

Invasive ctenophore *Mnemiopsis leidyi* in Norway

AINO HOSIA¹ AND TONE FALKENHAUG²

¹The Natural History Collections, University Museum of Bergen, University of Bergen, Bergen, Norway, ²Institute of Marine Research, Flødevigen, Norway

We present data on the occurrence of the invasive ctenophore Mnemiopsis leidyi in Norway after the initial observations made in 2005. Our data comes from several net sampling investigations conducted along the Norwegian coast in 2008–2014, as well as beach seine bycatch from the south coast (September–October 2005–2014). In 2008–2010, M. leidyi occurred in moderate abundances (≤ 0.56 lobate ind m^{-3}) during autumn, with northernmost observations from Trondheimsfjord. Mnemiopsis leidyi was not observed in 2011–2012 and was scarce in 2013, but in 2014 it was again abundant along the south and west coasts. While temperature and salinity conditions along the Norwegian south coast and its fjords are sufficient for survival and reproduction by M. leidyi, temperature may limit egg production rates. Biological factors including food limitation as well as competition and predation by native gelatinous predators can also constrain populations. Mnemiopsis leidyi populations in Norway are likely to exhibit source–sink dynamics, with advective losses and suboptimal conditions preventing overwintering in large areas along the coast. The presence of M. leidyi in the southern North Sea, coupled with the cyclonic circulation pattern, suggests that outbreaks may nevertheless be expected in years with favourable conditions and/or significant inflow from the southern North Sea. Climate change could enhance reproduction of M. leidyi in Norway and protected inner fjords may offer a suitable habitat for establishment of local populations in the future.

Keywords: introduced species, NIS, invasive species, Norwegian Coastal Current, North Sea, fjords, temperature, metapopulation, source–sink dynamics, jellyfish, comb jellies

Submitted 5 November 2014; accepted 20 January 2015

INTRODUCTION

The ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 is a successful invasive species with a bad reputation. From its native range along the temperate to subtropical Atlantic west coast, *M. leidyi* has embarked on several trans-Atlantic invasions, most likely in ballast waters. The notoriety of *M. leidyi* stems largely from its invasion of the Ponto-Caspian region towards the end of the last century. The arrival of the voracious planktivore in the Black Sea in the 1980s coincided with, and was partly blamed for, a collapse in commercial fisheries (Kideys, 2002). It is, however, likely that concurrent environmental problems including overfishing and eutrophication contributed to both the collapsing fish stocks and the invasive success of *M. leidyi* (Daskalov *et al.*, 2007). In the late 1990s the ctenophore further spread to the Caspian Sea, where its predatory impact had substantial effects on the ecosystem through trophic cascades (Roohi *et al.*, 2010).

In the beginning of the current millennium, *M. leidyi* spread to the North Sea and the Baltic Sea (Faasse & Bayha, 2006; Javidpour *et al.*, 2006; Boersma *et al.*, 2007; Oliveira, 2007; Tendal *et al.*, 2007; Antajan *et al.*, 2014) in what molecular studies suggest was a separate invasion event by a more northern source population than the one established in the

Ponto-Caspian (Reusch *et al.*, 2010). Simultaneously, *M. leidyi* has also spread to the Mediterranean, most likely through secondary invasion from the Black Sea (Ghabooli *et al.*, 2011; Bolte *et al.*, 2013).

The invasive success of *M. leidyi* can be attributed to a combination of ecological and life history traits conducive to the establishment of new populations. These include a wide tolerance for environmental conditions such as temperature, salinity and dissolved oxygen, opportunistic feeding with dietary flexibility and high potential ingestion rates, as well as the potential for rapid population increases due to high fecundity, short generation times and the capacity for self-fertilization (reviewed in Purcell *et al.*, 2001; Costello *et al.*, 2012). Abundant *M. leidyi* can have a considerable predatory impact on mesozooplankton populations (Granhag *et al.*, 2011), with the subsequent cascading effects on the rest of the ecosystem potentially resulting in socio-economic problems, as evidenced by experiences from the Ponto-Caspian region (Knowler, 2005). The recent appearance of *M. leidyi* in new European seas has, therefore, caused public concern and prompted research on the extent and consequences of the invasions.

The first confirmed observations of *M. leidyi* in Norwegian waters stem from Oslofjord in 2005 (Oliveira, 2007). In 2006, *M. leidyi* was also observed on the west coast, outside Bergen (Hansson, 2006). Unfortunately, monitoring of *M. leidyi* in Norwegian waters has been inconsistent and no further observations in Norway have been published. Here, we combine and present data on *M. leidyi* distribution and abundance in

Corresponding author:

A. Hosia

Emails: aino.hosia@um.uib.no; aino.hosia@gmail.com

Norwegian waters since the initial observations and discuss the factors influencing its spread and distribution along the Norwegian coast.

MATERIALS AND METHODS

Study area

The study area covers the Norwegian south and west coast up to $\sim 65^\circ\text{N}$ (Figure 1). Surface circulation along the Norwegian coast is dominated by the Norwegian Coastal Current (NCC) salinity $\sim 25-34.5$ flowing first south-west and then northwards along the entire coast. The NCC originates primarily

from brackish outflow from the Baltic Sea through the Skagerrak, and from Norwegian fjords and rivers (Sætre, 2007; Sætre & Aure, 2007). North Sea water contributing to the NCC is transported into the Skagerrak from the southern/central North Sea and the German Bight, and along the west coast of Denmark by the Jutland current – part of the generally cyclonic circulation in the North Sea (Sætre & Aure, 2007). *En route*, the NCC is mixed with the more saline Atlantic water (salinity $>34.5-35$) flowing below and outside it, increasing its salinity (Sætre, 2007; Sætre & Aure, 2007). The Norwegian coast is characterized by numerous fjords, often separated from the continental shelf outside by a sill of varying depth. Freshwater runoff to the fjords results in an estuarine circulation with a brackish surface layer, while more saline water is found in the fjord basins.

