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# Sightings of extraordinary marine species in the SW Baltic Sea linked to saline water inflows

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## ABSTRACT

The Baltic Sea, located in northern Europe, is one of the largest brackish water bodies in the world. Salinity levels range from fresh water conditions in the northeast to full strength saline waters at its transition zone to the North Sea in the west. Most of the water exchange happens in the SW Baltic Sea, the Belt Sea, where fresh water exits the Baltic Sea at the surface, while high saline, oxygen rich water is entering the Baltic at depth. Due to the extended salinity gradient of the Baltic Sea, a variety of species occur at the limit of their physiological tolerance and preference, i.e. in areas and habitats not representing their marine or fresh water origin. Additionally, the Baltic Sea is known for its high share of non-indigenous species, which have established. In this study, we compiled extraordinary sightings of transient, non-native or potentially range expanding species in the SW Baltic Sea for a period from 2001 to 2018. We focused on jellyfish, squid, fishes and marine mammals and linked their occurrences to the local hydrography. Hydrographic conditions, such as water temperature and salinity, were obtained from a high spatio-temporally resolved hydrodynamic Baltic Sea model, covering a daily resolved 40-year time series. We investigated that changes in the occurrence of exceptional species reflect the dynamics of water mass exchange between the Kattegat/Skagerrak and the SW Baltic Sea. Our analyses show that these changes could be related to the presence of anomalously high saline water masses. However, only a minor part of the sightings was caused by major Baltic inflow events, which are important to sustain oxygen rich deep water in the central Baltic Sea. This documents that the hydrographically highly dynamic SW Baltic Sea needs special attention for monitoring of non-indigenous species, as (i) high saline and warm water intrusions are more frequent than currently believed and ii) can be linked to sightings of exceptional species in the SW Baltic Sea. Additionally, most of the recent sightings occurred during anomalously warm periods. This supports the hypothesis, that the Baltic Sea is presently a predominant receiver area for non-indigenous species from warmer regions of the world.

## 1. Introduction

Extraordinary sightings of marine species outside their normal distribution range commonly attract large public attention, especially for animals easily observed by non-experts, such as mammals and charismatic fish or jellyfish species. Such sightings can either be related to active or passive range expansions, especially at the borders of the common distribution ranges (Van Gennip et al., 2017), or can be explained by the introduction of non-indigenous species due to climate-driven and/or human activities (Sorte et al., 2010). Non-indigenous species transported into a new environment can have profound effects

on marine ecosystems (Carlton and Geller, 1993). It has been suggested, that the highest establishment success of non-indigenous species occurs at intermediate salinities (Paavola et al., 2005), due to a minimum richness of native species (“Arten-minimum” sensu Remane, 1934). An example of an intermediate saline water body is the south-western Baltic Sea, located in northern Europe (hereafter SW Baltic Sea; Fig. 1). The Baltic Sea is one of the largest brackish water body of the world and its salinity spans fresh water conditions in the northeast to full strength saline waters at its transition to the North Sea in the west. In the Baltic Sea, many species occur at the limit of their physiological tolerance and preference, i.e. in areas and habitats not representing their marine or

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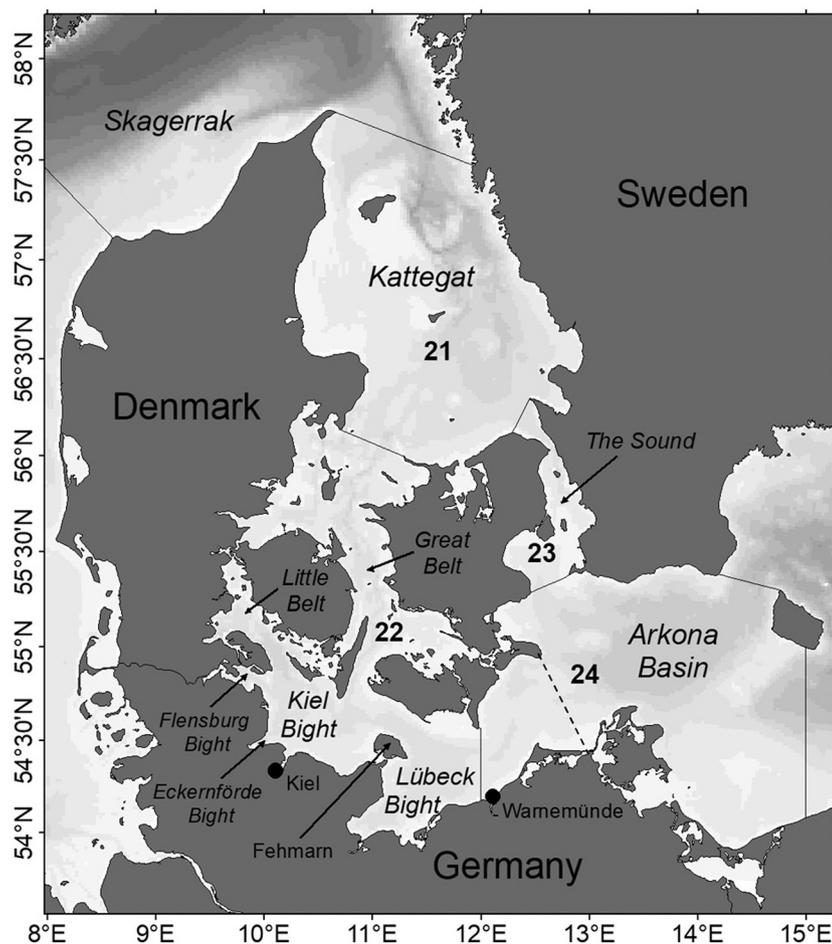
fresh water origin. Furthermore, Baltic species are often exposed to large environmental fluctuations (Bonsdorff, 2006; HELCOM, 2009). Generally, changes occur at higher amplitudes in coastal compared to open sea environments and cause hydrographic instability and biological fluctuations (Segerstråle, 1969).

The overall water balance of the Baltic Sea is controlled by in- and outflows through the Belt Sea, a part of the SW Baltic Sea with the Little Belt, the Great Belt and the Sound (Lehmann et al., 2002). Overall, river runoff and precipitation are causing a freshwater surplus, which forces a general outflow of brackish water within the upper layer of the Baltic Sea (Schinke and Matthäus, 1998). The surface water outflow is compensated by inflows of high saline water from the Kattegat at depth. Hence, the physical structure of the Baltic Sea is characterized by vertical and horizontal salinity gradients. Inflow of high saline bottom water is mainly caused by persistent, i.e. of a longer-term duration, strong westerly winds over the eastern North Atlantic and northern Europe (Schinke and Matthäus, 1998). For the long-term mean, the volume change of the Baltic Sea is zero, i.e. the freshwater surplus and the deep-water inflow are balanced by the surface water outflow. Thus, highly fluctuating in- and outflow is forced by the sea level inclination between the Kattegat and the SW Baltic Sea (Lehmann et al., 2002). Dynamics of the water exchange between the Baltic Sea and the North Sea have been studied in detail (e.g.: Gustafsson, 1997). However, dynamics of the hydrographic system in the SW Baltic Sea, especially the Belt Sea, remain largely neglected.

The Belt Sea is of fundamental importance for the water mass exchange between Kattegat and the central Baltic Sea. The Kattegat is a shallow water region with a mean depth of only 23 m and is directly connected to the Skagerrak in the north, which is part of the North Sea.

The Belt Sea is on average 13 m deep and strongly affected by water of Baltic origin in its surface. Water entering the Baltic Sea at depth has to pass the Darss Sill (Fig. 1), which is one of the shallowest obstacles for water masses entering the central Baltic (Fennel and Sturm, 1992). Hence, the Darss Sill (18 m deep) separates the Belt Sea to the east from the Arkona Basin, an area with maximum depths of about 45 m. The Belt Sea is further characterized by deep and narrow channels, such as the Great Belt and the Fehmarn Belt, which are responsible for most of the water mass exchange between the Kattegat and the Arkona Basin (Fennel and Sturm, 1992; Schinke and Matthäus, 1998). Another connection between the Kattegat and the Arkona Basin is the Sound. As it contains two sills east of Copenhagen with depths of only ca. 8 m, usually only a minor part of the bottom exchange is passing through this channel. However, near the surface, low saline water mainly exits the Baltic Sea through the Sound towards the Kattegat. The Little Belt, located between the Danish mainland and the island of Fyn, only plays a minor role for the water mass balance due to its small cross section, irrespectively of its high flow velocities.

