Density-driven water exchange controls seasonal declines in jellyfish (*Aurelia aurita*) abundance in a shallow fjord system

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ABSTRACT: The common jellyfish *Aurelia aurita* s.l. occurs in many coastal and shelf sea environments around the world, including fjord systems such as Kerteminde Fjord/Kertinge Nor (Denmark). As observed for the majority of temperate *A. aurita* populations, jellyfish appear in this fjord system each spring, go through gradual declines in their initially high abundance during summer/autumn and disappear by winter. While food limitation has been suggested to cause distinct seasonal declines in the local jellyfish abundance, the role of hydrodynamic forcing in the shallow, semi-enclosed fjord system is still unclear. Based on a 2 yr field campaign, we provide a dynamic description for the density-driven water exchange in Kerteminde Fjord/Kertinge Nor to quantify the dispersal of jellyfish from the local population to adjacent coastal waters. The predicted mean residence time (±SD) of 45 ± 1 d for the water masses in Kertinge Nor is in good agreement with an observed residence time of 41 ± 7 d during which jellyfish abundance in the fjord system was reduced to $e^{-1} = 37\%$. These results indicate that major fractions of 86.7 ± 8.9% and 82.6 ± 7.9% of observed declines in jellyfish abundance in the fjord system were controlled by the density-driven water exchange during 2013 and 2014, respectively. Our findings emphasize the relevance of hydrodynamic processes in context with jellyfish blooms by ensuring dispersal of jellyfish source populations from semi-enclosed, potentially food-limited regions to open coastal waters.

KEY WORDS: Jellyfish blooms · Hydrodynamic modeling · Open/source population · Scyphozoa · Fjord systems

INTRODUCTION

Jellyfish blooms occur with large fluctuations over broad temporal and regional scales (Lucas et al. 2012), challenging predictions on their intensity and frequency. Mass occurrences of jellyfish further have to be distinguished according to their origin; while true jellyfish blooms are directly attributable to demographic life cycle dynamics such as survival, growth and reproduction, apparent blooms are mainly associated with environmental properties, i.e. wind-driven or hydrodynamic processes (Graham et al. 2001). Information relating the intensity and frequency of jellyfish mass occurrence to hydrodynamic processes, however, has remained scarce (Johnson et al. 2001, Barz et al. 2006, Makabe et al. 2014, 2015). An improved understanding of the interplay between the complex life cycles of jellyfish and hydrodynamic processes is thus essential to identify the mechanisms underlying booms and busts of jellyfish blooms.

In the world's largest brackish water habitat, the Baltic Sea, a combination of freshwater discharge and water exchange with the North Sea generates far-reaching salinity gradients. The residence time of the bottom waters in the Baltic depends on the process of saltwater inflow and brackish-water outflow through the Danish straits (Kullenberg & Jacobsen 1981, Møller 1996). Resulting salinity changes give rise to density-driven currents in most coastal waters of this region, including the fjord system Kerteminde Fjord/Kertinge Nor (Jürgensen 1995, Riisgård et al. 1998). The cosmopolitan jellyfish *Aurelia aurita* s.l. (Scyphozoa, Cnidaria) is common in the Baltic Sea (Möller 1980, Barz et al. 2006) and shows seasonal mass occurrence in Kerteminde Fjord/Kertinge Nor. High numbers of *A. aurita* ephyrae (≥ 300 ind. m^{-3}) are released into the fjord system by benthic polyps each spring. Ephyrae grow and develop into medusae through summer, while their abundance shows gradual declines until the medusae disappear completely during the winter months (Olesen et al. 1994, Riisgård et al. 1995, 2010). The seasonal dynamics governing the local jellyfish population in the fjord system have remained unchanged over the last 25 yr (Goldstein & Riisgård 2016). Seasonal declines in the population size of *A. aurita* have previously been associated with senescence of medusae after spawning (Miyake et al. 1997, Marques et al. 2015), and increased mortality due to food limitation has been suggested as a major cause of the disappearance of medusae from the temperate fjord system during winter (Goldstein & Riisgård 2016). Further, the importance of hydrodynamic processes for the distribution of jellyfish in Kerteminde Fjord/Kertinge Nor and their additional supply with zooplankton prey from open coastal waters has been emphasized (Nielsen et al. 1997, Riisgård 1998). Although dispersal of jellyfish via density-driven water exchange may further explain decreasing abundances in the shallow cove during summer (Olesen et al. 1994, Riisgård et al. 2010), the actual contribution of the potential *A. aurita* source population to the open sea has to date never been quantified.

