Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) from a native to an exotic species: a review

J. H. Costello · K. M. Bayha · H. W. Mianzan · T. A. Shiganova · J. E. Purcell

Abstract The genus *Mnemiopsis* is comprised of a single species, *Mnemiopsis leidyi* A. Agassiz, 1865, that has recently made the transition from a distribution limited to the Atlantic coasts of North and South America to an invasive range that includes the Black, Caspian, Mediterranean, North, and Baltic seas. We review the foundations of the ctenophore's invasive success, which include the source-sink dynamics that characterize *Mnemiopsis* populations in temperate coastal waters where the ctenophore achieves its highest biomass levels and ecosystem impacts. Within its native temperate range, *Mnemiopsis* is frequently a dominant, seasonal, colonizing species with limited dispersal capacities. Cross-oceanic transport within ballast waters of intercontinental shipping vessels has altered this dispersal limitation and initiated a rapid global spread of *Mnemiopsis*. Owing to continuing transport via transoceanic shipping, we anticipate continued range expansion and review the variables most likely to determine whether introduction of *Mnemiopsis* to a novel community results in an inconspicuous addition or a disruptive invasion.

Keywords Invasion · Source-sink · Ballast transport · Niche flexibility · Range expansion

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Introduction

The lobate ctenophore, *Mnemiopsis leidyi* A. Agassiz, 1865, has an established record of ecological importance within its native range, but has most recently gained notoriety for its expansion into exotic habitats (reviewed in Purcell et al., 2001). Before the invasion of the Black Sea, there was little discussion of the invasive capabilities of *Mnemiopsis*. Yet this ctenophore has proven to be a highly successful invader and, consequently, the future of its expansion is an important issue for marine planktonic communities. Our goal here is to examine the factors promoting and limiting invasive success of *Mnemiopsis* in order to

review its potential for continued ecological range expansion.

Time course of invasive introductions

Range expansion of *Mnemiopsis* came into focus after the ctenophore was introduced to the Black Sea and surrounding areas (Vinogradov et al., 1989; Studenikina et al., 1991; Shiganova, 1993; Shiganova et al., 2001b; Shiganova & Malej, 2009) where fisheries' collapses and ecosystem disruptions were reported to be related to the introduction (Kideys, 2002; Knowler, 2005; Oguz et al., 2008). *Mnemiopsis* apparently was first transported accidentally in ballast water to the Black Sea (Ghabooli et al., 2010; Reusch et al., 2010). The ctenophores were first found in Sudak Bay in November, 1982 (Pereladov, 1988). By summer–autumn 1988, it had spread throughout the Black Sea, with average biomasses of up to 1 kg WW m^{-2} (40 g WW m^{-3}) and average numbers of up to 310 ctenophores m^{-2} (12.4 m^{-3}) (Vinogradov et al., 1989). Subsequently, *Mnemiopsis* moved through straits to adjacent basins (Fig. 1). It was first observed in the Sea of Azov in August, 1988 (Studenikina et al., 1991). Because *Mnemiopsis* cannot survive the winter low temperatures in the Sea of Azov, it must be reintroduced annually through the Kerch Strait from the Black Sea. The *Mnemiopsis* population spread from the Black Sea in the upper Bosporus current into the sea of Marmara, where it occurs all year in the upper water layer. It proceeded from the Sea of Marmara to the Mediterranean Sea, where it was first recorded in 1990 in the Aegean sea (Shiganova et al., 2001b). In subsequent accidental introductions, the ctenophore was transported from the Black Sea to the Caspian Sea in 1999 (Ivanov et al., 2000; Shiganova et al., 2001b) and from the northwestern Atlantic to the North and Baltic seas, where they were first reported in 2006 (Faasse & Bayha, 2006; Javidpour et al., 2006; Ghabooli et al., 2010; Reusch et al., 2010). It subsequently became apparent that *Mnemiopsis* was widely distributed in those waters (Hansson, 2006; Tendal et al., 2007; Schaber et al., 2011a, b).

Within the Mediterranean Sea, *Mnemiopsis* rapidly spread from the Aegean Sea to adjacent waters of the eastern Mediterranean (Levantine Sea), where it was found in Mersin Bay in spring 1992 (Kideys & Niermann, 1994) and in Syrian coastal waters in October 1993 (Shiganova, 1997). Until recently, *Mnemiopsis* was not reported from new locations in the Mediterranean. It was reported in the Northern Adriatic Sea in 2005 and from coastal waters of France in 2006 (Shiganova & Malej, 2009). Siapatis et al. (2008) developed a predictive model based on environmental conditions and water depth to identify the potential habitats of *Mnemiopsis* in the Mediterranean basin. Their model showed that many regions within the Mediterranean were potentially viable habitats for *Mnemiopsis* invasion. In 2009, blooms of *Mnemiopsis* were reported in waters of Israel (Galil et al., 2009; Fuentes et al., 2010), Italy (Boero et al., 2009), and Spain (Fuentes et al., 2010). *Mnemiopsis* from these locations genotypically resembled those from the northern Gulf of Mexico and the Black Sea (Fuentes et al., 2010). Both currents and shipping are probable methods of transport of *Mnemiopsis* within the Mediterranean Sea (Fuentes et al., 2010).

An uncorroborated report of *Mnemiopsis* came from the Indian Ocean (Sai Sastry & Chandramohan, 1989), while a more recent report, corroborated with photographs, comes from the Australian coast (Bayha, pers. obs.; Fig. 1). These reports are early indicators of *Mnemiopsis* presence in those regions but do not include biomass distributions or ecological interactions.

Genetic and physiological identity of *Mnemiopsis leidyi* global distributions

Knowledge of the specific identity of *Mnemiopsis* is an important starting point in order to insure that comparisons from different locations involve the same species. However, the taxonomic history of the genus over the past two centuries has been complicated and requires clarification regarding the true species diversity in the genus. Ctenophores closely resembling *Mnemiopsis* along the eastern coastline of the Americas have been described as three different genera: *Mnemia* (Eschscholtz, 1825), *Alcinoe* (Rang, 1828; Mertens, 1833) and *Mnemiopsis* (Agassiz, 1860, 1865; Mayer, 1900). While three *Mnemiopsis* species (*M. gardeni* L. Agassiz, 1860, *M. leidyi*, and *M. mccradyi* Mayer, 1900) are currently taxonomically valid (Cairns et al., 2002), *M. leidyi* and *M. mccradyi* are the only two species recognized in the recent literature (Harbison & Volovik, 1994). The species descriptions indicate that *M. leidyi* occurs north of Charleston,

Fig. 1 Contemporary global distribution and average peak biomass of *Mnemiopsis leidyi*. *Top* global distribution with *blue circles* representing native range, *red circles* representing the invasive range. *Orange circles* represent invasive locations for which no ctenophore biomass estimate is available. *Bottom* Latitudinal range of average peak biomass levels. *Colors* represent the same data points as in the *top panel*. (Color figure online)
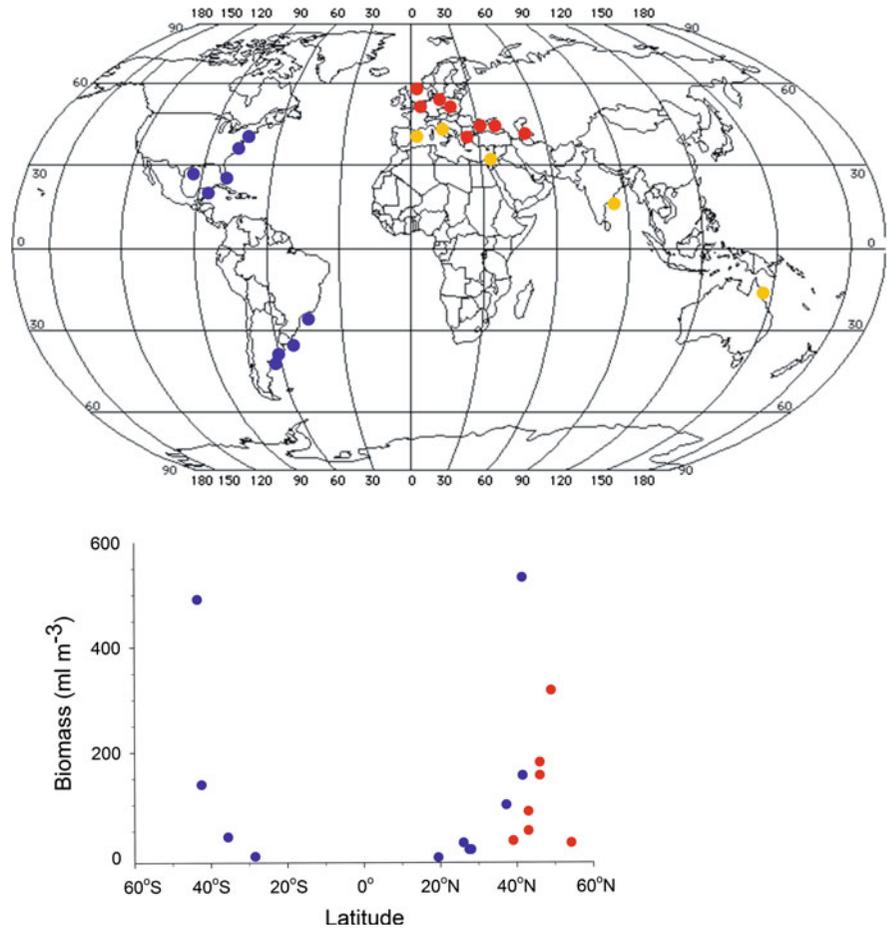
South Carolina, USA and *M. mccradyi* occurs from there south (Agassiz, 1865; Mayer, 1900); however, the main morphological character delineating the two species, the presence of papillate warts in *M. mccradyi*, was not in the original description (Mayer, 1900), but added later (Mayer, 1912). Harbison & Volovik (1994) and Seravin (1994a, b) effectively encapsulated doubts in the field regarding the establishment of two separate *Mnemiopsis* species, with Seravin (1994a, b) declaring *Mnemiopsis* to be monospecific, albeit-based solely on the examination of invasive animals in the Black Sea. Because the original invasive animals in the Black sea were initially identified alternatively as *M. mccradyi* (Zaika & Sergeeva, 1990) or *M. leidyi* (Vinogradov et al., 1989), the actual identity of ctenophores described in exotic regions has remained problematic. Taxonomic uncertainties in the Baltic sea (Gorokhova et al., 2009; Gorokhova & Lehtiniemi, 2010; Javidpour et al.,

2010) have underscored the importance of resolving species identification.

Although taxonomic conclusions based on morphological studies have indicated multiple species of *Mnemiopsis*, none of the genetic studies performed on *Mnemiopsis* to date have revealed evidence of more than one *Mnemiopsis* species (Bayha, 2005; Ghabooli et al., 2010; Reusch et al., 2010). While there is no standard for what degree of genetic variation separates species, in the absence of morphological data or when an animal's morphology renders morphological species delineation questionable, a common practice is to compare the genetic divergence between two specimens with that between recognized species of similar taxa (Schroth et al., 2002; Dawson, 2004). This technique has been especially prevalent with gelatinous zooplankton (Dawson & Jacobs, 2001; Bayha et al., 2004; Miranda et al., 2010) and, for species other than *Mnemiopsis*, genetic studies have indicated

significantly greater species diversity than was revealed based on morphology (Dawson & Jacobs, 2001; Bayha et al., 2004; Holland et al., 2004).

As of date, three studies have surveyed sequence divergence in the nuclear ribosomal internal transcribed spacer regions (ITS) to examine species diversity in *Mnemiopsis*. None of those studies found extensive sequence divergence among any of the worldwide populations that would be indicative of multiple species (Bayha, 2005; Ghabooli et al., 2010; Reusch et al., 2010). Given the extremely low divergence found among ctenophores for ribosomal genes (Podar et al., 2001), small divergence values would be expected, but Bayha (2005) showed that values were significantly lower than that found in other ctenophores. Additionally, sequence divergence values in *Mnemiopsis* cytochrome *b* (cyt*b*) also were lower than what is typically seen between invertebrate species, including other ctenophores (Bayha, 2005). In addition to indicating that *Mnemiopsis* is monospecific, all three genetic studies indicated that the invasive populations originated from the NW Atlantic, with the Black/Caspian population(s) from the vicinity of the Gulf of Mexico area (Bayha, 2005; Ghabooli et al., 2010; Reusch et al., 2010) and the northern European populations(s) from the northeastern coast of the USA (Reusch et al., 2010; Ghabooli et al., 2010; Fig. 2). These studies are consistent with the conclusion that only one species of *Mnemiopsis* occurs worldwide and that any morphological differences observed among native or invasive regions can be attributed to phenotypic plasticity.

Physiological evidence is also consistent with a monospecific identity of *Mnemiopsis* occupying diverse geographical regions. Comparisons between species previously described as *M. mccradyi* and *M. leidyi* revealed that physiological rates, including respiration, excretion, egg production, feeding, and growth, were indistinguishable at comparable conditions between the putative species (Kremer, 1994). Just as comparisons between populations within the endemic range of *Mnemiopsis* have yielded similar physiological patterns under comparable conditions, so also have comparisons between endemic and invasive populations indicated similar physiological patterns under comparable conditions. As a consequence, physiological traits of both endemic and invasive *Mnemiopsis* populations overlap to the extent that they are indistinguishable (Purcell et al., 2001).

These results suggest that the phenological and ecological variations found between regions reflect flexible responses of one species to a range of environmental conditions. Importantly, a monospecific view of *Mnemiopsis* allows evaluation of data from variable locations to be used for examination of broad patterns within a flexible, but single, species.

Population dynamics: the source-sink perspective

Mnemiopsis reaches its maximal biomass and ecological impact in temperate latitudes. Within its native range along the North and South American Atlantic coasts, the average values of peak seasonal biomass increase with latitude until the middle 40° latitudes both north and south of the equator (Fig. 1). In these regions, *Mnemiopsis* seasonally dominates the planktonic biomass (N. America—Deason, 1982; Condon & Steinberg, 2008; S. America—Mianzan & Guerrero, 2000) and planktonic community structure (Deason & Smayda, 1982; Purcell & Decker, 2005; Sullivan et al., 2008). Likewise, *Mnemiopsis* can dominate temperate planktonic communities within its invasive range (Purcell et al., 2001; Finenko et al., 2006; Shiganova et al., 2001a, b).

