Contribution of coastal nursery areas to the spring-spawning population of Atlantic herring (*Clupea harengus*) in the Western Baltic Sea

Dissertation

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Contents

Summary

Coastal ecosystems provide essential spawning and nursery areas for numerous economically important marine fish species. At the same time they are extremely exposed to anthropogenic modifications and habitat degradation. Potentially, effects of hazards acting on the local scale of coastal fish nursery habitats might become directly transported to the level of adult fish populations, eventually affecting population dynamics on far broader spatial scales.

Atlantic herring (*Clupea harengus*) is among the most intensely studied fish species in the world, but owing its high plasticity, there are still numerous uncertainties on the drivers of herring population dynamics and habitat dependency, emphasizing the risk to jeopardize population resilience by on-going habitat alterations.

Atlantic herring in the Western Baltic Sea is an extraordinarily important fishery target and simultaneously representing a crucial link between different trophic levels of the food web. Since herring recruitment decreased within the last 17 years for widely unknown reasons, it is assumed that multiple hazards have a cumulative impact on a local scale of important spawning grounds, being vital for Western Baltic herring reproduction. However, the quantitative contribution of single spawning areas to the overall population has not been empirically investigated. Western Baltic herring is considered to annually return to bays and estuaries for spawning their benthic eggs on submerged aquatic vegetation. This homing behavior potentially renders the population rather vulnerable against changes of those inherent areas. Hence, the knowledge on habitat dependency of herring throughout the life cycle is essential to understand recruitment variability.

The first part of this thesis deals with the identification of important nursery areas for the Western Baltic herring population. Elemental fingerprinting in age-0 herring otoliths from four different spawning areas along the Western Baltic coastline was used to identify habitat-specific chemical signatures. Additionally, these natal fingerprints were combined with otolith core signatures from adult herring to investigate the contribution of single spawning habitats to the overall population. Analysis revealed that the quantitative contribution of Greifswald Bay to the adult population was generally major, but the exact magnitude varied between the years.

Summary

According to herring homing behavior, this thesis provided first evidence that Atlantic herring in the Western Baltic Sea return to their natal spawning areas, revealing a strong, inherent dependency on certain inshore coastal spawning areas, such as Greifswald Bay.

The second part of the thesis deals with the identification of local drivers and stressors, acting on the nursery area Greifswald Bay to evaluate potential effects on population dynamics. Eutrophication-based cascading effects resulted in a decline of macrophyte spawning substrate in Greifswald Bay with current growth limits of about 3.5 m. This vertical distribution limit of spawning beds increases the vulnerability of benthic herring eggs to multiple stressors, such as storm-induced hydrodynamics and increased water temperatures, which could highly impact annual fish recruitment. In the framework of this thesis, a depth-related herring egg sampling in multiple years was conducted to investigate initial spawning, spawning intensity patterns and herring egg survival in one important spawning bed, located in southern Greifswald Bay. Herring spawn concentrations, vegetation biomass and egg mortalities were quantified, additionally prevailing water temperatures were used to analyze the impact of water temperature fluctuations on initial spawning and general spawning intensity. The results of this study confirmed that egg concentrations are generally related to macrophyte biomass. Initial spawning is mainly driven by prevailing temperature regime with no spawning activity below a 4°C threshold. Furthermore, strong inter-annual changes in spawning intensities and egg mortalities could be observed. The results further revealed a temperature-related shift in spawning depth. Herring preferred spawning in the shallow water (1 m) during the early season, while shifting their egg deposition to deeper water (2-3 m) in the late season, indicating that adult herring might avoid increasing temperatures during the season. Moreover, the impact of storm-induced hydrodynamics on herring egg mortality was investigated with a prior-post storm egg sampling and an additional quantification of herring eggs attached to plant litter, washed to the beach after a multiple-day storm event. The results showed that herring egg survival is negatively impacted by storm events, affecting the shallow littoral zone. Despite larval herring are considered as plankton and are therefore seen as passive particles in oceanographic dispersal models, results on the habitat use of early herring life stages demonstrated that active habitat selection might be an important subject to consider. Especially post-flexion larvae showed an active habitat selection of the vegetated littoral zone, hence highlighting the vital role for herring recruitment.

This thesis demonstrated that inshore coastal systems, including vegetated littoral zones, are particularly important for all herring life stages (from the egg to the larvae and juveniles to the matured adult herring). Their functions include nursery areas for juveniles, sheltered retention and development areas for eggs and larvae and spawning grounds for adult fish.

Considering the persistent level of eutrophication in combination with future climate change scenarios including increasing storm intensities, -frequencies and increasing temperatures, the results of this thesis underline the demand for an integrated and sustainable management of shallow coastal spawning grounds.

Zusammenfassung

Küstengewässer mit ihren geschützten Buchten, Lagunen und Ästuaren sind weltweit wichtige Laichgebiete und Kinderstuben für zahlreiche kommerziell genutzte Fischarten. Im Übergang vom Land zum Ozean und damit in der Zone der höchsten Bevölkerungsdichten, unterliegen diese Systeme einer enormen Veränderung durch menschliche Nutzung. Zudem unterliegt die Ökologie der flachen inneren Küstengewässer einer starken saisonalen Dynamik und reagiert unmittelbar auf klimatische Veränderungen. Je nach ihrem spezifischen Beitrag an Fischnachwuchs kann eine Verschlechterung der Umweltbedingungen auf der relativ lokalen räumlichen Skala dieser wichtigen Reproduktionsgebiete die Dynamik gesamter Fischpopulationen beeinflussen.

Der Atlantische Hering (*Clupea harengus*) zählt zu den am besten untersuchten Fischarten der Welt und dennoch gibt es immer noch Unklarheiten über wichtige Mechanismen der Populationsdynamik, über die räumliche Nutzung der Laichgebiete und somit über die gebietsspezifische Abhängigkeit der Adult-Population von bestimmten Reproduktionsgebieten. Diese Kenntnislücke birgt das Risiko, dass die Belastbarkeit von Populationen überschätzt wird und die Auswirkungen der anthropogen-verursachten Stressoren auf den Reproduktionserfolg des Herings weitaus größer sind, als bisher angenommen. Der Atlantische Hering der westlichen Ostsee ist der „Brotfisch" der lokalen Küstenfischer und somit einer der wichtigsten Zielarten für die kommerzielle Fischerei in der Ostsee. Zugleich spielt der Hering eine essentielle ökologische Rolle in marinen Nahrungsnetzen, da er ein wichtiges Bindeglied zwischen verschiedenen trophischen Ebenen darstellt. In den letzten 17 Jahren hat die Nachwuchsproduktion des Herings der westlichen Ostsee stark abgenommen. Es wird vermutet, dass zahlreiche lokale Stressoren einen negativen Einfluss auf den Reproduktionserfolg haben. Jedoch gibt es bislang keine Studien zu dem quantitativen Beitrag einzelner Laichgebiete und „Kinderstuben" zur Gesamtpopulation, um den Einfluss der lokalen Stressoren abschätzen zu können. Zudem weist der Hering ein besonderes Verhalten der Brutortstreue auf (Homing-Verhalten). Während seiner jährlichen Wanderungen kehrt der Hering jedes Frühjahr zu seinen Laichplätzen in den Lagunen und Buchten entlang der westlichen Ostseeküste zurück, um dort seine klebrigen

Eier an vorhandene Unterwasservegetation zu heften. Neben der Funktion als Laichgebiet fungieren die inneren Küstengewässer als Retentionsgebiete in denen die gesamte larvale Entwicklung abgeschlossen wird. Darum ist es besonders wichtig den Grad der Abhängigkeit dieser Fischart zu ihren Laichgründen zu untersuchen, um die Variabilität der Rekrutierung zu verstehen.

Der erste Teil dieser Arbeit beschäftigt sich mit der Identifikation der wichtigen Kinderstuben des Herings der westlichen Ostsee. Anhand von Otolithen-Mikrochemie wurden juvenile Heringsotolithen aus vier verschiedenen Laichgebieten auf ihre gebietsspezifischen, chemischen Unterschiede untersucht. Die gefundenen chemischen Signaturen wurden mit der Kernregion (juvenil-Phase) von adulten Heringsotolithen verglichen, um den Beitrag der vier untersuchten Gebiete zur Gesamtpopulation abzuschätzen. Die Analyse ergab, dass das Laichgebiet „Greifswalder Bodden" ein sehr wichtiges Aufwuchsgebiet für die frühen Entwicklungsstadien des Herings ist und dieses Laichgebiet quantitativ am Meisten zu der Adult-Population beigetragen hat. Der quantitative Beitrag variierte allerdings zwischen den beiden untersuchten Jahresklassen. Im Zusammenhang mit dem „Homing"-Verhalten des Herings wurde die räumliche Skala der Brutortstreue untersucht und die Hypothese aufgestellt, dass die adulten Heringe jedes Jahr zu ihrem Laichgebieten zurückkehren, wo sie einst selbst geschlüpft sind. In dieser Studie wurden die chemischen Signaturen des Laichgebietes „Greifswalder Bodden" mit den Kernregionen von adulten Heringen, die während der Laichzeit in diesem Gebiet gefangen wurden, verglichen. Die Ergebnisse haben gezeigt, dass der Hering im Zuge seiner jährlichen Migration zu seinem Ursprungslaichgebiet zurückkehrt. Diese Untersuchungen zeigen erstmals, dass einzelne Laichgebiete die gesamte Population zu tragen scheinen und beweisen die starke gebietsspezifische Abhängigkeit des Herings zu bestimmten Laichgebieten. Im zweiten Teil dieser Arbeit wurden lokale Faktoren untersucht, die auf dieses wichtige Gebiet einwirken und somit maßgeblich die gesamte Heringspopulation beeinflussen können. Der massive Eintrag von Nährstoffen aufgrund intensiver landwirtschaftlicher Nutzung und die resultierenden Kaskadeneffekte führten in der Vergangenheit zu einem starken Rückgang der Makrophyten, und somit zu einem Rückgang des Laichsubstrates. Die Unterwasservegetation ist heutzutage hauptsächlich im Litoral zu finden, mit einer Wachstumsgrenze von 3.5 m. Diese Tiefen-Verschiebung hin zum Flachwasser führt natürlich zu einer gesteigerten Exposition des Phytals und assoziierter Heringseier gegenüber Sturm-induzierter Hydrodynamik. Um kritische Aspekte der Laichbiologie des Herings besser zu verstehen, wurde im Rahmen dieser Arbeit eine mehrjährige Probennahme entlang eines Tiefengradienten in einem wichtigen Laichbett an der südlichen Küste des Greifswalder Boddens durchgeführt. Der Fokus lag dabei auf dem