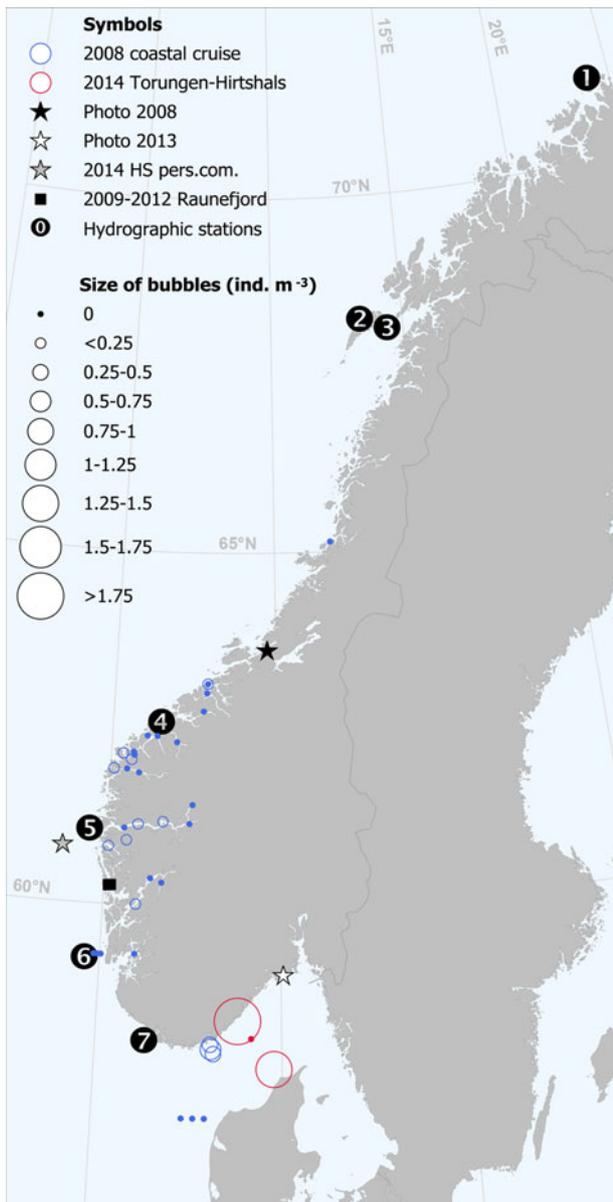


Fig. 1. *Mnemiopsis leidyi* observations along the Norwegian coast in November 2008 and the Torungen–Hirtshals transect in September 2014. Bubble size is relative to *M. leidyi* density. Also shown are the locations of WP₃ hauls without *M. leidyi* taken during these investigations, the approximate locations of the hydrographic stations (1 = Ingøy, 2 = Eggum, 3 = Skrova, 4 = Bud, 5 = Sognesjø, 6 = Indre Utsira, 7 = Lista) and the locations of miscellaneous additional *M. leidyi* observations.

Sampling

Net sampling was conducted on the following occasions, primarily using a WP₃ net (opening 1 m^2) with vertical hauls and a towing speed of $\sim 0.3\text{ m s}^{-1}$:

- (1) In November 2008, WP₃ hauls from a variable tow depth to the surface were made along the Norwegian coast up to $\sim 65^\circ\text{N}$ during a cruise on the R/V Håkon Mosby (Figure 1, Table S1 from the supplementary material).
- (2) From November 2009 to December 2011 and during the second half of 2012, \sim monthly ctenophore monitoring was carried out at two stations (St 1: $60^\circ 16.0'\text{N } 005^\circ 11.6'\text{E}$, bottom depth $\sim 128\text{ m}$; St 2: $60^\circ 15.597'\text{N } 005^\circ 08.386'\text{E}$, bottom depth $\sim 244\text{ m}$) in Rauneufjord, south of Bergen, using WP₃ hauls from above the seabed to the surface (Figure 1, Table S1).
- (3) In November 2009 and October 2010, samples were collected in Hardangerfjord, western Norway, during two cruises on the R/V Håkon Mosby as part of the Epigraph Project (Falkenhaus & Dalpadado, 2014). Vertical hauls were made with WP₃, WP₂ and Juday nets and depth stratified, oblique hauls with MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System; Wiebe *et al.*, 1985) along a transect extending from the inner fjord area to the fjord mouth (Figure 2, Table S1).
- (4) In September–October 2010, WP₃ samples were collected in conjunction with a beach seine survey cruise on R/V G.M. Dannevig along the south-eastern coast of Norway and in Oslofjord. WP₃ hauls from depths of 50 m , or from above the seabed (when bottom depth was $<50\text{ m}$) to the surface were made at 26 stations (Figure 2, Table S1).
- (5) In September 2014, WP₃ samples were collected along the Torungen–Hirtshals transect on the R/V Håkon Mosby. WP₃ hauls from depths of 50 m to the surface were made on three stations (Figure 1, Table S1).

Detailed information on the used gear, location, available environmental parameters and ctenophore size is provided in Table S1. For the net samples above, ctenophores were identified, enumerated and measured from live samples directly after sampling. Ctenophore size was measured as the oral–aboral length. Only specimens from transitional stage and above are considered in the present data, as larvae may not have been adequately sampled by the nets used and

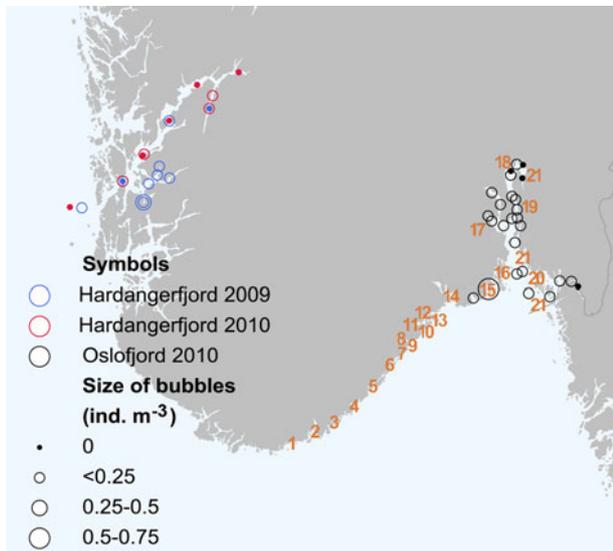


Fig. 2. *Mnemiopsis leidyi* observations in Hardangerfjord November 2009 and October 2010, and Oslofjord September–October 2010. Also shown are the locations of WP₃ hauls without *M. leidyi* taken during these investigations. Orange numbers indicate the approximate locations of the beach seine sampling areas along the coast; note that area 21 denotes extra sites, the location of which varies from year to year.

their morphological identification to species level can be difficult. CTD casts for temperature and salinity were taken at most stations.

In addition to net sampling, an index of lobate ctenophore bycatch abundance was recorded in September–October from 2005 to 2014 during the Norwegian Skagerrak beach seine survey, an annual monitoring program for juvenile fish ongoing since 1919 (Fromentin *et al.*, 1997; Durif *et al.*, 2011). The sampling comprised 84–138 sites annually, grouped into 21 areas along the south-east coast of Norway (Figure 2). The following index was used for ctenophore abundance in the beach seines: 0 = none, 1 = one, 2 = few, 3 = some, 4 = many, 5 = very many. We have calculated annual average indices for each area.