Temperate coastal regions vary seasonally between warm spring–fall periods capable of supporting extensive *Mnemiopsis* biomass, and cold winter periods when *Mnemiopsis* is unable to reproduce. During the non-reproductive winter months, *Mnemiopsis* populations cannot replace losses to advective flows with the result that local circulation patterns can flush *Mnemiopsis* populations from large portions of its coastal habitat. Because retention times of coast water systems are often of much shorter duration than *Mnemiopsis* winter non-reproductive periods (Costello et al., 2006a), the winter months can cause local disappearance of *Mnemiopsis* over extensive areas of its temperate range. Seasonal elimination from areas has important implications for *Mnemiopsis* distributions because *Mnemiopsis* is a holoplanktonic species (Fig. 3) with no known benthic resting eggs, cysts, or specialized overwintering stages (Hyman, 1940; Brusca & Brusca, 2003). This contrasts with many coastal jellyfish and copepods (e.g., Sullivan & MacManus, 1986; Marcus & Boero, 1998), which possess either benthic resting eggs or life stages that allow species persistence during periods when the
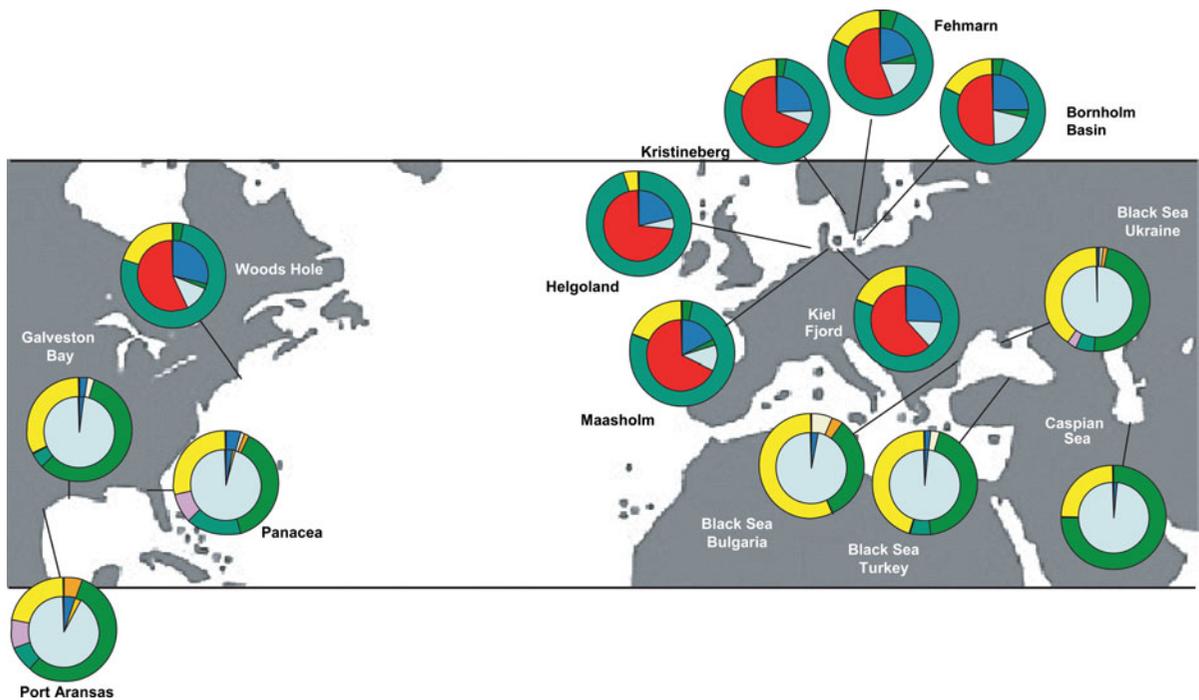
Fig. 2 Sampling locations of *Mnemiopsis leidyi* in their native distribution range along the North American Coast and in exotic locations within Eurasia. *Pie-diagrams* depict allele frequencies of two microsatellite loci that display five alleles (*inner circle*, MnleC1583) and seven alleles (MnleL13, *outer circle*), respectively. Note the overlap in the common alleles which suggests that both gene pools are not completely separated (from Reusch et al., 2010)

adult members of the species are not present in the water column. By contrast, overwintering *Mnemiopsis* populations persist in low advection regions, such as coastal embayments characterized by low water

Fig. 3 Variations in life histories of holoplanktonic genera. *Left* the genus *Acartia* (*black circles* represent resting eggs, *clear circles* represent planktonic eggs). *Right* the genus *Mnemiopsis* (only planktonic eggs)

exchange rates with surrounding areas (Costello et al., 2006a). These regions maintain persistent *Mnemiopsis* populations and are termed source regions (see Hanski (1999) for a discussion of metapopulation dynamics). When favorable temperature and feeding conditions arise during the temperate-zone spring, these overwintering refugia serve as sources for *Mnemiopsis* inocula that seed population growth throughout non-overwintering areas. The latter non-overwintering areas are termed sinks because they do not harbor persistent, reproducing populations. Instead, sink areas are characterized by a regular, annual pattern of local *Mnemiopsis* elimination and require re-inoculation each year to initiate seasonal growth (Fig. 4). Local currents provide the transport mechanism from source to sink regions and the seasonal expansion from source regions, evident as both the rate of *Mnemiopsis* distribution changes and the location of primary reproduction, follows predominant local circulation patterns (Kremer & Nixon, 1976; Deason, 1982; Condon & Steinberg, 2008). The expansion from source regions during favorable environmental periods may encompass multiple sink
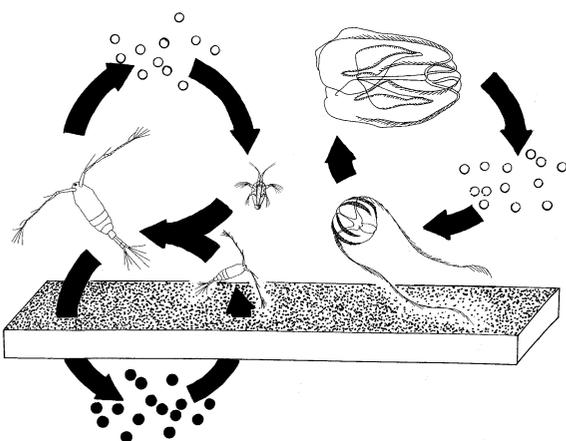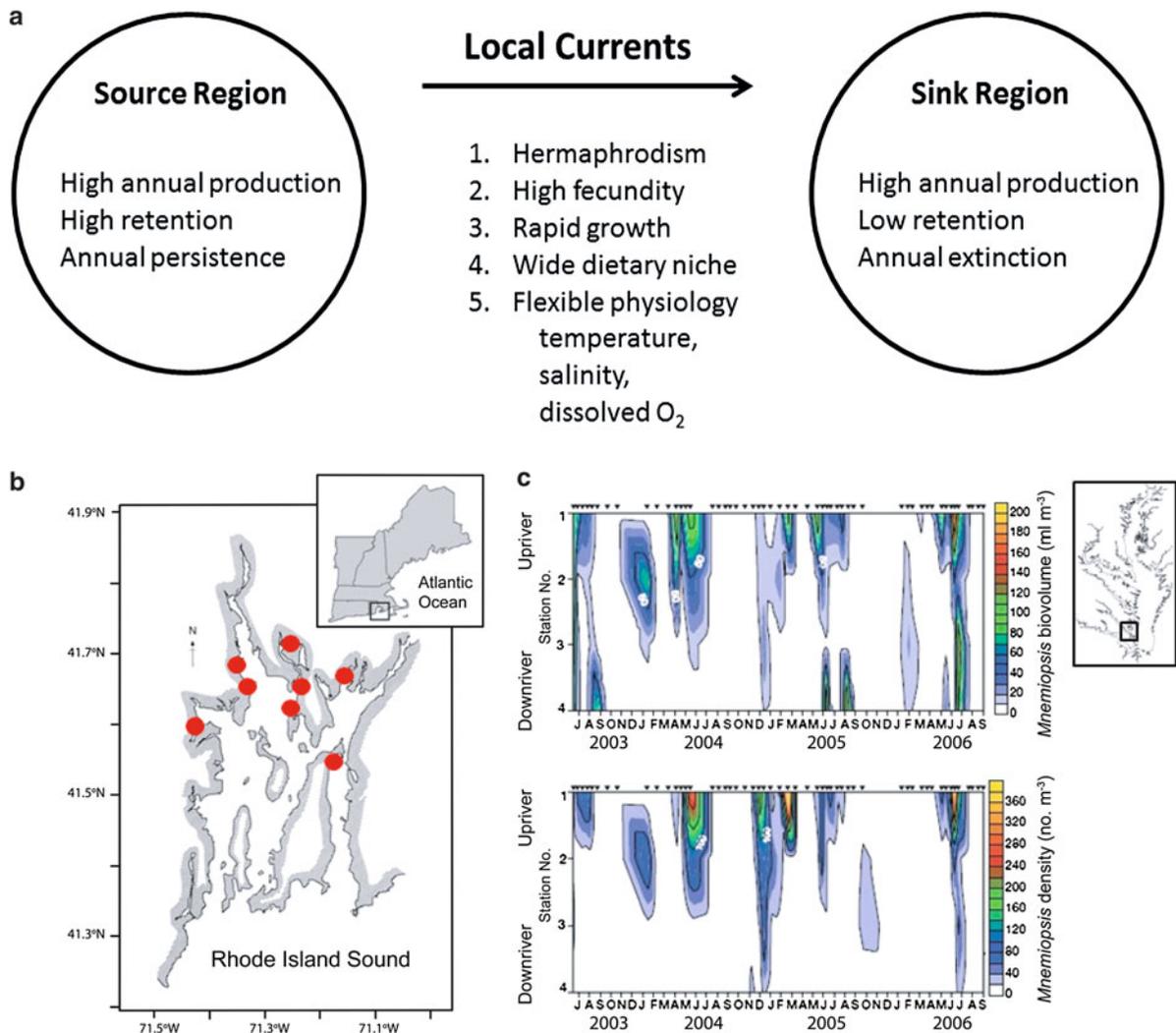
Fig. 4 *Mnemiopsis leidyi* metapopulation patterns. **a** Relationships between source regions and the factors enabling population growth in sink regions following dispersal via local currents. **b** Source regions in the native locale of Narragansett Bay, Rhode Island, USA. *Red dots* indicate embayments bordering the main Bay which can serve as source regions. *Mnemiopsis* populations persisted within these embayments throughout the winter of 2002 while no ctenophores were found within the central Bay during the same time period (Costello et al., unpublished data). **c** Seasonal source-sink distribution patterns within one embayment area, the York River estuary of Chesapeake Bay, USA (site location illustrated by inset panel). *Top* contour plots of average *Mnemiopsis* biomass (biovolume, ml ctenophore m^{-3}) and *bottom* density (no. ctenophores m^{-3}) for four stations plotted along an up-downstream gradient in the York River estuary. Note the predominance of *Mnemiopsis* presence upstream with periodic extensions of ctenophore biomass downstream, toward the estuary's convergence with the greater Chesapeake Bay (from Condon & Steinberg, 2008). (Color figure online)

regions and a large proportion of the total metapopulation range can exist in sink habitats if the source regions are sufficiently productive to subsidize the larger sink regions. The result of these interactions is a dynamic population distribution pattern involving seasonal refugia, current-driven dispersal, rapid population expansion and decline—all occurring within a mosaic of coastal source and sink areas. *Mnemiopsis* has achieved its greatest productivity levels (Fig. 1) with these source-sink population patterns. The dynamic nature of these population fluctuations favor life history traits that enable rapid conversion of plankton to ctenophore biomass under a range of local conditions occurring within temperate, coastal

habitats. The traits evolved by *Mnemiopsis* that have allowed it to successfully navigate these population dynamics affect the ctenophore's success in both native and exotic regions. This leads us to a question— which traits promote, and which constrain, this dynamic life history pattern?

Characteristics promoting the success of *Mnemiopsis* as an invader

Population growth capacities

Mnemiopsis has evolved a suite of life history traits enabling rapid population growth. Simultaneous, self-compatible hermaphrodism (Pianka, 1974; Reeve & Walter, 1978) permits production of fertile larvae by all egg-producing members of the population. Fecundity can be high—frequently in excess of 2,000 eggs ctenophore day^{-1} (Costello et al., 2006a) and as high as 12,000 eggs ctenophore day^{-1} for *Mnemiopsis* taken directly from Narragansett Bay (Baker & Reeve, 1974; Kremer, 1976). Egg production rates of similar magnitude are reported from the Black (Purcell et al., 2001) and Caspian (Finenko et al., 2006) seas. When grown under favorable temperature (15–30°C) and food (>25 µg C l^{-1}) conditions, larvae are characterized by high ratios of growth to metabolism (>2) and high-gross growth efficiencies (>30%) that permit rapid development (Kremer & Reeve, 1989). Generation times can be short and, at favorable temperatures and food levels, eggs can hatch and develop into reproducing adults within 14 days (Reeve & Walter, 1978). High fecundity, rapid growth, and short-generation times are common for colonizing species (Funk & Vitousik, 2007) and important components of the metapopulation dynamics underlying high-biomass production of *Mnemiopsis* in temperate regions (Fig. 4).

Broad physiological tolerance levels

Mnemiopsis has broad physiological tolerances to temperature, salinity, and dissolved oxygen (DO) levels (Purcell et al., 2001; Table 1). Nevertheless, few organisms are unaffected by alterations in physical regime and each physical factor plays an important role modifying *Mnemiopsis* distribution and abundance patterns.

The capacity to tolerate temperatures between 0 and 32°C permits *Mnemiopsis* to occupy a diverse geographical range that includes temperate through tropical marine communities (Harbison et al., 1978; Mianzan, 1999); however, within these broad temperature limits, temperature thresholds affect *Mnemiopsis* population dynamics. Most generally, the upper and lower temperature tolerances determine survival of individuals within habitats. There has been little research on the upper temperature limits of *Mnemiopsis*; however, it occurs in native habitats and now in eastern Mediterranean waters where summer temperatures reach 32°C (Table 1). Importantly, the Q_{10} estimated when temperatures changed seasonally (1.3) were much lower than those determined when temperatures were changed in the laboratory (≥ 3.4) (Purcell, 2009), indicating considerable physiological flexibility within temperature variations characterizing field distributions of *Mnemiopsis*.

The lower temperature limit for *Mnemiopsis* persistence appears to be around freezing. The precise level of the survival temperature threshold varies by region and may depend upon salinity levels. In Narragansett Bay, USA salinities varied between 22 and 33 and *Mnemiopsis* was collected from waters as low as −1°C by breaking holes in surface ice (Costello et al., 2006a); however, at lower salinities in the shallow sea of Azov (surface salinity 0–14), *Mnemiopsis* may not survive below ∼4°C (Purcell et al., 2001). Similarly, in the northern Caspian Sea, *Mnemiopsis* cannot survive when salinity is lower than 4 (Shiganova et al., 2004b). *Mnemiopsis* populations disappear in the Sea of Azov when water temperatures become colder than 3°C (Shiganova et al., 2001b, 2003). These reports indicate that low-salinity levels can adversely impact winter survival of *Mnemiopsis* populations.