Here, we study to which degree the observed seasonal declines in jellyfish abundance in the model system Kerteminde Fjord/Kertinge Nor can be explained by hydrodynamic processes. Based on regular field samplings during 2013 and 2014, we describe the water exchange as a function of salinity differences between the fjord system and the adjacent Great Belt considering temporal and spatial variation of the dispersive transport. Using a simple water exchange model, we compare observed sea-

sonal patterns in jellyfish abundance to predictions based on the residence time of water masses in Kertinge Nor. Our findings emphasize the importance of hydrodynamic dispersal for the population ecology of jellyfish in Danish waters and suggest a minor role of mortality due to starvation.

MATERIALS AND METHODS

Study area

Great Belt is one of the Danish straits that connect the Baltic Sea to the North Sea. The adjacent fjord system, Kerteminde Fjord and Kertinge Nor (Fig. 1A), covers an area of 8.5 km^2 and comprises a total volume of 17×10^6 m^3 with a mean water depth of 2 m and a maximum depth of 8 m (Riisgård et al. 2008). A diurnal tide with an average amplitude of 20 cm forces water masses from Great Belt over a shallow sill into the fjord system (Riisgård et al. 1996). Frequent salinity changes in the Danish straits due to water exchange between the North Sea and the Baltic (Lass et al. 1987, Gustafsson & Andersson 2001) result in a density-driven circulation of the water masses in the fjord system (Jürgensen 1995, Møller 1996). Strength and direction of the density-driven circulation are determined by salinity differences between Kerteminde Fjord/Kertinge Nor and Great Belt, resulting in either bottom layer inflow of more saline water (Fig. 1B) or in surface layer inflow of less saline water (Fig. 1C) (Jürgensen 1995, Nielsen et al. 1997). Temperature is an unimportant parameter compared to salinity for the driving density differences between water masses in this region (Jürgensen 1995). No significant freshwater discharge affects the shallow fjord system.

Salinity measurements

During the study period from May to December 2013 and from April to December 2014, we measured salinity at 5 locations in the fjord system Kertinge Nor (Locations 1−3)/Kerteminde Fjord (Locations 4−5) and at the reference location in Great Belt (Location 6; Table 1, Fig. 1A) every second week. We recorded salinity (S; PSU) in vertical profiles with 0.5 m depth intervals at each sampling location using an YSI 650 multiparameter display system (MDS) with integrated optical monitoring sonde (accuracy: ±0.1 PSU). Comparative salinity data from Great Belt (Location STB53; 55° 30′ 46″ N, 10° 51′ 27″ E) was provided by the Danish Environmental Protection Agency (EPA).

Jellyfish abundance

Along with salinity measurements, we collected jellyfish *Aurelia aurita* by horizontal surface net hauls (haul length: 5.4 ± 0.2 m; depth: 0.5 m) with a 500 µm meshed plankton net (mouth area: 0.25 m²) at the 6 sampling locations in Kertinge Nor, Kerteminde Fjord and Great Belt (Locations 1–6; Table 1, Fig. 1A) during 2013 and 2014. After each haul, we gently rinsed the jellyfish off the plankton net for subsequent counting in the laboratory. The jellyfish abundance N (ind. m⁻³) at each sampling location was determined as the number of ephyrae and medusae per volume of seawater filtered during each net haul (i.e. 5.4 m × 0.25 m² = 1.35 m³).

Medusae originating from the innermost part of the fjord system (cf. Olesen et al. 1994) are characterized by their smaller size and a red-brownish color compared to the much larger, blueish medusae from Great Belt, which makes the 2 populations distinguishable. By excluding all individuals from Great Belt ($N \le 3$ ind. m⁻³) from our counts, we set the advection of medusae from Great Belt to zero. While the abundance of medusae in Great Belt was below the detection limit of the methods described above during the entire study period ($N <$ 0.1 ind. m⁻³; J. Goldstein pers. obs.), we occasionally observed medusae from Kertinge Nor in Great Belt.