For marine systems, hydrographic regimes are of significant importance to shape and sustain species distribution ranges (Gaylord and Gaines, 2000). Additionally, ocean currents and current driven interconnectivity between regions play a fundamental role in secondary spread dynamics of non-indigenous species and have been documented to explain invasion dynamics and range expansions of marine holoplanktonic species (Jaspers et al., 2018). However, climate change leads to wide ranging shifts of marine habitats with changing ocean currents impacting the future distribution range of passively dispersed plankton organisms (Van Gennip et al., 2017). Furthermore, ocean warming affects actively swimming species, which expand their



**Fig. 1.** Investigation area showing the extended SW Baltic Sea with its transition (Skagerrak) to the North Sea. ICES subdivision (SD) numbers are indicated by solid line. The Belt Sea (SD 22 + 23) with the Little Belt, Great Belt, and The Sound, being part of the SW Baltic Sea, where the Darss Sill (indicated by dashed line) separates the SW from the Central Baltic Sea. Grey shading corresponds to areas of similar bottom depth. Kiel fjord is indicated by locality name Kiel, Fehmarn Belt is located above the island Fehmarn.

distribution polewards (Burrows et al., 2011).

Here, we present sightings of uncommon passively drifting as well as actively swimming species from various taxonomic groups (invertebrates, fishes and marine mammals), which seem to have expanded their geographic distribution into the SW Baltic Sea during recent years: European common squid (*Alloteuthis subulata*), lion's mane jellyfish (*Cyanea capillata*), angler fish (*Lophius piscatorius*), ocean sunfish (*Mola mola*), common bottlenose dolphin (*Tursiops truncatus*), white-beaked dolphin (*Lagenorhynchus albirostris*) and fin whale (*Balaenoptera physalus*) (Table 1).

Some of the selected species have sporadically been reported from various parts of the SW Baltic Sea for a long time. As an example, records of the European common squid in the Belt Sea date back to the 1930s (Jaeckel, 1937, 1958). It is the most abundant squid in the North Sea and its easternmost distribution is generally considered to be the Skagerrak/Kattegat (Hastie et al., 2009). The occurrence of extraordinary species has always been sparse, and they have been considered either to be vagrants, immigrants or being introduced. Most of them, such as the ocean sunfish or the fin whale are elusive and their sightings commonly attract large public and media attention. Environmental or hydrographic changes that could be responsible for the expanded geographic distribution range of the species mentioned above remain unknown and have so far not been linked to local hydrographic anomalies in the SW Baltic Sea. In this study we explore if occurrence and abundance of selected non-indigenous species in the Belt Sea reflect the dynamics of water mass exchange between the higher saline Kattegat/Skagerrak and the SW Baltic Sea.

Based on scientific literature, reports from media as well as own citizen science information, we will first provide a detailed compilation on extraordinary marine species sightings in the SW Baltic Sea. In detail, the present study uses a hydrodynamic modelling approach to provide retrospective and statistical analyses on (i) the spatially resolved variability of the daily abiotic environmental conditions (temperature, salinity) in the Belt Sea. In particular, our objectives are (ii) to statistically classify the variability of the past water mass distribution and (iii) to present it in terms of regional time series. Another objective of this study is (iv) to assign observational evidence of the exceptional occurrence of cnidarians, cephalopods, fishes and marine mammals to statistically specified temperature and salinity anomalies in the Belt Sea. By linking actual physical environmental conditions during exceptional

sightings of marine animals in the Belt Sea to the average condition over a 40 years period (1979–2018), we aim to understand the importance of high saline water intrusion on the current and expected future distribution of marine life in the SW Baltic Sea.

## 2. Material and methods

### 2.1. Hydrodynamic modelling

We used an established hydrodynamic model configuration described and evaluated in Lehmann et al. (2014) and Lennartz et al. (2014). This configuration combines a coupled sea ice-ocean model for the entire Baltic Sea (BSIOM; Lehmann, 1995; Lehmann and Hinrichsen, 2000; Lehmann et al., 2002). This high-resolution hydrodynamic model has a horizontal resolution of 2.5 km with 60 vertical levels. The upper 102 m are resolved at levels of 3 m thickness and further below at levels of 6 m thickness, respectively. The model domain includes the entire Baltic Sea including the Kattegat as well as the Skagerrak. The hydrodynamic model is realistically forced using the ERA-Interim atmospheric re-analysis fields (Dee et al., 2011), with a 6-hourly temporal and approximately 80 km spatial resolution, respectively. The forcing data were interpolated on the model grid with a 3-hourly resolution and include surface air pressure, precipitation, cloudiness, and air- and dew point temperatures at 2 m height from sea surface. Wind speed and wind direction at 10 m height from sea surface were calculated from geostrophic winds with respect to different degrees of roughness on the open sea and off the coast (Bumke et al., 1998). BSIOM forcing functions, such as wind stress, radiation and heat fluxes were calculated according to Rudolph and Lehmann (2006). Additionally, river runoff was prescribed from a monthly mean runoff data set (Kronsell and Andersson, 2012). Prognostic variables of the model are the baroclinic current field, the 3-D temperature, salinity and oxygen distributions, the 2-D surface elevations and the barotropic transport. Physical properties simulated by the model agree well with known circulation features and observed physical conditions in the Baltic Sea (for further description see Hinrichsen et al., 1997; Lehmann et al., 2014).

### 2.2. Oceanographic baseline and noise

The quasi-realistic temperature and salinity output of BSIOM

**Table 1**

Representative sightings of eight actively swimming species from various taxonomic groups that probably have expanded their geographical distribution into the SW Baltic Sea.

| Group                 | Common name           | Species name                      | Sighting location             | Sighting date            | Reference   |
|-----------------------|-----------------------|-----------------------------------|-------------------------------|--------------------------|---|
| Invertebrates         |                       |                                   |                               |                          |   |
| Cnidaria, Scyphozoa   | Lion's mane jellyfish | <i>Cyanea capillata</i>           | Kiel Bight                    | 2014 Aug                 | this study, see Fig. 4                              |
|                       |                       |                                   | Kiel Bight                    | 2018 Aug                 | Kieler Nachrichten, 30.8.2028, interview C. Jaspers |
| Mollusca, Cephalopoda | European common squid | <i>Alloteuthis subulata</i>       | Kiel Bight, Bellevue Pier     | 1999 Nov                 | Piatkowski, pers. obs.                              |
|                       |                       |                                   | Kiel Bight, off Kiel Fjord    | 2001 Jan                 | Herrmann et al. (2001)                              |
|                       |                       |                                   | Mecklenburg Bay, Warnemünde   | 2003 Dec                 | Ostsee-Zeitung, 11.12.2003                          |
|                       |                       |                                   | Kiel Bight, off Schilksee     | 2010 Dec                 | Schröder, pers. comm.                               |
|                       |                       |                                   | Kiel Bight, Eckernförde Bight | 16.12.2014               | Piatkowski, pers. obs.                              |
|                       |                       |                                   | Kiel Bight, Eckernförde Bight | 19.11.2015               | Eckernförder Zeitung, 2.12.2015                     |
| Vertebrates           |                       |                                   |                               |                          |   |
| Actinopterygii        | Ocean sunfish         | <i>Mola mola</i>                  | Kiel Bight, Hohwacht          | 15.12.2018               | Deutsche Presse Agentur, 17.12.2018                 |
|                       |                       |                                   | Little Belt, Kiel Bight       | 2016 Jan local fishermen |   |
| Cetacea               | Angler fish           | <i>Lophius piscatorius</i>        | Kiel Bight, Eckernförde Bight | 2015 Jan                 | Petereit, pers. obs.                                |
|                       | Bottlenose dolphin    | <i>Tursiops truncatus</i>         | Lübeck Bight, near Fehmarn    | 2015 Dec                 | Kieler Nachrichten, December 2015                   |
|                       | White-beaked dolphin  | <i>Lagenorhynchus albirostris</i> | Kiel Bight, off Olpenitz      | 2018 Jun                 | Schweinswal e.V.                                    |
|                       | Fin whale             | <i>Balaenoptera physalus</i>      | Kiel Bight, Kiel harbour      | 2003 Jul                 | Jensen and Kinze (2011)                             |
|                       |                       |                                   | Little Belt, Flensburg Bight  | 2006 Aug                 | Jensen and Kinze (2011)                             |

provides the basis for detailed analyses of the abiotic environment in the Belt Sea. If we want to know about the environmental status of water mass distribution at any time it is mandatory to know about the mean conditions (baseline) and furthermore about the width of its natural fluctuations in space and time (noise). For three selected sub-areas (Eckernförde Bight, Kiel Bight and Little Belt) with a size of  $\sim 100 \text{ km}^2$  in the Belt Sea (Fig. 1), data were aggregated daily for 3 m depth layers. For each of these sub-areas we calculated vertically resolved long-term averages of temperature and salinity (baseline). Our study is mainly focused on the westernmost part of the SW Baltic Sea (Eckernförde, Kiel and Lübeck Bight), because here we can expect that the sighted extraordinary and/or non-indigenous species mainly passed through the Little and Great Belt. However, averaged data provided no information about their variability (noise). Thus, for a more comprehensive presentation regarding the variance of temperatures and salinities we have calculated their standard deviations. As an example, Fig. 2 shows the baseline and noise patterns for temperature and salinity at three different depths (4.5 m, 10.5 m and 16.5 m) in the Kiel Bight area. Because of a high degree of similarity of the hydrography between the sub-areas, we have decided not to provide any further detailed graphic information.