A second temperature threshold directly affects *Mnemiopsis* population growth—the reproductive temperature threshold. Purcell et al. (2001) reported egg production of *Mnemiopsis* from Chesapeake Bay to occur between the temperatures of 12–29°C and results from Costello et al. (2006a) in Narragansett Bay broadly match those results (Fig. 5), with minor egg release at temperatures as low as 6°C. Conservatively, we expect that 10°C is an approximate lower temperature threshold for successful egg production by a developing *Mnemiopsis* population and egg production rates increase with higher temperatures,

Table 1 Comparison of systems over the native and invaded range of *Mnemiopsis leidyi*

Location	Native or invaded (year)	Temp. (°C)	Salinity	Predators	Zooplankton biomass or density (mg C or no. m⁻³)		Ctenophore biomass or density (mg C, ml WW, or no. m⁻³)			Reference
					Peak season	Range	Peak (present)	Range	Years (No.)	
Narragansett Bay, RI	Native	1–25	25–32	*Beroe*	June–July	30–110 C[a]	August–September (Spring–Fall)	6-100 C	>8	Hulsizer (1976), Kremer (1976), Kremer & Nixon (1976), Durbin & Durbin (1981), Deason (1982), Deason & Smayda (1982), Smayda (1988)
Mid Chesapeake Bay, MD	Native	2–30	5–16	Bay group	Summer	30–180 C[b]	June–September (all year)	10–100 C	16	Lonsdale (1981), Olson (1987), Purcell et al. (1994)
Biscayne Bay, FL	Native	18–32	14–45	*Beroe*	Fall to Winter	11 C[c]	Fall (all year)	ND	1+	Baker (1973)
Nueces Estuary, TX	Native	7–31	20–38		Variable	50 C	Summer (all year)	8–20 C	1	Buskey (1993)
Rio de la Plata estuary, ARG	Native	7.5–25	9–24	Several fish species	Spring	37 C	Spring	2–15 C	1	Mianzan et al. (1996), Sorarrain (1998)
Blanca bay, ARG	Native	5–24	24–38	*Beroe*	Spring–Summer	40,000 m⁻³	Spring and Fall	ND	3	Mianzan & Sabatini (1985), Mianzan (1986)
Nord Patagonic Tidal front, ARG	Native	10–16	33	Several fish species			Summer	140 ml	1	Mianzan et al. (1996, 2010), Mianzan pers. Obs
Black Sea (before *Beroe* arrival)	Invaded 1982	0–27	12–22	*Beroe*	March–May; July–August	33,000 m⁻³ [d]; 243–418 mg m⁻³	All year	0.5–130 C	12	Purcell et al. (2001), Shiganova & Malej (2009)
Sea of Azov (before *Beroe* arrival)	Invaded 1988	−0.8 to 30	0–14	*Beroe*	May–June; July–August	350–390 mg m⁻³	Spring–Fall	67–143 C	12	Shiganova et al. (2001b), Shiganova & Malej (2009)
Northern Caspian	Invaded 1999	0–28	0.1–11	No indigenous gelatinous predators	April–May; July–August	289 ± 296 mg WW m⁻³	August–November	0.32–105 C	7–8	Shiganova et al. (2004b)
Middle		0–25	12.6–13			37.6 ± 58 mg WW m⁻³	June–November			
Southern Caspian		10–30	12.6–13		July; September–October	66 ± 72 mg WW m⁻³	All year			
Sea of Marmara	Invaded	8–29	18–29	*Beroe*			All year		11	Shiganova et al. (2001b)

Table 1 continued

Location	Native or invaded (year)	Temp. (°C)	Salinity	Predators	Zooplankton biomass or density (mg C or no. m⁻³)		Ctenophore biomass or density (mg C, ml WW, or no. m⁻³)			Reference
					Peak season	Range	Peak (present)	Range	Years (No.)	
Aegean Sea	Invaded 1990	13–29	33–40	Med group	Spring; Summer	0.8–6 mg DW m^{-3}	All year	0.1–20	11	Shiganova et al. (2004a)
Turkey (Mediterranean coast)	Invaded 1992	23–24	~38	Med group	Summer	0.02 ml m^{-3}	ND			Kideys & Niermann (1994)
Gulf of Trieste	Invaded 2005	10–26	32–38	Med group		3.6–9 C	Not established			Shiganova & Malej (2009)
France	Invaded 2006	?–31.5	39.5	Med group			ND		4	Shiganova & Malej (2009)
Catalan Sea	Invaded 2009	12–26	37–39	Med group	Spring; Fall	500–8000 m^{-3} d	Spring			Fuentes et al. (2010)
Italy	Invaded 2009	13–26	37.5–38	Med group		500–4000 m^{-3} d	ND			Boero et al. (2009)
Israel	Invaded 2009	16–32	39–40	Med group		0–2598 m^{-3}	ND			Fuentes et al. (2010)
North Sea Helgoland	Invaded 2006	7–14	~36	N Sea group	Spring–Summer	<40,000 m^{-3} d	ND	<0.3	3	Greve et al. (2004), Hamer et al. (2011)
Baltic Sea Limfjorden	Invaded 2006	5–15	32–19	N Sea group	Summer	<250 C	Summer	<80 C	3	Riisgård et al. (2012), Javidpour et al. (2009b), Schaber et al. (2011a)
Kiel Bight		5–17	11–22	N Sea group	Spring	<2 C	Spring–Fall (all year)	<75 C		

Bay Group = *Chrysaora quinquecirrha*, *Beroe ovata*, *Cyanea capillata* (Linnaeus)

Med. group = *Beroe cucumis* Fabricius, *Beroe forskalii* Milne Edwards, *Chrysaora hysoscella* Eschscholtz, *Pelagia noctiluca* (Forsskål) *Aequorea forskalea* Peron & Lesueur

N Sea group = *B. ovata*, *C. capillata*, *C. hysoscella*, *Aequorea vitrina* Gosse

C carbon, *ND* no data

[a] >153 µm fraction, assuming C = 35%DW, or 1 ml displacement volume = 60 mg C (Kremer 1994)

[b] Converted from counts assuming 3 µg C per copepodite or adult (Kremer 1994)

[c] >202 µm fraction, assuming C = 35%DW (Kremer 1994)
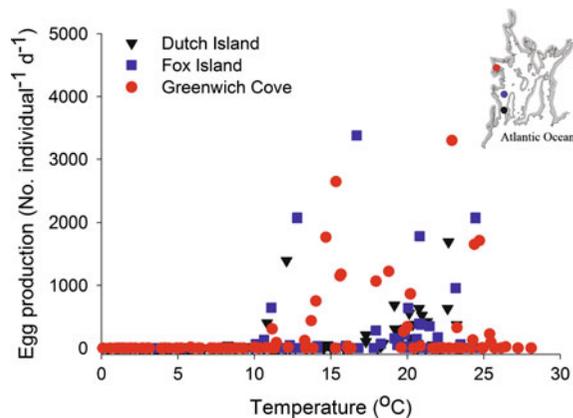
[d] Before *Mnemiopsis*

Fig. 5 Egg production by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay during weekly sampling between the years 2001–2003. *Circles* of *different color* represent sites of *similar color* on the station map of Narragansett Bay, *upper right corner of figure* (from Costello et al., 2006a)

with maxima occurring between 15 and 30°C (Fig. 5; Purcell et al., 2001). These data also suggest several important relationships between temperature and *Mnemiopsis* population growth. First, optimal temperatures are a necessary but insufficient condition for *Mnemiopsis* population growth. Temperatures in the reproductive range of *Mnemiopsis* alone are not effective predictors of population growth; many sampling dates with adequate temperatures supported little or no egg production by *Mnemiopsis* field populations (Fig. 5; Purcell et al., 2001). Likewise, many regions with favorable temperature regimes in the subtropics and tropics do not generally support high *Mnemiopsis* biomass levels (Table 1; Fig. 1). Instead, favorable temperature levels may be viewed as a condition that permits high-population growth, but only when combined with sufficient prey concentrations and limited predation pressure (Kremer, 1994; Purcell et al., 2001). Second, during several months of the year, temperatures of temperate zone waters are below the reproductive threshold for *Mnemiopsis*. As noted previously, this affects annual distribution patterns and overwintering survival of *Mnemiopsis* populations. Third, climate change is altering the annual duration of this overwintering period in temperate waters. The number of days per year that are too cold for *Mnemiopsis* reproduction has decreased in recent years (Fig. 6a), and the coastal areas most affected by this climactic trend are inshore embayments that serve as *Mnemiopsis* source regions

(Fig. 6b). One result of this trend is that *Mnemiopsis* population growth may now often begin earlier and persist longer on a seasonal basis in temperate coastal systems than during previously recorded periods (Costello et al., 2006b; Condon & Steinberg, 2008).

Mnemiopsis also has extremely wide salinity tolerances, from nearly freshwater to hypersaline lagoons (Table 1). A recent physiological study showed *Mnemiopsis* to be a hyper-osmoconformer (Yazdani Foshtomi et al., 2007). Its broad salinity tolerance has several important effects. First, it created confusion about identification of *M. leidyi*, which generally lacks warts in low-salinity environments (*M. leidyi*) but is firmer-bodied and generally has warts in high-salinity environments (mistakenly called *M. mccradyi*). Second, because dry weights (DWs) of *Mnemiopsis* reflect the salinity of its environment, physiological rates standardized by DW can appear to differ widely among habitats; thus, standardization by DW should be avoided and salinities should always be reported (Purcell, 2009). Third, its wide salinity tolerance allows the ctenophores to extend from offshore regions into embayments that experience wide fluctuations influenced by rain and runoff (Table 1; Kremer, 1994; Purcell et al., 2001). These low-salinity habitats serve as important refuges from less-euryhaline predators, such as *Chrysaora quinquecirrha* Desor, 1848 and *Beroe* spp. Gronov, 1760 (Purcell et al., 2001). This physiological flexibility has led to a perception that *Mnemiopsis* populations are not constrained by salinity variations (Reeve et al., 1989; Kremer, 1994; Purcell & Decker, 2005). However, although *Mnemiopsis* has wide salinity tolerances, low salinities can lead to reduced low-temperature survival, smaller maximum body size (Purcell et al., 2001), and decreased reproductive success (C. Jaspers, pers. comm.).

The capacity to function over a wide range of DO concentrations is an additional physiological trait with important adaptive advantages for *Mnemiopsis*. Low DO concentrations generally occur in shallow marine systems during summer months when water column stratification limits mixing and aeration of bottom waters. A variety of coastal mesoplankton are adversely affected by low O_2 levels (<3 mg O_2 l^{-1}), but *Mnemiopsis* is tolerant of low DO levels. *Mnemiopsis* feeding rates on copepods are undiminished at low DO levels and such large, lobate ctenophores actually experience elevated clearance rates in low DO
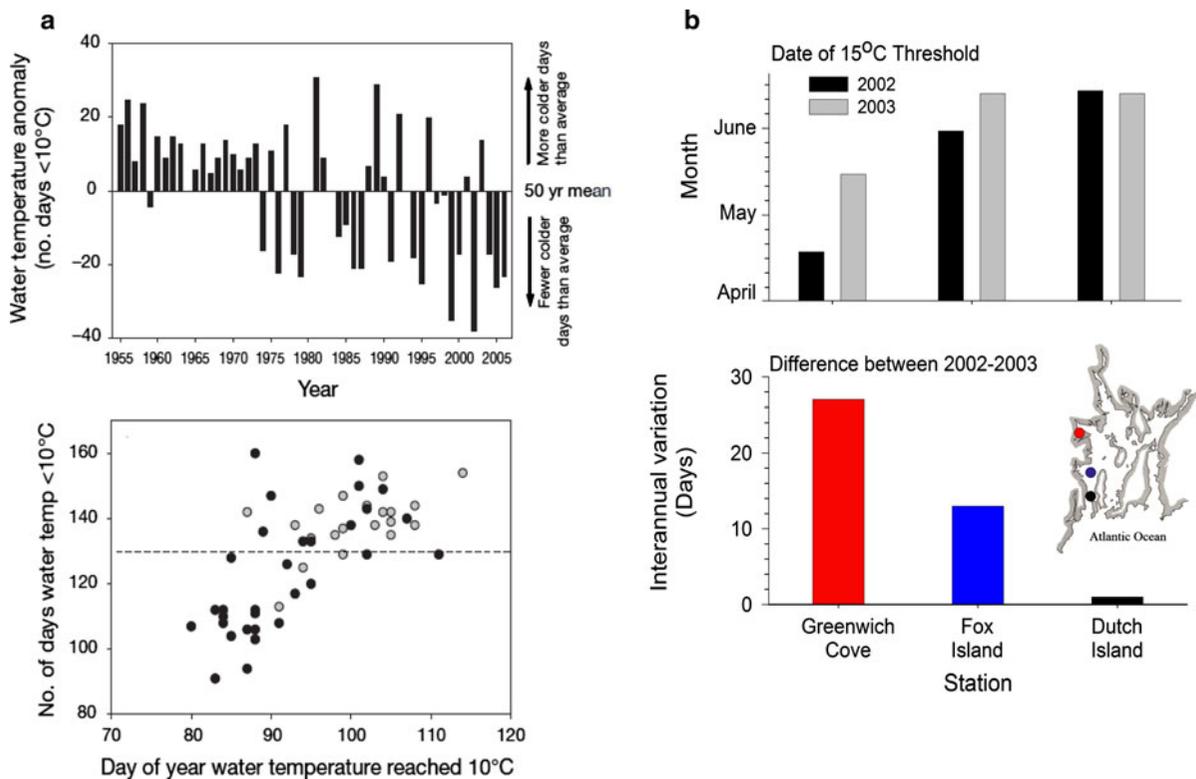
Fig. 6 The impact of climate change on threshold temperatures for *Mnemiopsis leidyi* population growth in North American, temperate habitats in the ctenophore's native range. **a** Warming temperatures in the York River estuary of Chesapeake Bay. *Upper left panel* comparison of water temperature anomaly from 1955 to 2006 against 50 year mean. York River water temperature anomaly was defined as the number of days per year winter–spring water temperatures were <10°C, minus the 50 year annual mean. Negative anomalies reflect increased water temperatures over the winter–spring period. *Lower left panel* Frequency of cold days (<10°C) in relation to when water temperature increased to and remained above the 10°C threshold (*x*-axis). Note the recent trend toward years with earlier warming and consequently fewer cold (<10°C), non-reproductive days. *Grey circle* 1955–1974; *black circle* 1975–2006; *dotted line* 50 year mean of the water temperature anomaly (from Condon & Steinberg, 2008). **b** Amplification of temperature warming within shallow embayments of Narragansett Bay, USA. *Upper right panel* date at which the 15°C threshold was reached during the spring months of 2002 and 2003 for three stations in Narragansett Bay (station locations illustrated by colored points of inset map). *Lower right panel* the advance, in days, of the 15°C threshold in the warm spring of 2002 relative to the colder spring of 2003. Note that whereas the timing of warming at the seaward-most station is relatively unaffected between years, the shallow embayment at Greenwich Cove is strongly affected. Greenwich Cove is a *Mnemiopsis* source population location (from Costello et al., 2006a)

conditions (Decker et al., 2004). Large (but not small) *Mnemiopsis* had lower growth and egg production in low DO concentrations (1.5 and 2.5 mg O_2 l^{-1}) than in saturated DO (Grove & Breitburg, 2005). Clearance rates of *Mnemiopsis* on fish eggs and larvae were the same at low- and high-DO concentrations (1.5 and 7.0 mg O_2 l^{-1}), and ctenophore densities were high in the bottom layer even in low DO (Kolesar et al., 2010). Tolerance to low DO levels provides *Mnemiopsis* a predatory advantage over prey experiencing impaired escape performance in low DO and a competitive advantage over zooplanktivorous fish with similar diets and higher sensitivity to hypoxia (Purcell et al., 2007). Thus, tolerance of hypoxia is a beneficial trait that enables *Mnemiopsis* to inhabit highly eutrophic coastal habitats.