Water exchange model

Our water exchange model takes into account the physical processes between the water masses of a fjord system and an open boundary. For conceptual understanding, we divided the fjord system Kertinge Nor/Kerteminde Fjord into 5 different compartments with an open boundary in Great Belt (Figs. 1A & 2). The applied method is based on 4 basic assumptions: (I) Conservation of volume: the water exchange discharges between compartments are of equal magnitude. (II)
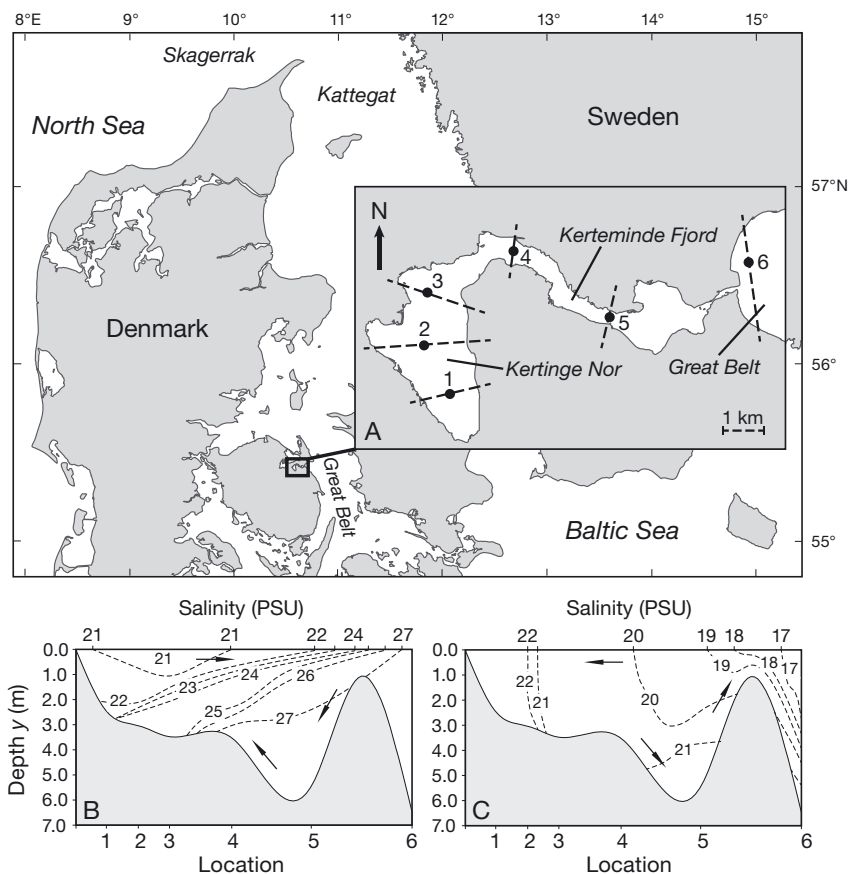

Fig. 1. (A) Investigation area with jellyfish sampling locations in the fjord system (inset) Kertinge Nor (Location 1: 55° 25″ 44″ N, 10° 34′ 23″E, Location 2: 55° 26′ 15″ N, 10° 33′ 54″ E, Location 3: 55° 26′ 53″ N, 10° 33′ 54″ E)/Kerteminde Fjord (Location 4: 55° 27′ 30″ N, 10° 35′ 43″ E, Location 5: 55° 26′ 43″ N, 10° 37′ 31″ E) and the adjacent Great Belt (Location 6: 55° 27′ 12″ N, 10° 40′ 59″ E). Broken lines mark different fjord compartments. Salinity differences between the fjord system and Great Belt result in density-dependent water exchange. Circulation of the water masses in Kerteminde Fjord/Kertinge Nor is driven by either (B) bottom layer inflow of more saline water into the fjord (arrows) or (C) surface layer inflow of less saline water into the fjord (arrows)

Table 1. Physical properties of different fjord compartments corresponding to the water masses between adjacent sampling locations in Kertinge Nor/Kerteminde Fjord (Fig. 1A). *L*: length; *w*: mean width; *y*: mean depth; *A*: surface area; $V (= A \times y)$: volume

Compartment *n*	*L* (m)	*w* (m)	*y* (m)	*A* (×10⁶ m²)	*V* (×10⁶ m³)
1	1086	891	2.1	0.6	1.26
2	1176	1411	2.6	1.5	3.90
3	2434	1266	2.4	2.0	4.80
4	2493	378	2.4	1.7	4.08
5	2788	241	3.9	0.9	3.51

Conservation of mass: the salinity change in Kerteminde Fjord/Kertinge Nor is driven by the inflow of water masses with variable salinity from the open boundary (Great Belt) and the outflow of mixed water from the fjord system as a function of water exchange
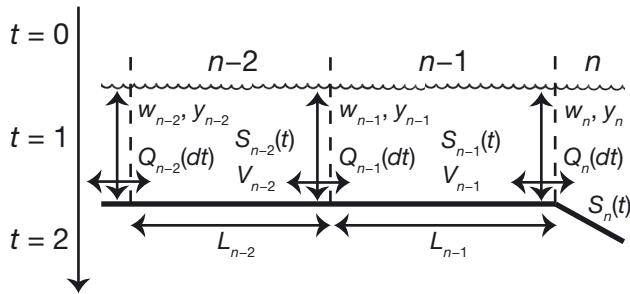
Fig. 2. Conceptual illustration of the governing physical processes in the fjord system Kerteminde Fjord/Kertinge Nor. Properties of the different compartments (broken lines) from the open boundary ($n = 6$) towards the innermost part of the fjord system ($n = 1$) are defined for time step dt. t: time; n: compartment number; w: width; y: water depth; S: salinity; V: volume; L: length; Q: exchange discharge