Other observations

Some observations were also obtained by searching the web for underwater images of *Mnemiopsis leidyi* in Norway and soliciting help from UW photographers. Photographic documentation was required in order to exclude observations of the externally similar lobate *Bolinopsis infundibulum* (O.F. Müller, 1776), native along the entire coast.

Prevailing environmental conditions

To evaluate *Mnemiopsis leidyi*'s potential for survival and reproduction in Norwegian waters, we looked at a time series of monthly average temperatures at several depths during the past ~40–80 years until 2012 at seven permanent hydrographical stations located along the coast (<http://www.imr.no/forskning/forskningsdata/stasjoner/>) (Figure 1). Prior to analysis, years with incomplete sampling during the period of minimum and/or maximum temperatures were manually removed from the time series. We then extracted a time series on the annual temperature minima and maxima

for each station, to compare with *M. leidyi*'s temperature requirements for survival and reproduction, obtained from literature.

Presentation of data

Figures were prepared using R version 2.15.3 (R Core Team, 2013) and Manifold System 8.0.

RESULTS

Net sampling

During the cruise in November 2008, *Mnemiopsis leidyi* were encountered at several locations along the south and west coasts, with the northernmost individuals sampled at Sunndalsfjord (Figure 1, Table S1). The highest concentrations, 0.54 ind m⁻³ in the upper 50 m, were encountered in the south, close to Oksøy. In the west coast fjords, the abundance of *M. leidyi* was greatest towards the mouth of the fjord, with the species mostly absent from the inner fjords.

In Raunefjord, *Mnemiopsis leidyi* were observed during the first sampling efforts in November 2009, as well as in October–November 2010 (Figure 3, Table S1). No *M. leidyi* were observed during sampling in 2011 or 2012. The highest abundance (0.1 ind m⁻³ in the upper 100 m) was recorded in November 2009. Other ctenophores commonly observed during the sampling included *Bolinopsis infundibulum*, *Pleurobrachia pileus* (O.F. Müller, 1776) and *Beroe cucumis* Fabricius, 1780 (Figure 3).

In Hardangerfjord, *M. leidyi* was recorded at eight out of 27 stations in November 2009, and at four out of 24 stations in October 2010. Abundances were generally higher in November 2009 (≤ 0.40 ind m⁻³) than in October 2010 (< 0.2 ind m⁻³). The highest concentrations were found in the outer fjord area, and in one of the fjord branches (Figure 2, Table S1). Depth stratified sampling revealed that *M. leidyi* was mainly distributed in the upper 25 m, with few records below 50 m (Table S1).

In September–October 2010, *M. leidyi* was observed at most stations in and outside Oslofjord, with abundances reaching 0.56 ind m⁻³ in the upper 50 m (Figure 2, Table S1).

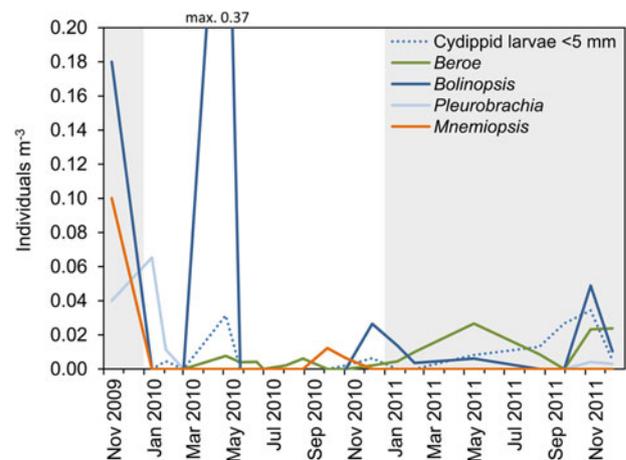


Fig. 3. Seasonal abundance of common ctenophores at Raunefjord. Average from stations 1 and 2, ~monthly WP₃ hauls from bottom to surface.

In September 2014, *M. leidy* was observed at both ends of the Torungen–Hirtshals transect, but not at the middle station (Figure 1, Table S1). The abundances were the highest recorded during our monitoring efforts – up to 1.96 ind m^{-3} in the upper 50 m.

When considering the observed abundances in our data, it should be taken into account that the haul depths and the proportion of the sampled water column vary (Table S1). The calculated concentrations per cubic metre assume even distribution within the sampled layer; however, this is hardly realistic, as also shown by our depth stratified MOCNESS data.

Beach seine bycatch

Lobate ctenophore bycatch in beach seines was first noted in 2005, at a few stations. Abundant lobate ctenophores were caught in 2007–2010, followed by their disappearance from the beach seines in 2011–2013. In 2014, high abundances were again observed (Figure 4). It should be noted that not all lobate bycatch was identified to species, but the combination of its sudden appearance in 2005, the timing of the investigation during the *Mnemiopsis leidy* peak season in the autumn (as opposed to *Bolinopsis infundibulum*, which peaks in the spring) and the available photographic evidence suggest that it is likely primarily *M. leidy*.

Environmental conditions

According to the time series on temperature minima and maxima at the hydrographic stations, surface temperature should consistently reach an annual maximum sufficient for

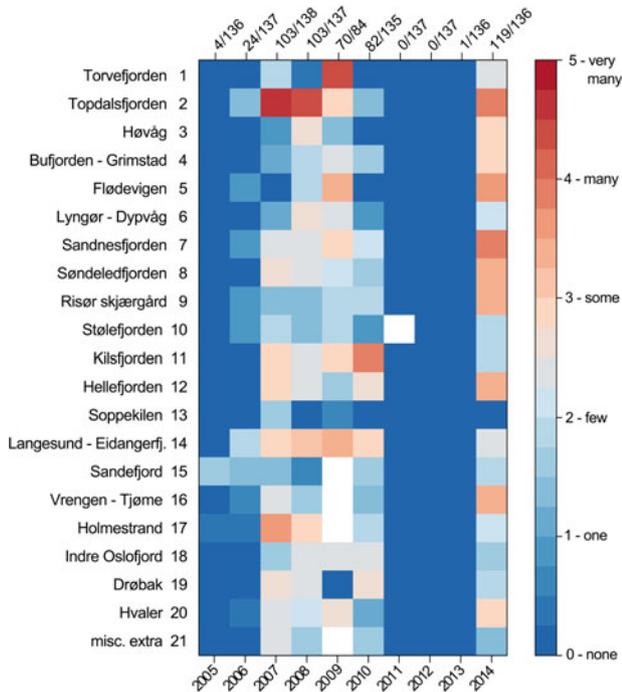


Fig. 4. Mean index of lobate ctenophore bycatch in beach seines from 21 areas along the Norwegian south coast, autumn 2005–2014 (for locations, see Figure 1). White fill indicates missing data. Upper x-axis labels show number of sites with lobate ctenophores vs total number of sampled sites for the given year.