Zeitpunkt des ersten Laichens, der generellen Laichintensität und der Überlebensrate von Heringseiern. Eikonzentrationen, die vorhandene Pflanzenbiomasse, sowie Eimortalitäten wurden bestimmt und die Wassertemperaturen aufgenommen, um den generellen Temperatureinfluss auf den Zeitpunkt des ersten Laichgeschäftes, aber auch auf die tiefen-basierte Laichkonzentration zu untersuchen. Die Ergebnisse zeigen, dass die Eikonzentrationen abhängig von der vorhandenen Pflanzenbiomasse sind. Die erste Laichablage ist abhängig von den vorherrschenden Wassertemperaturen, es wurde keine Laichaktivität unterhalb der 4°C-Grenze beobachtet. Es konnten zudem starke zwischenjährliche Unterschiede in der Laichintensität und in den Eimortalitäten beobachtet werden. Weitere Ergebnisse haben einen Temperatur-abhängigen Wechsel der Laichtiefe entlang der Saison aufgezeigt. Die Heringe bevorzugten das Flachwasser (1 m) zu Beginn der Laichsaison (März) und laichten im späteren Verlauf der Saison (April) in tiefere Wasserzonen (2-3 m), um womöglich die schnell ansteigenden und generell höheren Temperaturen in der Flachwasserzone zu vermeiden. Des Weiteren wurde der Einfluss von Stürmen und dem dadurch bedingten Wellenschlag auf die Mortalität von Heringseiern untersucht. Auf definierten experimentellen Flächen wurden die Konzentrationen der Heringseier vor- und nach einem mehrtägigen Sturmereignis, sowie die Eikonzentrationen auf der angespülten Pflanzenbiomasse an einem Strandabschnitt bestimmt. Die Ergebnisse haben gezeigt, dass Sturm-induzierte Hydrodynamik in der bewachsenen Flachwasserzone zu einer drastischen Ei-Sterblichkeit führen kann. Des Weiteren wurde eine Untersuchung durchgeführt, in der die Wichtigkeit der Litoralzone für Heringslarven aufgezeigt wurde. Obwohl allgemein Heringslarven als Ichthyoplankton angesehen werden, welche passiv ohne aktive Bewegung in der Wassersäule treiben, konnte die Studie zeigen, dass Larven im Post-Flexion-Stadium aktiv ihren Lebensraum wählen können und vermehrt in der Litoralzone zu finden sind. Zusammenfassend kann aus den Ergebnissen dieser Arbeit geschlossen werden, dass einzelne Gebiete (wie der Greifswalder Bodden) von enormer Wichtigkeit für den Fortbestand des Herings der westlichen Ostsee sind. Zudem sind alle Lebensstadien (vom Ei über die Larve bis hin zum adulten Hering) stark auf die bewachsene Litoralzone in den inneren Küstengewässern angewiesen, da diese wichtige Funktionen als Kinderstube für juvenile Heringe, als schützende Retentionsgebiete für Heringseier und Heringslarven, sowie als Laichgebiete für die adulten Heringe übernimmt. Obwohl die Nährstoffeinträge in den letzten Jahren reduziert werden konnten, wird der Greifswalder Bodden immer noch als eutrophes Gewässer eingestuft und ein Anstieg der Makrophytenbiomasse ist in näherer Zukunft nicht zu erwarten. In Hinblick auf die immer noch reduzierte Pflanzenbiomasse und dem Klimawandel, der steigende Sturmintensitäten und –frequenzen, sowie steigende Wassertemperaturen mit sich bringen wird, unterstreichen

die Ergebnisse die Forderung nach einem nachhaltigen Küstenzonen-Management, um diese wichtigen Laichgründe vor weiteren anthropogenen Einflüssen zu schützen und somit den Fortbestand der Heringspopulation der westlichen Ostsee für zukünftige Generationen zu sichern.

General Introduction

Herring Biology

Geographic distribution

Herring is a small pelagic teleost fish (Clupeiformes, family: Clupeidae), typically occurring in the epipelagial of the temperate northern hemisphere (Klinkhardt 1996), inhabiting the Pacific, Atlantic and Arctic oceans (Haegele & Schweigert 1985). On species level, herring is divided into Pacific herring (*Clupea pallasii*) and Atlantic herring (*Clupea harengus*). Both species include several local populations and "races", depending on spawning time, spawning location, migration patterns and morphologic characteristics (Haegele & Schweigert 1985, Klinkhardt 1996).

The Food and Agriculture Organization of the United Nations (FAO) stated that Atlantic herring is with 1.6 kilotons of landings (in 2014) one of the most economically important fish species in the world (FAO 2016). In the Atlantic, *C. harengus* is divided into spring and autumn/winter spawning populations (Aneer & Nellbring 1982, Dickey-Collas et al. 2010, Geffen et al. 2011) which are considered genetically distinct (Barrio et al. 2016). The spawning areas of the northwest Atlantic populations are located in the Gulf of St. Lawrence, along the coast of Nova Scotia, up to Newfoundland (Wheeler & Winters 1984, Haegele & Schweigert 1985, Messieh & Rosenthal 1989). In the north eastern Atlantic, herring reproduction areas are geographically distributed around Iceland, the Faroe Islands, along the British Isles and Ireland, along the coast of Norway, as well as in the Kattegat-Skagerrak area and the Baltic Sea up to the Bothnian Bay in Finland (Dragesund et al. 1980, Rosenberg & Palmén 1982, Klinkhardt 1986, Kääriä et al. 1997, Brophy et al. 2006). It is also known that herring is geographically distributed up to the north to the White Sea, where individuals seem to be morphometrically similar to the Pacific herring, showing one small-sized spring spawning and one large-sized summer spawning herring (Soin 1971, Klinkhardt 1996). *C. pallasii* in the Pacific Ocean is known to be a winter-spring spawning herring and usually spawns in the intertidal and upper subtidal zones along the Pacific coast of North America (California (US), Washington State

(US), British Columbia (CAN), Alaska (US)), in the Bering Sea and all the way to the Pacific coast of Japan (Haegele & Schweigert 1985).

In the Atlantic, the commercially exploited herring stocks in the North Sea belong to autumn spawning populations, spawning their eggs on gravel and stones in deeper coastal shelf areas down to approximately 70 m (Hempel & Schubert 1968, Blaxter 1985). Although formerly abundant, only residuals of those autumn spawners currently occur in the Baltic Sea as they did not yet recover from major fishery pressure during the 1970's (MacKenzie & Ojaveer 2018). Nowadays, most of the recent Baltic Sea herring populations are spring spawners, showing a similar spawning mode as the Pacific herring (Haegele et al. 1981, Hay 1985, Polte et al. 2014), using mainly macrophytes as spawning substrate in the immediate shore zone. Regarding the fact that herring is one of the most studied fish species worldwide, it is striking that there seems to be a great uncertainty and lack of current knowledge on the characterization of spawning grounds and the degree of their dependence on estuarine habitats (Able 2005). This is presumably due to the diversity of different herring populations and their individual spawning and migration patterns (Haegele & Schweigert 1985).

Herring in the Western Baltic Sea

The Western Baltic spring spawning herring population is one of the most important fishery targets in the Baltic Sea region. This herring population is genetically distinct from neighboring herring populations (i.e. North Sea or Central Baltic) (Bekkevold et al. 2005, Jørgensen et al. 2005, Gaggiotti et al. 2009) and is considered to be a metapopulation, consisting of multiple spawning components with the "Rügen herring", being one of the main components of this population (Clausen et al. 2007). Herring spawning areas are located in the vicinity of the Island of Rügen and along the Western Baltic coastline (Fig. 1). Besides the economic relevance for human nutrition, this small pelagic clupeid plays a key-role in marine food webs, transporting energy from the lower level of zooplankton to the higher trophic levels of predators (Blaxter & Hunter 1982, Möllmann et al. 2004, Kotterba 2015). While there is often a high number of species at the lowest (i.e. phytoplankton, zooplankton) and highest trophic levels (i.e. large fish predators), the representatives, serving the function as intermediate link, are often based on only single species (Bakun 2006). Especially in the Baltic Sea, with its strong salinity gradient with marine conditions (Kattegat-Skagerrak, 35 PSU), mesohaline conditions along the Western Baltic up to almost fresh water conditions in the Bothnian Bay, the species richness in this trophic position is rather poor (Elmgren 1984), indicating the crucial importance of single species such as herring and sprat (*Sprattus sprattus*) for the entire ecosystem function.