discharges between different compartments. Salinity S in fjord compartment n at time $t + 1$ is determined using the concept of mass conservation, as expressed by the following equation:

$$S_n(t+1) = S_n(t) + \frac{dt}{V_n}\{Q_{n-1}(dt)\times[S_{n-1}(t+1)-S_n(t)]$$
$$+ Q_n(dt)\times[S_{n+1}(t)-S_n(t)]\} \quad (1)$$

where $S_n(t)$ is the salinity in compartment n at time t, dt the model time step, and V_n (m³) the volume of compartment n, while $Q_{n-1}(dt)$ and $Q_n(dt)$ (m³ s⁻¹) describe the water exchange discharges between the adjacent compartments $n-1$ and n during time step dt (Fig. 2). (III) Density-driven water exchange: the exchange discharge between compartments is determined based on the concept for maximum density-driven exchange (Armi & Farmer 1986), for which the discharge Q depends on the cross-sectional area $y \times w$ (m²), obtained from depth y (m) and width w (m) of the fjord compartment (Table 1), the maximum flow velocity v_{max} (m s⁻¹), and an efficiency coefficient α:

$$Q = \alpha\, y\, w\, v_{max} \quad (2)$$

Considering the energy difference that limits the density-driven water exchange between the fjord system and the adjacent Great Belt, Eq. (2) can be expressed as

$$Q = \alpha\, y\, w \sqrt{g' \frac{y_U y_L}{y_U + y_L}} \quad (3)$$

with $y_U = y_L = \frac{1}{2}y$, where y_U and y_L refer to the depth of an upper (U) and a lower (L) water layer (cf. Armi & Farmer 1986) according to the salinity difference between the open boundary and the fjord system. The reduced gravity term g' can further be substituted by the density of the lower and the upper water layer, ρ_L and ρ_U, respectively, as follows:

$$g' = g\frac{\rho_L - \rho_U}{\rho_L} \quad (4)$$

where the density ρ (kg m⁻³) can be approximated from the depth-integrated mean salinity S as $\rho = 1000 + (0.8S)$. Inserting the above parameters in Eq. (3) results in the following equation for the density-driven exchange discharge Q in compartment n during time step dt:

$$Q_n(dt) = \alpha\frac{1}{2}y_n w_n \sqrt{g\frac{0.8}{1000}}\sqrt{y_n}\sqrt{|S_n(t)-S_{n+1}(t)|} \quad (5)$$

The discharge hence depends on the dynamic variable S, the fixed geometric variables y and w of each compartment and on the constant g; and the relationship among the variables can be calibrated using α. Since the net exchange discharges follow the dimensions of each fjord compartment, the dispersion coefficient D (m² s⁻¹) for each time step dt and compartment n can be estimated using the equation:

$$D_n(dt) = \frac{Q_n(dt)}{y_n w_n} L_n \quad (6)$$

where L_n denotes compartment length (Table 1). (IV) Numerical criterion: a basic numerical criterion is that the water masses of a fjord compartment cannot be emptied during a modeling time step. The following criterion (Courant criterion) has to be fulfilled to avoid water exchange discharges Q (from both sides of the compartment) that exceed the volume of the compartment over time step dt: $V \le 2\,Q\,dt = 2\,y\,w\,v_{max}\,dt$, so that $dt \ge V/(2\,y\,w\,v_{max}) = \frac{1}{2}L/v_{max}$. For the mean distance $L = 2025$ m between adjacent sampling locations (Table 1) and a maximum flow velocity $v_{max} = 0.1$ m s⁻¹ (order of magnitude as observed in central parts of Kerteminde Fjord), this results in a maximum time step dt ($= \frac{1}{2}\,2025$ m/0.1 m s⁻¹) ~3 h. Since our dataset includes measurements for every second week, we estimated the variation in salinity at the open boundary in half-weekly intervals to take into account the frequency of salinity changes in Great Belt (cf. Jürgensen 1995). This was necessary to reproduce the observed longitudinal salinity gradient in the fjord system based on the efficiency coefficient α (detailed information on the model calibration is available in Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m597p137_supp.pdf). Finally, salinity estimates for the open boundary were interpolated for each 3 h time step to fulfill the numerical criterion. Independent salinity measurements in Great Belt by the Danish EPA (2017, F. Nørgaard pers. comm.) were used to confirm our estimates for the open boundary salinity.

