores and scyphozoan jellyfish of the U.S. Atlantic and Gulf of Mexico. Ph.D. Dissertation, The University of Delaware, Newark.

Bayha, K. M., G. R. Harbison, J. H. McDonald & P. M. Gaffney, 2004. Preliminary investigation on the molecular systematics of the invasive ctenophore *Beroe ovata*. In Dumont, H., T. A. Shiganova & U. Niermann (eds), Aquatic Invasions in the Black, Caspian and Mediterranean Seas. Kluwer Academic Publishers, Dordrecht: 167–175.

Boero, F., M. Putti, E. Trainito, E. Prontera, S. Piraino & T. Shiganova, 2009. Recent changes in Western Mediterranean Sea biodiversity: the establishment of *Mnemiopsis leidyi* (Ctenophora) and the arrival of *Phyllorhiza punctata* (Cnidaria). Aquatic Invasions 4: 675–680.

Calbet, A., S. Garrido, E. Saiz, M. Alcaraz & C. M. Duarte, 2001. Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. Journal of Plankton Research 23: 319–331.

CAMERI (Coastal and Marine Engineering Institute of the Technion), 2008. Annual report for the Israel Ports Development & Assets Company Ltd, http://eng.israports.co.il/.

Coll, M., I. Palomera, S. Tudela & F. Sardà, 2006. Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. Journal of Marine Systems 59: 63–96.

Costello, J. H., B. K. Sullivan & D. J. Gifford, 2006a. A physical–biological interaction underlying variable phonological responses to climate change by coastal zooplankton. Journal of Plankton Research 28: 1099–1105.

Costello, J. H., B. K. Sullivan, D. Van Keuren & D. J. Gifford, 2006b. Seasonal refugia, shoreward thermal amplification, and metapopulation dynamics of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. Limnology and Oceanography 51: 1819–1831.

Cushing, D. H., 1989. A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. Journal of Plankton Research 11: 1–13.

Dawson, M. N., K. A. Raskoff & D. K. Jacobs, 1998. Preservation of marine invertebrate tissues for DNA analyses. Molecular Marine Biology and Biotechnology 7: 145–152.

Estrada, M., 1996. Primary production in the northwestern Mediterranean. Scientia Marina 60(Suppl. 2): 55–64.

Faasse, M. A. & K. M. Bayha, 2006. The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in coastal waters of the Netherlands: an unrecognized invasion? Aquatic Invasions 1: 270–277.

Faris, S., 2009. A gelatinous invasion. Time 174: 47–48.

Fernández de Puelles, M. L., F. Alemany & J. Jansá, 2007. Zooplankton time-series in the Balearic Sea (Western Mediterranean): variability during the decade 1994–2003. Progress in Oceanography 74: 329–354.

Font, J., J. Salat & J. Tintoré, 1988. Permanent features of the circulation in the Catalan Sea. Oceanologica Acta 1988: 51–57.

Foshtomi, M. Y., B. Abtahi, A. E. Sari & M. Taheri, 2007. Ion composition and osmolarity of Caspian Sea ctenophore, *Mnemiopsis leidyi*, in different salinities. Journal of Experimental Marine Biology and Ecology 352: 28–34.

Fuentes, V. L., D. Atienza, J.-M. Gili & J. E. Purcell, 2009. First records of *Mnemiopsis leidyi* A. Agassiz 1865 off the NW Mediterranean coast of Spain. Aquatic Invasions 4: 671–674.

Galil, B. S., 2007. Seeing red: alien species along the Mediterranean coast of Israel. Aquatic Invasions 2: 281–312.

Galil, B. S., E. Spanier & W. W. Ferguson, 1990. The scyphomedusae of the Mediterranean coast of Israel, including two Lessepsian migrants new to the Mediterranean. Zoologische Mededelingen 64: 95–105.