To provide spatio-temporal information about the noise level of temperature and salinity data for every sub-area, we have calculated their temporal variability as their differences with regard to the mean and corresponding standard deviations as a baseline. We have developed an index of salinity fluctuations ( $SF$ ) by calculating differences between daily data and daily mean data (40-years averages), both provided by the hydrodynamic model, and normalized by the standard deviation of the long-term daily mean,

$$SF = (S_{daily} - S_{mean}) / S_{stdv} \quad (1)$$

with  $S_{mean}$  the 40-years daily mean salinity data and  $S_{stdv}$  the standard deviations, while  $S_{daily}$  represents the daily quasi-realistic data of salinity. Furthermore, with the same approach we have calculated a data set for temperature ( $TF$ ). For further analyses we have divided the environmental information into three categories:  $TF1$  and  $SF1 < -1$  (noise),  $-1 \geq TF2$  and  $SF2 \leq 1$  (baseline), and  $TF3$  and  $SF3 > 1$  (noise). Information on the physical environmental conditions during the time window of exceptional marine animal sightings in the Belt Sea together with the average hydrographic conditions over a 40 years period (1979–2019), will allow us to understand the importance of high saline water intrusions on the distribution of such animals in the area.

### 2.3. Observational evidence of sightings of extraordinary marine species in the physical environment

We conducted a comprehensive literature review to extract information about exceptional sightings for species with a distribution range that does not include reproducing sub-populations in the Belt Sea. Due to the sporadic nature of exceptional species sightings, especially considering marine mammals, we also considered information from local newspapers as well as scientific expert confirmed sightings from local fishermen and diving clubs (see Table 1). In order to account for the uncertainty of correct first occurrence date of the respective species in the Belt Sea, we have assigned the date of the species occurrence to the statistically specified factors ( $SF$  and  $TF$ ) for temperature and salinity. Hereby, only environmental data in a time window 60 days backward of the confirmed sighting were considered.

To get high resolution information about population fluctuation over

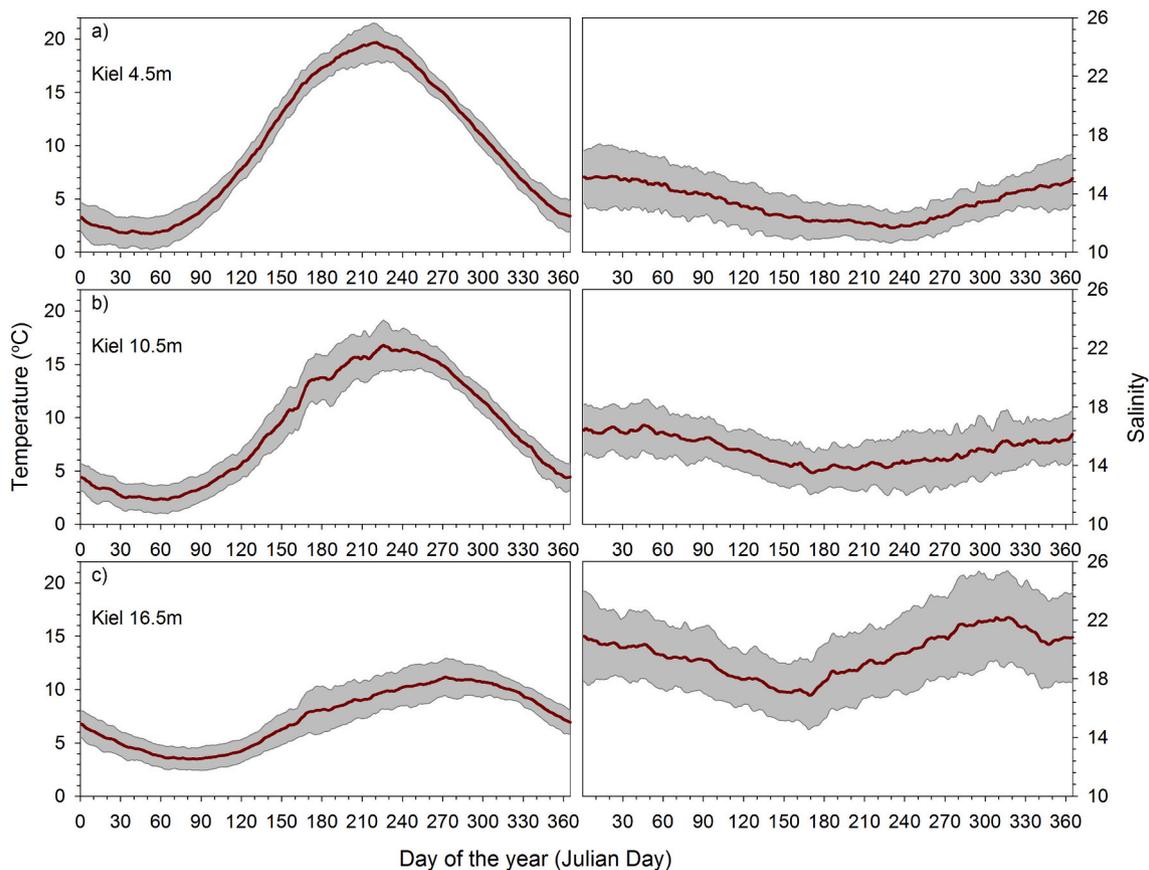


Fig. 2. Annual mean hydrographic conditions in Kiel Bight for three different depth layers (a: 4.5, b: 10.5, c: 16.5 m). 40 year averaged (red line 1979–2018) temperature (left) and salinity (right) profiles with  $\pm 1SD$  (grey area). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

short time periods, large (>15 cm diameter) individuals of the lion's mane jellyfish (*C. capillata*) were monitored in the outer part of Kiel Fjord, which is a larger water inlet connecting Kiel Bight with the city of Kiel. Sampling was performed from 2nd of June until 8th of November 2014 along 4 transects of 180 to 330 m lengths. Transects were investigated at least once a week and jellyfish abundances are presented as average *C. capillata* abundance 100 m transect<sup>-1</sup> ± SD. Observations were performed visually during low wave action, when the bottom could be seen. An area of 5 m in width along the transect down to the bottom was covered.

#### 2.4. Time series analysis of categorized environmental conditions

To obtain long-term information of the physical environment in the SW Baltic Sea we constructed a 40 years-time series for each of the different temperature and salinity categories. Besides categories, the environmental data were calculated for 3 different depth levels (4.5 m, 10.5 m and 16.5 m) as well as for all quarters of a year.

Generally, we made our analyses in order to more clearly state that hydrographic properties (temperature and salinity) at the time of exceptional sighting of species compared with 40-year means, were substantially different compared to the long-term mean.

### 3. Results

#### 3.1. Observations of extraordinary sightings in relation to current physical conditions

Daily resolved abiotic environmental conditions in the Belt Sea (Fig. 1) have been extracted as hydrodynamic model results for the observation period 1979–2018 for subsequent analysis. The baseline (±1SD) of average salinity and temperature annual cycles for three depth strata (4.5 m, 10.5 m, 16.5 m) in Kiel Bight is shown in Fig. 2.

An example of an exceptional sighting is the common bottlenose dolphin (*T. truncatus*) during December 2015 in the Belt Sea, SW Baltic Sea (Fig. 3). Its occurrence is presented along with data on the 40-year average as well as actual physical environment. Data show that temperature and salinity values during the sighting period were on average higher than the long-term mean (Fig. 3a). Furthermore, vertical profiles of *TF* and *SF* show that for relatively warm temperatures extremely high saline water masses are present during this exceptional sighting, with a

maximum *SF*-ratios of 2.5 (Fig. 3b).

Additional vertical temperature and salinity profiles of the baseline (±1SD) along with simulated temperature and salinity depth profiles, which correspond to the exceptional sighting of invertebrates (Fig. S1), fish and marine mammals (Fig. S2), show that during the exceptional sightings, extreme salinity and/or temperature conditions persist.