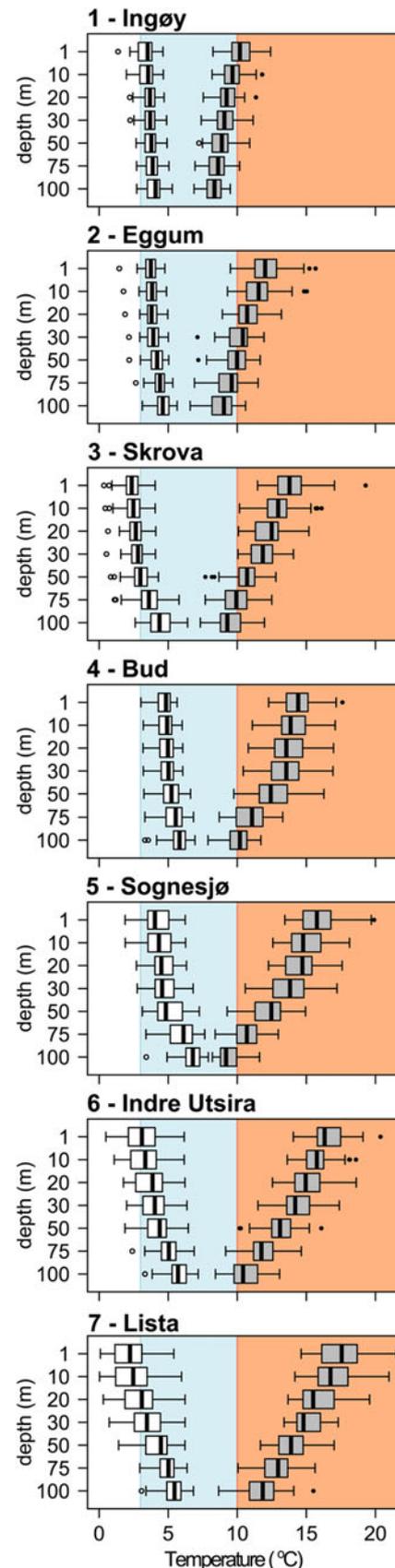


Fig. 5. Boxplots of time series of annual minimum (white) and maximum (grey) temperatures for past 40–80 years at seven hydrographical stations along the Norwegian coast (for locations, see Figure 1). The blue and orange backgrounds indicate conservative estimates of temperature ranges allowing *Mnemiopsis leidy* survival ($>3^{\circ}\text{C}$) and reproduction ($>10^{\circ}\text{C}$), respectively.

reproduction at least up to the level of Bud at $\sim 63^{\circ}\text{N}$ (Figure 5). Below freezing temperatures were never observed in the time series, which should allow for the survival of *Mnemiopsis leidyi* at the salinities predominating along the Norwegian coast.

Other observations

Most observations from divers corresponded with the geographic range and timing of observations from net sampling and/or beach seine observations (data not shown). However, they also included the northernmost confirmed observation from outside Selva, Trondheimsfjord, in September 2008 (K. Telnes; http://www.seawater.no/fauna/ctenophora/images/IMG2008_2828.jpg) as well as the only confirmed observation in 2013 from outside Stavern, Larviksfjord (S. Sarre; <https://www.flickr.com/photos/52065318@N03/10312589883/>) (Figure 1).

DISCUSSION

Environmental conditions

Mnemiopsis leidyi is native along the West Atlantic coast, from Argentina in the south to New England in the North, with the highest abundances found in temperate latitudes on both hemispheres (Costello *et al.*, 2012). It is a primarily neritic species, rarely found in large numbers in the less productive oceanic waters (Costello *et al.*, 2012). The species exhibits morphological variation both in its native and introduced ranges, and the genus *Mnemiopsis* has previously been divided into several species based on morphology and distribution. Recent molecular studies support a single species, *M. leidyi* A. Agassiz, 1865, that exhibits various morphotypes related to environmental conditions (reviewed in Costello *et al.*, 2012). Genetic studies suggest that while the southern European invaders stem from the Gulf of Mexico region, the invaders to northern Europe originate from the coast of New England (Reusch *et al.*, 2010) and could thus be expected to be better adapted to the North East Atlantic climatic conditions.

Mnemiopsis leidyi tolerates a wide range of salinities and temperatures, $\sim 0\text{--}32^{\circ}\text{C}$ and $< 2\text{--}39$ PSU (Purcell *et al.*, 2001; Costello *et al.*, 2012). Egg production of *M. leidyi* from Gullmarsfjorden, Sweden, increases with salinity (range 6–33), with the highest reproductive rates observed at salinities of 25 and 33, and salinity < 10 compromising reproduction (Jaspers *et al.*, 2011). Salinity is thus unlikely to be a limiting factor along the Norwegian coast, where the NCC has a salinity of 25–34.5 and fjords feature a varying brackish surface layer and more saline bottom water influenced by Atlantic water with salinity $> 34.5\text{--}35$ (Sætre, 2007; Aure *et al.*, 2007). At comparable salinities, *M. leidyi* is in its native range encountered at temperatures ranging from 0 to $> 30^{\circ}\text{C}$ (reviewed in Haraldsson *et al.*, 2013). In Narragansett Bay, live *M. leidyi* have even been observed under ice in below freezing temperatures (Costello *et al.*, 2006). Winter minimum temperatures at the hydrographical stations along the Norwegian coast were consistently higher when deeper in the water column (Figure 5), suggesting *M. leidyi* could also find refuge from cold temperatures by overwintering at depth. While this would suggest that

winter temperatures are not the main factor limiting survival along the Norwegian coast, *M. leidyi* were nevertheless not to be found after the exceptionally cold winters of 2010 and 2011.

Summer water temperatures along the southern Norwegian coast are sufficient for *M. leidyi* reproduction, although temperatures may constrain the reproductive rates. The approximate lower temperature limit for successful egg production by *M. leidyi* is around $10\text{--}12^{\circ}\text{C}$ (Costello *et al.*, 2012; Lehtiniemi *et al.*, 2012), but egg production is highly temperature dependent above this minimum requirement (Purcell *et al.*, 2001). The annual maximum temperature along the Norwegian coast is consistently above 12°C , at least to the level of Bud, with most years being notably warmer (Figure 5). Our ranges of minimum and maximum temperatures do not take into account the warming that has occurred during the long observation period over several decades, and are, therefore, conservative estimates of the current situation. Many of our *M. leidyi* observations are from temperatures that would be expected to restrict egg production (Table S1). The highest *M. leidyi* concentrations in Norway were recorded in 2014 and coincided with the warmest water temperatures during our study.