The present exchange model was calibrated and verified based on salinity changes in the fjord system

Kertinge Nor/Kerteminde Fjord and the adjacent Great Belt in the time period May to December 2013 and April to December 2014. With reference to field observations, we applied the water exchange model for predicting seasonal declines in the jellyfish abundance due to dispersal. For this purpose, predicted and observed *A. aurita* abundances for the study period were standardized by their annual maxima to obtain comparable estimates for the residence time of jellyfish and the corresponding residence time of the water masses in the fjord system.

Statistical analyses

Hydrodynamic modeling and statistical data analyses were performed in R version 3.1.3 (R Core Team 2015). A linear model was used to explore differences between the calibrated mean salinity at the open boundary (Fig. 1A) and independent salinity measurements in Great Belt (Location STB53) during the study period. A linear mixed-effect model from R package lme4 (Bates et al. 2015) was parameterized to test for differences between measured and simu-

lated (fixed effect) salinity while correcting for time (random effect). Model assumptions were met without the need for fitting generalized models.

RESULTS

Model predictions of salinity

Salinity predictions of our water exchange model are in full agreement with mean (depth-integrated) salinity in Kertinge Nor/Kerteminde Fjord over the study periods in 2013 and 2014 (cf. Table S1 and Figs. S1 & S2 in the Supplement). The range and variation of depth-integrated salinity measured at the open boundary towards Great Belt coincide with independent salinity measurements at Location STB53 in the central Great Belt, confirming our model estimates for the open boundary salinity (Fig. 3A). Our water exchange model was calibrated and verified based on salinity in Kertinge Nor/Kerteminde Fjord (Fig. 3B) using an efficiency factor $\alpha = 0.15$, indicating that the density-driven current in the fjord system is only about 15% as efficient as the
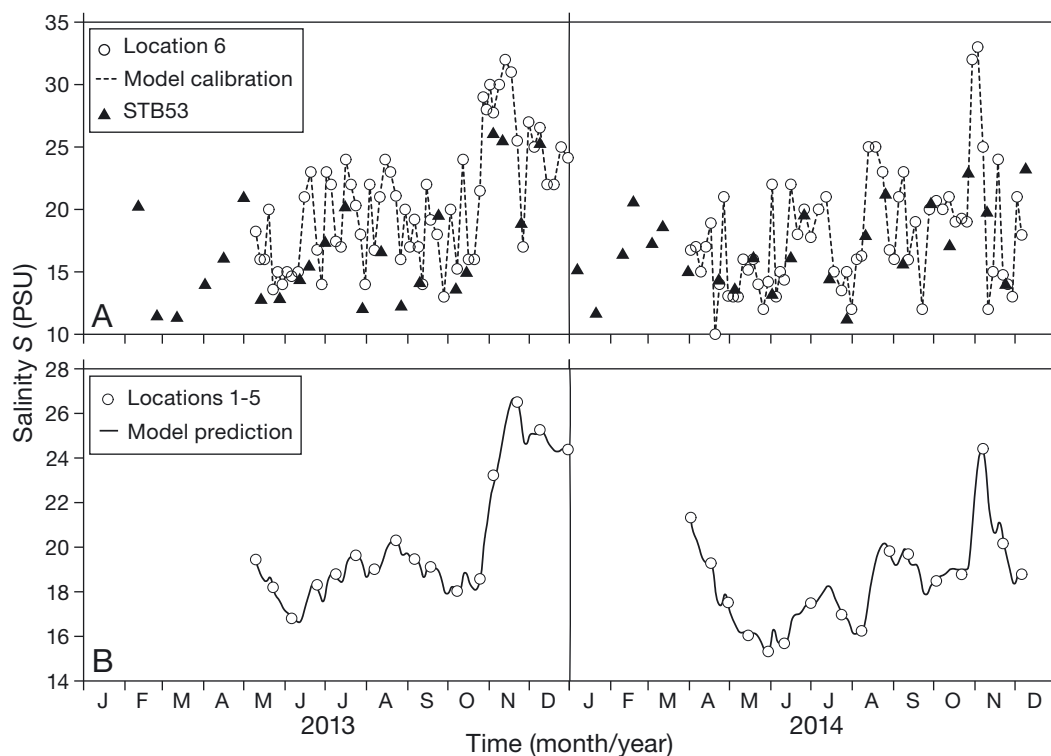