During August 2014 and August 2018, exceptionally high abundances of the lion's mane jellyfish (*C. capillata*) were observed in Kiel Bight with high salinity ratios (*SFs*) ranging between around 0,8 to >3 and low temperature ratios (*TFs*), ranging between -2 to 0. This indicates inflow of higher saline, colder water masses from the Kattegat/Skagerrak via Belt Sea into Kiel Fjord (Figs. 4, S1). During summer and autumn, temperatures in high saline areas were typically colder compared to long-term mean conditions of the Baltic Sea (Fig. S1). Similarly, the occurrence of European common squid (*A. subulata*) is characterized by anomalously high temperature and salinity in mid-depth water layers (Fig. S1). For the *SFs* maxima of 2.5 and almost 2 were obtained during January 2001 and December 2014, respectively (Figs. S1). However, the *TFs* show inverse patterns compared to the situation observed during intense *C. capillata* sightings in summer and autumn (Fig. 4). Hence, exceptional squid sightings were characterized by positive water temperature ratios (*TF* > 1) above the baseline for both, January 2001 and December 2014. The corresponding high saline waters from Kattegat/Skagerrak (> 30 psu) origin were characterized by a higher water temperature during winter and spring.

Marine mammals are characterized by anomalously colder temperatures compared to the long-term mean (Fig. S2) with *TFs* ranging from -2.5 to 2 for all observations covering the months June, July and August along with positive salinity anomalies and *SFs* maximum values up to 4 (Fig. 4c). For both investigated fish species (*M. mola* and *L. piscatorius*), the vertical salinity distribution was generally above the baseline conditions with maximum *SFs* ranged between -1 and 2.7, with corresponding *TFs* between -1.5 and 1.5, respectively (Figs. 4d, S2). The latter resulted from the different temperature conditions between the years (2015-2018) at the sighting location Kiel Bight.

In summary, salinity was higher than the 40 year mean in their normal depth range during the sighting of 6 out of 10 species. For the occurrences of *C. capillata*, anomalously high positive fluctuations (*SF*) were obtained for salinity in summer, while for most of the observations temperature deviations (*TF*) were negative. For the occurrence of *A. subulata*, both the *SFs* and the *TFs* were mainly positive for winter

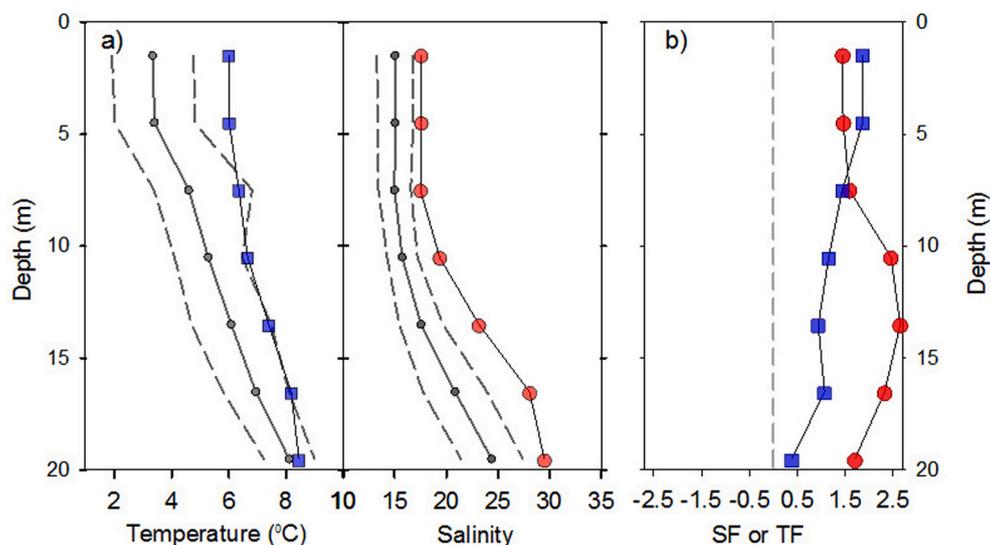
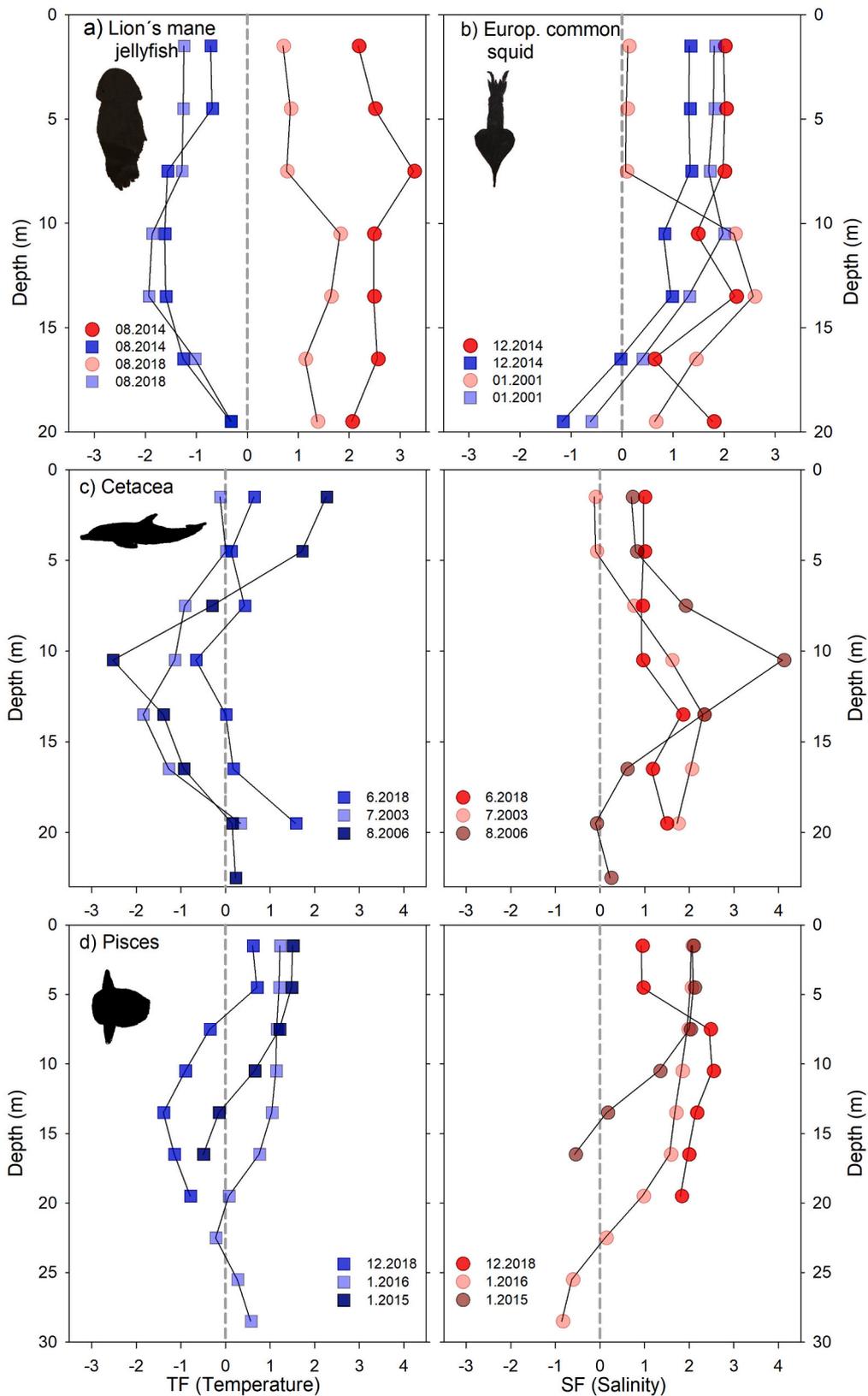


Fig. 3. Depth profiles of a) temperature and salinity during sighting of a common bottlenose dolphin (*Tursiops truncatus*) in the Belt Sea, SW Baltic Sea in December 2015 (colored symbols) compared to the long-term mean (black solid line) and standard deviation (dashed line), and b) the indices of temperature and salinity fluctuations (see formula 1).



**Fig. 4.** Exceptional sightings of uncommon species in the Belt Sea, SW Baltic Sea (see Table 1). Temperature (TFs, square, blue) and salinity (SFs, circle, red) versus depth for invertebrates a) the lion's mane jellyfish *Cyanea capillata* in Kiel Bight; b) the European common squid *Alloteuthis subulata*, in Eckernförde Bight (light red/blue) and in Kiel Bight (medium red/blue); as well as marine mammals c) white-beaked dolphin *Lagenorhynchus albirostris* in Kiel Bight (medium red/blue), and fin whale *Balaenoptera physalus* in Kiel Bight (light red/blue) and in Little Belt (dark red/blue); and fish d) ocean sunfish *Mola mola* in Kiel Bight (medium red/blue), in Little Belt (light red/blue), and the angler fish *Lophius piscatorius* in Eckernförde Bight (dark red/blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. 4). For the exceptional fish distributions  $TF$  values were less pronounced compared to invertebrates (Fig. 4). Recordings of the white-beaked dolphin (*L. albirostris*) and the fin whale (*B. physalus*) could be linked to variable  $SFs$ , ranging from 0 to 4, though maximum  $SFs$  only occurring in mid-depth layers (Fig. 4). In general, the sightings of non-indigenous marine mammals could mainly be associated with anomalously cold-water masses only in the mid-depth water layer.