Wide dietary niche

Dietary flexibility allows *Mnemiopsis* to exploit a variety of planktonic food sources, including micro-plankton, mesozooplankton, and ichthyoplankton, in environments characterized by diverse assemblages. The annual population growth cycle of *Mnemiopsis* in

temperate waters of its native range involves transitions between regions characterized by different spectra of available prey. For example, in Narragansett Bay, USA, overwintering embayments are often highly productive environments (Fig. 7a), with more diverse metazoan planktonic assemblages than the central Bay regions. Whereas copepods typically dominate the mesozooplankton assemblages in the more central Bay waters (Fig. 7b), a variety of invertebrate larvae and other groups (e.g., molluscs, barnacles, polychaetes, ascidian larvae, rotifers) can numerically predominate in shallow embayments so that copepods may be a minority of prey encountered (Fig. 7c) by ctenophores in these embayments. The flexible feeding capacity of *Mnemiopsis* allows it to successfully exploit the variety of prey environments encountered during the regular annual population expansion cycle from embayments to the central Bay. A result of this dietary flexibility is that *Mnemiopsis* ingestion patterns vary widely depending upon the available prey and, consequently, these variations are reflected in the literature on *Mnemiopsis* (Table 2). Although characteristic of *Mnemiopsis* feeding patterns in its native environment, dietary flexibility is also an essential trait associated with invasive success by introduced species (Caut et al., 2008; Zhang et al., 2010).

The dietary breadth of *Mnemiopsis* is, however, life-stage dependent. Eggs are small, about 0.3 mm in diameter and the cydippid larval stage that hatches from an egg is of similar small dimensions and possesses delicate tentacles (Fig. 8) used for prey capture. The small size and low organic structure of newly hatched larvae render their tentacles vulnerable to physical damage during encounters with larger, more powerful metazoan prey (Greve, 1977; Stanlaw et al., 1981). Although all sizes of cydippid larvae are capable of capturing nauplii of the copepod *Acartia tonsa*, encounters of cydippid larvae less than 0.65 mm diameter with *A. tonsa* nauplii (NI–NII) often result in loss of the delicate cydippid tentacles. For small larvae (0.3–2.0 mm diameter), retention of nauplii was related to cydippid diameter (Waggett & Sullivan, 2006). Larger than 2.0 diameter, *Mnemiopsis* larvae retain copepod nauplii effectively (~90%) and larvae >2.5 mm retained >60% of *A. tonsa* copepodites. During the earliest cydippid stages, ingestion of a wide array of protists including both autotrophic and heterotrophic prey—diatoms,
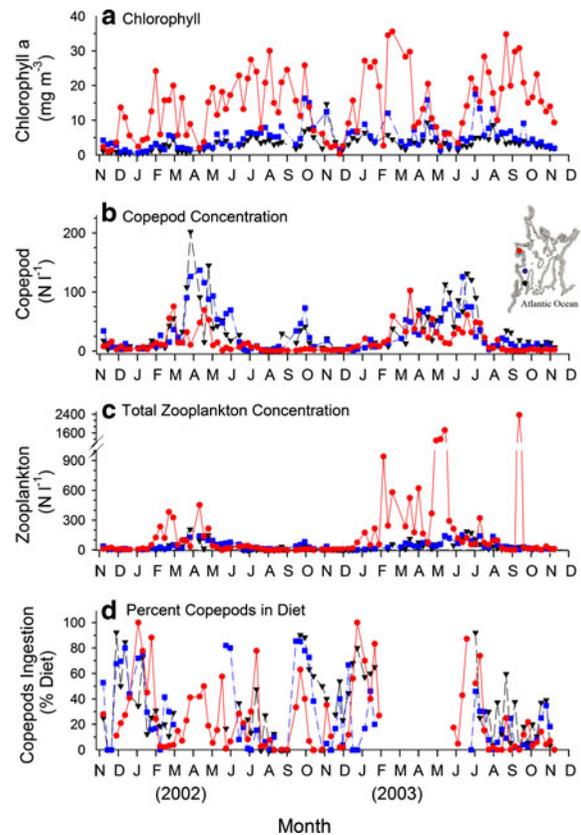

Fig. 7 Variation in plankton community composition and diet of *Mnemiopsis leidyi* at three locations (locations shown by colors within *inset* of panel **b**) during 2 years in Narragansett Bay, USA. The three sites possessed different **a** chlorophyll biomass, **b** different relative proportions of copepods and **c** other types of zooplankton. Note that diet composition, measured as the (**d**) proportion of the diet comprised of copepods, often varied between sites within Narragansett Bay on the same sample dates. Samples from different sites were taken within a 4 h period on each sample date (**a–c** from Costello et al., 2006a; **d** from Costello et al., unpublished)

dinoflagellates, euglenoids, aloricate, and tintinnid ciliates—are an important nutritional resource for *Mnemiopsis* (Sullivan & Gifford, 2004). These prey do not mechanically damage the cydippid larvae and provide a safe nutritional alternative to more powerful metazoan plankton. Immediately upon hatching, cydippid larvae begin consuming protistan microplankton. Protistan microplankton at densities representative of temperate coastal waters can provide sufficient nutrition for growth up to approximately 5 mm in diameter (Sullivan & Gifford, 2007), at which size *Mnemiopsis* begins the morphological transition to the lobate phase (Rapoza et al., 2005).

Table 2 *Mnemiopsis leidyi* prey ingestion based on in situ gut contents from various geographical locations

Site	Dominant prey	Reference
Indian River estuary, FL, USA	Copepod nauplii, barnacle nauplii, mollusc veligers, A*cartia* sp. adults & copepodites, *Oithona* sp.	Larson (1987)
Narragansett Bay, RI, USA	Copepod nauplii, *Acartia* sp. adults & copepodites, mollusc veligers, barnacle nauplii, rotifers	Newton et al., (2009)
Barnegat Bay, NJ, USA	Mollusc larvae, invertebrate larvae	Nelson (1925)
Woods Hole, MA, USA	*Acartia* sp. adults & copepodites, copepod nauplii, mollusc larvae, cladocera (*Penilia* sp.)	Rapoza et al. (2005)
Northern Black Sea, summer	Copepods (mainly A*cartia* sp. and *Calanus* sp.), *Penilia* sp., copepod nauplii, mollusc veligers, barnacle cyprids	Tzikhon-Lukanina et al. (1991)
Northern Black Sea, summer	Cladocerans, mollusc veligers, copepods, appendicularians, tintinnids, cyprid, gastropod and polychaete larvae, fish eggs	Zaika & Revkov (1998)
Southern Black Sea, summer	Copepods (mainly *Acartia* sp. and *Calanus* sp.), *Oithona* sp., *Pseudocalanus* sp., *Paracalanus* sp.	Mutlu (1999)
Southern Black Sea, winter	Copepods (*Acartia* sp., *Pseudocalanus* sp., *Calanus* sp., *Oithona* sp., mollusc larvae	Mutlu (1999)
Kiel Bight, Baltic Sea	Barnacle nauplii, copepods (*Acartia* sp., *Pseudocalanus* sp.), cladocera, scyphozoan planula larvae, ctenophore larvae	Javidpour et al. (2009a)
Gullmar Fjord, Baltic Sea	Tintinnids, appendicularians, *Penilia* sp., *Acartia* sp., copepodites, copepod nauplii, mollusc veligers, dinoflagellates, *Sagitta* sp.,	Granhag et al. (2011)

Capture and ingestion of protists continues throughout development of the lobate stage, but the transition from cydippid to lobate forms entails a dramatic broadening in diversity of metazoan prey consumed (Fig. 9). Small prey continue to be ingested by lobate *Mnemiopsis*, but probably are not a substantial nutritional source for larger lobate stages (Stanlaw et al., 1981). Although ingestion of metazoan prey has been the primary focus of *Mnemiopsis* trophic impacts (e.g., Table 2), microzooplanktonic feeding by *Mnemiopsis*, particularly larvae, may play an important role in microzooplankton dynamics when larvae are abundant (Stoecker et al., 1987; Sullivan & Gifford, 2004). Unfortunately, the short digestion times (2–6 min for copepod nauplii, <2 min for aloricate ciliates; Sullivan, 2010) make ctenophore feeding on microzooplankton difficult to quantify using conventional in situ gut content methods.

The wide dietary breadth of lobate stage *Mnemiopsis* is based on structurally simple but functionally complex feeding mechanisms. The simple component of the feeding system is the structural basis of encounter with prey. Prey entrained within a relatively uniform, laminar feeding current (Fig. 10) that provides transport to two major capture surfaces—the tentillae and the inside surfaces of the oral lobes. The

functional elegance of the *Mnemiopsis* feeding system relies upon the matching of feeding current hydrodynamic traits with the sensory systems of zooplankton prey. Slowly swimming and low mobility prey (e.g., many larvae of crustaceans, molluscs, invertebrates, and fish eggs) are simply entrained in the feeding current and collected by sticky colloblasts on the tentillae (Waggett & Costello, 1999; Waggett & Buskey, 2006) and transported to the mouth via ciliary currents within a food groove (Main, 1928; Moss et al., 2004). Larger prey with sophisticated sensory and escape capabilities (e.g., copepods and fish larvae) are also entrained in the flows but are usually unresponsive to transport within these flows until the prey are surrounded by the ctenophore's lobes and escape probabilities are greatly reduced (Costello et al., 1999). The inability of prey to detect their transport prior to capture is due to the low-shear profiles of the feeding current flows generated by *Mnemiopsis* (Fig. 11). Prey, such as copepods, do eventually detect the presence of stronger shear gradients adjacent to the ctenophore's body, but attempted escape by these prey usually entails contact with the sticky inner oral lobe surfaces where the prey are captured by the ctenophore. The unique combination of morphological structure and hydrodynamic stealth allows *Mnemiopsis* a dietary
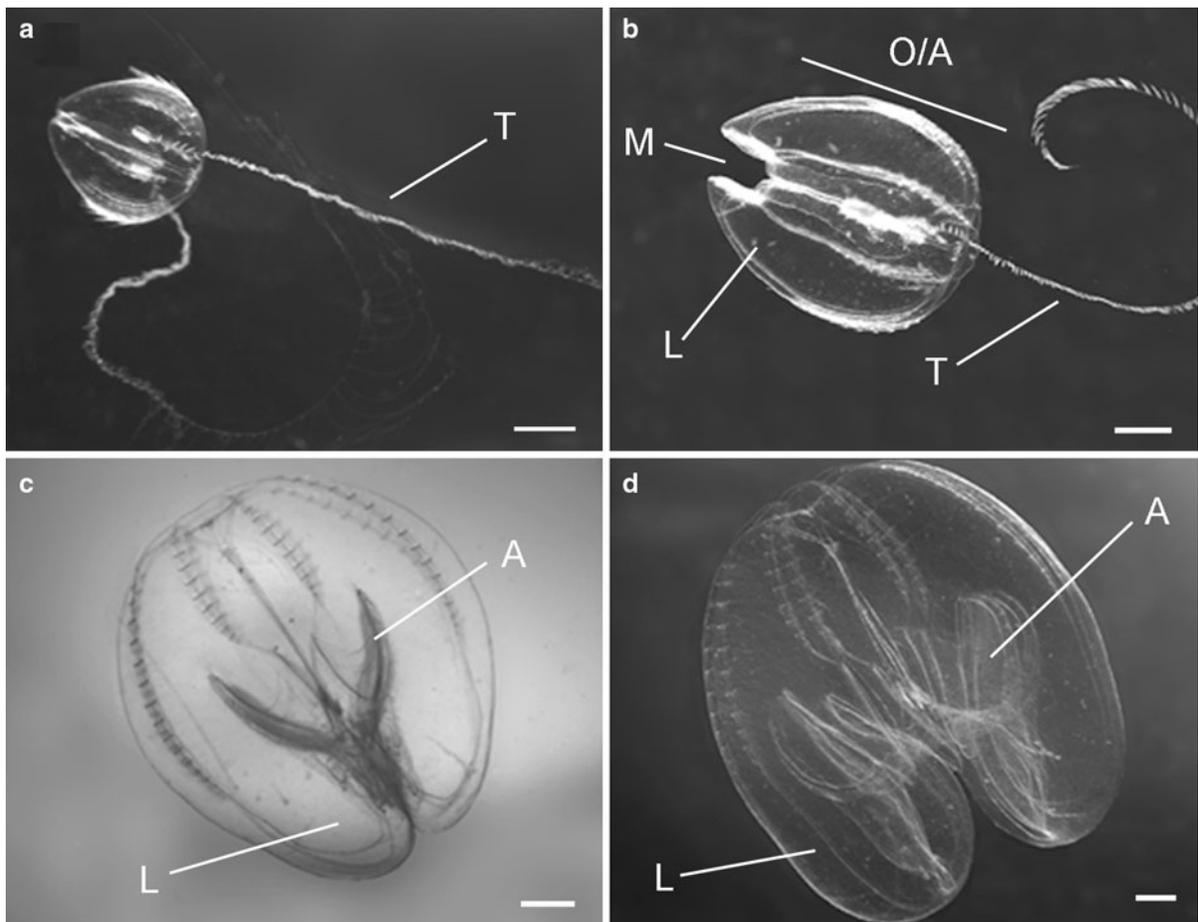
Fig. 8 *Mnemiopsis leidyi* life history stages. **a** Tentaculate-stage cydippid larva with trailing tentacles (T). **b** Transition-stage larva with tentacles and small oral lobes (L). Only one of the two tentacles is in focus. *O/A* oral–aboral axis; *M* mouth. **c** Lobate-stage larva, with developing auricles (a) and oral lobes. **d** Post-larval *Mnemiopsis* with completely developed auricles and oral lobes. *Scale bars* are 1.0 mm (from Sullivan & Gifford, 2004)

breadth that encompasses a wide portion of the diverse prey spectra it frequently encounters in its native and exotic ranges.