The seasonal monitoring from Raunefjord, on the west coast, shows *M. leidyi* occurring only late in the fall. Both their late appearance and the concurrent low temperatures imply that the *M. leidyi* were advected to the area with the coastal current, rather than produced locally. As our data only show autumnal snapshots from the Skagerrak area, it is not possible to say whether an actively reproducing population was present earlier in the summer, when water temperatures were higher, or whether these observations also reflect advection from a more favourable source area. A recent study modelling habitat suitability in the North Sea has identified Skagerrak as a high risk area for *M. leidyi* establishment due to relatively warm temperatures and high food availability (Collingridge *et al.*, 2014).

Biological interactions

While temperature and salinity set the boundaries for survival and reproductive success of *Mnemiopsis leidyi*, biological interactions are important in controlling population size. Egg production in *M. leidyi* is sensitive to food availability (Reeve *et al.*, 1989) and the species tolerates starvation relatively poorly (Anninsky *et al.*, 2005; Costello *et al.*, 2012). Relatively high prey abundances are, thus, a prerequisite for population expansion (Costello *et al.*, 2012). *Mnemiopsis leidyi* is rarely found where mesozooplankton prey concentrations are below 3 mg C m^{-3} (Kremer, 1994) and concentrations higher by an order of magnitude are needed for unlimited growth. In addition, larvae require microplankton prey concentrations of $> 40\text{ mg C m}^{-3}$ for growth (reviewed in Collingridge *et al.*, 2014). According to a recent modelling study, food availability could limit winter survival in large parts of the North Sea (Collingridge *et al.*, 2014). In comparison, the annual minimum concentration of mesozooplankton in coastal areas of Skagerrak and western Norway occurs in November–January, and varies between 0.3 and 2 mg C m^{-3} , assuming a carbon content of 50% dry weight T. Falkenhaus, unpublished data). However, patches of higher zooplankton concentrations ($8\text{--}14\text{ mg C m}^{-3}$) may be present in inner fjord areas during autumn and winter (Falkenhaus & Dalpadado, 2014), making these areas

potentially suitable for overwintering. Respiration demands of *M. leidy* are also significantly correlated with temperature (Lilley *et al.*, 2014) and would, thus, be relatively low in the cold Nordic waters.

The Norwegian coast has a rich gelatinous fauna (Hosia & Bamstedt, 2007) and competition from native gelatinous predators could reduce *M. leidy* numbers or prevent establishment (Riisgård *et al.*, 2010). A superficially similar lobate, *Bolinopsis infundibulum*, is native along the entire Norwegian coast. It reproduces at lower temperatures than *M. leidy* and its seasonal timing allows it to better utilize the high zooplankton abundances following the spring bloom. *Bolinopsis infundibulum* could also be better at exploiting low prey densities; studies from the Bahamas and the Aegean suggest that *M. leidy* requires an order of magnitude for higher ambient prey concentrations than the co-occurring lobate *Bolinopsis vitrea*, and that the latter dominates in the less productive areas (Kremer *et al.*, 1986; Shiganova *et al.*, 2004).

Predation, particularly by gelatinous predators, can also regulate *M. leidy* populations, with cascading effects on the pelagic ecosystem (reviewed in Costello *et al.*, 2006; Purcell *et al.*, 2001). The devastating effects of the *M. leidy* invasions in the Ponto-Caspian were partly due to the initial lack of predators in these systems. In comparison, a host of native North-East Atlantic gelatinous predators capable of feeding on *M. leidy* have been identified, including *Beroe cucumis* and *Cyanea capillata*, common in Norwegian waters, as well as the more rarely observed *Beroe gracilis*, *Chrysaora hysoscella* and *Pelagia noctiluca* (Hosia & Titelman, 2011; Hosia *et al.*, 2011; Tilves *et al.*, 2012; Galil & Gevili, 2013). In addition, *M. leidy*'s native West Atlantic predator *Beroe ovata*, *sensu* Mayer 1912, credited for reducing the *M. leidy* populations of the Black Sea after its accidental introduction there in the late 1990s, has recently been observed for the first time in the Danish Straits adjacent to the North Sea (Shiganova *et al.*, 2014).

On the other hand, intraguild predation by *M. leidy* could have a negative impact on native gelatinous predators, both through competition for common prey and direct predation on juvenile stages. The ctenophore has been shown to prey on *Beroe* larvae in incubation experiments (Hosia *et al.*, 2011) and high numbers of *Aurelia aurita* planulae have been found in *M. leidy* stomachs from the Kiel Bight (Javidpour *et al.*, 2009). This raises questions about whether the *M. leidy* invasion could play a role in the diminishing *A. aurita* observations in the North Sea (Hosia *et al.*, 2014).

The North European populations of *M. leidy* also carry larvae of the parasitic sea-anemone *Edwardsiella* sp. (Selander *et al.*, 2010). In our Norwegian samples, *Edwardsiella* larvae were seldom observed, but can, for example, be seen infesting the specimen photographed from Trondheimsfjord (http://www.seawater.no/fauna/ctenophora/images/IMG2008_2828.jpg). In 2014, the infection rate in Flødevigen appears to be higher than in earlier years (T. Falkenhaus, personal observation). *Edwardsiella lineata* have been shown to reduce growth rates and, subsequently, reproductive output of infected *M. leidy* in its native range (Bumann & Puls, 1996).

Source–sink dynamics

Mnemiopsis leidy exhibits pronounced source–sink dynamics with local extinctions at less favourable locations combined

with repeated annual re-colonization from adjacent seed areas in both its native and introduced ranges (Purcell *et al.*, 2001; Costello *et al.*, 2006, 2012; Bolte *et al.*, 2013). During the non-reproductive period, advective losses can result in the disappearance of *M. leidy* from large areas (Costello *et al.*, 2006, 2012). Successful overwintering takes place in regions with low water exchange, which allows the populations to persist over winter (Costello *et al.*, 2006, 2012). These regions then serve as source populations for the annual reintroduction of *M. leidy* to the sink areas.