High resolution investigation in the Kiel Fjord indicates that during the period of exceptional high saline water inflows, *C. capillata* appeared in Kiel Fjord during August 2014, while they were not observed from June throughout start of August (Fig. 5). During the high saline anomaly situation observed, *C. capillata* abundances reached a maximum of 14 individuals 100 m-transect<sup>-1</sup> (average  $\pm$  SD;  $10.4 \pm 2.7$ , see Fig. 5) on 15th of August.

### 3.2. Time series analysis of categorized environmental conditions

As obtained from the analyses on the observational evidence of the considered species, it was expected that these species predominately occur in the SW Baltic Sea during periods of anomalously high salinity conditions ( $SF > 1$ ). Fig. 6 presents the within- and between year variation of exceptional high salinity conditions ( $SF > 1$ ). The salinity category showed large differences between years and seasons, without general pattern, like trends or periodic structures. However, for all depth layers (4.5 m, 10.5 m and 16.5 m) highest frequencies of salinity anomalies were observed during the 1st quarter, while lowest frequencies were observed for the 3rd quarter.

For the high salinity-category, the simultaneous occurrence of a relatively cold environment ( $TF < -1$ ) is temporally (quarters of years) and spatially (depth layers: 4.5 m, 10.5 m and 16.5 m) highly variable (Fig. 7). In the top water layer high evidence of cold environmental conditions was only obtained during the 2nd quarter at the beginning of the time series, while the presence of such conditions during quarter 1, 3 and 4 were only weak. In comparison, the frequency patterns at the mid-depth layer (10.5 m) differed. The occurrence of a cold environment for quarters 1, 2 and 4 was similar to the conditions in the top water layer. However, in quarter 3 for many years during the 1980ies the number of days exhibiting cold temperatures was extremely high. In the deepest water layer of the Kiel Bight area (16.5 m) extremely cold environmental conditions were not observed during the first quarter of the years, but were relatively low and variable during the other quarters. In general, we have identified temporally decreasing trends for this cold-water category.

The frequency distribution of the baseline temperature category ( $-1 \geq TF \leq 1$ ; not shown) revealed relatively high variability for all time-series. Generally, for all layers the highest number of days representing these environmental categories was obtained for the 2nd and the 3rd quarters.

Highest fractions of relatively warm temperature conditions ( $TF > 1$ ) appeared for the upper and the mid-depth water layer during the 1st and the 4th quarters (Fig. 7). The same was obtained for the 1st quarter in the deep-water layer, while for all other depths and quarters warm water masses occurred only occasionally.

## 4. Discussion

The Belt Sea connects the high saline Kattegat/Skagerrak in the northwest with the low saline central Baltic Sea in the east, and is known as a hydrographically dynamic transition zone, influenced by seasonal and large-scale atmospheric forcing (Lehmann et al., 2011). However, extraordinary sightings of transient non-indigenous or range expanding species from high saline environments have so far not been linked to the hydrographic conditions in the Belt Sea.

Variability of physical processes at larger spatial scales includes active movements of larger individuals as well as passive transport of small individuals. Thus, the distributions of extraordinary and/or non-indigenous species are both determined by habitat availability in terms of temperature, salinity, etc., but are also limited through life stage specific dispersal and migration patterns of species. While the distribution of passively transported individuals (e.g. small invertebrates) is limited by ocean currents, motile animals (e.g. squid, fish or marine mammals) may actively stay in water masses, which represent their familiar habit. As an example, marine mammals could passively stay in the high saline water mass and drift with the currents into the SW Baltic Sea due to exceptional hydrographic conditions. However, passive drift or active foraging activity to follow passively drifted prey items, is difficult to decipher.

The European common squid (*A. subulata*), which is an abundant cephalopod in the North Sea, has its easternmost distribution in the Skagerrak/Kattegat area (Hastie et al., 2009; Gebhardt and Knebelberger, 2015). During this century, however, *A. subulata* has been increasingly reported and caught in the Kiel Bight and even further east, off Fehmarn and Warnemünde (Herrmann et al., 2001; Piatkowski, pers. obs.). We assume that this squid might become a range expanding nekton species in the Belt Sea during pulses of high saline water influses in autumn and winter months, because our study links exceptional

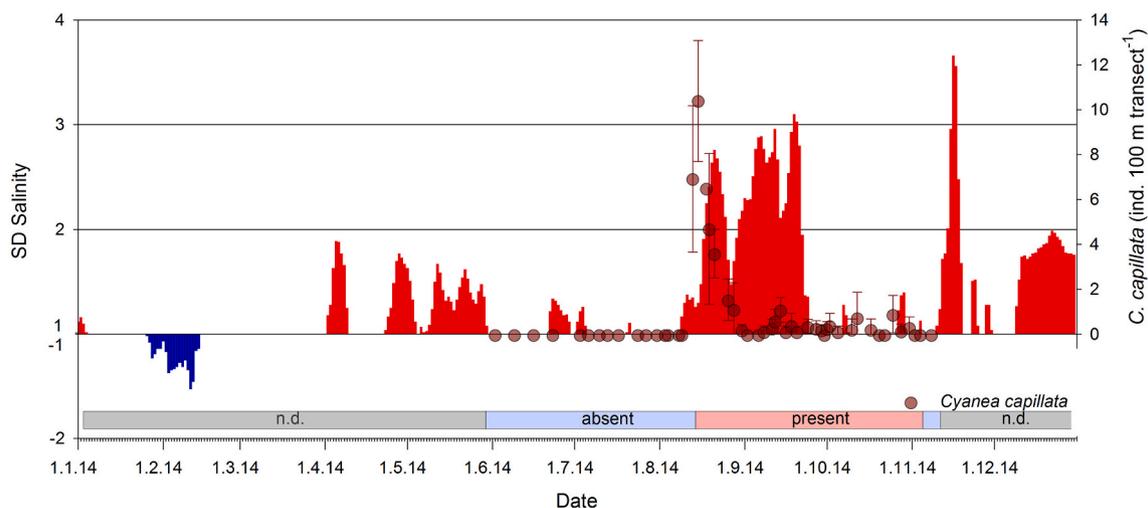
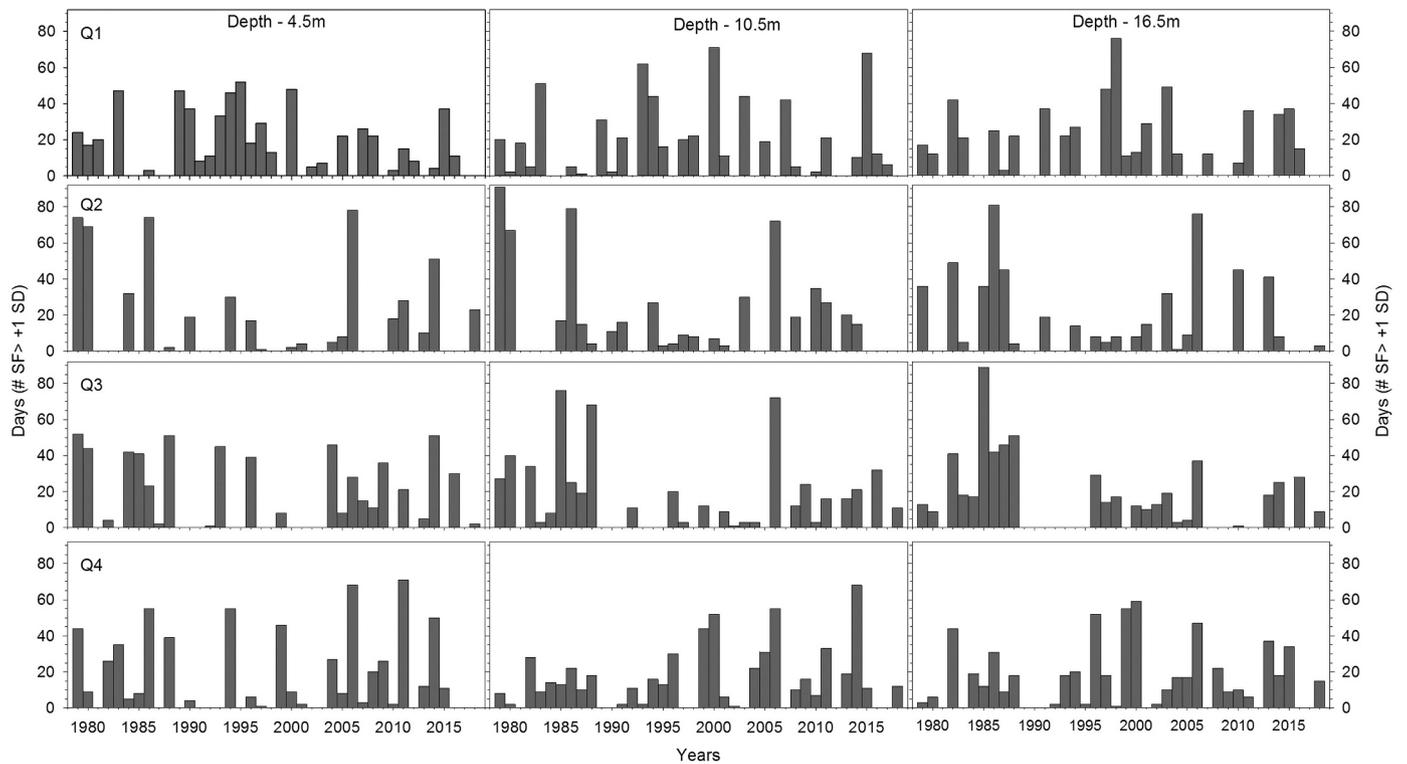
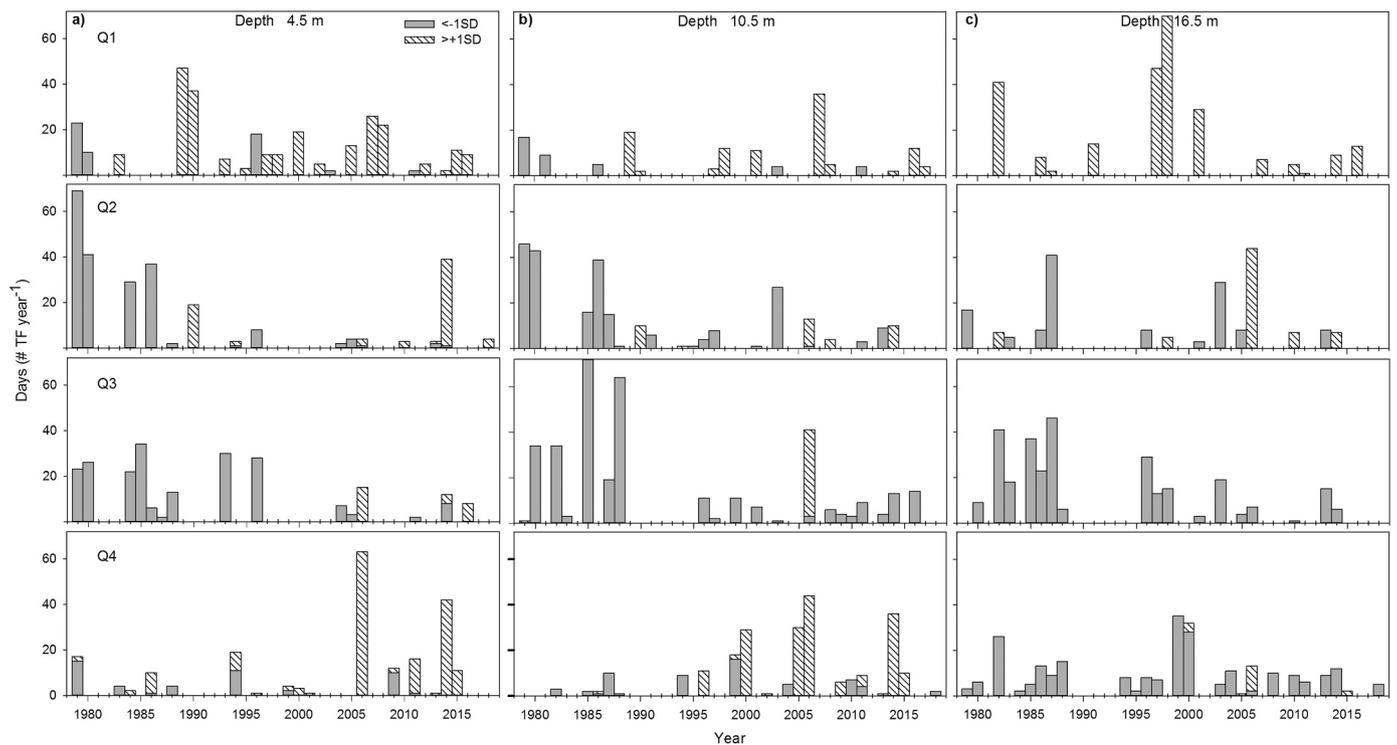