Fig. 3. Water exchange model for the fjord system Kertinge Nor/Kerteminde Fjord based on salinity variations in the adjacent Great Belt during 2013 and 2014. (A) Model calibration based on measured depth-integrated mean salinities at Location 6 in Great Belt (cf. Fig. 1A) and independent salinity measurements at Location STB53 in Great Belt (data source: Danish EPA; linear model, $F_{1,64} = 6.2$, p = 0.015). (B) Predicted mean salinity and measured depth-integrated mean salinity for Locations 1–5 in the fjord system (linear mixed-effect model, $t_{1.4,319} = 0.18$, p = 0.857)

theoretical maximum exchange (i.e. constant, frictionless flow between 2 infinite and homogeneous basins). Vertical salinity profiles in the fjord system and the adjacent Great Belt indicate that density-driven circulation resulted from surface layer inflow of less saline water from the open sea in 69% of the 32 sampling days over both years, while bottom layer inflow was only observed in 31% of sampling days (Table S1).

Resulting exchange discharges showed gradual attenuation from the fjord outlet to the adjacent Great Belt towards the innermost part of the fjord system, as expressed by an almost linear decrease in mean dispersion coefficients ($\pm$SD) from $41.4 \pm 17.0 \ m^2 \ s^{-1}$ at Location 5 to $26.9 \pm 10.7 \ m^2 \ s^{-1}$ at Location 4, $15.2 \pm 6.1 \ m^2 \ s^{-1}$ at Location 3, $5.7 \pm 2.3 \ m^2 \ s^{-1}$ at Location 2 and $3.8 \pm 1.5 \ m^2 \ s^{-1}$ at Location 1 (Fig. S3). Regional variability by an approximate factor of 10 is additionally demonstrated by a decrease in median dispersion from $\sim 40 \ m^2 \ s^{-1}$ in the outermost part of Kerteminde Fjord towards $\sim 4 \ m^2 \ s^{-1}$ in the innermost part of Kertinge Nor. The strength of dispersion seems to vary over time by the same order of magnitude, as reflected by the 90th and 10th percentiles approximately 50% above and below the median value (Fig. S4). Despite that the temporal variability of dispersion showed a typical period of about 2 wk, there was no indication for a seasonal dependency of the dispersive transport.

Model predictions of jellyfish abundance

Observed seasonal declines in the abundance of *Aurelia aurita* ephyrae and medusae in the fjord system Kertinge Nor/Kerteminde Fjord during 2013 and 2014 (Table S2) were predominantly due to hydrodynamic processes, as indicated by the predictions of our water exchange model (Fig. S5). Exponential regression functions reflect mean reductions by $-2.6 \pm 0.3\%$ d^{-1} and $-2.4 \pm 0.6\%$ d^{-1} in the observed jellyfish abundance in Kertinge Nor (Locations 1–3; Fig. 1A) during 2013 and 2014, respectively. Corresponding residence times, i.e. the times at which jellyfish abundance in Kertinge Nor was reduced to e^{-1} (= 0.37) times its initial value, were 39.4 ± 4.1 d and 42.7 ± 10.6 d, respectively. These observed jellyfish residence times are in good agreement with the residence times of the water masses, indicating decreases in jellyfish abundance to 37% after 45.0 ± 0.1 d and 44.0 ± 0.1 d, respectively, due to hydrodynamic forcing (Table S3). Predicted seasonal declines in the abundance of *A. aurita* in Kerteminde Fjord/Kertinge Nor resemble major fractions of $86.7 \pm 8.9\%$ and
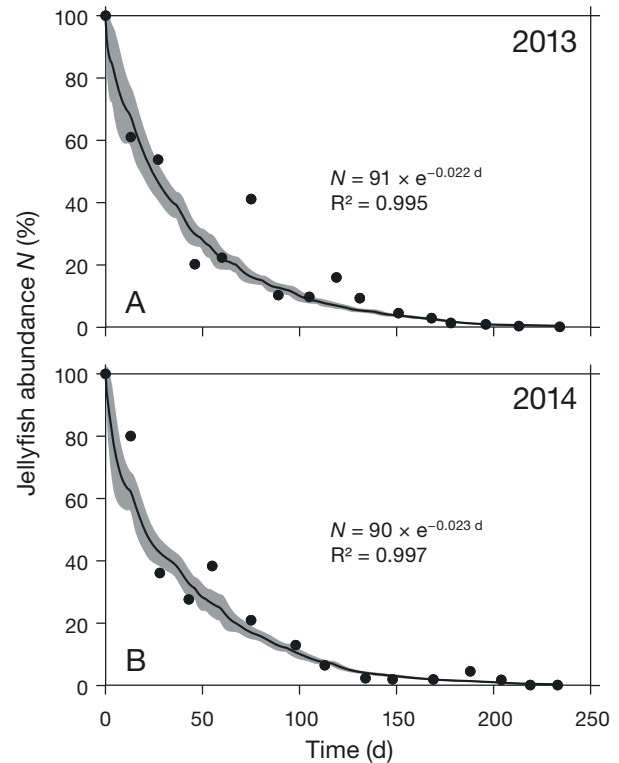