The Western Baltic spring spawning herring conducts annual migrations between their feeding grounds in Kattegat and Skagerrak during summer (Oeberst et al. 2009), their overwintering habitat in the Öresund Strait (Nielsen et al. 2001) and their inshore coastal spawning grounds along the Western Baltic Sea (Fig. 1).
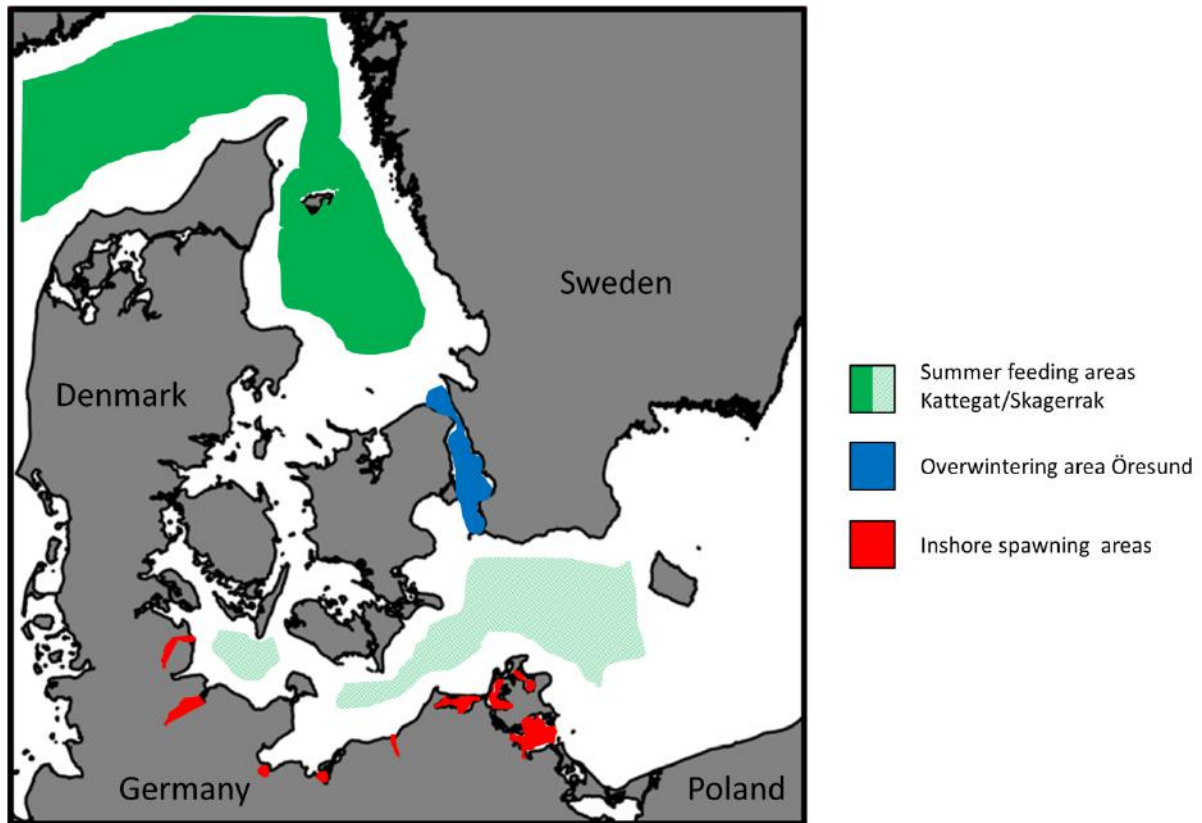
Figure 1: Annual migration route of Atlantic herring in the Western Baltic Sea. Adult herring summer feeding areas in the Kattegat and Skagerrak are indicated by green color, the overwintering area in the Öresund Strait is colored in blue and the known inshore coastal spawning areas along the Western Baltic coast are colored in red (Figure is modified after P. Kotterba).

In February, matured adult herring aggregations can be found in coastal waters, ready to enter the inshore spawning areas from March until May in spawning cohorts with the larger repeated spawning individuals arriving first, followed by the small and younger individuals in the later season (Haegele & Schweigert 1985, Hay 1985, Lambert 1987). The number of spawning cohorts varies, depending on population and geographic location (Haegele & Schweigert 1985, Scabell 1988, Rajasilta et al. 1993). Spawning activity is mainly triggered by prevailing water temperatures. Rügen herring is considered to start spawning at about 4°C in Greifswald Bay, which is a major spawning area for this population (Klinkhardt 1986, Scabell 1988, Klinkhardt 1996). Herring is classified as a litho-phytophilous spawner (Balon 1975), attaching their

extremely adhesive eggs to benthic substrates (aquatic macrophytes) in the shallow littoral zone. Spawning in Baltic Sea inshore waters is often described to occur with an active contact to substrate (Hourston et al. 1976, Klinkhardt 1996 and literature therein), highlighting the importance of vegetation for the reproduction success of the Western Baltic herring population.

Greifswald Bay: Spawning area characteristics

Greifswald Bay is a semi-enclosed inshore lagoon, formed by the Island of Rügen northwards and the German mainland in the south with a connection to the Baltic Sea by a narrow sound (Strelasund) westward and a wide, but shallow opening in eastern direction (Fig. 2). This brackish lagoon covers approximately 514 km^2. With a mean salinity of 7.3 PSU (Kell 1989), Greifswald Bay is a shallow, mesohaline ecosystem with a mean water depth of 5.8 m (max. depth of 13.6 m).
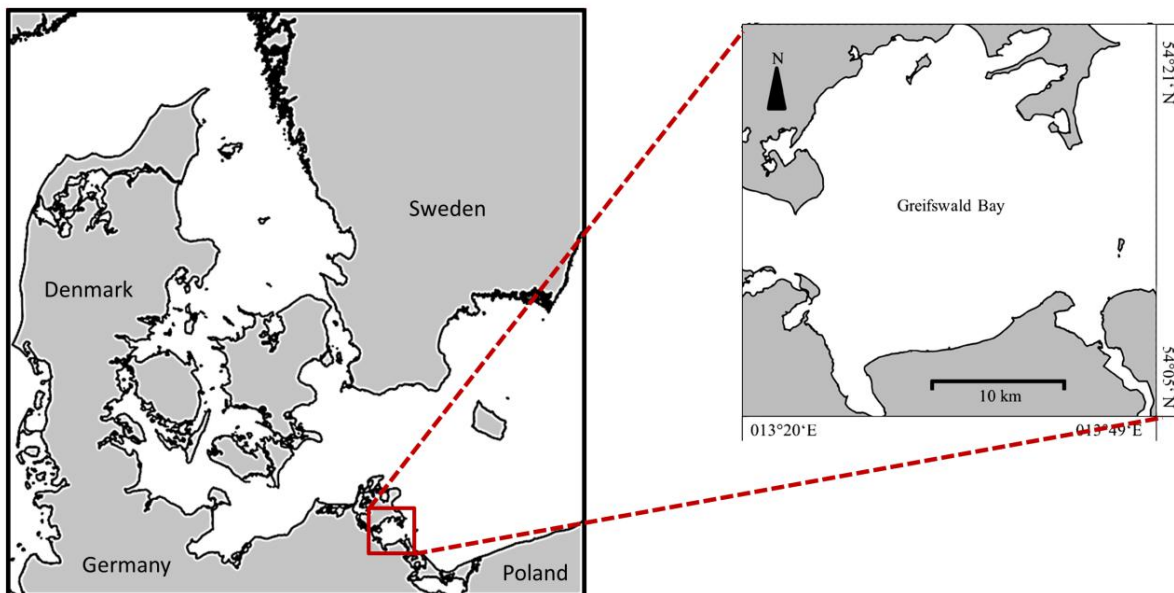
Figure 2: Location of one important spawning area for the Western Baltic herring population. Greifswald Bay is a shallow coastal lagoon in the vicinity of the Island of Rügen in the Western Baltic Sea (Greifswald Bay map modified after Kotterba et al. 2014)

Owing to the topographic features and the marginal lunar tidal amplitude in the inner coastal waters (< 10 cm), there is only a limited water exchange rate with the open Baltic Sea which is mainly wind driven (Schnese 1973, Stigge 1989, Schiewer 2008). The water temperatures range seasonally from sub 0°C surface waters with regularly closed ice coverage in winter to more than 20°C during summer. The shallow water depth results in a rapid warming during springtime and water temperatures decrease quickly in autumn. Due to wind mixing, thermoclines are a rare event and the water body is generally well-oxygenated throughout the season (Schnese

1973, Schiewer 2008). The shallow littoral zone is characterized by extended beds of submerged aquatic vegetation, showing growth limits of approximately 3.5 m water depth (Munkes 2005b, Kanstinger et al. 2016). These vegetated areas in the shallow littoral serve as suitable herring spawning beds. The spawning beds are stratified by depth and dominated by flowering plants such as pondweeds (mainly *Stuckenia* spec.) or marine seagrass (*Zostera marina*) in addition to a diverse macroalgal community (i.e. *Furcellaria* spec.; *Fucus* spec.) with also fast-growing filamentous brown and green algae (Geisel & Messner 1989).

Greifswald Bay is classified as a eutrophic ecosystem, according to the water quality assessment of Mecklenburg-Western Pomerania (state agency water quality report, 2003-2006). Although the total nitrogen and total phosphor input could be reduced within three decades, the water quality of Greifswald Bay is still exceeding the thresholds according to the EU-Water Framework Directive (Robakowski 2012). The annual nitrogen and phosphor inflow into the Bay is generally dominated by river discharge, mainly depending on meteorological and hydrological conditions and on non-located diffuse sources (Robakowski 2012). Eutrophication processes, resulted from high nutrient loads in the past, led to a severe decline in vegetation biomass in Greifswald Bay from 90% (Seifert 1938) to 7-15% (Messner & von Oertzen 1990, 1991, Kanstinger et al. 2016). Bartels & Klüber (1999) even stated that the vegetated area in Greifswald Bay was only 4% (22.54 km^2) of the total area in 1990.

Homing

Homing (or spawning site fidelity) is a well-documented behavioral trait in diadromous fish species (Vladykov 1971, Tesch 1975, Youngson et al. 1994, Quinn et al. 1999, Zimmerman et al. 2013) and is also observed for some purely marine, economic relevant species, such as Atlantic cod (*Gadus morhua*), North Sea plaice (*Pleuronectes platessa*), Baltic Sea turbot (*Psetta maxima*) and Atlantic herring (Wheeler & Winters 1984, Robichaud & Rose 2001, Hunter et al. 2003, Florin & Franzén 2010). Considering herring homing behavior, there is some confusion about the exact meaning of the term "homing". Often "homing" is used describing "natal homing", which means that the fish is returning to the spawning area, where it was once spawned (Hay et al. 2001). Besides "natal" homing, there is another form, described as "repeated" homing, meaning that herring return to a distinct spawning area, but not certainly to the spawning area of natal origin. Generally, homing behavior to spawning areas could be observed for Atlantic and Pacific herring populations respectively (Hourston 1982, Wheeler & Winters 1984), but results are mainly based on tagging investigations. Those mark-recapture studies cannot differentiate between "natal homing" and "repeated homing" (MacLean & Evans 1981,

McQuinn 1997), although herring is assumed to home to their natal spawning sites, due to their genetic population structure (Bekkevold et al. 2005, Ruzzante et al. 2006). Studies on the spatial scale herring home to their coastal spawning areas in the Western Baltic Sea are missing. However, if habitat conditions become unfavorable for successful reproduction and adult herring continue their migrations to these unfavorable habitats due to this specific behavioral traits, this could lead to severe impacts on population level. Hence, there is a strong need to investigate herring homing behavior to implement a coastal zone management of regional spawning sites which may have an essential function for the persistence of populations (Polte et al. 2014).