Fig. 5. Daily salinity anomalies during 2014 expressed as  $>1$  SD (red) and  $<1$  SD (blue) of the averaged salinity over the 40-year period (1979–2018) for the upper water column (4.5 m) in Kiel Fjord. The large lion's mane jellyfish *Cyanea capillata* ( $>15$  cm) is indicated by red dots ( $\pm$ SD). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 6.** Number of days per quarter of the year (jan-mar/apr-jun/jul-sep/oct-dec) with exceptional salinity conditions ( $SFs > 1$ ) in the Kiel Bight area for the depth intervals 4.5, 10.5 and 16.5 m.



**Fig. 7.** Number of days per quarter of the year (jan-mar/apr-jun/jul-sep/oct-dec) with exceptional temperature conditions ( $TFs < -1$  and  $TFs > 1$ ) during salinity conditions ( $SFs \geq 1$ ; Fig. 6) with the number of days where the observed temperature was  $SD \geq 1$  (hatched) and  $SD \leq -1$  (grey) in the Kiel Bight area for the depth intervals 4.5, 10.5 and 16.5 m.

hydrographic conditions in the Belt Sea to the presence of *A. subulata*. This is in accordance with increasing trends that nektonic squids from the North Sea appear in the SW Baltic Sea. An example is the broadtail

shortfin squid *Illex coindetii* which has been sampled in the Kattegat as well as the adjoining Great Belt and The Sound (Oesterwind and Scahber, 2020).

Apart from passive processes related to ocean currents which are important for less mobile plankton species, active range expansions have been documented for actively swimming species such as pelagic fishes. For Northern Europe it has been shown that more southerly nekton species like the European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) are re-occurring in the north-eastern North Sea and Skagerrak/Kattegat area, following a total disappearance until the 1980ies (Alheit et al., 2012). For the North Sea, climate variability has an important role for the dynamics of European anchovy, and their occurrence has been linked to warm phases of the Atlantic multi-decadal oscillation with an associated expansion of its thermal habitat and distribution range (Petitgas et al., 2012). It also re-occurred in the Kattegat and Skagerrak, including sporadic observations in the SW Baltic Sea (Niels et al., 2015).

For other higher saline and economically non-important fish species, documentation of their distribution in the Baltic Sea is sporadic and has not been systematically linked to the hydrographic environment. The ocean sunfish (*M. mola*), is an example of an unusual sighting, which attracts large public attention. It is the largest teleost fish and 23 individuals have so far been recorded in the Baltic Sea from 1860 and 2015 (Moritz et al., 2018). It is suggested that ocean sunfish are transported into the Baltic Sea via major inflow events, however lately this view has been changed as it only explains part of the sightings (Moritz et al., 2018). However, our results indicate that unusual sightings can be related to periods of exceptional hydrographic conditions, which do not classify as “Major Baltic Inflows” (Mohrholz et al., 2015). In the oceanic northeast Atlantic they occur year-round foraging on jellyfish, their major prey (Breen et al., 2017), which they sometimes might follow in relatively warm and saline water masses towards the Baltic Sea.

Dolphins and whales have been recorded since a long time in the Belt Sea and adjacent waters (e.g., Schultz, 1970; Skóra, 1991; Kinze et al., 2011). In recent years, sightings are primarily based on reports from the media or citizen science information (see Table 1). Unfortunately, scientific monitoring activity targeting whales are limited and sightings are still sparse and sometimes anecdotic. However, new records increased and have been documented in detail (Harder et al., 2011; Jensen and Kinze, 2011; Kinze et al., 2011, 2018). Nevertheless, there have not been any thorough studies to relate the occurrence of whales and dolphins to the water mass characteristics in the SW Baltic Sea.

Here we report on a collection of exceptional sightings of species, which cannot be regarded to belong to the common species assemblage of the Belt Sea. All exceptional sightings were recorded between 2001 and 2018. For all events, periods of water fluxes were evident due to advective transport of more saline Kattegat/Skagerrak water into the relatively low saline SW Baltic Sea. This caused an unusual increase of salinity to about >25 psu in the Belt Sea area, which represents values of larger than a 2-fold standard deviation from the average salinity observed during a 40-year period. We consider these uncommon hydrographic events to be responsible for the sudden occurrence of the exceptional species sighted in the Belt Sea. The hypothesis that changes in the occurrence of exceptional species in the Belt Sea reflect the dynamics of water mass exchange in the Kattegat/Skagerrak and the SW Baltic Sea, has been successfully investigated and confirmed by our study.