Fig. 4. *Aurelia aurita.* Mean observed jellyfish abundance (closed circles) and predicted abundance due to water exchange (solid lines; grey areas: SD) in Kertinge Nor (Locations 1–3) during (A) 2013 and (B) 2014. Exponential regression equations indicate residence times of $1/0.022 \ d^{-1}$ = 45 d and $1/0.023 \ d^{-1}$ = 44 d, i.e. the time at which the jellyfish population is reduced to e^{-1} (= 37%) due to water exchange

$82.6 \pm 7.9\%$ of observed declines in 2013 and 2014, respectively (Fig. 4).

DISCUSSION

Hydrodynamic forcing in a shallow fjord system

The present study indicates that $\geq 82.6\%$ of observed declines in the jellyfish abundance in the shallow fjord system Kerteminde Fjord/Kertinge Nor were caused by hydrodynamic forcing. Our 2 yr campaign of consistent measurements of salinity and jellyfish abundance provides a detailed quantification of the dispersal of jellyfish from the local population to adjacent coastal waters due to density-driven water exchange. The common jellyfish is a keystone species in controlling the trophic structure in Kertinge Nor (Olesen 1995). During summer, the dense *Aurelia aurita* population has a severe predatory impact on the local zooplankton community, as it can filter a water volume corresponding to several times

the whole water volume of Kertinge Nor daily (Riisgård et al. 1996), which results in estimated copepod half-lives as short as <1 d (Olesen 1995, Riisgård et al. 2010, Goldstein & Riisgård 2016). As a consequence of food limitation, medusae show restricted individual growth rates and generally small umbrella diameters (Olesen et al. 1994).

In general, medusa size depends on the availability of food resources relative to jellyfish abundance (Schneider & Behrends 1994, Lucas 2001, Goldstein & Riisgård 2016). Near-identical mean residence times of ~45 d for the water masses in Kertinge Nor during 2013 and 2014 are in good agreement with previous estimates of between 1 wk and a few months, i.e. 1.5 mo on average (Jürgensen 1995, Riisgård et al. 1996, 2008), and suggest gradual dispersal of the jellyfish population to adjacent coastal waters at a comparable rate during both years. Considering the simultaneous advection of zooplankton prey (Riisgård et al. 1995, Nielsen et al. 1997, Riisgård 1998), the present findings suggest seasonal declines in jellyfish abundance as an essential mechanism determining food availability inside the fjord system.

Apart from the number of released ephyrae, i.e. observed annual maximum jellyfish abundances, and the hydrodynamic dispersal of jellyfish from Kertinge Nor, the population size in the fjord system further depends on mortality rates. Mortality of *A. aurita* ephyrae and premature medusae generally seems to be low (Möller 1980, Fu et al. 2014). In temperate regions, sexual maturation is typically followed by shrinkage (degrowth) of medusae and simultaneous declines in population density (Hamner & Jenssen 1974, Möller 1980, Olesen et al. 1994, Lucas 2001, Uye & Shimauchi 2005, Marques et al. 2015, Goldstein & Riisgård 2016). While shortage of zooplankton prey controls seasonal degrowth and, consequently, reduced energy allocation to reproduction (Lucas 1996, Ishii & Båmstedt 1998), our findings indicate that death by starvation (or senescence) plays a minor role in the disappearance of medusae from Kertinge Nor (cf. Goldstein & Riisgård 2016). Hydrodynamic dispersal is suggested as a key mechanism to increase the survival probability of jellyfish in open coastal waters versus semi-enclosed and hence potentially food-limited regions.

Dispersal of medusae from semi-enclosed habitats to open coastal regions

The present study highlights the role of shallow, semi-enclosed fjord systems and estuaries as nursery grounds for scyphozoan jellyfish, while hydrodynamic dispersal of such (open) source populations may decisively contribute to the intensity and frequency of jellyfish blooms in adjacent coastal waters. In the shallow Kerteminde Fjord/Kertinge Nor, seasonal declines in jellyfish abundance are primarily subject to hydrodynamic forcing, pointing out the protected, food-limited fjord system as a source region for small *A. aurita*, which are frequently flushed out into Great Belt, where they may grow big (cf. Riisgård et al. 2010).