Herring early life stages

Impact factors — Besides the fact that parental factors are known to impact egg and larval size (Chambers & Leggett 1996, Evans & Geffen 1998), the development of stationary benthic eggs is subject to local climate variability and spawning site specific drivers and stressors. Salinity is an important abiotic driver for ontogenetic development (Klinkhardt 1986). Herring gametes generally show a wide salinity tolerance, ranging from 4 to 35 PSU, depending on geographical location and population (Holliday & Blaxter 1960, Haegele & Schweigert 1985, Klinkhardt 1986). For Baltic Sea herring larvae, critical salinity levels of 2–3 PSU could be observed (Illing et al. 2016). Water temperatures are one of the most influential abiotic factors for successful reproduction, controlling embryonic growth rates and biochemical reactions (Blaxter 1956, Laurence & Howell 1981). Prevailing water temperatures during spawning and egg development determine the time of hatch, larvae size at hatch, duration of yolk utilization (Peck et al. 2012) and influence the development of myotomal muscles required for swimming in herring larvae (Vieira & Johnston 1992, Moyano et al. 2016), hence consequently driving survival of early life stages (Rannak 1958, Peck et al. 2012). For Western Baltic herring, the optimal temperature window for successful hatching is determined between 5-17°C (Peck et al. 2012). It is assumed that the duration of herring egg development is approximately 12 days at 10°C (Klinkhardt 1984, Peck et al. 2012). Larval size at hatching varies between 5.5-7.3 mm, depending on temperature (Klinkhardt 1986, Peck et al. 2012) and duration of yolk utilization is about 6.5 days at 8°C (Klinkhardt 1996). The point, when herring larvae shift from yolk consumption to active feeding, predominately preying on zooplankton, such as copepods, nauplii and copepodite stages (Checkley Jr. 1982, Möllmann et al. 2004, Paulsen et al. 2014), is considered to be the most critical period in early larval stages and is assumed to determine year-class strength of fish populations (Hjort 1914).
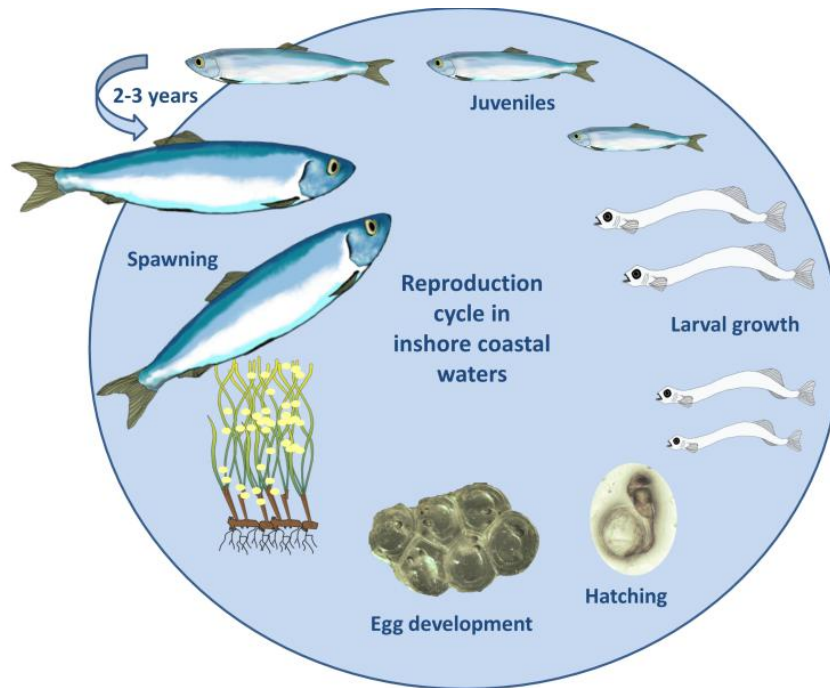
Figure 3: Herring life cycle in inshore coastal waters. Spawning herring attach their demersal eggs on submerged vegetation. After successful egg development, herring larvae hatch, grow, metamorphosed and become juveniles. Juveniles migrate to outer coastal waters and after 2-3 years, matured herring migrate into the spawning area to complete the life cycle. Symbols for diagrams courtesy of the Integration and Application Network (ian.umces.edu/symbols) and symbols of adult herring and larvae are created by Paul Kotterba, pictures of eggs and hatching larvae: D. Moll.

Habitat use — Whereas some clupeids spawn pelagic eggs, where successful egg development and hatching success is mainly dependent on hydrodynamic drift patterns (such as sprat (*Sprattus sprattus*), anchovies (*Engraulis* spec.) and sardine (*Sardina pilchardus*), see Shelton & Hutchings 1982, Nissling et al. 2003, Santos et al. 2007), herring spend their entire early life stages (from egg to juvenile fish) within their inshore coastal spawning grounds (Fig. 3).

Generally, larval fish is considered as ichthyoplankton, implying they are not able to influence their spatial distribution actively, being passive drifting particles. Hence one important research aspect to understand recruitment variability is larval dispersal (Hjort 1914, 1926, Cushing 1975, Iles & Sinclair 1982, Bauer et al. 2013). Research on the capability of active habitat use of fish larvae was quite unattended, even though studies showed an active habitat selection for coral reef fish larvae (Dudley et al. 2000, Paris & Cowen 2004). Furthermore, a study on larval herring swimming capability revealed different critical swimming speeds for different herring developmental stages (yolk-sac to post-flexion stadium), indicating that even small and fragile-looking herring larvae are able (to a certain degree) to actively select their habitats (Moyano et al. 2016). Since different environmental hazards could affect distinct early life stage-habitats, it is necessary to investigate the habitat use of early fish life stages in inshore

coastal reproduction areas. At larval sizes of 25-30 mm, schooling behavior in larval herring can be observed (Rosenthal 1968) and active migration to outer coastal areas usually starts after metamorphosis is completed, when herring reach a total length of 35-40 mm (Blaxter & Hunter 1982, Klinkhardt 1996). After 2-3 years, juvenile herring are matured, entering their spawning area in spring for their first spawning season, completing the life cycle.

Survival bottlenecks — Although recent studies from the Pacific and Atlantic herring populations provide the hypothesis that year-class strength is rather determined during the juvenile life after metamorphosis (Sætre et al. 2002, Bishop et al. 2015) or by the magnitude of spawning stock biomass (Toresen 2001), there is evidence that Western Baltic herring recruitment is driven by bottlenecks, located predominately in the early life stages previous to metamorphosis (Oeberst et al. 2009, Arula et al. 2014, Polte et al. 2014).

Herring populations are considered to be "bet-hedging" strategists, spreading their spawning activity in waves over time, increasing the chances of successful reproduction by avoiding poor feeding conditions (Lambert & Ware 1984, Lambert 1990, Arula et al. 2014). This reproductive effort is required to ensure recruitment and therefore the survival of populations (Duarte & Alcaraz 1989).

It is a common assumption that availability of suitable prey organisms during the larval phase is one of multiple factors, driving fish recruitment variability (Cushing 1975, Sinclair & Tremblay 1984). Polte et al. (2014) stated distinct larval hatching peaks along the Western Baltic herring spawning season with differing contribution to Western Baltic herring recruitment, assuming distinct cohort bottlenecks. In Greifswald Bay, the survival bottleneck for the first cohort (usually occurring in late March) is rather located in the larval stage, whereas the bottleneck for the second cohort, which usually occurs in late April and mainly drives recruitment, is supposed to be located in the pre-hatching period at the egg stage (Polte et al. 2014).

Benthic herring eggs are subject to several stressors (Fig. 4), such as predation of the local predator community, since eggs are easy accessible energy sources. Recent studies revealed a strong predation pressure by the local threespine stickleback (*Gasterosteus aculeatus*) on herring eggs, deposited in an important western Baltic Sea spawning ground (Kotterba et al. 2014, Kotterba et al. 2017). Moreover, depth-limitation of vegetation, which is observed in Greifswald Bay spawning area due to eutrophication processes in the past, increases the vulnerability to storm-induced mechanic forces, as well-described for the Pacific herring population around Vancouver Island, British Columbia, Canada (Hart & Tester 1934, Hay & Miller 1982, Haegele & Schweigert 1989). Since the Baltic Sea herring shows a similar spawning mode as the
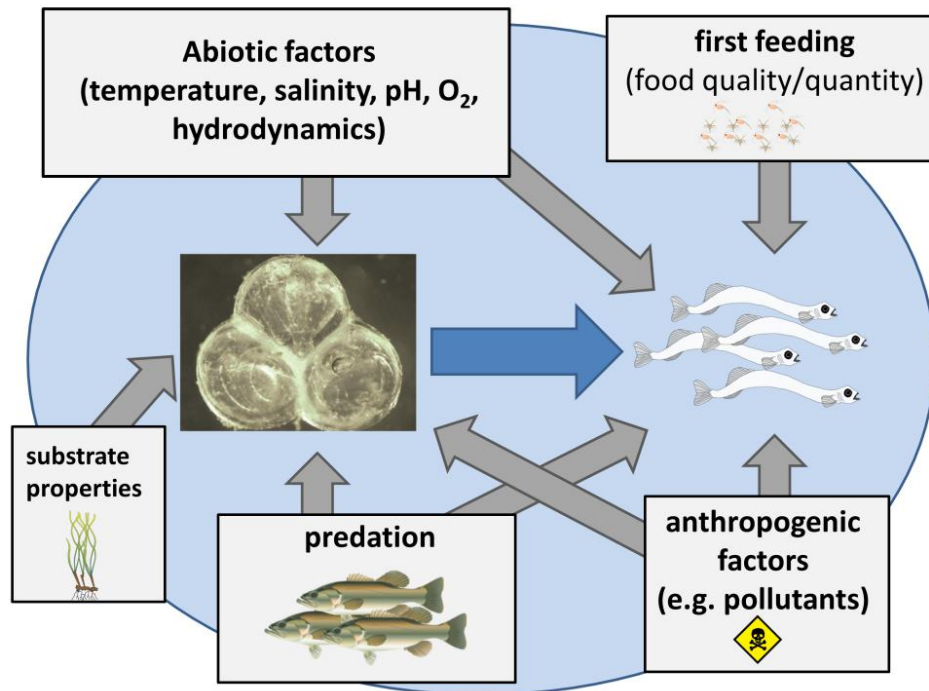
Figure 4: Drivers and stressors acting on early herring life stages (egg stage and larvae) with potential bottleneck functions in inshore coastal waters. Symbols for diagrams courtesy of the Integration and Application Network (ian.umces.edu/symbols), herring larvae symbols are created by P. Kotterba, pictures of eggs originated from D. Moll.