One consequence of the delicate hydrodynamic equilibrium involved in prey capture is that *Mnemiopsis* predation is likely to be highly sensitive to variations in ambient hydrodynamic conditions, such as turbulent mixing. The delicate morphology and very low shear levels observed in the feeding current of *Mnemiopsis* suggests that even low levels of ambient turbulence could potentially interfere with prey entrainment and encounter processes, reducing feeding proficiency. Field data (Fig. 12) suggest that *Mnemiopsis* avoids highly mixed regions when possible and can migrate vertically to minimize exposure to turbulent mixing (Miller, 1974; Costello &

Mianzan, 2003; Mianzan et al., 2010). The interactions between mixing processes, ctenophore feeding currents, and prey escape behavior involves a variety of undocumented interactions that, when quantified, may provide insight in variations in predation patterns related to physical conditions.

The combination of effective feeding and rapid growth potential provide *Mnemiopsis* the ability to strongly impact planktonic communities. Early quantitative estimates suggested relatively low average (5–10% day^{-1}) capacities of *Mnemiopsis* to crop copepod standing stocks (Kremer, 1979). However, more recent estimates indicate substantially higher predatory potential (>100% of zooplankton standing stock day^{-1}; Table 3). These higher estimates of predatory potential are consistent with rapid declines
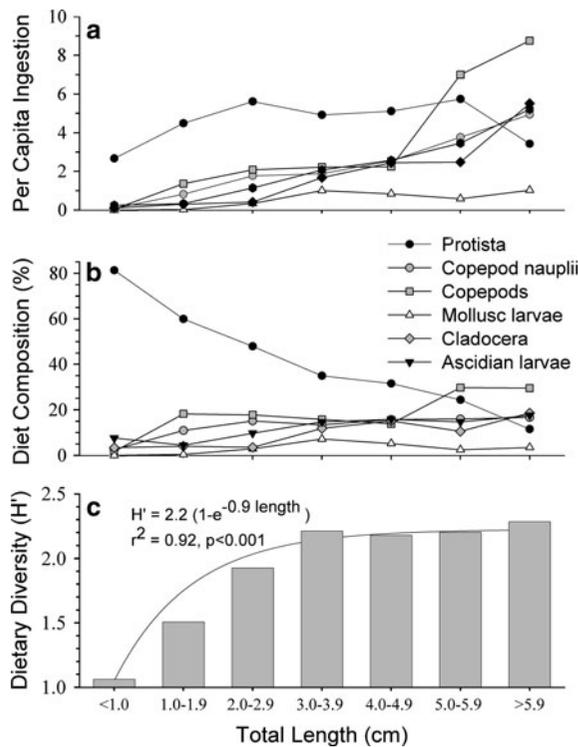
Fig. 9 Dietary patterns in relation to body size of *Mnemiopsis leidyi*. **a** Per capita consumption of different prey categories, **b** relative proportion of diet as reflected by in situ gut contents and **c** the diversity (H') of the diet (from Rapoza et al., 2005)

in zooplankton populations that often accompany increases in *Mnemiopsis* biomass (e.g., Fig. 13). The increasing appreciation of *Mnemiopsis* predatory impacts is related to methodological changes, particularly the use of larger volume experimental feeding containers and field ingestion estimates. For example, experiments with 10–50 mm sized ctenophores in containers ranging from 3.5 to 1,000 l demonstrated that ratios of container volume to ctenophore volume of <2,500:1 resulted in reduced ctenophore clearance rates. Clearance rates were greater in the larger containers and greatest in 1,000-l containers (Purcell, 2009). In addition, feeding rates determined from field gut contents and digestion rates were generally higher than from containers (reviewed in Purcell, 1997). For example, clearance rates of 40-mm-long (~15 g WW) *Mnemiopsis* on *Acartia* sp. copepods estimated from gut contents in the Baltic sea (8.3 l ind.$^{-1}$ h^{-1}) were 4-times those of similarly sized ctenophores measured in 1,000-l containers (Granhag et al., 2011). These high-predation rates

make *Mnemiopsis* a competitive threat to fish larvae and zooplanktivorous (forage) fish species when their diets overlap (Darvishi et al., 2004). Indeed, competition for zooplankton prey has been assumed to be the main cause of inverse abundances of ctenophore and forage fish in the Black Sea region (e.g., Purcell et al., 2001; Oguz, 2005; Daskalov et al., 2007; Oguz & Gilbert, 2007; Oguz et al., 2008; Mutlu, 2009).

The role of *Mnemiopsis* as a direct fish predator currently presents a more complex picture. A variety of studies demonstrate direct predation on fish eggs and larvae (reviewed by Purcell & Arai, 2001; Purcell et al., 2001). However, recent studies in the Baltic region describe differing distributions of *Mnemiopsis* relative to fish eggs and larvae (Haslob et al., 2007; Schaber et al., 2011b) and a low clearance rate of the ctenophores on Baltic cod eggs (Jaspers et al., 2011). The variation in these results suggests that behavioral details of ctenophore–prey interactions need greater examination for more complete understanding. These details will help clarify the pathways through which ctenophore predatory impacts cascade through planktonic communities in native (Deason & Smayda, 1982; Purcell & Decker, 2005; Sullivan et al., 2008) and exotic (Shiganova et al., 2004a, b; Finenko et al., 2006; Kideys et al., 2008) habitats.

Constraints on the invasiveness of *Mnemiopsis*

Requirement for high-prey availability

Rapid population growth of *Mnemiopsis* requires high prey ingestion rates. Kremer & Reeve (1989) estimated that a minimum prey biomass of >24 µg C l^{-1} is required to support population growth of field populations. This is roughly an order of magnitude greater than average prey concentrations found in more oligotrophic oceanic waters (Kremer et al., 1986). *Mnemiopsis* is rarely found in waters less than 3 µg C l^{-1} (Kremer, 1994). Instead, a genus with many structural similarities but lower feeding effort at high-prey concentrations, *Bolinopsis* L. Agassiz, 1860, appears to replace *Mnemiopsis* in many less productive waters (Kremer et al., 1986). Reproduction by *Mnemiopsis* is sensitive to food supply and egg production declines within 24 h when feeding stops. No eggs are produced after 3–4 days of starvation (Reeve et al., 1989). The protein-dominated body
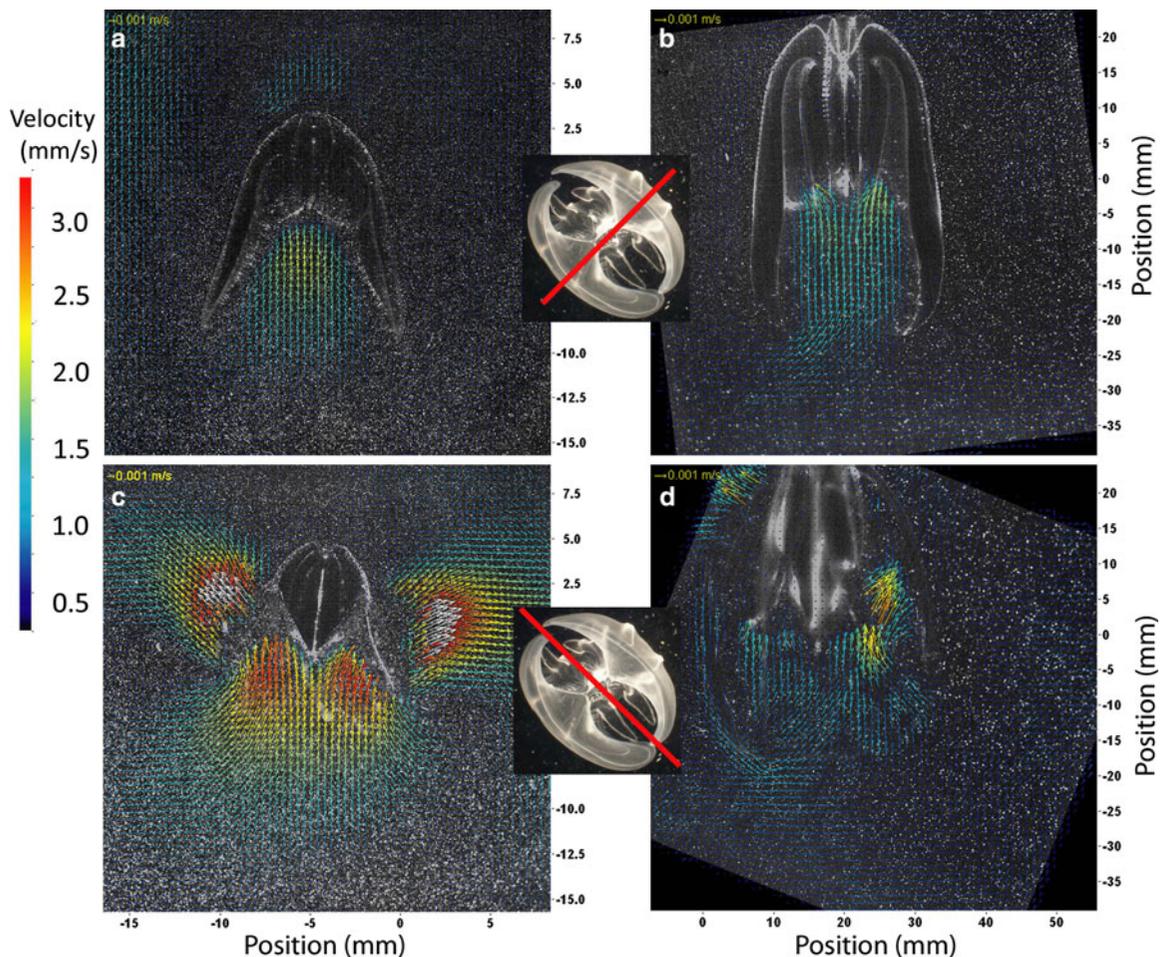
Fig. 10 Representative velocity vector fields around a small (1.3 cm long; **a**, **c**) and large (4.8 cm long; **b**, **d**) *Mnemiopsis leidyi*. Both ctenophores were stationary (i.e., swimming velocity of 0) and actively entrained fluid between their lobes. The laser sheet used for digital particle image velocimetry (DPIV) was directed through the center of the ctenophore at two perpendicular orientations (laser orientation illustrated by *red line*, *insets*). DPIV is shown with the laser directed through the lobes (**a**, **b**) and between the lobes (**c**, **d**). This view is through the transparent lobe to show particle velocities between the lobes. *White vectors* represent velocities greater than 3.5 mm s^{-1} (from Colin et al., 2010). (Color figure online)

tissues of *Mnemiopsis* (Kremer, 1976; Anninsky et al., 2005) are not well suited to low food supplies. *Mnemiopsis* possesses very limited lipid and carbohydrate body reserves, which are quickly utilized during non-feeding periods (Anninsky et al., 2005). The use of body proteins to satisfy metabolic demands leads to organic dilution of tissues (Reeve et al., 1989) and, after several days of starvation, body shrinkage (reviewed in Reeve & Walter, 1978). Loss of organic weight by *Mnemiopsis* during starvation averages 5.9% day^{-1} at 12°C (Anninsky et al., 2005), indicating that body shrinkage can be rapid at low prey concentrations. As a consequence of high-reproductive sensitivity to low-food levels and very limited starvation tolerance, *Mnemiopsis* appears incapable of extending population growth into regions of low-prey concentrations, such as oceanic waters.

Vulnerability to predation

Mnemiopsis biomass levels can be limited by influential predators. A wide array of predators consume *Mnemiopsis* (Table 1), including vertebrate (Mianzan et al., 1996) and gelatinous (reviewed in Purcell et al., 2001; Arai, 2005) predators. Gelatinous predators appear to be particularly influential (Purcell & Cowan,