In detail, we found a close match between the occurrence of large sized lion’s mane jellyfish *C. capillata* during August 2014 and August 2018 and the intrusion of exceptionally high saline waters into Kiel Bight. More specifically, during a five months investigation period, higher occurrence of this species could be linked to salinity anomalies >2 SD. Similarly, it has already been suggested that *C. capillata* in the coastal waters of the SW Baltic Sea originates from high saline water inflows from the Kattegat (Möller, 1980), where it actively reproduces (Gröndahl, 1988). So far high-resolution field-based hydrographic measurements were lacking to proof the findings by Möller (1980). Drift model analyses by Barz et al. (2006) documented that adult jelly fish (*A. aurita* and *C. capillata*) observed in the Bornholm Basin (central Baltic

Sea) can stem from higher saline waters of the SW Baltic and southern Kattegat. Similarly, the occurrence of European common squid in the Belt Sea could be linked to higher saline water inflow events, which occurred during winter and were characterized by higher temperature and higher salinities, which was also the situation for uncommon fish species in the Belt Sea. For example, angler fish only very rarely occur in the Belt Sea and to our knowledge, no information outside citizen science observations are available. Interestingly, most of the marine mammals were observed during summer during hydrographic situations characterized by lower temperatures and higher salinities, which indicate inflow of water from North Sea areas into the SW Baltic Sea. However, we also found observations of marine mammal occurrences during winter, where their presence was linked to higher temperatures along with higher salinities due to the general pattern that North Sea waters are warmer during quarter 4 and 1 and colder during quarter 2 and 3. In our study we have shown that in mid-depth water layers the white-beaked dolphin (*L. albirostris*) occurred at relatively normal temperatures, but high saline water masses during the summer months in the Kiel Bight area. Different scenarios are suggested for the fin whale (*B. physalus*) sightings in Kiel Bight and in the Little Belt, which occurred in relatively cold water-masses (Fig. 4c). However, sighting of the common bottlenose dolphin (*Tursiops truncatus*) in the Belt Sea during winter 2015 could be related to a different hydrographic situation, with relatively high temperature and salinity anomalies obtained for mid-depth and deep-water layers (Fig. 3).

Our species list is only selective, however, our data provide compelling evidence for the potential of species dispersal and introduction into the SW Baltic Sea due to exceptional hydrographic conditions. Inflows of high saline, oxygen rich water masses from the Kattegat into the Baltic Sea are known as the basic hydrographic process to provide variations in the physical environment (Schinke and Matthäus, 1998; Lehmann et al., 2002). However, direct determination of these variations is often limited by a lack of observations. In contrast to e.g. time consuming CTD-sampling, the utilization of a hydrodynamic model is to our knowledge the first approach to investigate the abiotic environment in the SW Baltic Sea on a daily time scale considering high resolution spatial coverage of the SW Baltic Sea. This highlights the need for monitoring the current and historical physical environments along with species distribution ranges in order to understand how climate change will expend the geographic distribution of transient non-native species, as well as how climate change could impact the food web structure and the functioning in the Baltic Sea.

The main objectives of fishery science and management are to ensure long term sustainability of fish stocks, for example due to minimization of ecosystem disruption (Rutherford, 2002). Medium to long-term predictions of fish stock sizes commonly rely on different stock recruitment relationships. A probably less well-known recruitment hypothesis suggests that impacts on marine fish stocks may be influenced through predation by gelatinous zooplankton on early life stages of fish (Fraser, 1970; Anderson, 1988). Recent studies report on mass occurrence of jellyfish and ctenophores in different ecosystems around the world (Richardson et al., 2009) as well as an increase of gelatinous invasive species in the Baltic Sea (Jaspers et al., 2021), potentially posing high predation pressure in marine ecosystems. This highlights that a close application of hydrographic information is essential for understanding species accumulations in localized areas as well as determining their potential reproduction and source areas. Similarly, it has been documented that ocean currents can sustain species in less favorable habitats by re-current re-seedings following local extinctions (Jaspers et al., 2018).

For computational reasons, predictions of abiotic environmental variability driving the introduction of exceptional species into marine ecosystems, as in our analysis, have so far typically been performed in a hindcast mode, rather than in real time. However, due to increasing computational capacity, model runs in forecast mode can be pursued by coupling hydrodynamic models with real time and forecasted forcing

conditions (e.g. weather forecasts; Brüning et al., 2014). These model results could be easily applied to quickly provide species forecast maps. To improve sampling of spatially heterogeneous species and thereby might help to provide the assessment of ecosystems dynamics. Additionally, this information could also be highly applicable for establishing an early warning system for expected stinging jellyfish landings along highly frequented bathing beaches.

During the most recent decades, the hydrographic conditions in the Belt Sea were influenced by large-scale climate conditions. Especially, for the recent 3 decades, Baltic Sea surface temperature warming trends have been determined between 0.4 and 0.7 °C per decade (Lehmann et al., 2011; BACC II, 2015). Thus, because of its ecological and evolutionary history, the Baltic Sea is presently a predominant receiver area for exceptional and/or non-indigenous species, with most of the observed exceptional species originating from warmer water climates (Leppäkoski and Olenin, 2001). As increasing water temperatures are observed and expected for the Baltic Sea, more species from warmer regions of the world can be expected to establish in the Baltic Sea (BACC, 2008).

## 5. Conclusion

We have shown that biological sightings of marine life have to be considered in its physical environment, which urges to more closely combine efforts of marine ecologists with physical oceanographers in order to understand species distribution and response to global change. This is of importance as knowledge on the occurrence and persistence of non-indigenous and exceptional species in the Belt Sea is essential to assess if these species are really established and hence form a potential to become invasive or, if they are occasional visitors from other areas where they actively reproduce.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2022.102175>.

## Declaration of Competing Interest

The authors declare no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## References