Pacific herring, storm events could also immensely affect Western Baltic herring recruitment. There is evidence that climate change will increase storm frequency and -intensity and sea surface temperatures (Woth et al. 2006, Coumou & Rahmstorf 2012). Regarding the essential role of water temperatures for successful development of herring eggs, larvae and therefore recruitment, these forecasts will drastically affect coastal ecosystems, especially shallow coastal waters (Rijnsdorp et al. 2009).

Eutrophication related cascade effects

Submerged aquatic vegetation provides substantial spawning substrate for benthic spawning fish species (Haegele & Schweigert 1985, Beauchamp et al. 1992, Polte & Asmus 2006) and is also essential for juvenile and nursery habitats (Rooker et al. 1998, Nagelkerken et al. 2001, Verweij et al. 2008). High agricultural land use and massive use of fertilizer overcharged the natural buffering capacity of sensible coastal ecosystems during the last centuries worldwide and high nutrient loads resulted in massive growth of phytoplankton, leading to increased water turbidity and decreased light penetration and therefore to drastic declines of extension and growth rates for submerged aquatic vegetation (Moore & Wetzel 2000). In Greifswald Bay, eutrophication

resulted in loss of vegetated areas, generally reduced depth distribution of existing macrophyte beds and resulted in a decline in general vegetation diversity (Munkes 2005a, Kanstinger et al. 2016). However, structural complexity of vegetation evidently facilitates the successful development of herring eggs (von Nordheim et al. 2018). Besides eutrophication related cascade effects such as the example of increased epiphyte growth, reducing the photosynthetic rate of vegetation (Sand-Jensen 1977, 1990), there are also several observations on eutrophication-triggered occurrence of filamentous algae cloaked together in lumps or thick mats (Bonsdorff 1992, Pihl et al. 1999), assumed to negatively impact herring egg survival (Aneer 1985, 1987, von Nordheim unpublished) (Fig. 5).

Eutrophication also drives the occurrence of harmful algal blooms and pathogenic organisms (Braga et al. 2000), showing a global expansion in recent years with an increasing impact on fish mortality (Anderson et al. 2000, Anderson et al. 2002). Altogether, the human-induced impact on coastal habitats is substantial. Although many commercially important fish species rely on coastal habitats, either for spawning or as juvenile areas and nurseries, there is still insufficient information on the connectivity between these habitats and fish population dynamics on fishery target species (Seitz et al. 2014). Research on juvenile-adult habitat connectivity for exploited fish species is highly relevant, since understanding fish population dynamics and identification of essential nursery habitats could enhance sustainable management strategies for fisheries (Hamer et al. 2003). One example for a negative impact of multiple threats on a herring population is the Cherry Point herring, a local Pacific herring (*Clupea pallasii*) population on the coast of Washington State (USA). The interaction of high fishery pressure, the intense anthropogenic alteration of the coastal region (oil refineries and aluminium smelter) and the shift from a cold to a warm climate period led to a change in age structure, a decreased reproduction capacity and therefore caused a severe decline in fish abundances (Landis et al. 2004). All primary and secondary threats acting on this herring population demonstrate that knowledge on the impact of drivers and stressors is strongly required to understand year class variability and set the baseline to successful fishery management strategies.

Herring recruitment failure — For stock assessment purposes the Thünen Institute of Baltic Sea Fisheries conducts a weekly larvae survey in Greifswald Bay (and the adjacent Strelasund) every year during the spawning season to investigate the spatial and temporal distribution of herring larvae in this important reproduction area. Survey data are used to estimate the total annual amount of probable survivors as determined by older larvae of 20 mm total length, expressed by the recruitment index (N20-index, for more information see Oeberst et al. 2009,
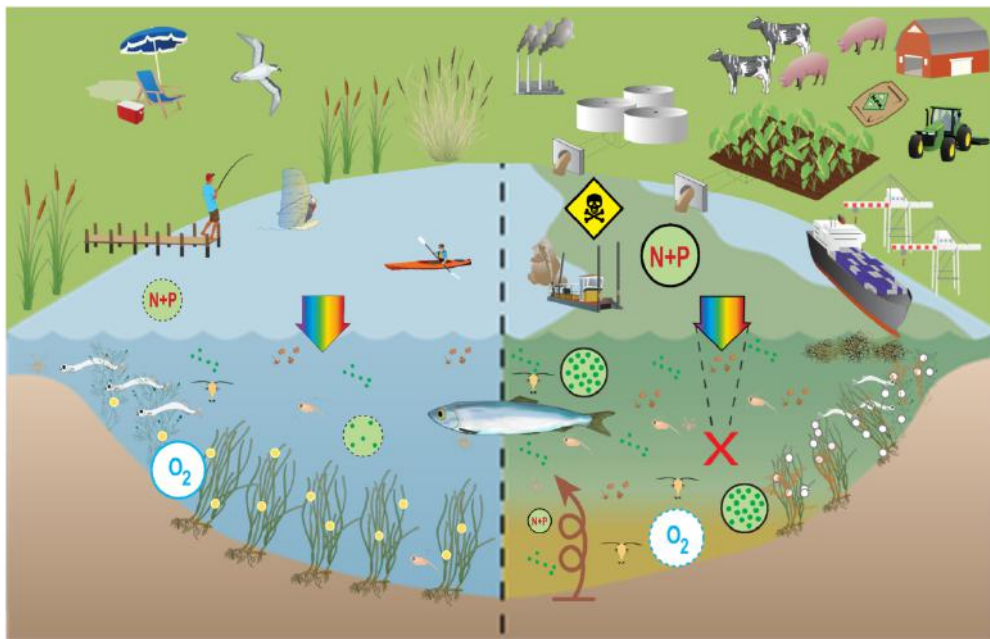
Figure 5: Conceptual diagram on environmental deterioration and anthropogenic-caused effects on herring spawning habitats, resulting in a decreased herring egg survival. Left: spawning habitat in a good ecological condition. Right: Impact of eutrophication and habitat alterations, such as dredging activities, causing internal eutrophication, but also have lethal and sub-lethal effects on fish eggs, fish larvae and adult fish (Auld & Schubel 1978, Wilber & Clarke 2001, Griffin et al. 2009), symbols for diagrams courtesy of the Integration and Application Network (ian.umces.edu/symbols).

Polte et al. 2014). This N20-index is considered to represent the year-class strength of offspring that will grow into the adult population during the following 2-3 years (Oeberst et al. 2009). The Western Baltic herring recruitment continuously decreased during the past two decades and reached its lowest level in 2016 (ICES Advice 2017). The reasons for this decline are still unknown, but it is assumed that multiple stressors are acting on a local scale of important spawning grounds, which are of high importance for herring reproduction.

The chart shows a scatter plot with regression line. The equation is $y = 0.0629x + 492.05$ and $R^2 = 0.696$. The y-axis is labeled "GERAS Age-1 (millions)" ranging from 0 to 2,500. The x-axis is labeled "N20 Age-0 (millions)" ranging from 0 to 25,000. A red data point is labeled "2015".
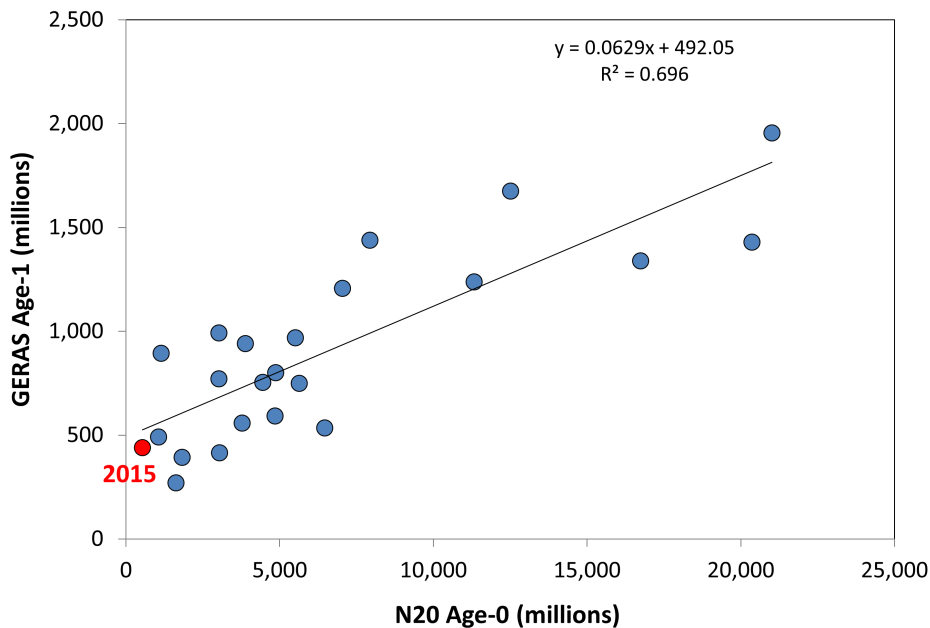
Figure 6: Correlation of the recruitment N20-index with abundance data of age-1 herring, caught in the entire western Baltic Sea during an acoustic survey in autumn (GERAS) from 1993-2015, indicating a relation between Western Baltic herring recruitment and larval production in Greifswald Bay. The year 2015 indicates the lowest N20 within the time-series and is highlighted in red (slightly modified after Polte & Gröhsler 2018).

Although the actual contribution of the spawning area Greifswald Bay to the Western Baltic herring population is unknown, Greifswald Bay is assumed to be one of the main reproduction areas for this population. Correlations of > 20 mm sized larvae (N20-index) with abundance data of age-1 juveniles, caught in the entire western Baltic Sea, indicated that herring recruitment is not independent from the larval production in Greifswald Bay (Fig. 6). This is underlined by a further analysis of the low larval production year 2016, which also resulted in low age-1 juveniles in 2017 (not depicted in Fig 6, personal communication T. Gröhsler). Besides spawning areas in the vicinity of the Island of Rügen, other herring spawning grounds and juvenile areas along the Western Baltic Sea are barely described and information is rather anecdotal (but see Weber 1971, Schnack 1974, Lupatsch & Nellen 1981). Hence, there is no

comprehensive understanding on the quantitative contribution of single juvenile areas to the adult Western Baltic herring population. For responsible future management strategies, there is a strong need to identify regional hazards, acting on a local scale of important spawning grounds, having the potential to be transported to the population level.