Galil, B. S., N. Kress & T. A. Shiganova, 2009. First record of *Mnemiopsis leidyi* A. Agassiz, 1865 (Ctenophora Lobata Mnemiidae) off the Mediterranean coast of Israel. Aquatic Invasions 4: 356–362.

García, E., J. Tintoré, J. Pinot, J. Font & M. Manríquez, 1994. Surface circulation and dynamics of the Balearic Sea. Coastal and Estuarine Studies 46: 73–91.

GESAMP (IMO/FAO/UNESCO-IOC/WMO/WHO/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection), 1997. Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* invasion in the Black Sea. Report and Studies GESAMP 58: 84 pp.

Gili, J. M. & F. Pagés, 2005. Les proliferacions de meduses. Bolletí de la Societat d'Història Natural de les Balears 48: 9–22.

Gili, J. M., V. Fuentes & D. Atienza, 2007. Medusa project: data year 2007. Technical report No. 1: 98 pp.

Gili, J. M., V. Fuentes & D. Atienza, 2008. Medusa project: data year 2008. Technical report No. 2: 198 pp.

Gorokhova, E., M. Lehtiniemi, S. Viitasalo-Frosen & S. H. D. Haddock, 2009. Molecular evidence for the occurrence of ctenophore *Mertensia ovum* in the northern Baltic Sea and implications for the status of the *Mnemiopsis leidyi* invasion. Limnology and Oceanography 54: 2025–2033.

Hamad, N., C. Millot & I. Taupier-Letage, 2005. A new hypothesis about the surface circulation in the eastern basin of the Mediterranean Sea. Progress in Oceanography 66: 287–298.

Herut, B., E. Shefer & Y. Cohen, 2005. Environmental quality of Israel's Mediterranean coastal waters in 2004. IOLR Report H34/2005.

Herut, B., Y. Cohen, E. Shefer, N. Gordon, B. Galil, G. Tibor & M. Tom, 2006. Environmental quality of Israel's Mediterranean coastal waters in 2005. IOLR Report H25/2006.

Herut, B., E. Shefer, N. Gordon, B. Galil, G. Tibor & M. Tom, 2008. Environmental quality of Israel's Mediterranean coastal waters in 2007. IOLR Report H52/2008.

IEC (Israel Electric Corporation), 2009. Environmental report 2009 (in preparation).

Isinibilir, M. & A. N. Tarkan, 2002. Distribution of the invasive ctenophore *Mnemiopsis leidyi* in the north-eastern Aegean Sea in August 1998. Turkish Journal of Fisheries and Aquatic Sciences 2: 129–132.

Ivanov, V. P., A. M. Kamakin, V. B. Ushivtsev, T. A. Shiganova, O. P. Zhukova, N. Aladin, S. I. Wilson, G. R. Harbison & H. J. Dumont, 2000. Invasion of the Caspian Sea by the comb jellyfish *Mnemiopsis leidyi* (Ctenophora). Biological Invasions 2: 255–258.

Javidpour, J., U. Sommer & T. A. Shiganova, 2006. First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. Aquatic Invasions 1: 299–302.

Javidpour, J., J. Molinero & J. Peschutter, 2008. Seasonal changes and population dynamics of the ctenophore *Mnemiopsis leidyi* after its first year of invasion in the Kiel Fjord, Western Baltic sea. Biological Invasions. doi:10.1007/s10530-008-9300-8.

Kamburska, L. & S. Fonda-Umani, 2009. From seasonal to decadal inter-annual variability of mesozooplankton biomass in the Northern Adriatic Sea (Gulf of Trieste). Journal of Marine Systems 78: 490–504.

Kideys, A. E. & U. Niermann, 1993. Intrusion of *Mnemiopsis mccradyi* (Ctenophora; Lobata) into the Mediterranean Sea. Senckenbergiana Maritima 23: 43–47.

Kideys, A. E. & U. Niermann, 1994. Occurrence of *Mnemiopsis* along the Turkish coasts (from northeastern Mediterranean to Istanbul). ICES Journal of Marine Science 51: 423–427.