Such dynamics are probably also pertinent to the Norwegian coast. Overwintering *M. leidy* have been observed in southern areas of the North Sea (Van Ginderdeuren *et al.*, 2012; van Walraven *et al.*, 2013) as well as in the Bay of Seine on the south coast of the English Channel (Antajan *et al.*, 2014). These regions with established populations can act as seed areas, with the cyclonic circulation in the North Sea and the NCC transporting ctenophores to and along the Norwegian coast. The decreasing amounts of *M. leidy* observed towards the inner fjords along the Norwegian west coast in 2008 and the late appearance of the ctenophores in Raunefjord in 2010 would also agree with advection of the ctenophores with the coastal current. In addition to our observations from the south coast in 2014, there are also several unconfirmed *M. leidy* observations from the vicinity of Bergen this year. Large numbers of *M. leidy* together with *Pleurobrachia pileus* (~50/50, >3.5 kg combined) were also caught in a trawl from 20–40 m off the Norwegian coast, just south of Sognefjord, in mid-October 2014 (Figure 1), suggesting spreading of the ctenophores with the coastal current also this year (at 60.7967°N 3.7483°E on 15 October 2014, during an R/V G.O. Sars cruise by the Department of Biology, University of Bergen; H. Savolainen, personal communication). Transport time from the German Bight to the Skagerrak has been estimated to be on the order of 1–3 months (Kristensen, 1991). This transport is highly dependent on the wind regime and may vary between years (Heilmann *et al.*, 1991), possibly contributing to the interannual differences in *M. leidy* abundances in Norway, evident, for example, in the beach seine bycatch. Assuming a coastal current velocity of ~0.5 knots, a further month would be spent in reaching the vicinity of Bergen. Southern North Sea *M. leidy* could also overwinter at an intermediate location *en route* (van der Molen *et al.*, 2014), or periodic new inoculations could occur from further afield through ballast water transport.

Within its native range in Narragansett Bay, *M. leidy* overwinter in shallow inshore retention areas (Costello *et al.*, 2006; Beaulieu *et al.*, 2013). Protected inner fjords or polls (offshoot of a fjord with a narrow entrance and a shallow sill) with limited water exchange could also provide a suitable habitat for the establishment of permanent populations in Norway. These habitats feature varying brackish water, higher summer temperatures than the open ocean and refuge from advective losses. While the upper layers of fjords are characterized by estuarine circulation transporting brackish water out of the fjord and, below it, coastal water into the fjord, water exchange below sill level is much reduced, facilitating the retention of plankton and formation of resident populations (Aksnes *et al.*, 1989; Sørnes *et al.*, 2007; Hosia & Bamstedt, 2008). This kind of overwintering strategy is used by the lobate ctenophore *Bolinopsis infundibulum* in Malangen fjord, northern Norway (Falkenhaus, 1996). The

ctenophore overwinters in extremely low concentrations deep in the innermost basin of the fjord, where advection is limited, as well as in a nearby semi-enclosed bay. These seed populations then give rise to a rapid increase in biomass in the spring.

Protected fjords could also provide a favourable habitat in the sense that *M. leidyi* tends to avoid turbulent waters, possibly due to the ambient fluid motion interfering with its feeding currents (Mianzan *et al.*, 2010; Sutherland *et al.*, 2014). In terms of food availability, mesozooplankton concentrations in inner Hardangerfjord are equivalent to $\sim 2\text{--}9.5\text{ mg C m}^{-3}$ in the spring, with patches of $8\text{--}14\text{ mg C m}^{-3}$ found in autumn and winter (Falkenhaus & Dalpadado, 2014). The predatory ctenophore *Beroe cucumis* is also known to inhabit fjord basins year round, potentially limiting the survival of overwintering lobates (Falkenhaus, 1996). Also in the current study, *Beroe cucumis* was observed more or less continuously in Raunefjord. As it is, the monitoring of ctenophores in Norway is insufficient for discovering *M. leidyi* populations potentially establishing in inner fjords, fjord basins or polls before they become noticeably abundant.

CONCLUSIONS

Even though temperature and salinity along the south-western Norwegian coast are within the limits for successful overwintering and reproduction by *Mnemiopsis leidyi*, populations are likely limited by advective losses, temperature constraints on reproductive rates and biological factors including limiting prey densities as well as intraguild competition and predation by native gelatinous predators. The highest *M. leidyi* abundances in the current study were observed in the Skagerrak area, which has also been identified as a high risk area for *M. leidyi* blooms (Collingridge *et al.*, 2014). The populations in Norwegian waters probably exhibit source–sink dynamics, either with the southern North Sea – with its year-round populations acting as a source area – or, speculatively, by *M. leidyi* establishing overwintering seed populations in protected fjords or polls in southern Norway. Considering the high fecundity of *M. leidyi* and the cyclonic circulation in the North Sea, it seems highly likely that outbreaks along the south and west Norwegian coasts may be expected in future years, with favourable conditions or significant inflow from the southern North Sea. Higher water temperatures due to climate change could, in the future, enhance reproductive success and facilitate overwintering of *M. leidyi* in Norwegian waters. In *M. leidyi*'s native range, spatiotemporal expansion due to a warming climate seems to have increased its potential for inflicting a negative impact on the plankton community (Beaulieu *et al.*, 2013). Suggested future research includes the systematic monitoring of *M. leidyi* in Norwegian waters in order to identify environmental parameters influencing the interannual patterns of abundance, a focus on *M. leidyi*'s overwintering ecology including identifying and monitoring potential overwintering habitats as well as the modelling of the potential source–sink dynamics at scales relevant to the Norwegian coast.

Supplementary material and methods

The supplementary material for this article can be found at <http://www.journals.cambridge.org/MBD>.

ACKNOWLEDGEMENTS

This work was supported by the Research Council of Norway (RCN) program HAVKYST (A.H. and T.F., project no. 190304), the ForBio Research School funding from RCN (A.H., project no. 210460) and the Norwegian Taxonomy Initiative (A.H., project no. 70184215). We wish to thank the crews of R/Vs Håkon Mosby, Hans Brattstrøm and G.M. Dannevig for help with sampling; Ø. Paulsen, M.J. Ohldieck and other participants in the beach seine project; J. Albretsen for help with hydrography and K. Telnes, S. Sarre and other UW photographers and divers for responding to our queries.