Fig. 11 Shear deformation rates of the two largest components of deformation in different regions of the feeding current of a small stationary *Mnemiopsis leidyi* (1.3 cm long). *Top* S_{yx} represents alterations in u_x (*x* component of fluid velocity) along the *y* axis. Three transects at outer, middle, and inner lobe positions (*top, right*) are compared with minimum threshold deformation rates that elicit escape responses of common coastal copepods (indicated by *green lines with letters* designating different copepod species). Deformation rate thresholds are from Kiørboe et al., 1999 (*Acartia*), Burdick et al., 2007 (*Centropages, Temora, Tortanus*), and Green et al., 2003 (*Eurytemora*). *Bottom* S_{yy} represents alterations in u_y (*y* component of fluid velocity) along the *y* axis. Two transects depict S_{yy} across the lobe opening and along a central axis from the lobe opening to the ctenophore's mouth (indicated by *red lines*, bottom). The observed deformation rates for this small ctenophore are large compared with those of larger ctenophores. Despite this, much of the feeding current is undetectable to prey. We would expect a greater portion of the feeding current of larger ctenophores to be below the threshold of prey detection (from Colin et al., 2010). (Color figure online)
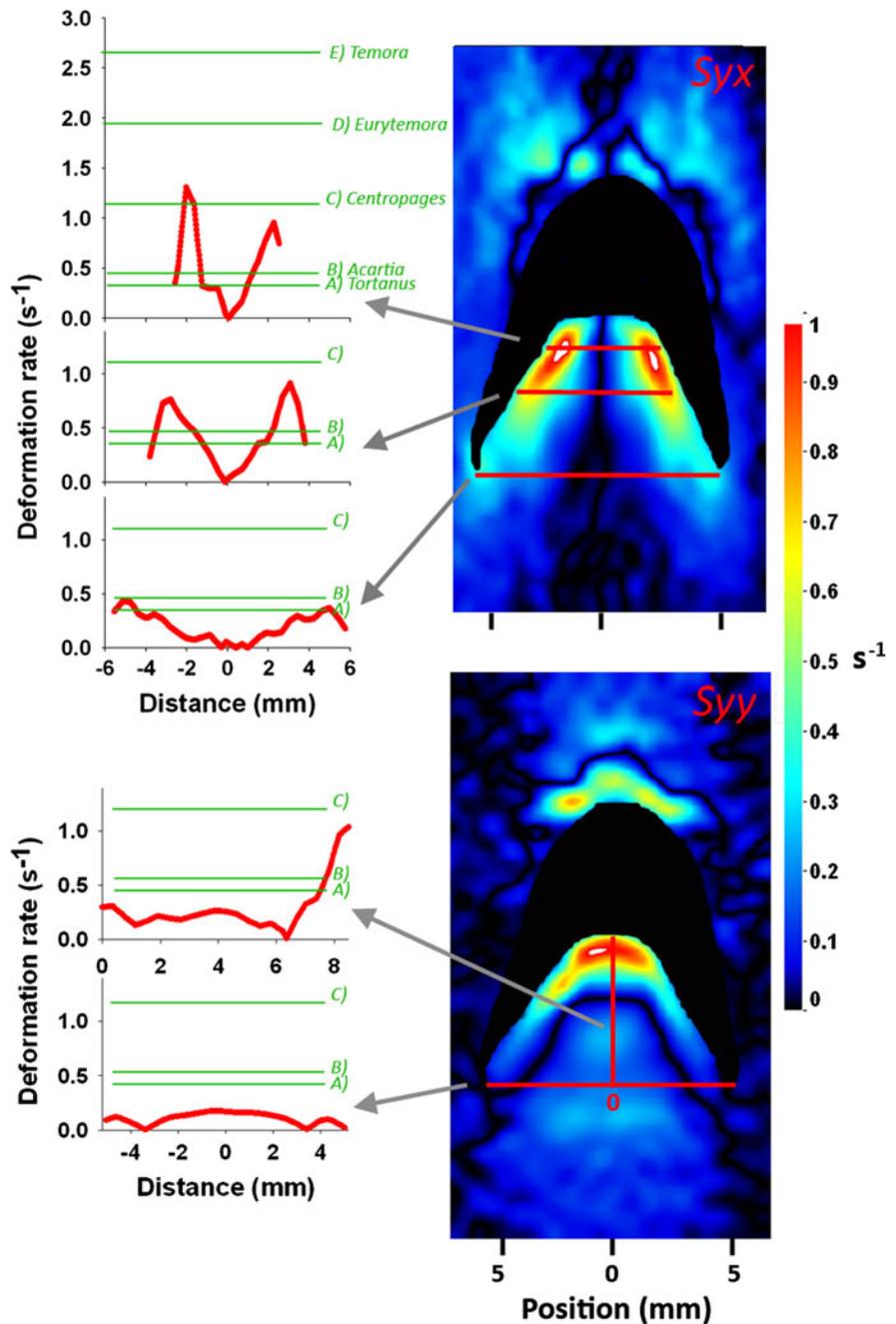
1995; Shiganova et al., 2001a, 2004a; Finenko et al., 2003; Purcell & Decker, 2005; Condon & Steinberg, 2008), although little information exists on predation by fish. The regulatory effect of these gelatinous predators can dominate *Mnemiopsis* population biomass and have cascading effects through the plankton community (Fig. 14). The dominant influence of gelatinous predators on *Mnemiopsis* biomass is remarkable in light of the rapid population growth potential of *Mnemiopsis* and the high frequency (>90%) with which the ctenophores may evade predators (Kreps et al., 1997; Hosia & Titelman, 2011; Titelman et al., 2012). However, as evaluated by Condon and Steinberg (2008), the ability of predators
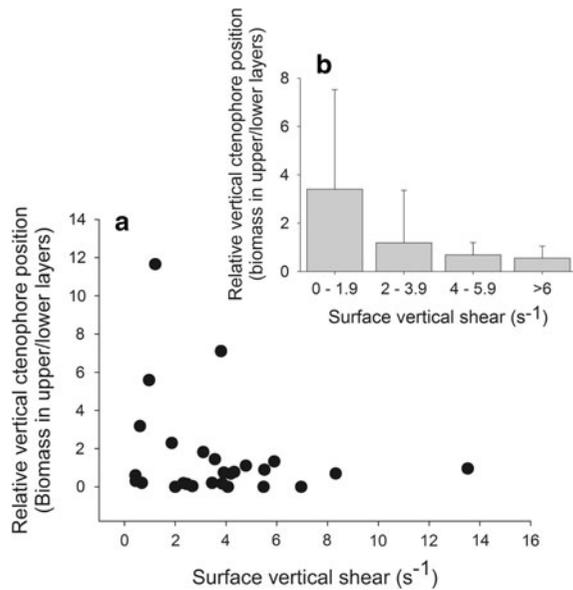
Fig. 12 Relative vertical position of *Mnemiopsis leidyi* biomass versus surface vertical shear in the Peninsula Valdes region during December, 1989. **a** Data for all individual stations, and **b** grouping of stations by shear levels allowing comparison relative positions of *Mnemiopsis* biomass in relation to surface vertical shear. Note that the proportion of ctenophores in the surface layers were always low when surface vertical shear was high (>4.0 s^{-1}); however, when surface vertical shear was low, the vertical positions of ctenophore biomass were more variable (from Mianzan et al., 2010)
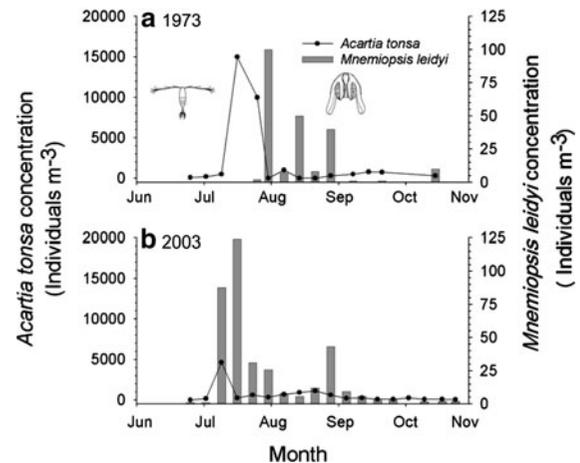

Fig. 13 Relationship between timing of population maxima for the copepod *Acartia tonsa* and the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, RI, USA. *A. tonsa* has historically been the dominant summer copepod in Narragansett Bay and the copepod's population peaked before the onset of *Mnemiopsis* population growth (e.g., **a**; see also Deason, 1982). However, in recent years, *Mnemiopsis* populations have increased earlier (Costello et al., 2006b), and *A. tonsa* has become rare in Narragansett Bay during much of the summer (from Sullivan et al., 2007)

such as *C. quinquecirrha* to crop *Mnemiopsis* biomass exceeds the population growth potential of *Mnemiopsis* in even the most favorable food and temperature

Table 3 Predation rates of *Mnemiopsis leidyi* on copepods and *Chrysaora quinquecirrha* on *Mnemiopsis*

Month	Size (mm)	B_p	D_p	I	DPP	DC
Mnemiopsis consuming copepods						
April	43–43	0.7–10.7	119–1775	<0.1–0.5	<1–21	8–84
May	10–39	0.7–9.1	110–1520	0.7–2.5	27–127	144–697
June	12–13	0.0–6.4	81–1065	0.2–1.8	24–208	39–299
July	22–63	2.9–7.6	477–1271	0.0–1.2	0–43	0–206
August	0–34	3.6–113.6	594–18929	0.0–0.1	0–2	0–23
Chrysaora quinquecirrha consuming *Mnemiopsis*						
April	0	0.2–35.2	<1–38	0	0	0
May	0	19.9–32.8	32–425	0	0	0
June	23–133	5.3–50.2	82–170	0.1–13.5	2–27	0–3
July	76–152	0.0–12.5	0–86	0.6–72.7	37–242	<3–425
August	80–134	0.0–17.7	0–28	<0.1–28.1	<1–159	<1–107

Predicted monthly carbon (C) ingestion rates for populations at a upriver York River station. Ingestion rates based on mean-sized predator (mm), and predator and prey C standing stocks (mg C m^{-3}). Values are upper and lower monthly range estimates for April–August 2003–2006. Calculations were made using equations listed in Condon & Steinberg (2008). B_p = biomass of prey (mg C m^{-3}); D_p = density of prey (no. prey m^{-3}); I = population ingestion rates (mg C m^{-3} day^{-1}); DPP = daily population predation pressure rates (% prey C day^{-1}); DC = C-based daily prey consumption rates (no. prey m^{-3} day^{-1}) (From Condon & Steinberg, 2008)

conditions for the ctenophore (Table 3). *Mnemiopsis* introductions have been comparatively devastating in regions without other gelatinous predators, such as the Caspian sea (Roohi et al., 2008, 2009), but they may be moderated in the presence of established indigenous gelatinous predators, such as in recently invaded European regions (Hosia & Titelman, 2011) or where other gelatinous predators have been introduced, such as *Beroe ovata* Bruguiève, 1789 in the Black Sea (Finenko et al., 2003; Shiganova et al., 2003). Consequently, the presence of predators, particularly gelatinous carnivores, can override other favorable conditions and diminish *Mnemiopsis* biomass both in its native (Kremer & Nixon, 1976; Purcell & Decker, 2005; Condon & Steinberg, 2008) and exotic ranges (Finenko et al., 2003; Shiganova et al., 2003).

Population dynamics and invasive patterns of *Mnemiopsis*

The same traits enabling high-biomass production and influential ecological impacts by *Mnemiopsis* in temperate regions of its native habitat are the basis for the ctenophore's success as an invader in exotic habitats. *Mnemiopsis* possesses many traits associated with "weed" species—wide physiological tolerances, wide dietary niche, rapid growth, short-generation times, and high fecundity (Sakai et al., 2001). These traits have been a consistent feature of *Mnemiopsis* population dynamics within its native range and are now shared by the ctenophore's populations in its exotic range. From this perspective, the high-invasive success of *Mnemiopsis* in exotic habitats can be viewed as an extension of the source-sink population dynamics enabling the ctenophore to successfully dominate temperate regions of its native range.

The transition from a historically stable to a contemporary invasive distribution was initiated by reducing limitations on dispersal of *Mnemiopsis*. Although dispersal between source and sink regions has historically been limited by local and regional circulation patterns, the contemporary marine environment also features trans-oceanic transport vectors in the form of ballast tanks within commercial sea vessels (Fig. 15). Molecular markers trace the pathways of these trans-oceanic *Mnemiopsis* introductions (Fig. 2) and similar patterns have been confirmed by multiple, independent studies (Ghabooli et al., 2010;
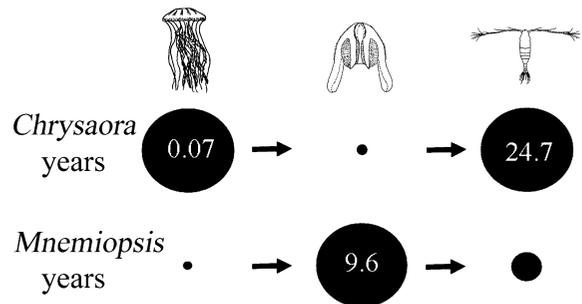

Fig. 14 The role of selective feeding by the scyphomedusa, *Chrysaora quinquecirrha*, on a planktonic community in mesohaline regions of Chesapeake Bay, USA, that contain the ctenophore *Mnemiopsis leidyi* and copepods. Data based on Purcell & Decker (2005; annual variations detailed therein). The circumference of the spheres under each organism represents the relative average proportions of those species in the plankton during years of high abundance in individuals of *C. quinquecirrha* (*Chrysaora* years: 1987–1990 and 1995) or *Mnemiopsis* (*Mnemiopsis* years: 1996–2000). The maximum concentrations of each organismal group are normalized to the same circumferences. Within each organismal group, the relative circumferences of the two time periods are proportionately dimensioned and the average abundances of each group (no. m^{-3} for *C. quinquecirrha* and *Mnemiopsis*, no. l^{-1} for copepods) are listed within the *circles*. Values for *smaller circles* (*C. quinquecirrha*: 0.007 m^{-3}, *Mnemiopsis*: 1.1 m^{-3}, copepods: 7.7 l^{-1}) were not listed in the figure. *Arrows* represent a simplification of trophic interactions because members of *C. quinquecirrha* prey upon both individuals of *Mnemiopsis* and copepods, but selectively prey upon ctenophores relative to copepods. Predation by individuals of *C. quinquecirrha* upon the ctenophore *Mnemiopsis* reduces the latter with a cascading effect on the ctenophore's principle prey items, the copepods. Consequently, the relative abundance of copepods in the plankton is dominated by trophic interactions that depend on the prey selection characteristics of the scyphomedusa *C. quinquecirrha*

Reusch et al., 2010). These data demonstrate an ongoing pattern that includes relatively recent introductions from North America to areas such as the North and Baltic Seas.

It is likely that *Mnemiopsis* will continue to expand into exotic areas in the near future. The reasons for this projection are based on the processes driving invasive expansion by the ctenophore. Successful invasion of a novel area by *Mnemiopsis* is dependent both on the recipient environment (the area's "invasibility"—Leung & Mandrake, 2007) and on the ability to reach these new areas (the ctenophore's "propagule pressure"—Lockwood et al., 2005). Upon arrival, invaders must persist in the new habitat and persistence depends upon the match between the individual
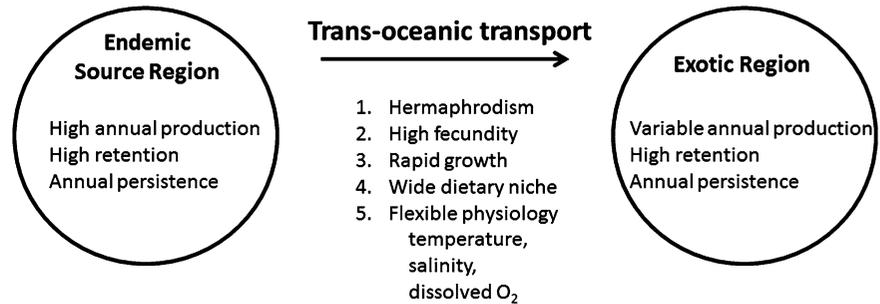
species' traits and the new environment. The broad physiological tolerances of *Mnemiopsis* (Table 1) suggest that a wide array of productive coastal environments have high-invasibility levels for *Mnemiopsis* and could potentially be suitable habitats for the ctenophore; however, the ctenophore first has to reach those habitats. Historically, the expanse of low-productivity oceanic waters likely has prevented extension of *Mnemiopsis* beyond its native coastlines of the Atlantic North and South Americas (Harbison & Volovik, 1994). However, this historical limitation has been relaxed by ballast water transport via contemporary transoceanic shipping. Ballast water regulation is a developing field with limited prospects for reducing transfer of inocula in the near future (David & Gollasch, 2008). Hence, the key obstacle to *Mnemiopsis* invasion of new regions is relaxed during a period when the number of source regions for inocula has increased. Increasing the number of source regions can dramatically increase overall invasion rates—within 50 years of initial invasion, a new source region may supply inocula for invasion to an additional 300 ports (Kaluza et al., 2010). This combination of factors—a wide variety of high invasibility regions, reduction of dispersal limitation, and increasing propagule pressure—favors continued range expansion by *Mnemiopsis*.

We expect that the ecological role played by introduced *Mnemiopsis* populations will depend upon community structure in the novel environments. Within its native range, the ctenophore's ecological role is constrained by the variables previously considered (i.e., temperature and production regimes, predator dynamics). These same constraints will influence invasive populations of *Mnemiopsis* in

exotic habitats. In a variety of native habitats, *Mnemiopsis* is a persistent but relatively inconspicuous community member (Kremer et al., 1986; Kremer, 1994). Even in areas that experience periodic, high *Mnemiopsis* biomass, fluctuations in ctenophore biomass depend upon predator population dynamics (Fig. 14). The dramatic effects following *Mnemiopsis* introductions documented in the Black (e.g., Kideys, 2002; Shiganova et al., 2004a) and Caspian (e.g., Shiganova et al., 2004b; Roohi et al., 2008, 2009) seas occurred in habitats that lacked gelatinous predators (Purcell et al., 2001). Recent introductions to the Baltic and North Seas occurred in habitats containing potentially influential gelatinous predators (Hosia & Titelman, 2011) that may impact the eventual role of *Mnemiopsis* in these communities. We expect that the variables favoring and constraining *Mnemiopsis* population dynamics in previously studied habitats will provide insight into the fate of introduced populations as the world community adjusts to the ctenophore's expanded the presence in coastal marine communities.