Kremer, P., 1994. Patterns of abundance for *Mnemiopsis* in US coastal waters: a comparative overview. ICES Journal of Marine Science 51: 347–354.

Kube, S., L. Postel, C. Honnef & C. B. Augustin, 2007. *Mnemiopsis leidyi* in the Baltic Sea – distribution and overwintering between autumn 2006 and spring 2007. Aquaic Invasions 2: 137–145.

Lehtiniemi, M., J. P. Pääkkönen, J. Flinkman, T. Katajisto, E. Gorokhova, M. Karajalanein, S. Viitasalo & H. Björk, 2007. Distribution and abundance of the American comb jelly (*Mnemiopsis leidyi*) – a rapid invasion to the northern Baltic Sea during 2007. Aquatic Invasions 2: 445–449.

Leonard, J. & F. Maynou, 2003. Fish stocks assessment in the Mediterranean: state of the art. In Ulltang, O. & G. Blom (eds), Fish Stocks Assessments and Predictions: Integrating Relevant Knowledge. Scientia Marina 67 (Suppl. 1): 37–49.

Lotan, A., R. Ben-Hillel & Y. Loya, 1992. Life cycle of *Rhopilema nomadica*: a new immigrant scyphomedusan in the Mediterranean. Marine Biology 112: 237–242.

Monserrat, S., J. L. López-Jurado & M. Marcos, 2008. A mesoscale index to describe the regional circulation around the Balearic Islands. Journal of Marine Systems 71: 413–420.

OCEANA, 2008. Illes Balears: propuesta para la gestión de habitat amenazados y la pezca, http://oceana.org/fileadmin/oceana/uploads/europe/reports/Illes_Balears_OCEANA.pdf.

Oguz, T., 2005. Long-term impacts of anthropogenic forcing on the Black Sea ecosystem. Oceanography 18: 112–121.

Oguz, T., B. Fach & B. Salihoglu, 2008. Invasion dynamics of the alien ctenophore *Mnemiopsis leidyi* and its impact on anchovy collapse in the Black Sea. Journal of Plankton Research 30: 1385–1397.

Pisanty, S. & E. Grofit, 1991. Limiting effort in the Israeli trawl fishery. Fisheries and Fishbreeding in Israel 24: 100–133. (in Hebrew with English abstract).

Podar, M., S. H. D. Haddock, M. L. Sogin & G. R. Harbison, 2001. A molecular genetic framework for the phylum Ctenophora using 18s rRNA genes. Molecular Phylogenetics and Evolution 21: 218–230.

Purcell, J. E., 1988. Quantification of *Mnemiopsis leidyi* (Ctenophora, Lobata) from formalin-preserved plankton samples. Marine Ecology Progress Series 45: 197–200.

Purcell, J. E., 1991. Predation by *Aequorea victoria* on other species of potentially competing pelagic hydrozoans. Marine Ecology Progress Series 72: 255–260.

Purcell, J. E. & M. B. Decker, 2005. Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987–2000. Limnology and Oceanography 50: 376–387. http://aslo.org/lo/toc/vol_50/issue_1/0376.pdf.

Purcell, J. E., T. A. Shiganova, M. B. Decker & E. D. Houde, 2001. The ctenophore *Mnemiopsis* in native and exotic habitats: U.S. estuaries versus the Black Sea basin. Hydrobiologia 451: 145–176.

Rapoza, R., D. Novak & J. H. Costello, 2005. Life-stage dependent, in situ dietary patterns of the lobate ctenophore *Mnemiopsis leidyi* Agassiz 1865. Journal of Plankton Research 27: 951–956.

REMPEC (Regional Marine Pollution Emergency Response Centre for the Mediterranean Sea), 2008. Study of maritime traffic flows in the Mediterranean Sea. Final report, Unrestricted Version, EU-Funded MEDA Regional Project MED 2005/109-573.