Danish estuaries are for the most part shallow (<3 m depth), have short water residence times, and tend to be heavily loaded with nutrients (Conley et al. 2000), reasons for which they may provide highly suitable habitat for the early developmental stages of jellyfish. The appearance of *A. aurita* ephyrae in distinct annual cohorts in shallow Danish waters such as Kertinge Nor and Mariager Fjord has previously been documented (Goldstein & Riisgård 2016, Lüskow & Riisgård 2016), and suggests the presence of polyps (Olesen et al. 1994). Little field evidence exists for polyp populations, in particular outside protected fjords and lagoons (Gröndahl 1988). Proliferation of artificial settlement substrates by human-made structures, however, may promote the occurrence of scyphozoan polyps in coastal and offshore areas severely (Duarte et al. 2012, Lucas et al. 2012, van Walraven et al. 2016). Port enclosures along the Inland Sea of Japan have previously been pointed out as seeding grounds for newly released *A. aurita* ephyrae which are transported offshore via tidal exchange (Makabe et al. 2014, 2015). In the Danish straits, density-driven currents are very common (Jürgensen 1995, Møller 1996, Riisgård 1998) and hence, similar hydrodynamic properties as observed in Kerteminde Fjord/Kertinge Nor apply to the majority of fjord systems in this region (cf. Josefson & Rasmussen 2000). These characteristics indicate dispersal of *A. aurita* medusae from inner-Danish shallow waters into coastal regions of Great Belt, Kattegat, Skagerrak and parts of the central Baltic Sea (cf. Barz et al. 2006) where they may restock local polyp populations.

Longevity of *A. aurita* medusae seems to range from ~4–8 mo to >1 yr in temperate waters (reviewed by Lucas et al. 2012); however, such field estimates are often only based on the presence or absence of distinct seasonal cohorts. The present study emphasizes the fundamental importance of hydrodynamic processes for jellyfish life histories in semi-enclosed and open coastal regions, in particular since age determination of scyphomedusae has remained challenging (cf. Lucas 2001, Widmer 2005, Sötje et al. 2017).

The model system Kerteminde Fjord/Kertinge Nor

While numerical solutions for the temporal and spatial variation in dispersive transport typically require high-resolution modeling of climatological phenomena and geographical properties (e.g. Signell & Butman 1992, Stohl et al. 2005), the characteristics of Kerteminde Fjord/Kertinge Nor allow for a simple hydrodynamic description based on salinity variations in the adjacent Great Belt. Our water exchange description takes into account physical principles including conservation of volume and mass, as well as an exchange discharge condition for stratified confined flows. The model is based on variable dispersion coefficients, hence reflecting geographical properties of Kerteminde Fjord/Kertinge Nor as well as meteorologically forced inflow- and outflow events in the adjacent Great Belt. The density-driven circulation was dominated by surface water inflow into the fjord system during 2013 and 2014, while bottom layer inflow from the open sea was less frequent and mostly observed from late August to December, matching the time frame of major Baltic inflows from the North Sea (Matthäus & Franck 1992, Schinke & Matthäus 1998). The present water exchange model reveals an uncertainty of ≤17.4 % with respect to observed declines in jellyfish abundance in the fjord system. This uncertainty is attributable to mortality and/or changes in the jellyfish distribution due to stratification which may occur during periods of stable salinity in Great Belt (Nielsen et al. 1997). While wind, waves and currents may constrain the distribution of gelatinous zooplankton in deeper offshore regions (e.g. Mianzan et al. 2010), vertical mixing is a key parameter in homogenizing the entire water column of the shallow Kerteminde Fjord/Kertinge Nor (Nielsen et al. 1997, Riisgård et al. 1998). During the study periods in 2013 and 2014, the probability of stable stratification was generally low, as reflected by a mean salinity gradient of 2.3 ± 1.8 PSU between the innermost part of Kertinge Nor and Great Belt. The adaptation time of *A. aurita* to this salinity difference, i.e. the time it takes jellyfish to enter a water mass of higher or lower salinity, can be estimated to 0.89 × 2.3 PSU = 2 h (Nielsen et al. 1997, their Fig. 4) which is within the time step dt ~3 h of our model.

CONCLUSIONS

The present water exchange model emphasizes the major importance of hydrodynamic dispersal for the boom-and-bust dynamics characterizing jellyfish mass occurrence. Shallow, semi-enclosed regions such as Danish fjords and estuaries are suggested as nursery grounds for jellyfish source populations which may constitute jellyfish blooms in adjacent coastal areas. Due to a strong impact of jellyfish abundance on the food resources available per individual, hydrodynamic forcing may further be a key variable for the longevity of medusae. This work may encourage future research to shed further light on the interplay between jellyfish life histories and hydrodynamic processes.

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