REFERENCES

- Aksnes D.L., Aure J., Kaartvedt S., Magnesen T. and Richard J. (1989) Significance of advection for the carrying capacities of fjord populations. *Marine Ecology Progress Series* 50, 263–274.
- Anninsky B.E., Finenko G.A., Abolmasova G.I., Hubareva E.S., Svetlichny L.S., Bat L. and Kideys A.E. (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.
- Antajan E., Bastian T., Raud T., Brylinski J.-M., Hoffman S., Breton G., Cornille V., Delegrange A. and Vincent D. (2014) The invasive ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 along the English Channel and the North Sea French coasts: another introduction pathway in northern European waters? *Aquatic Invasions* 9, 167–173.
- Aure J., Asplin L. and Sætre R. (2007) Coast/fjord water exchange. In Sætre R. (ed.) *The Norwegian Coastal Current*, Trondheim: Tapir Academic Press, pp. 115–124.
- Beaulieu W.T., Costello J.H., Klein-Macphée G. and Sullivan B.K. (2013) Seasonality of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Journal of Plankton Research* 35, 785–791.
- Boersma M., Malzahn A.M., Greve W. and Javidpour J. (2007) The first occurrence of the ctenophore *Mnemiopsis leidyi* in the North Sea. *Helgoland Marine Research* 61, 153–155.
- Bolte S., Fuentes V., Haslob H., Huwer B., Thibault-Botha D., Angel D., Galil B., Javidpour J., Moss A.G. and Reusch T.B.H. (2013) Population genetics of the invasive ctenophore *Mnemiopsis leidyi* in Europe reveal source–sink dynamics and secondary dispersal to the Mediterranean Sea. *Marine Ecology Progress Series* 485, 25–36.
- Bumann D. and Puls G. (1996) Infestation with larvae of the sea anemone *Edwardsia lineata* affects nutrition and growth of the ctenophore *Mnemiopsis leidyi*. *Parasitology* 113, 123–128.
- Collingridge K., van der Molen J. and Pitois S. (2014) Modelling risk areas in the North Sea for blooms of the invasive comb jelly *Mnemiopsis leidyi* A. Agassiz, 1865. *Aquatic Invasions* 9, 21–36.
- Costello J.H., Bayha K.M., Mianzan H.W., Shiganova T.A. and Purcell J.E. (2012) Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) from a native to an exotic species: a review. *Hydrobiologia* 690, 21–46.
- Costello J.H., Gifford D.J., Van Keuren D. and Sullivan L.J. (2006) Seasonal refugia, shoreward thermal amplification, and metapopulation dynamics of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Limnology and Oceanography* 51, 1819–1831.
- Daskalov G.M., Grishin A.N., Rodionov S. and Mihneva V. (2007) Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences of the United States of America* 104, 10518–10523.

- Durif C.M., Gjosaeter J. and Vollestad L.A.** (2011) Influence of oceanic factors on *Anguilla anguilla* (L.) over the twentieth century in coastal habitats of the Skagerrak, southern Norway. *Proceedings of the Royal Society B: Biological Sciences* 278, 464–473.
- Faasse M.A. and Bayha K.M.** (2006) The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in coastal waters of the Netherlands: an unrecognized invasion? *Aquatic Invasions* 1, 270–277.
- Falkenhaus T.** (1996) Distributional and seasonal patterns of ctenophores in Malangen, northern Norway. *Marine Ecology Progress Series* 140, 59–70.
- Falkenhaus T. and Dalpadado P.** (2014) Diet composition and food selectivity of sprat (*Sprattus sprattus*) in Hardangerfjord, Norway. *Marine Biology Research* 10, 203–215.
- Fromentin J.-M., Stenseth N.C., Gjosaeter J., Bjørnstad O.N., Falck W. and Johannessen T.** (1997) Spatial patterns of the temporal dynamics of three gadoid species along the Norwegian Skagerrak coast. *Marine Ecology Progress Series* 155, 209–222.
- Galil B.S. and Gevili R.** (2013) A moveable feast: *Beroe cucumis* sensu Mayer, 1912 (Ctenophora; Beroidea; Beroidea) preying on *Mnemiopsis leidyi* A. Agassiz, 1865 (Ctenophora; Lobata; Bolinopsidae) off the Mediterranean coast of Israel. *BioInvasions Records* 2, 191–194.
- Ghabooli S., Shiganova T., Zhan A., Cristescu M., Eghtesadi-Araghi P. and MacIsaac H.** (2011) Multiple introductions and invasion pathways for the invasive ctenophore *Mnemiopsis leidyi* in Eurasia. *Biological Invasions* 13, 679–690.
- Granhag L., Møller L.F. and Hansson L.J.** (2011) Size-specific clearance rates of the ctenophore *Mnemiopsis leidyi* based on *in situ* gut content analyses. *Journal of Plankton Research* 33, 1043–1052.
- Hansson H.G.** (2006) Ctenophores of the Baltic and adjacent seas – the invader *Mnemiopsis* is here! *Aquatic Invasions* 1, 295–298.
- Haraldsson M., Jaspers C., Tiselius P., Aksnes D.L., Andersen T. and Titelman J.** (2013) Environmental constraints of the invasive *Mnemiopsis leidyi* in Scandinavian waters. *Limnology and Oceanography* 58, 763–763.
- Heilmann J.P., Olsen O.V. and Danielssen D.S.** (1991) The potential of the Jutland coastal current as a transporter of nutrients to the Kattegat. *International Council for the Exploration of the Sea (CM Documents)*, CM 1991/C:34, 20 pp.
- Hosia A. and Bamstedt U.** (2007) Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway. *Marine Ecology Progress Series* 351, 113–127.
- Hosia A. and Bamstedt U.** (2008) Seasonal abundance and vertical distribution of siphonophores in western Norwegian fjords. *Journal of Plankton Research* 30, 951–962.
- Hosia A., Falkenhaus T. and Naustvoll L.J.** (2014) Trends in abundance and phenology of *Aurelia aurita* and *Cyanea* spp. at a Skagerrak location, 1992–2011. *Marine Ecology Progress Series* 498, 103–115.
- Hosia A. and Titelman J.** (2011) Intraguild predation between the native North Sea jellyfish *Cyanea capillata* and the invasive ctenophore *Mnemiopsis leidyi*. *Journal of Plankton Research* 33, 535–540.
- Hosia A., Titelman J., Hansson L.J. and Haraldsson M.** (2011) Interactions between native and alien ctenophores: *Beroe gracilis* and *Mnemiopsis leidyi* in Gullmarsfjorden. *Marine Ecology Progress Series* 422, 129–138.
- Jaspers C., Møller L.F. and Kiorboe T.** (2011) Salinity gradient of the Baltic Sea limits the reproduction and population expansion of the newly invaded comb jelly *Mnemiopsis leidyi*. *PLoS ONE* 6, e24065, doi: 10.1371/journal.pone.0024065.
- Javidpour J., Molinero J.C., Peschutter J. and Sommer U.** (2009) Seasonal changes and population dynamics of the ctenophore *Mnemiopsis leidyi* after its first year of invasion in the Kiel Fjord, Western Baltic Sea. *Biological Invasions* 11, 873–882.
- Javidpour J., Sommer U. and Shiganova T.** (2006) First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. *Aquatic Invasions* 1, 299–302.
- Kideys A.E.** (2002) Fall and rise of the Black Sea ecosystem. *Science* 297, 1482–1484.
- Knowler D.** (2005) Reassessing the costs of biological invasion: *Mnemiopsis leidyi* in the Black sea. *Ecological Economics* 52, 187–199.
- Kremer P.** (1994) Patterns of abundance for *Mnemiopsis leidyi* in US coastal waters: a comparative overview. *ICES Journal of Marine Science* 51, 347–354.
- Kremer P., Reeve M.R. and Syms M.A.** (1986) The nutritional ecology of the ctenophore *Bolinopsis vitrea*: comparisons with *Mnemiopsis mccradyi* from the same region. *Journal of Plankton Research* 8, 1197–1208.
- Kristensen K.B.** (1991) *The Jutland Coastal Current*. Series Paper, Vol. 53, Institute of Hydrodynamics and Hydraulic Engineering, Technical University of Denmark, Denmark.
- Lehtiniemi M., Lehmann A., Javidpour J. and Myrberg K.** (2012) Spreading and physico-biological reproduction limitations of the invasive American comb jelly *Mnemiopsis leidyi* in the Baltic Sea. *Biological Invasions* 14, 341–354.
- Lilley M.K.S., Thibault-Botha D. and Lombard F.** (2014) Respiration demands increase significantly with both temperature and mass in the invasive ctenophore *Mnemiopsis leidyi*. *Journal of Plankton Research* 36, 831–837.
- Mianzan H.W., Martos P., Costello J.H. and Guerrero R.A.** (2010) Avoidance of hydrodynamically mixed environments by *Mnemiopsis leidyi* (Ctenophora: Lobata) in open-sea populations from Patagonia, Argentina. *Hydrobiologia* 645, 113–124.
- Oliveira O.M.P.** (2007) The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic Seas. *Aquatic Invasions* 2, 185–189.
- Purcell J.E., Shiganova T.A., Decker M.B. and Houde E.D.** (2001) The ctenophore *Mnemiopsis* in native and exotic habitats: U.S. estuaries versus the Black Sea basin. *Hydrobiologia* 451, 145–176.
- R Core Team** (2013) *R: a Language and environment for statistical computing*. R Foundation for Statistical Computing: Vienna, Austria, ISBN 3-900051-07-0 at <http://www.R-project.org/>
- Reeve M.R., Syms M.A. and Kremer P.** (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.B.H., Bolte S., Sparwel M., Moss A.G. and Javidpour J.** (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., Barth-Jensen C. and Madsen C.V.** (2010) High abundance of the jellyfish *Aurelia aurita* excludes the invasive ctenophore *Mnemiopsis leidyi* to establish in a shallow cove (Kertinge Nor, Denmark). *Aquatic Invasions* 5, 347–356.
- Roohi A., Kideys A.E., Sajjadi A., Hashemian A., Pourgholam R., Fazli H., Khanari A.G. and Eker-Develi E.** (2010) Changes in biodiversity of phytoplankton, zooplankton, fishes and macrobenthos in the Southern Caspian Sea after the invasion of the ctenophore *Mnemiopsis leidyi*. *Biological Invasions* 12, 2343–2361.