Herring and the nursery concept

Inner coastal waters are main drivers of ocean productivity and serve as vital and ecologically important habitats for marine fishes and their early life stages, providing important spawning substrates for benthic spawning fish (Fonds et al. 1974, Haegele et al. 1981, Polte & Asmus 2006), increased food availability for juvenile organisms (Blaber et al. 1995, Nagelkerken et al. 2001), plenty of hiding places to avoid predation during the early life stages (Orth et al. 1984, Shulman 1985, Parrish 1989, Caddy 2007) and it is assumed that the shelter from hydrodynamics could also positively affect distribution of juveniles in these coastal inshore waters (Blaber & Whitfield 1977). All these characteristics underline the essential function as considerable spawning and juvenile habitats for many temperate and tropical fish species around the world (Blaber & Blaber 1980, Beck et al. 2001, Nagelkerken et al. 2001), generally leading to high abundances of larval and juvenile fish in these specific areas (Heck & Thoman 1984, Vasconcelos et al. 2010). Instead of the frequent, universal use of the term "nursery area" summarizing all coastal habitats where juveniles of a given species occur, there was a demand for a clear and unambiguous definition of the term in the recent literature (Carlson & Straty 1981, Robertson & Duke 1987, Bennett 1989, Nagelkerken et al. 2002, Tse et al. 2008).

The definition after Beck et al. (2001) emphasizes the concept of a nursery area, revealing the importance to identify the quantitative contribution of particular areas to the adult population of fish or invertebrates (Beck et al. 2001). According to the authors, a nursery area is not just one of multiple areas inhabited by juveniles of a population, but it is defined as "an area, which contributes a greater than average number of individuals to the adult population on a per-unit area basis" (Beck et al. 2001) (Fig. 7). A few years later, this definition was extended by Dahlgren et al. (2006), remarking that the nursery definition after Beck et al. (2001) did not consider larger habitats as nurseries, contributing a smaller number of individuals per-unit area, but perhaps in total contributing a majority of individuals to the adult population (Dahlgren et al. 2006). According to these quantitative aspects, research is nowadays increasingly focused on studies on juvenile-adult habitat connectivity and dependency of fish species to certain habitats (Thorrold et al. 2001, Forrester & Swearer 2002, Gillanders 2002). This connectivity
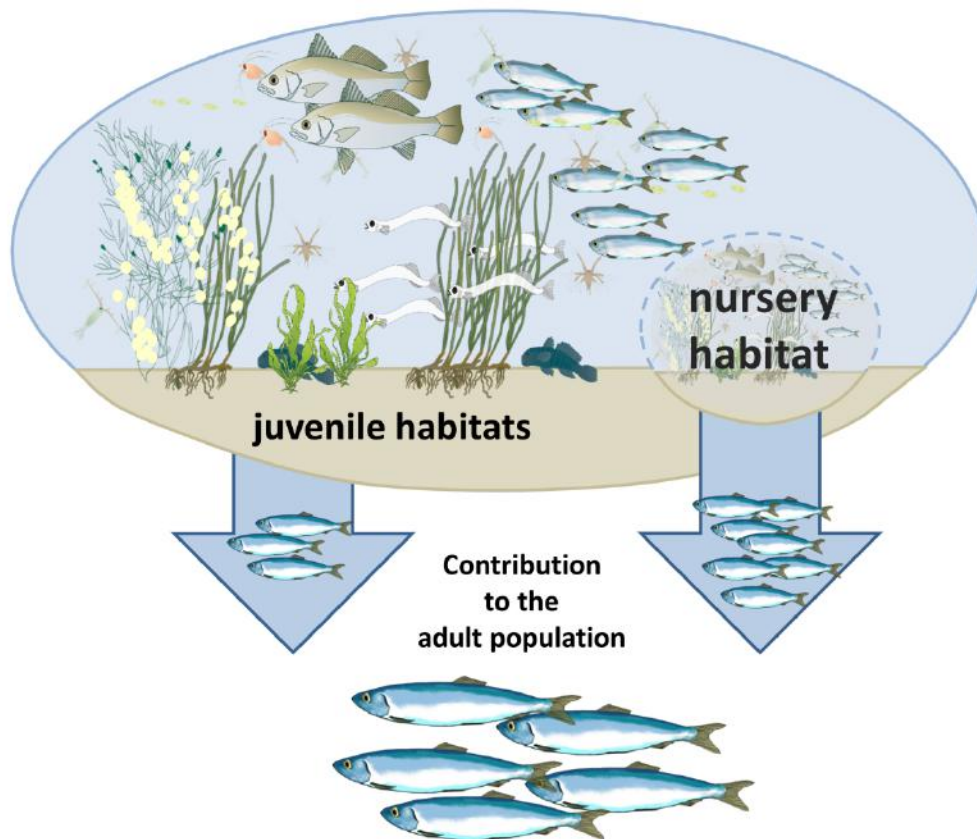
Figure 7: Nursery-role concept, modified after Beck et al. 2001. Juveniles of a species can inhabit multiple juvenile habitats within a system, but the major quantitative contribution to the adult population is often provided by one or few nursery areas. Symbols for diagrams courtesy of the Integration and Application Network (ian.umces.edu/symbols) and especially symbols of adult herring and larvae originated from P. Kotterba.

and dependency aspect is highly relevant to evaluate the relation between habitat availability, spawning habitat degradation and fish population dynamics and at the same time exposed a great lack of knowledge on general life history and migratory patterns of economic important fish species with a great uncertainty of obligate or facultative habitat use (Able 2005).

Aims of the thesis

Since coastal ecosystems suffer from eutrophication, but simultaneously serve the function of important spawning and juvenile habitats for ecologically and economically relevant fish species worldwide, the evaluation of fish habitat dependency has rarely been implemented into current coastal zone management plans. Atlantic herring in the Western Baltic Sea shows a strong dependency on inner coastal waters for recruitment, since the early life history is taking place in coastal inshore bays and estuaries and adults returning to these specific areas every year for spawning, even though under unfavorable ecological conditions. Regarding the current state of knowledge on general herring ecology in the Western Baltic Sea and particularly the effects of regional hazards and their potential impacts on population dynamics, there is a strong need to (1) estimate the importance of single spawning and juvenile areas to the total Western Baltic herring population and to (2) identify local drivers and stressors and evaluate their impact on Western Baltic herring recruitment.

Identification of coastal nurseries

Since the contribution of single spawning and juvenile habitats along the Western Baltic Sea to the overall population is unknown but essential to understand recruitment variability and population dynamics, the promising tool of otolith chemistry was used to identify habitat specific elemental signals in four different known herring spawning habitats along the Western Baltic Sea, hypothesizing that these specific signals were different between the investigated juvenile habitats. Elemental composition of the age-0 herring otolith core regions were set as a baseline (Chapter 1) for subsequent contribution estimations of single habitats. In Chapter 2, elemental composition data of age-0 herring otoliths were combined with elemental data of the otolith core region of adult herring, sampled in the overwintering and accumulation area, to estimate the contribution of single juvenile habitats to the overall adult population, hypothesizing that Greifswald Bay function as an important nursery habitat for Western Baltic herring. Since herring shows the important behavioral aspect of homing to their spawning areas, herring homing behavior was investigated with the help of otolith specific element

signatures from adult herring otoliths, sampled in Greifswald Bay during spawning season, hypothesizing that spawning migrations of Atlantic herring populations in the Western Baltic Sea are driven by homing behavior on quite small spatial scales, where adult herring home to their natal spawning areas (Chapter 3).

Reproductive stressors on the level of nurseries

In order to the changing environmental conditions of coastal juvenile herring habitats, research on herring spawning ecology is essential to understand herring reproduction success and productivity, especially in an eutrophic ecosystem like Greifswald Bay. Since important recruitment bottlenecks are located in the egg stage, the identification of local stressors with the aim to evaluate their impact on herring egg survival and reproduction is subject to the following chapters. Chapter 4 presents a study on general herring spawning ecology, regarding temperature-based initial spawning in one shallow spawning bed, depth-related egg distribution along the littoral depth gradient to investigate the impact of prevailing water temperatures on herring egg survival in these shallow vegetated spawning beds. Since investigations in the Pacific region reveal high egg loss rates due to wave action, a second study deals with the impact on storm events on herring egg mortality in the shallow coastal waters of the Western Baltic Sea (Chapter 5). Furthermore, distribution patterns of herring larvae and potential active habitat selection of early herring life stages were investigated (Chapter 6), hypothesizing that even small and fragile-looking larvae are able to actively select their habitat, emphasizing the importance of shallow coastal habitats for herring recruitment and population persistence.

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Chapter 1

Using elemental fingerprinting in Western Baltic juvenile herring (*Clupea harengus*) otoliths to distinguish different juvenile habitats

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Abstract

For many fish species, coastal areas are ecologically important by providing essential spawning and juvenile habitats. However, these habitats are often highly impacted by multiple anthropogenic threats. Atlantic herring (*Clupea harengus*) shows a distinct homing behavior, returning to particular coastal spawning grounds (e.g. estuaries, brackish lagoons and bays) every year during spring, attaching adhesive eggs to benthic substrates. Attributed to early life stage mortality, herring recruitment decreased in the western Baltic Sea during the past two decades. Since major drivers and stressors for herring reproduction are potentially introduced on the local scale of important spawning grounds, the knowledge of the contribution of different juvenile habitats to population dynamics is essential. We used elemental fingerprinting in otoliths of early herring life stages, caught in four known spawning and juvenile habitats and offshore along the Western Baltic Sea, to detect differences in the chemical composition based on varying water chemistry in particular areas. Results from the laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) analysis revealed a distinct chemical separation between age-0 herring caught in the vicinity of the Island of Rügen (south-western Baltic Sea) and other areas further west in the Baltic Sea with high significant differences among the areas. Furthermore, we created an innovative elemental fingerprinting index (*EFI*), which allows us comparisons of otolith multi-element patterns within and between certain juvenile habitats, indicating that otolith chemistry is a suitable tool for future habitat connectivity estimates. The aim is the identification of herring offspring origin and the contribution of particular juvenile areas to the adult population, which could lead towards a more directed coastal zone management.