Riisgård, H. U., L. Bøttiger, C. V. Madsen & J. E. Purcell, 2007. Invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark) in late summer 2007 – assessment of abundance and predation effects. Aquatic Invasions 2: 395–401.

Rosentraub, Z. & S. Brenner, 2007. Circulation over the southeastern continental shelf and slope of the Mediterranean Sea: direct current measurements, winds, and numerical model simulations. Journal of Geophysical Research: Oceans 112(C11001): 1–21.

Sabatés, A., M. P. Olivar, J. Salat, I. Palomera & F. Alemany, 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. Progress in Oceanography 74: 355–376.

Sabatés, A., F. Pagès, D. Atienza, V. Fuentes, J. E. Purcell & J.-M. Gili, this volume. Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* from near shore to open sea in the NW Mediterranean. Hydrobiologia. doi: 10.1007/s10750-010-0221-z.

Saiz, E., A. Calbet, D. Atienza & M. Alcaraz, 2007. Feeding and production of zooplankton in the Catalan Sea (NW Mediterranean). Progress in Oceanography 74: 313–328.

Salat, J., 1995. The circulation between the Catalan and Balearic currents in the southern Catalan Sea. Oceanologica Acta 18: 227–234.

Shiganova, T. A. & A. Malej, 2009. Native and non-native ctenophores in the Gulf of Trieste, Northern Adriatic Sea. Journal of Plankton Research 31: 61–71.

Shiganova, T. A., Z. A. Mirzoyan, E. A. Studenikina, S. P. Volovik, I. Siokou-Frangou, S. Zervoudaki, E. D. Christou, A. Y. Skirta & H. J. Dumont, 2001. Population development of the invader ctenophore *Mnemiopsis leidyi* in the Black Sea and other seas of the Mediterranean basin. Marine Biology 139: 431–445.

Shiganova, T. A., E. D. Christou, J. V. Bulgakova, I. Siokou-Frangou, S. Zervoudaki & A. Siapatis, 2004. Study on the distribution and biology of the invader *M. leidyi* in the northern Aegean Sea, comparison with indigenous species Bolinopsis vitrea. In Dumont, H., T. A. Shiganova & U. Niermann (eds), The Ctenophore *Mnemiopsis leidyi* in the Black, Caspian and Mediterranean Seas and Other Aquatic Invasions. NATO Science Series: IV. Earth and Environmental Sciences, Vol. 35. Kluwer Academic Publishers, Dordrecht: 113–135.

Siapatis, A., M. Giannoulaki, V. D. Valavanis, A. Palialexis, E. Schismenou, A. Machias & S. Somarakis, 2008. Modelling potential habitat of the invasive ctenophore *Mnemiopsis leidyi* in Aegean Sea. Hydrobiologia 612: 281–295.

Spanier, E., & B. S. Galil, 1991. Lessepsian migration: a continuous biogeographical process. Endeavour 15: 102–106.

Sullivan, L. J., & D. J. Gifford, 2004. Diet of the larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). Journal of Plankton Research 26: 417–431.

Sullivan, B. K., D. Van Keuren & M. Claucy, 2001. Timing and size of blooms of the ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, RI. Hydrobiologia 451: 113–120.

Vinogradov, M. E. & E. A. Shushkina, 1992. Temporal changes in community structure in the open Black Sea. Oceanology 32: 485–491.

Vinogradov, M. E., E. A. Shushkina, E. I. Musayeva & P. Y. Sorokin, 1989. A newly acclimated species in the Black Sea: the ctenophore *Mnemiopsis leidyi* (Ctenophora: Lobata). Oceanology 29: 220–224.

Vollmer, S. V. & S. R. Palumbi, 2004. Testing the utility of internal transcribed spacer sequences in coral phylogenetics. Molecular Ecology 13: 2763–2772.

Zviely, D., E. Kit & M. Klein, 2007. Longshore sand transport estimates along the Mediterranean coast of Israel in the Holocene. Marine Geology 238: 61–73.