- Selander E., Møller L., Sundberg P. and Tiselius P. (2010) Parasitic anemone infects the invasive ctenophore *Mnemiopsis leidyi* in the North East Atlantic. *Biological Invasions* 12, 1003–1009.
- Shiganova T.A., Christou E.D., Bulgakova J.V., Sioukou-Frangou I., Zervoudaki S. and Siapatis A. (2004) Distribution and biology of *Mnemiopsis leidyi* in the Northern Aegean Sea, and comparisons with the indigenous *Bolinopsis vitrea*. In Dumont H., Shiganova T. and Niermann U. (eds) *Aquatic invasions in the Black, Caspian and Mediterranean Seas. The ctenophores Mnemiopsis leidyi and Beroe in the Ponto-Caspian and other aquatic invasions*. Netherlands: Springer, pp. 113–135.
- Shiganova T.A., Riisgård H.U., Ghabooli S. and Tendal O.S. (2014) First report on *Beroe ovata* in an unusual mixture of ctenophores in the Great Belt (Denmark). *Aquatic Invasions* 9, 111–116.
- Sutherland K.R., Costello J.H., Colin S.P. and Dabiri J.O. (2014) Ambient fluid motions influence swimming and feeding by the ctenophore *Mnemiopsis leidyi*. *Journal of Plankton Research* 36, 1310–1322.
- Sætre R. (2007) Properties of coastal water masses. In Sætre R. (ed.) *The Norwegian Coastal Current*. Trondheim: Tapir Academic Press, pp. 59–72.
- Sætre R. and Aure J. (2007) Characteristic circulation features. In Sætre R. (ed.) *The Norwegian Coastal Current*. Trondheim: Tapir Academic Press, pp. 99–114.
- Sørnes T.A., Aksnes D.L., Bamstedt U. and Youngbluth M.J. (2007) Causes for mass occurrences of the jellyfish *Periphylla periphylla*: a hypothesis that involves optically conditioned retention. *Journal of Plankton Research* 29, 157–167.
- Tendal O.S., Jensen K.R. and Riisgård H.U. (2007) Invasive ctenophore *Mnemiopsis leidyi* widely distributed in Danish waters. *Aquatic Invasions* 2, 455–460.
- Tilves U., Purcell J.E., Marambio M., Canepa A., Olariaga A. and Fuentes V. (2012) Predation by the scyphozoan *Pelagia noctiluca* on *Mnemiopsis leidyi* ctenophores in the NW Mediterranean Sea. *Journal of Plankton Research* 35, 218–224.
- van der Molen J., van Beek J., Augustine S., Vansteenbrugge L., van Walraven L., Langenberg V., van der Veer H.W., Hostens K., Pitois S. and Robbens J. (2014) Modelling survival and connectivity of *Mnemiopsis leidyi* in the southern North Sea and Scheldt estuaries. *Ocean Science Discussion* 11, 1561–1611.
- Van Ginderdeuren K., Hostens K., Hoffman S., Vansteenbrugge L., Soenen K., De Blauwe H., Robbens J. and Vincx M. (2012) Distribution of the invasive ctenophore *Mnemiopsis leidyi* in the Belgian part of the North Sea. *Aquatic Invasions* 7, 163–169.
- van Walraven L., Langenberg V.T. and van der Veer H.W. (2013) Seasonal occurrence of the invasive ctenophore *Mnemiopsis leidyi* in the western Dutch Wadden Sea. *Journal of Sea Research* 82, 86–92.
- and
- Wiebe P.H., Morton A.W., Bradley A.M., Backus R.H., Craddock J.E., Barber V., Cowles T.J. and Flierl G.R. (1985) New developments in the MOCNESS, an apparatus for sampling zooplankton and micro-nekton. *Marine Biology* 87, 313–323.

Correspondence should be addressed to:

A. Hosia
 The Natural History Collections
 University Museum of Bergen
 University of Bergen
 P.O. Box 7800
 NO-5020 Bergen, Norway
 emails: aino.hosia@um.uib.no, aino.hosia@gmail.com