- Alheit, J., Pohlmann, T., Casini, M., Greve, W., Hinrichs, R., Mathis, M., et al., 2012. Climate variability drives anchovies and sardines into the north and Baltic seas. *Prog. Oceanogr.* 96, 128–139.
- Anderson, J.T., 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *J. Northwest Atl. Fish. Sci.* 8, 55–56.
- BACC, 2008. Assessment of climate change for the Baltic Sea basin. In: *Regional Climate Studies. XII.* Springer Verlag, Berlin, p. 474.
- BACC, 2015. Second Assessment of Climate Change for the Baltic Sea Basin. Springer International Publishing, p. 501.
- Barz, K., Hinrichsen, H.-H., Hirche, H.-J., 2006. *Scyphozoa* in the Bornholm Basin (Central Baltic Sea) – the role of advection. *J. Mar. Syst.* 60, 167–176.
- Bonsdorff, E., 2006. Zoobenthic diversity-gradients in the Baltic Sea: continuous post-glacial succession in a stressed ecosystem. *J. Exp. Mar. Biol. Ecol.* 330, 383–391.
- Breen, P., Cañadas, A., Cadhla, O.Ó., Mackey, M., Scheidat, M., Geelhood, S.C.V., Rogan, R., Jessopp, M., 2017. New insights into ocean sunfish (*Mola mola*) abundance and seasonal distribution in the Northeast Atlantic. *Sci. Rep.* 7, 2025.
- Brüning, T., Janssen, F., Kleine, E., Komo, H., Maßmann, S., Menzenhauer-Schumacher, I., Jandt, S., Dick, S., 2014. Operational Ocean forecasting for German coastal waters. *Die Küste* 81, 273–290. <https://vzb.baw.de/die-kueste/0/k081118.pdf>.
- Bumke, K., Karger, U., Hasse, L., Niekamp, K., 1998. Evaporation over the Baltic Sea as an example of a semi-enclosed sea. *Contr. Atmosph. Phys.* 71, 249–261.
- Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., et al., 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334, 652–655.
- Carlton, J.T., Geller, J.B., 1993. Ecological roulette: the global transport of non-indigenous marine organisms. *Sci. New Ser.* 261 (5117), 78–82.
- Dee, D.P., Uppala, S.M., Simmons, A.J., Berrisford, P., Poli, P., Kobayashi, S., et al., 2011. The ERA-interim reanalysis: configuration and performance of the data assimilation system. *Quart. J. Royal Meteorol. Soc.* 137, 553–597.
- Fennel, W., Sturm, M., 1992. Dynamics of the western Baltic. *J. Mar. Syst.* 3, 183–205.
- Fraser, J.H., 1970. The ecology of the ctenophore *Pleurobrachia pileus* in Scottish waters. *ICES Journal du Conseil* 33, 149–168.
- Gaylor, B., Gaines, S.D., 2000. Temperature or transport? Range limits in marine species mediated solely by flow. *Am. Nat.* 155, 769–789.
- Gebhardt, K., Knebelberger, T., 2015. Identification of cephalopod species from the north and Baltic Sea using morphology, COI and 18S rDNA sequences. *Helgol. Mar. Res.* 69, 259–271.
- Gröndahl, F., 1988. A comparative ecological study on the scyphozoans *Aurelia aurita*, *Cyanea capillata* and *Cyanea lamarckii* in the Gullmar Fjord, Western Sweden, 1982–1986. *Mar. Biol.* 97, 541–550.
- Gustafsson, B., 1997. Interaction between Baltic Sea and North Sea. *Deut. Hydrograph. Zeitg.* 49, 65–183.
- Harder, K., Kinze, C.C., Schulze, G., Benke, H., 2011. Bartenwale in der Ostsee: eine Übersicht. *Meer und Museum* 23, 163–184.
- Hastie, L.C., Pierce, G.J., Wang, J., Bruno, I., Moreno, A., Piatkowski, U., Robin, J.-P., 2009. Cephalopods in the north-East Atlantic: species, biogeography, ecology, exploitation and conservation. *Oceanogr. Mar. Biol.* 47, 111–190.
- HELCOM, 2009. Biodiversity in the Baltic Sea - an Integrated Thematic Assessment on Biodiversity and Nature Conservation in the Baltic. *Balt. Sea Environ. Proc. No.* 116B.
- Herrmann, M., Gonschior, H., Piatkowski, U., 2001. Hydrographic changes push European common squid *Alloteuthis subulata* into Kiel Bay, western Baltic Sea. In: *International Council for the Exploration of the Sea, ICES CM 2001/K:13.* ICES, Copenhagen.
- Hinrichsen, H.H., John, M.A., Lehmann, A., Brügge, B., 1997. Modelling the cod larvae drift in the Bornholm Basin in summer 1994. *Cont. Shelf Res.* 17, 1765–1784.
- Jaekel, S., 1937. Tintenfische in der westlichen Ostsee. *Archiv für Molluskenkunde* 69, 129–136.
- Jaekel, S., 1958. Cephalopoden. In: *Remane, A. (Ed.), Die Tierwelt der Nord- und Ostsee*, 37, pp. 480–723, 9b.
- Jaspers, C., Huwer, B., Antajan, E., Hosiá, A., Hinrichsen, H.-H., Biastoch, A., et al., 2018. Ocean current connectivity propelling the secondary spread of a marine invasive comb jelly across western Eurasia. *Glob. Ecol. Biogeogr.* 27, 814–827.
- Jaspers, C., Bezio, N., Hinrichsen, H.-H., 2021. Diversity and physiological tolerance of native and invasive jellyfish/ctenophores along the extreme salinity gradient of the Baltic Sea. *Diversity* 13, 57.
- Jensen, T., Kinze, C.C., 2011. Finn- und Buckelwalsichtungen in der Ostsee 2003–2011: Verhalten in einem fremden Gewässer. *Meer und Museum* 23, 185–198.
- Kinze, C.C., Schulze, G., Skóra, K., Benke, H., 2011. Zahnwale als Gastarten in der Ostsee. *Meer und Museum* 23, 53–82.
- Kinze, C.C., Thøstesen, C.B., Olsen, M.T., 2018. Cetacean stranding records along the Danish coastline: records for the period 2008–2011 and a comparative review. *Lutra* 61, 87–105.
- Kronsell, J., Andersson, P., 2012. Total regional runoff to the Baltic Sea. In: *HELCOM Indicator Fact Sheets 2011.* Online. <http://www.helcom.fi/environment2/ifs>.
- Lehmann, A., 1995. A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. *Tellus A* 47, 1013–1031.
- Lehmann, A., Hinrichsen, H.-H., 2000. On the thermohaline variability of the Baltic Sea. *J. Mar. Syst.* 25, 333–357.
- Lehmann, A., Krauss, W., Hinrichsen, H.-H., 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus A* 54, 299–316.
- Lehmann, A., Getzlaff, K., Harlaß, J., 2011. Detailed assessment of climate variability of the Baltic Sea area for the period 1958–2009. *Clim. Res.* 46, 185–196.
- Lehmann, A., Hinrichsen, H.-H., Getzlaff, K., Myrberg, K., 2014. Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. *J. Mar. Syst.* 134, 20–28. <https://doi.org/10.1016/j.jmarsys.2014.02.012>.
- Lennartz, S.T., Lehmann, A., Herrford, J., Malien, F., Hansen, H.P., Biester, H., Bange, H.W., 2014. Long-term trends at the time Series Station Boknis Eck (Baltic Sea), 1957–2013: does climate change counteract the decline in eutrophication? *Biogeosci.* 6323–6339.
- Leppäkoski, E., Olenin, S., 2001. The meltdown of biogeographical peculiarities of the Baltic Sea: the interaction of natural and man made processes. *Ambio* 30, 202–209.
- Mohrholz, V., Naumann, M., Nausch, G., Krüger, S., Gräwe, U., 2015. Fresh oxygen for the Baltic Sea – an exceptional saline inflow after a decade of stagnation. *J. Mar. Syst.* 148, 152–166.
- Möller, H., 1980. A summer survey of large zooplankton, particularly Scyphomedusae, in North Sea and Baltic. *Meeresforsch.* 28, 61–68.
- Moritz, T., Augustin, C.B., Winkler, H.M., Pagel, H.J., 2018. Records of the Ocean Sunfish (*Mola mola*, Tetraodontiformes) in the German Baltic Sea. *Bullet. Fish Biol.* 17, 45–51.

- Niels, D., Heessen, H., Ellis, J., 2015. Fish atlas of the Celtic Sea, North Sea, and Baltic Sea - Based on International Research-Vessel Surveys, pp. 1–572.
- Oesterwind, D., Scahber, M., 2020. First evidence of *Illex coindetii* (Vérany, 1839) in the Baltic Sea and the Kattegat. *Thalassas: An Int. J. Mar. Sci.* 36, 143–147.
- Paavola, M., Olenin, S., Leppäksöki, 2005. Are invasive species most successful in habitats of low native species richness across European brackish water seas? *Estuar. Coast. Shelf Sci.* 64, 738–750.
- Petitgas, P., Alheit, J., Peck, M.A., Raab, K., Irigoien, X., Huret, M., et al., 2012. Anchovy population expansion in the North Sea. *Mar. Ecol. Prog. Ser.* 444, 1–13.
- Remane, A., 1934. Die Brackwasserfauna. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 36, 34–74.
- Richardson, A.J., Bakun, A., Hays, G.C., Gibbons, M.J., 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends Ecol. Evol.* 24, 312–322.
- Rudolph, C., Lehmann, A., 2006. A model-measurements comparison of atmospheric forcing and surface fluxes of the Baltic Sea. *Oceanologia* 48, 333–380.
- Rutherford, E.S., 2002. Fishery management. In: Fulman, L.A., Werner, R.G. (Eds.), *Fishery Science. The Unique Contribution of Early Life Stages*. Blackwell Science Ltd., Malden, MA (USA), pp. 206–221.
- Schinke, H., Matthäus, W., 1998. On the causes of major Baltic inflows - an analysis of long time series. *Cont. Shelf Res.* 18, 67–97.
- Schultz, W., 1970. Über das Vorkommen von Walen in der Nord- und Ostsee (Ordnung Cetacea). *Zool. Anz.* 185, 172–264.
- Segerstråle, S.G., 1969. Biological fluctuations in the Baltic Sea. *Prog. Oceanogr.* 5, 169–184.
- Skóra, K.E., 1991. Notes on cetacea observed in the polish Baltic Sea: 1979–1990. *Aquat. Mamm.* 17, 67–70.
- Sorte, C.J.B., Williams, S.L., Carlton, J.T., 2010. Marine range shifts and species introductions: comparative spread rates and community impacts. *Glob. Ecol. Biogeogr.* 19, 303–316.
- Van Gennip, S.J., Popova, E.E., Yool, A., Pecl, G.T., Hobday, A.J., Sorte, C.J.B., 2017. Going with the flow: the role of ocean circulation in global marine ecosystems under a changing climate. *Glob. Chang. Biol.* 23, 2602–2617.

## Glossary

*hydrodynamic model*: tool to quantify key physical processes in waters, capable to assess environmental impacts

*geostrophic winds*: balance between Coriolis and pressure gradient force

*baroclinic flows*: pressure gradient force changes with depth

*barotropic flows*: driven by horizontal pressure gradients induced by sea surface slopes

*drift*: current-driven movement of particles and organisms

*major Baltic inflows*: transport of large amounts of high saline/oxygenated waters

*water mass characteristic*: ocean water with a distinctive narrow range of physical and chemical parameter

*CTD-sampling*: vertical measurements of the physical environment in open & coastal seas

*Marine mammals*: surface breathing animals living in aquatic environments, such as whales (cetaceans), seals etc.

*Marine invertebrates*: multicellular aquatic animals that lack a vertebral column, e.g. squid & jellyfish, compared to vertebrates, with vertebral column e.g. pisces (fishes)

*Non-indigenous species*: living organisms observed outside their native distribution range

*Invasive species*: non-indigenous species with documented ecosystem impact