Introduction

Coastal ecosystems are of high ecological importance, since these systems are highly productive, serving as considerable spawning and juvenile habitats for many temperate and tropical fish species around the world (Blaber & Blaber 1980, Orth et al. 1984, Shulman 1985, Levin et al. 1997, Nagelkerken et al. 2002). However, coastal waters are increasingly impacted by increased multiple anthropogenic threats, affecting the natural buffering potential of these ecosystems during the last centuries. Due to this interaction of coastal habitats, being anthropogenic stressed ecosystems and simultaneously being important fish reproduction areas, the knowledge of the importance of juvenile habitats for the overall fish population is crucial. However, evaluations on the nursery functions are often performed by comparing juvenile fish abundance and species richness between differing habitats (Kerstan 1991, Reichert & van der Veer 1991, van der Veer et al. 2001, Nagelkerken et al. 2002, Tse et al. 2008). Since Beck et al. (2001) stated the "nursery-role hypothesis", defining a juvenile habitat to be a nursery area for a particular fish species, when its contribution to the adult population is higher than from other juvenile habitats (Beck et al. 2001), the research effort is more focused on evaluations of juvenile habitat productivity to adult population (Gillanders & Kingsford 1996, Forrester & Swearer 2002, Gillanders 2002a). However, quantifying the contribution of a particular juvenile habitat to the overall adult population is quite challenging.

While otoliths, the calcified ear stones of teleost fish, were formerly used for annual age and growth estimations (Beamish 1979, Hoyer et al. 1985, Newman et al. 2000, Newman 2002), the scope of otolith research further developed during last decades (Campana 2005), resulting in new scientific applications such as otolith microstructure analyses for estimating age of early life stages on a daily scale (Nishimura & Yamada 1984, Campana & Moksness 1991, Lecomte-Finiger 1992, Secor & Dean 1992, Campana & Thorrold 2001) and otolith chemical analyses to investigate the spatial origin of offspring (Dove et al. 1996, Thresher 1999, Volk et al. 2000, Gillanders & Kingsford 2003, Swan et al. 2006, Ranaldi & Gagnon 2010).

The otolith chemistry approach takes advantage of the specific fish otolith characteristics, being metabolic inert, growing continuously without resorption and acting like life history recorders by incorporating elements into their growing surface and therefore reflecting the physical and chemical characteristics of the ambient water, where the fish is residing during the early ontogeny (Campana & Neilson 1985, Campana 1999). With the implementation of otolith microchemistry, a new age of fishery research was established, resulting in several studies concerning stock discrimination analyses (Edmonds et al. 1989, Kalish 1990, Campana et al.

1994, Swan et al. 2006, Heidemann et al. 2012) and fish migration patterns of diadromous fish species, e.g. for European eel *Anguilla anguilla* (Tzeng et al. 1997), American shad *Alosa sapidissima* (Limburg 1995) and Chinook salmon *Oncorhynchus tshawytscha* (Ingram & Weber 1999, Barnett-Johnson et al. 2008), mainly based on the elements Sr and Ba, known to be markers for salinity gradients (Kennedy et al. 2002, Kraus & Secor 2004, Elsdon & Gillanders 2005, Gillanders 2005a, Zimmerman 2005, Brennan et al. 2015). Further approaches to investigate habitat connectivity, predominately based only on a few selected elements, extended the knowledge on habitat use of different early life stages and the connectivity to adult habitats, especially conducted on tropic and sub-tropic fishes (Gillanders & Kingsford 1996, Milton et al. 1997, Rooker et al. 2001, Thorrold et al. 2001) and on some temperate species (see Yamashita et al. 2000, Secor et al. 2001, Brown 2003). However, studies concerning habitat connectivity of commercially important fish species in the northern hemisphere (such as flatfishes, cod and herring) are rather scarce (but see Geffen et al. 2003, Vasconcelos et al. 2008, Geffen et al. 2011, Thorisson et al. 2011). Investigations on *C. harengus* are mainly based on the detection of a few elements in larval and juvenile otoliths (Brophy et al. 2003, Brophy et al. 2004) or element ratio variability related to environmental parameters, e.g. temperature (Radtke et al. 1990, Townsend et al. 1992).

The Atlantic herring is one of the most important marine fishery target species in the world with high landings (1.6×10^6 tons) in 2014 (FAO 2016). Moreover this small pelagic fish is of high ecological relevance, acting as a link between different trophic levels in the marine food web (Casini et al. 2004, Möllmann et al. 2004). The Western Baltic spring spawning herring is a highly migratory population, accomplishing annual migrations between their feeding grounds in the Kattegat and Skagerrak in summer and their coastal spawning grounds located in bays, estuaries and lagoons along the coastal Western Baltic Sea during spring. In contrast to many other small pelagic fish species, *C. harengus* is a litho-phytophilous spawner (Balon 1975), attaching numerous adhesive eggs to benthic substrates, either on gravel beds in deeper waters, reported for North Sea herring (Hempel & Schubert 1968, Hempel 1971), or on submerged aquatic vegetation in the shallow littoral zone (Klinkhardt 1986, Aneer 1989, Kotterba et al. 2014). The Western Baltic herring spawns predominantly on macrophytes, showing the same spawning mode as the Pacific herring (*Clupea pallasii*) (Taylor 1964). Herring seems to return to the same spawning grounds every year, showing a distinct homing behavior (Wheeler & Winters 1984, McQuinn 1997). Hence, these sensitive coastal ecosystems are essential for herring reproduction success and at the same time reproduction is affected by multiple biotic factors, e.g. condition of adults (see Laine & Rajasilta 1999, Engelhard & Heino 2006) and

egg predation (Richardson et al. 2011, Kotterba et al. 2014), as well as abiotic environmental variables, e.g. water temperatures, oxygen supply, suitable spawning substrate (see Blaxter 1956, Braum 1973, Peck et al. 2012, Kanstinger et al. 2016) and additionally human induced stressors, e.g. eutrophication and pollution (Kinne & Rosenthal 1967, Dethlefsen et al. 1996, Munkes 2005). Herring recruitment in one important Western Baltic spawning area decreased during the past two decades and remained on a low level ever since, reaching the lowest value of the time-series in 2016 (ICES Advice 2017). The reasons are still unclear, but it is assumed that climate change, eutrophication related cascade effects and therewith interacting multiple regional stressors, negatively affected egg and larval survival in important spawning areas. Quantitative studies on the contributions of single coastal juvenile habitats to the adult Western Baltic herring population are lacking, but those are vital to understand the impact of these local hazards to the overall population. Hence, otolith chemistry has the potential to broaden our understanding of fish population dynamics and the connectivity between juvenile and adult fish habitats and might result in improved management strategies for the Western Baltic herring population in the future. Based on a multiple-element approach, we analyzed the elemental composition of age-0 herring otoliths from inshore spawning areas and offshore sampling sites along the Western Baltic coastline. Furthermore we modified an ecologically established index to create an elemental fingerprinting index (*EFI*) for comparing otolith chemical signatures within and between different inshore sampling areas, hypothesizing that herring otoliths from different juvenile areas along the Western Baltic Sea differ in their elemental composition.

Material and Methods

Outer coastal sampling sites

Age-0 herring were caught during a standardized pelagic trawl fishery survey in autumn 2014. Six sampling sites were selected along the coastline of the Western Baltic Sea, (Fig. 1), where salinity varied from approx. 15-20 PSU (Schaber & Gröhsler 2014) at the most northern station, located within a strait between the two Danish islands Funen and Zealand (the Great Belt), to approx. 7-10 PSU in the most eastern stations around the Island of Rügen (Fig. 1). Assuming that age-0 herring collected in the outer coastal sampling stations do not migrate long distances but are rather located in the vicinity of their spawning areas, elemental differences of those otoliths were analyzed with solution based-inductively coupled plasma-mass spectrometry (SB-ICP-MS) to detect potential differences between western and eastern sampling locations.
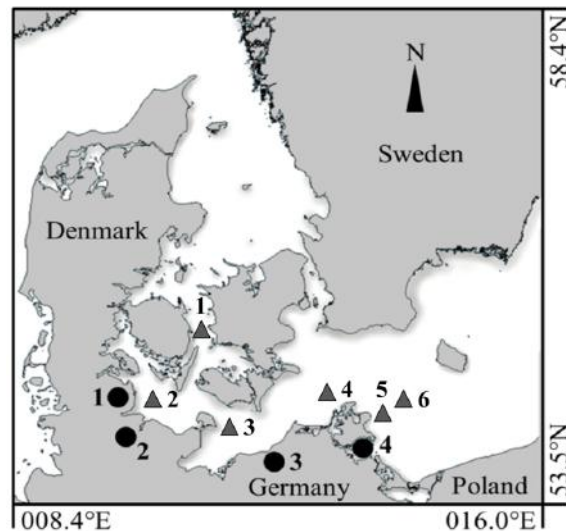
Figure 1: The inshore and offshore sampling locations in the Western Baltic Sea. Sampling locations of outer coastal age-0 herring from 2014 are represented by grey triangles: (**1**) Denmark (Great Belt), (**2**) Kiel Bay, (**3**) Mecklenburg Bay and (**4-6**) sampling locations in the vicinity of the Island of Rügen. The four inshore sampling sites from 2016 are indicated by black circles (**1**) Schlei Fjord (SF), (**2**) Kiel Canal (KC), (**3**) Warnow Estuary (WE) and (**4**) Greifswald Bay (GB).

Inner coastal study sites

All four inner coastal study sites are known juvenile habitats for the Western Baltic spring spawning herring population. Sampling was conducted in the Schlei Fjord (SF) (N 54° 35′; E 09° 51′), Kiel Canal (KC) (N 54° 21′; E 09° 50′), in the Warnow Estuary (WE) (N 54° 07′; E 12° 05′) and Greifswald Bay (GB) (N 54° 13′; E 13° 32′) in summer 2016 (Fig. 1). To analyze habitat-specific chemical signatures, 30 otoliths from each juvenile area were used for chemical analysis, except for Greifswald Bay (n=15). The chosen sample size (n=30) was above the commonly accepted standard for this kind of analysis (Gillanders 2002b, de Pontual et al. 2003, Kraus & Secor 2004, Hamer & Jenkins 2007) and was assumed to be adequate to test our hypotheses. Hereafter, the abbreviations of the different sampling areas are used in the following text. The characteristics of each sampling site, including abiotic parameters (sea surface temperatures (SST) and salinity) during sampling, mean total length (TL mm) of juvenile herring, as well as numbers of individuals per sampling site are summarized in Tab. 1.