References

Agassiz, L., 1860. Contributions to the Natural History of the United States of America, Vol. 3. Little, Brown & Co., Boston.

Agassiz, A., 1865. Illustrated Catalogue of the Museum of Comparative Zoology. Vol. II. North American Acalephae. Welch, Bigelow & Co, Cambridge, MA.

Anninsky, B. E., G. A. Finenko, G. I. Abolmasova, E. S. Hubareva, L. S. Svetlichny, L. Bat & A. E. Kideys, 2005. Effect of starvation on the biochemical compositions and respiration rates of ctenophores *Mnemiopsis leidyi* and *Beroe ovata* in the Black Sea. Journal of the Marine Biological Association of the United Kingdom 85: 549–561.

Arai, M. N., 2005. Predation on pelagic coelenterates: a review. Journal of the Marine Biological Association of the United Kingdom 85: 523–536.

Baker, L. D., 1973. The ecology of the ctenophore *Mnemiospsis mccradyi* in Biscayne Bay, Florida. University of Miami Technical Report, University of Miami-Rosenstiel School of Marine and Atmospheric Science: 131 pp.

Baker, I. D. & M. R. Reeve, 1974. Laboratory culture of the lobate ctenophore *Mnemiopsis mccradyi* with notes on feeding and fecundity. Marine Biology 26: 57–62.

Bayha, K., 2005. The molecular systematics and population genetics of four coastal ctenophores and scyphozoan jellyfish of the US Atlantic and Gulf of Mexico. PhD Dissertation. University of Delaware, Newark.

Bayha, K. M., G. R. Harbison, J. H. McDonald & P. M. Gaffney, 2004. Preliminary investigation on the molecular systematic 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.

Brusca, R. C. & G. J. Brusca, 2003. Invertebrates. Sinauer Associates, Sunderland, USA.

Burdick, D. S., D. K. Hartline & P. H. Lenz, 2007. Escape strategies in co-occurring calanoids copepods. Limnology and Oceanography 52: 2373–2385.

Buskey, E. J., 1993. Annual pattern of micro- and mesozooplankton abundance and biomass in a subtropical estuary. Journal of Plankton Research 15: 907–924.

Cairns, S. D., D. R. Calder, A. Brinckmann-Voss, C. B. Castro, D. G. Fautin, P. R. Pugh, C. E. Mills, W. C. Jaap, M. N. Arai, S. H. D. Haddock & D. M. Opresko, 2002. Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Cnidaria and Ctenophora, 2nd ed. American Fisheries Society Special Publication 28, Bethesda: 1–115.

Caut, S., E. Angulo & F. Courchamp, 2008. Dietary shift of an invasive predator: rats, seabirds and sea turtles. Journal of Applied Ecology 45: 428–437.

Colin, S. P., J. H. Costello, L. J. Hansson, J. Titelman & J. O. Dabiri, 2010. Stealth predation: the ecological success of the invasive ctenophore *Mnemiopsis leidyi*. Proceedings of the National Academy of Sciences of the United States of America 107: 17223–17227.

Condon, R. H. & D. K. Steinberg, 2008. Development, biological regulation, and fate of ctenophore blooms in the York River estuary, Chesapeake Bay. Marine Ecology Progress Series 369: 153–168.

Costello, J. H. & H. W. Mianzan, 2003. Sampling field distributions of *Mnemiopsis leidyi* (Ctenophora, Lobata): planktonic or benthic methods? Journal of Plankton Research 25: 455–459.

Costello, J. H., R. Loftus & R. Waggett, 1999. Influence of prey detection on capture success for the ctenophore *Mnemiopsis leidyi* feeding upon adult *Acartia tonsa* and *Oithona colcarva* copepods. Marine Ecology Progress Series 191: 207–216.

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

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

Darvishi, F., A. Esmaili Sari & P. Farshchi, 2004. Dietary overlap between invasion ctenophora (*M. leidyi* and anchovy (*C. engrauliformis*) in the southern parts of Caspian Sea. International Journal of Environmental Science and Technology 1: 89–95.

Daskalov, G. M., A. N. Grishin, S. Rodionov & V. Mihneva, 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proceedings of the National Academy of Science of the United States of America 104: 10518–10523.

David, M. & S. Gollasch, 2008. EU shipping in the dawn of managing the ballast water issue. Marine Pollution Bulletin 56: 1966–1972.

Dawson, M. N., 2004. Some implications of molecular phylogenetics for understanding biodiversity in jellyfishes, with emphasis on Scyphozoa. Hydrobiologia 530/531: 249–260.

Dawson, M. N. & D. Jacobs, 2001. Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria, Scyphozoa). Biological Bulletin 200: 92–96.

Deason, E. E., 1982. Mnemiopsis leidyi (Ctenophora) in Narragansett Bay, 1975–79: abundance, size composition and estimation of grazing. Estuarine, Coastal and Shelf Science 15: 121–134.

Deason, E. E. & T. J. Smayda, 1982. Ctenophore-zooplankton-phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972–1977. Journal of Plankton Research 4: 203–217.

Decker, M. B., D. L. Breitburg & J. E. Purcell, 2004. Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. Marine Ecology Progress Series 280: 163–172.

Durbin, A. G. & E. G. Durbin, 1981. Standing stock and estimated production rates of phytoplankton and zooplankton in Narragansett Bay, Rhode Island. Estuaries 4: 24–41.

Eschsholtz, F., 1825. Berichtüber die zoologischeAusbeute während der Reise von Kronstadtbis St. Peter und Paul. Isis 1: 733–747.

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.

Finenko, G. A., Z. A. Romanova, G. I. Abolmasova, B. E. An-ninsky, L. S. Svetlichny, E. S. Hubareva, L. Bati & A. E. Kideys, 2003. Population dynamics, ingestion, growth and reproduction rates of the invader *Beroe ovata* and its impact on plankton community in Sevastopol Bay, the Black Sea. Journal of Plankton Research 25: 539–549.

Finenko, G. A., A. E. Kideys, B. E. Anninsky, T. A. Shiganova, A. Roohi, M. R. Tabari, H. Rostami & S. Bagheri, 2006. Invasive ctenophore *Mnemiopsis leidyi* in the Caspian Sea: feeding, respiration, reproduction and predatory impact on the zooplankton community. Marine Ecology Progress Series 314: 171–185.

Fuentes, V. L., D. L. Angel, K. M. Bayha, D. Atienza, D. Edelist, C. Bordehore, J.-M. Gili & J. E. Purcell, 2010. Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, span the Mediterranean Sea in 2009. Hydrobiologia 645: 23–37.

Funk, J. L. & P. M. Vitousik, 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature 446: 1079–1081.

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.

Ghabooli, S., T. A. Shiganova, A. Zhan, M. Cristescu, P. Egh-tesadi-Araghi & H. MacIsaac, 2010. Multiple introductions and invasion pathways for the invasive ctenophore *Mnemiopsis leidyi* in Eurasia. Biological Invasions. doi:10.1007/s10530-010-9859-8.

Gorokhova, E. & M. Lehtiniemi, 2010. Comment: Reconsid-ering evidence for *Mnemiopsis* invasion in European waters. Journal of Plankton Research 32: 93–95.

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* inva-sion. Limnology and Oceanography 54: 2025–2033.

Granhag, L., L. F. Møller & L. J. Hansson, 2011. Size-specific clearance rates of the ctenophore *Mnemiopsis leidyi* based on in situ gut content analyses. Journal of Plankton Research doi. doi:10.1093/plankt/fbr010.

Green, S., A. W. Visser, J. Titelman & T. Kiørboe, 2003. Escape responses of copepod nauplii in the flow field of the blue mussel, *Mytilus edulis*. Marine Biology 142: 727–733.

Greve, W., 1977. Interspecific interaction: the analysis of com-plex structures in carnivorous zooplankton populations. Helgolander Wissenschaftliche Meeresunters 30: 83–91.

Greve, W., F. Reiners, J. Nast & S. Hoffmann, 2004. Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. Helgoland Marine Research 58: 274–288.

Grove, M. & D. L. Breitburg, 2005. Growth and reproduction of gelatinous zooplankton exposed to low dissolved oxygen. Marine Ecology Progress Series 301: 185–198.

Hamer, H. H., A. M. Malzahn & M. Boersma, 2011. The invasive ctenophore *Mnemiopsis leidyi*: a threat to fish recruitment in the North Sea? Journal of Plankton Research 33: 137–144.

Hanski, I., 1999. Metapopulation Ecology. Oxford University Press, New York, USA.

Hansson, H. G., 2006. Ctenophores of the Baltic and adjacent Seas – the invader *Mnemiopsis* is here! Aquatic Invasions 1: 295–298.

Harbison, G. R. & S. P. Volovik, 1994. The ctenophore, *Mnemiopsis leidyi*, in the Black Sea: a holoplanktonic organism transported in the ballast water of ships. In Nonindigenous Estuarine and Marine Organisms (NEMO), Proceedings of the Conference and Workshop, Seattle, WA, April 1993. U. S. Department of Commerce, National Oceanic and Atmospheric Administration, Washington, DC: 25–36.

Harbison, G. R., L. P. Madin & N. R. Swanberg, 1978. On the natural history and distribution of oceanic ctenophores. Deep-Sea Research 25: 233–256.

Haslob, H., C. Clemmesen, M. Schaber, H. H. Hinrichsen, J. O. Schmidt, R. Voss, G. Kraus & F. W. Köster, 2007. Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. Marine Ecology Progress Series 349: 303–306.

Holland, B., M. N. Dawson, G. Crow & D. Hofmann, 2004. Global phylogeography of *Cassiopea* (Scyphozoa: Rhizo-stomeae): molecular evidence for cryptic species and multiple invasions of the Hawaiian Islands. Marine Biol-ogy 145: 1119–1128.

Hosia, A. & J. Titelman, 2011. Intraguild predation between the native North Sea jellyfish *Cyanea capillata* and the inva-sive ctenophore *Mnemiopsis leidyi*. Journal of Plankton Research 33: 535–540.

Hulsizer, E. E., 1976. Zooplankton of lower Narragansett Bay 1972–1973. Chesapeake Science 17: 260–270.

Hyman, L. H., 1940. The Invertebrates: Protozoa Through Ctenophora. McGraw-Hill Co., New York.

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

Jaspers, C., J. Titelman, L. J. Hansson, M. Haraldsson & C. R. Ditlefsen, 2011. The invasive ctenophore *Mnemiopsis leidyi* poses no direct threat to Baltic cod eggs and larvae. Limnology and Oceanography 56: 431–439.

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

Javidpour, J., J. C. Molinero, A. Lehmann, T. Hansen & U. Sommer, 2009a. Annual assessment of the predation of *Mnemiopsis leidyi* in a new invaded environment, the Kiel Fjord (Western Baltic Sea): a matter of concern? Journal of Plankton Research 31: 729–738.

Javidpour, J., J. C. Molinero, J. Peschutter & U. Sommer, 2009b. Seasonal changes and population dynamics of the cteno-phore *Mnemiopsis leidyi* after its first year of invasion in the Kiel Fjord, Western Baltic Sea. Biological Invasions 11: 873–882.

Javidpour, J., J. C. Molinero & U. Sommer, 2010. Reconsidering evidence for *Mnemiopsis* invasion in European waters: reply. Journal of Plankton Research 32: 97–98.

Kaluza, P., A. Kölzsch, M. T. Gastner & B. Blasius, 2010. The complex network of global cargo ship movements. Journal of the Royal Society Interface. doi:10.1098/rsif.2009.0495.

Kideys, A. E., 2002. Fall and rise of the Black Sea ecosystem. Science 297: 1482–1484.

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

Kideys, A. E., A. Roohi, E. Eker-Develi, F. Melin & D. Beare, 2008. Increased chlorophyll levels in the Southern Caspian Sea following an invasion of jellyfish. Research Letters in Ecology. doi:10.1155/2008/185642.

Kiørboe, T., E. Saiz & A. Visser, 1999. Hydrodynamic signal perception in the copepod *Acartia tonsa*. Marine Ecology Progress Series 179: 97–111.

Knowler, D., 2005. Reassessing the costs of biological invasion: *Mnemiopsis leidyi* in the Black sea. Ecological Economics 52: 187–199.

Kolesar, S. E., D. L. Breitburg, J. E. Purcell & M. B. Decker, 2010. Effects of hypoxia on *Mnemiopsis leidyi*, ichthyoplankton and copepods: clearance rates and vertical habitat overlap. Marine Ecology Progress Series 411: 173–188.

Kremer, P., 1976. Population dynamics and ecological energetics of a pulsed zooplankton predator, the ctenophore *Mnemiopsis leidyi*. In Wiley, M. L. (ed.), Estuarine Processes, Vol. 1. Academic Press, New York: 197–215.

Kremer, P., 1979. Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. Estuaries 2: 97–105.

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

Kremer, P. & S. Nixon, 1976. Distribution and abundance of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay. Estuarine and Coastal Marine Science 4: 627–639.

Kremer, P. & M. R. Reeve, 1989. Growth dynamics of a ctenophore (*Mnemiopsis*) in relation to variable food supply. II. Carbon budgets and growth model. Journal of Plankton Research 11: 553–574.

Kremer, P., M. R. Reeve & M. A. Syms, 1986. The nutritional ecology of the ctenophore *Bolinopsis vitrea*: comparison with *Mnemiopsis mccradyi* from the same region. Journal of Plankton Research 8: 1197–1208.

Kreps, T. A., J. E. Purcell & K. B. Heidelberg, 1997. Escape of the ctenophore, *Mnemiopsis leidyi* from the scyphomedusa predator, *Chrysaora quinquecirrha*. Marine Biology 128: 441–446.

Larson, R. J., 1987. In situ feeding rates of the ctenophore *Mnemiopsis mccradyi*. Estuaries 10: 87–91.

Leung, B. & N. E. Mandrake, 2007. The risk of establishment of aquatic invasive species: joining invasibility and propagule pressure. Proceedings of the Royal Society B 274: 2603–2609.

Lockwood, J. L., P. Cassey & T. Blackburn, 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20: 223–228.

Lonsdale, D. J., 1981. Regulatory role of physical factors and predation for two Chesapeake Bay copepod species. Marine Ecology Progress Series 5: 341–351.

Main, R. J., 1928. Observations of the feeding mechanism of a ctenophore, *Mnemiopsis leidyi*. Biological Bulletin 55: 69–78.

Marcus, N. H. & F. Boero, 1998. Minireview: the importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. Limnology and Oceanography 43: 763–768.

Mayer, A. G., 1900. Descriptions of new and little-known medusae from the Western Atlantic. Bulletin of the Museum of Comparative Zoology Harvard 37: 1–9.

Mayer, A. G., 1912. Ctenophores of the Atlantic Coast of North America. Carnegie Institute Publishing, Washington.

Mertens, H., 1833. Beobachtungen und Untersuchungenüber die beroeartigenAkalephen. Mémoires de L'AcademieImperiale des Sciences de St. Petersbourg (6th Sér.) 2: 479–543.

Mianzan, H. W., 1986. *Beroe ovata* en aguas de la bahía Blanca, Argentina (Ctenophora). Spheniscus 2: 29–32.

Mianzan, H., 1999. Ctenophora. In Boltovskoy, D. (ed.), South Atlantic Zooplankton. Backhuys Publishers, Leiden: 561–573.

Mianzan, H. W. & R. Guerrero, 2000. Environmental patterns and biomass distribution of gelatinous macrozooplankton. Three study cases in the Southwestern Atlantic. Scientia Marina 64(Supl. 1): 215–224.

Mianzan, H. W. & M. Sabatini, 1985. Estudio preliminar sobre distribución y abundancia de *Mnemiopsis maccradyi* en el estuario de bahía Blanca, Argentina (Ctenophora). Spheniscus 1: 53–68.

Mianzan, H. W., N. Mari, B. Prenski & F. Sanchez, 1996. Fish predation on neritic ctenophores from the Argentine continental shelf: a neglected food resource? Fisheries Research 27: 69–79.

Mianzan, H. W., P. Martos, J. H. Costello & R. Guerro, 2010. Avoidance of hydrodynamically mixed environments by *Mnemiopsis leidyi* (Ctenophora: Lobata) in open-sea populations from Patagonia, Argentina. Hydrobiologia 645: 113–124.

Miller, R. J., 1974. Distribution and biomass of an estuarine ctenophore population, *Mnemiopsis leidyi* (A. Agassiz). Chesapeake Science 15: 1–8.

Miranda, L., A. Collins, A. Marques & S. Vollmer, 2010. Molecules clarify a Cnidarian life cycle: the "Hydrozoan" *Microhydrulalimopsicola* is an early life stage of the Staurozoan *Haliclystu santarcticus*. PLoS ONE 5: e10182.

Moss, A. G., B. Wells & L. Muellner, 2004. A mechanosensory system that controls feeding in adult *Mnemiopsis*. Hydrobiologia 530(531): 145–153.

Mutlu, E., 1999. Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. II. *Mnemiopsis leidyi*. Marine Biology 135: 603–614.

Mutlu, E., 2009. Recent distribution and size structure of gelatinous organisms in the southern Black Sea and their interactions with fish catches. Marine Biology 156: 935–957.

Nelson, T. C., 1925. On the occurrence and food habits of ctenophores in New Jersey inland coastal waters. Biological Bulletin 48: 92–111.

Newton, C., J. H. Costello, B. K. Sullivan & S. P. Colin, 2009. Feeding mechanisms and prey selection by the ctenophore *Mnemiopsis leidyi*. ASLO, abstract.

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

Oguz, T. & D. Gilbert, 2007. Abrupt transitions of the top-down controlled Black Sea pelagic ecosystem during 1960–2000: evidence for regime-shifts under strong fishery exploitation and nutrient enrichment modulated by climate-induced variations. Deep-Sea Research Part I 54: 220–242.

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.

Olson, M. M., 1987. Zooplankton. In Heck, K. L., Jr. (ed.), Ecological Studies in the Middle Reach of Chesapeake Bay. Springer-Verlag, New York: 38–81.

Pereladov, M. V., 1988. Some observations for biota of Sudak Bay of the Black Sea. III All-Russian conference of marine biology. Naukova Dumka, Kiev 1: 237–238. (in Russian).

Pianka, H. D., 1974. Ctenophora. In Giese, A. C. & J. S. Pearse (eds), Reproduction of Marine Invertebrates, Vol. I. Academic Press, New York: 201–265.

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

Purcell, J. E., 1997. Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates and effects on prey populations. Annales de l'Institut océanographique, Paris 73: 125–137.

Purcell, J. E., 2009. Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. Hydrobiologia 616: 23–50.

Purcell, J. E. & M. N. Arai, 2001. Interactions of pelagic cnidarians and ctenophores with fishes: a review. Hydrobiologia 451 (Developments in Hydrobiology 155): 27–44.

Purcell, J. E. & J. H. Cowan, 1995. Predation by the scyphomedusan Chrysaora quinquecirrha on Mnemiopsis leidyi ctenophores. Marine Ecology Progress Series 129: 63–70.

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.

Purcell, J. E., J. R. White & M. R. Roman, 1994. Predation by gelatinous zooplankton and resource limitation as potential controls of Acartia tonsa copepod populations in Chesapeake Bay. Limnology and Oceanography 39: 263–278.

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.

Purcell, J. E., S.-I. Uye & W.-T. Lo, 2007. Anthropogenic causes of jellyfish blooms and direct consequences for humans: a review. Marine Ecology Progress Series 350: 153–174.

Rang, P. C. A. L., 1828. Établissement de la famille des Béroïdesdansl'ordre des acalèphes libres, et description de deux genres nouveaux qui luiappartiennent Mémoires. Société d'Histoire Naturelle de Paris 4: 166–173.

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.

Reeve, M. R. & M. A. Walter, 1978. Nutritional ecology of ctenophores – a review of recent research. Advances in Marine Biology 15: 249–287.

Reeve, M. R., M. A. Syms & P. Kremer, 1989. Growth dynamics of a ctenophore (Mnemiopsis) in relation to variable food supply. I. Carbon biomass, feeding, egg production, growth, and assimilation efficiency. Journal of Plankton Research 11: 535–552.

Reusch, T., S. Bolte, M. Sparwell, A. Moss & J. Javidpour, 2010. Microsatellites reveal origin and genetic diversity of Eurasian invasions by one of the world's most notorious marine invader, Mnemiopsis leidyi (Ctenophora). Molecular Ecology 19: 2690–2699.

Riisgård, H. U., C. V. Madsen, C. Barth-Jensen, & J. E. Purcell, 2012. Population dynamics and zooplankton-predation impact of the indigenous scyphozoan Aurelia aurita and the invasive ctenophore Mnemiopsis leidyi in Limfjorden (Denmark). Aquatic Invasions (in press).

Roohi, A., Z. Yasin, A. E. Kideys, A. T. S. Hwai, A. G. Khanari & E. Eker-Develi, 2008. Impact of a new invasive ctenophore (Mnemiopsis leidyi) on the zooplankton community of the Southern Caspian Sea. Marine Ecology 29: 421–434.

Roohi, A., A. E. Kideys, A. Sajjadi, A. Hashemian, R. Pourgholam, H. Fazli, A. G. Khanari & E. Eker-Develi, 2009. Changes in biodiversity of phytoplankton, zooplankton, fishes and macrobenthos in the southern Caspian Sea after the invasion of the ctenophore Mnemiopsis leidyi. Biological Invasions. doi:10.1007/s10530-009-9648-4.

Sai Sastry, A. G. R. & P. Chandramohan, 1989. Planktonic coelenterates of Vasishta Godavari estuary, east coast of India. Indian Journal of Marine Sciences 18: 160–164.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson & S. G. Weller, 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32: 305–332.

Schaber, M., H. Haslob, B. Huwer, A. Harjes, H.-H. Hinrichsen, F. W. Köster, M. Storr-Paulsen, J. O. Schmidt & R. Voss, 2011a. The invasive ctenophore Mnemiopsis leidyi in the central Baltic Sea: seasonal phenology and hydrographic influence on spatio-temporal distribution patterns. Journal of Plankton Research. doi:10.1093/plankt/fbq167.

Schaber, M., H. Haslob, B. Huwer, A. Harjes, H.-H. Hinrichsen, M. Storr-Paulsen, J. O. Schmidt, R. Voss, V. Neumann & F. W. Köster, 2011b. Spatio-temporal overlap of the alien invasive ctenophore Mnemiopsis leidyi and ichthyoplankton in the Bornholm Basin (Baltic Sea). Biological Invasions. doi:10.1007/s10530-011-9936-7.

Schroth, W., G. Jarms, B. Streit & B. Schierwater, 2002. Speciation and phylogeography in the cosmopolitan marine moon jelly, Aurelia sp. BMC Evolutionary Biology 2: 1.

Seravin, L. N., 1994a. The systematic revision of the genus Mnemiopsis (Ctenophora, Lobata). 1. The history of description and study of species belonging to the genus Mnemiopsis. Zoologichesky Zhurnal 73: 9–18.

Seravin, L. N., 1994b. The systematic revision of the genus Mnemiopsis (Ctenophora, Lobata). 2. Species attribution on Mnemiopsis from the Black Sea and the species composition of the genus Mnemiopsis. Zoologichesky Zhurnal 73: 19–34.

Shiganova, T. A., 1993. Ctenophore Mnemiopsis leidyi and ichthyoplankton in the Sea of Marmara in October of 1992. Oceanology 33: 900–903.

Shiganova, T. A., 1997. Mnemiopsis leidyi abundance in the Black Sea and its impact on the pelagic community. In Ozsoy, E. & A. Mikaelyan (eds), Sensitivity of North Sea, Baltic Sea and Black Sea to Anthropogenic and Climatic

Changes. Kluwer Academic Publishers, Dordrecht: 117–130.

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., Y. V. Bulgakova, S. P. Volovik, Z. A. Mirzoyan & S. I. Dudkin, 2001a. The new invader *Beroe ovata* Brown 1756 and its effect on the ecosystem in the northeastern Black Sea in August-September 1999. Hydrobiologia 451: 187–197.

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, 2001b. 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. I. Musaeva, Y. V. Bulgakova, Z. A. Mirzoyan & M. L. Martynuk, 2003. Ctenophores invaders *Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* Mayer 1912, and their effect on the pelagic ecosystem of the north-eastern Black Sea. Biological Bulletin Russian Academy of Sciences, Moscow 2: 225–235.

Shiganova, T. A., H. J. Dumont, A. Mikaelyan, D. M. Glazov, Y. V. Bulgakova, E. I. Musaeva, P. Y. Sorokin, L. A. Pautova, Z. A. Mirzoyan & E. I. Studenikina, 2004a. Interaction between the invading ctenophores *Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* Mayer 1912, and their Influence on the pelagic ecosystem of the northeastern Black Sea. 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: 33–70.

Shiganova, T. A., H. J. Dumont, A. F. Sokolsky, A. M. Kamakin, D. Tinenkova & E. K. Durasheva, 2004b. Population dynamics of *Mnemiopsis leidyi* in the Caspian Sea, and effects on the Caspian ecosystem. 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: 71–111.

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

Smayda, T. J., 1988. Final report: environmental conditions and plankton dynamics in Narragansett Bay during an annual cycle characterized by a brown tide. Narragansett Bay Project.

Sorarrain, D., 1998. Cambios estacionales en la biomasa de organismos gelatinosos en relación con otros zooplánteres en la bahía Samborombón. MSc Thesis, Facultad de Ciencias Exactas y Naturales, Departamento de Ciencias Marinas, Universidad Nacional de Mar del Plata, Argentina, Mar del Plata: 35 pp.

Stanlaw, K. A., M. R. Reeve & M. A. Walter, 1981. Growth, food and vulnerability to damage of the ctenophore *Mnemiopsis mccradyi* in its early life history stages. Limnology and Oceanography 26: 224–234.

Stoecker, D. K., P. G. Verity, A. E. Michaels & L. H. Davis, 1987. Feeding by larval and post-larval ctenophores on microzooplankton. Journal of Plankton Research 9: 667–683.

Studenikina, E. I., S. P. Volovik, I. A. Miryozan & G. I. Luts, 1991. The ctenophore *Mnemiopsis leidyi* in the Sea of Azov. Oceanology 3: 722–725.

Sullivan, L. J., 2010. Gut evacuation of larval *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). Journal of Plankton Research 32: 69–74.

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, L. J. & D. J. Gifford, 2007. Growth and feeding rates of the newly hatched larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). Journal of Plankton Research 29: 949–965.

Sullivan, B. K. & L. T. MacManus, 1986. Factors controlling seasonal succession of the copepods *Acartia hudsonica* and *A. tonsa* in Narragansett Bay, RI: temperature and resting egg production. Marine Ecology Progress Series 28: 121–128.

Sullivan, B. K., J. H. Costello & D. VanKeuen, 2007. Seasonality of the copepods *Acartia hudsonica* and *Acartia tonsa* in Narragansett Bay, RI, USA during a period of climate change. Estuarine, Coastal and Shelf Science 73: 259–267.

Sullivan, B. K., D. J. Gifford, J. H. Costello & J. R. Graff, 2008. Narragansett Bay ctenophore-zooplankton-phytoplankton dynamics in a changing climate. In Desbonnet, A. & B. A. Costa-Pierce (eds), Science for Ecosystem-Based Management: Narragansett Bay in the 21st Century. Springer, New York: 485–498.

Tendal, O. S., K. R. Jensen & H. U. Riisgård, 2007. Invasive ctenophore *Mnemiopsis leidyi* widely distributed in Danish waters. Aquatic Invasions 2: 272–277.

Titelman, J., L. J. Hansson, T. Nilsen, S. P. Colin & J. H. Costello, 2012. Predator-induced vertical behavior of a ctenophore. Hydrobiologia. doi:10.1007/s10750-012-1056-6.

Tzikhon-Lukanina, E. A., O. G. Reznichenko & T. A. Lukasheva, 1991. Quantitative aspects of feeding in the Black Sea ctenophore *Mnemiopsis leidyi*. Oceanology 31: 272–276.

Vinogradov, M. E., E. A. Shushkina, E. I. Musaeva & P. Yu. Sorokin, 1989. Ctenophore *Mnemiopsis leidyi* (A. Agassiz) (Ctenophora: Lobata) – new settlers in the Black Sea. Oceanology 29: 293–298.

Waggett, R. J. & E. J. Buskey, 2006. Copepod sensitivity to flow fields: detection by copepods of predatory ctenophores. Marine Ecology Progress Series 323: 205–211.

Waggett, R. & J. H. Costello, 1999. Different mechanisms used by the lobate ctenophore, *Mnemiopsis leidyi*, to capture nauplii and adult life stages of the copepod *Acartia tonsa*. Journal of Plankton Research 21: 2037–2052.

Waggett, R. J. & L. J. Sullivan, 2006. Feeding efficiency of the larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). Journal of Plankton Research 28: 719–723.

Yazdani Foshtomi, M., B. Abtahi, A. Esmaili 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.

Zaika, V. E. & N. K. Revkov, 1998. Nutrition of the Black Sea ctenophore in dependence on zooplankton abundance. Gydrobiologichesky Zhurnal 34: 29–35. (in Russian).

Zaika, V. Ye. & N. G. Sergeeva, 1990. Morphology and development of *Mnemiopsis mccradyi* (Ctenophora, Lobata) in the Black Sea. Zoologicheskiy Zhurnal 69: 5–11. (in Russian).

Zhang, W., P. F. Hendrix, B. A. Snyder, M. Molina, J. Li, X. Rao, E. Siemann & S. Fu, 2010. Dietary flexibility aids Asian earthworm invasion in North American forests. Ecology 91: 2070–2079.