Sample preparation and analytical methods

Offshore age-0 herring — Available otoliths from age-0 herring (TL ~ 84.9 mm ± 1.1 mm) were washed in ultrapure water (TKA-GenPure, 0.2 µm capsule filter, Hartmann GmbH). The ultrapure water used for the analysis (18.2 MΩ cm^{-1}) was obtained from a MilliQ Element /

Table 1: Description of each inshore sampling area with respective water body type and salinity gradients, sampling dates, abiotic parameters and number of analyzed individuals with mean total length [mm] (and standard deviation) of caught juvenile herring. The SST and salinity for GB are averaged due to different pooled stations.

Location	Water body type	Salinity range PSU	Sampling date	SST °C	Salinity PSU	No. of individ.	Mean TL mm
SF	Fjord 54 km^2	mesohalin 5-18	28th June 2016	20.8	4.03	30	37.2 ($\pm$ 2.9)
KC	Artificial water way 100 km	mesohalin 2.5-15	08th June 2016	20.0	7.05	30	38.0 ($\pm$ 1.8)
WE	Estuary 12.6 km^2	mesohalin 5-18	23rd June 2016	20.1	10.7	30	23.2 ($\pm$ 3.5)
GB	Lagoon 514 km^2	mesohalin 5-10	15th June 2016	$\varnothing$18.3	$\varnothing$7.8	15	22.7 ($\pm$ 2.2)

Elix 3 water purification system (Merck Millipore, Schwalbach, Germany). Nitric acid as well as hydrochloric acid (both suprapure quality) were obtained from Merck (Merck Darmstadt, Germany). To achieve a sufficient blank level both acids were doubly purified in a sub boiling distillation cascade, operated under clean room conditions (class 10000). All labware (sampling bottles, sample tubes etc.) were cleaned according to a procedure, which includes the leaching of the material over a period of approximately 1.5 month using different acids (HCl and HNO$_3$ respectively) of different purities to minimize the blank level of the material. Depending on individual otolith size of each sampling station, two to five otoliths were pooled in cleaned plastic vials. Otoliths from each sampling location were dissolved in approximately 1 ml of 2% nitric acid (volume was filled up to 50 ml with ultrapure water) for chemical analysis using a SB-ICP-MS approach. Pooled otoliths were used to increase the weighed portion, due to the specific sensibility of the used ICP-MS (Agilent Technologies 8800 ICP-MS Triple Quad). Multi element standard solutions covering the targeted element selection were obtained from Inorganic Ventures (Inorganic Ventures, Christiansburg, Virginia, USA). Diluted stock solutions for the preparation of the calibration standards were prepared fresh and directly before the start of the different measurements. For quality control during the measurements the following certified standard reference materials have been used: SLEW-3, CASS-4, CASS-5 NASS-5, NASS-6. All reference materials have been obtained from LGC (LGC Standards GmbH, Wesel, Germany). External calibration solutions were always freshly prepared and stabilized by adding either subboiled HNO$_3$ and subboiled HCl to a final calibration solution volume of 50 ml. All calibration solutions were prepared using acid cleaned DigiTube vials (SCP Science, SPrpep, Germany). To minimize contamination effects, the instrument was operated in a class 10000 clean room environment with restricted access. All sample preparation steps were performed inside a clean bench (class 100).

Inner coastal age-0 herring — Age-0 herring were caught by beach seine (7 m opening, 5 mm mesh size, wing height 1.5 m) in the SF sampling area. In KC, sampling was conducted with a purse seine (40 m length, 4 mm mesh size, 3 m height). The sampling areas WE and GB were sampled with a ring trawl of 1 meter diameter (1550 µm mesh size) onboard a research vessel. Hydrological parameters (SST and salinity) were either recorded with a hand held field probe (YSI Professional Plus) or a remotely operated CTD. Herring were frozen immediately after the catch and were transported to the laboratory. Prior to otolith dissection, microscope slides were washed in 2% nitric acid (Rotipuran Supra 69%, Carl Roth), were rinsed with ultrapure water and were dried under a flow cabin to keep them free from dust particles. Double-sided adhesive transparent pads, placed on the cleaned glass slides, were used as otolith fixing material. Herring otoliths were dissected under a microscope (Olympus SD 30). Sagittal otoliths were removed with non-metallic equipment (e.g. ceramic forceps) to minimize potential contamination. After dissection, each otolith (either left or right sagittal otolith) was rinsed in ultrapure water, approximately three times, to remove any adhesive tissue. Thereafter, all otoliths from each sampling area were transferred and placed on the adhesive pad. Microscope slides with attached otoliths were stored in a plastic vials until the otolith core region was analyzed with the laser ablation-inductively coupled plasma-mass spectrometry technique (ThermoFinnigan ELEMENT2 ICP-MS with a Nd:YAG UP213 laser ablation system). The certified reference material NIST612 (National Institute of Standards and Technology) and the micro analytical reference material MACS3 (United States Geological Survey) were used for calibration (Jochum et al. 2007, Jochum et al. 2011) and were analyzed prior to measurement and measurements were constantly repeated to ensure quality. Otolith core regions were ablated with 80 µm laser spot size at 60% power with a pulse repetition rate of 10 Hz and energy densities of ~10.2 J cm^{-2}. Otolith samples were measured with dwell duration setting of 70 seconds. Further technical information of the New Wave laser ablation system and the operating parameters for the ELEMENT2 ICP-MS are given in the appendix (C1, Tab. A1).

Elemental fingerprinting index (EFI)

We visualized chemical otolith signatures for each spawning area (based on the inshore sampling in 2016) by radar plots, based on the relative mean proportion of 17 element concentrations in a defined order. Additionally, we created the elemental fingerprinting index (*EFI*), adapted to the ecologically well-established overlap index (Schoener index), representing a new interdisciplinary measure of similarity in herring otolith elemental composition. This index is

derived by the congruence of radar plot areas, resulting from specific element concentrations of two comparing individuals and reflects the percentage overlap of plot area comparison. The *EFI* ranges from 0 to 1, where a value of 0 indicates that two compared individuals are most different in otolith elemental composition, whereas a value of 1 indicating the highest similarity in elemental composition of two compared individuals. We conducted elemental concentration comparisons for all individuals within one sampling area (with 435 comparisons for each sampling area, except GB: 105 comparisons) and comparisons of all individuals between different sampling areas (900 comparisons in total, except for GB: 450). *EFI* was used to identify similarities within one group and differences in scope of elements concentration between groups.
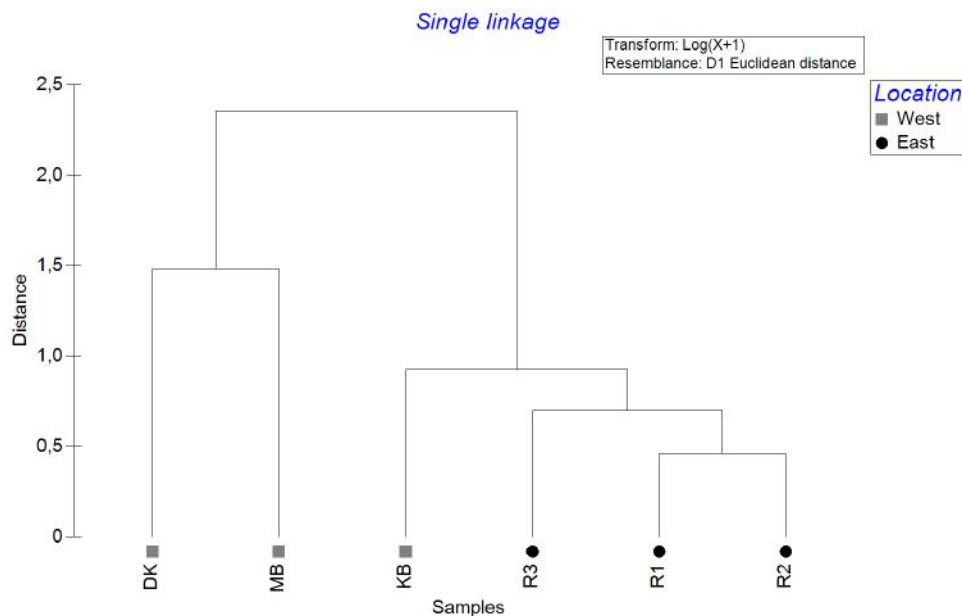
Data Analysis

Values near the detection limits were excluded from the analysis and only elements with no more than two missing concentration values were considered for further analysis (in total 17 elements). Illustrations (Cluster-Analysis and MDS-plots) were created with the PRIMER Software (Version 6.1.13) with the dissimilarity matrix of calculating the Euclidean distances and elemental concentrations were $\log(x + 1)$-transformed for standardization. Statistical analyses were performed with the software STATISTICA 12 (Statsoft) and SPSS, statistical significance (significance level of $p < 0.05$) was tested by using one-way analysis of variance (ANOVA). Data sets were tested for variance homogeneity by Levene's test. Due to variance heterogeneity and unequal sample sizes, statistical significance was tested with ANOVA including Welch correction (Welch 1938) and post-hoc tests for inhomogeneous variances and sample sizes (Games Howell test). *EFI* values were tested for significant differences within and between sampling areas using Welch-Test and Games Howell post-hoc test to investigate significant differences between the four sampling sites.

Results

Otolith chemical signatures

Offshore samples — In total, the concentrations of 44 elements could be determined in juvenile otoliths from the outer coastal sampling sites by SB-ICP-MS (see appendix C1, Tab. A2). All elements and their respective concentration in µg g^{-1} for each sampling location were included in a cluster analysis for distinguishing outer coastal sampling sites on the basis of their chemical otolith signatures. We found a separation between the western and the eastern samples (Fig. 2) with a clear clustering of the western sampling sites DK and MB and the Rügen samples (R1, R2, R3). KB samples are more similar to the eastern located Rügen samples.

Figure 2: Cluster analysis, using the Euclidean distance to classify groups of all detectable elements (in total 44 elements) for the outer coastal herring samples. Otoliths were pooled and data were log(x+1)-transformed for standardization. The grey squares indicate samples from western locations Denmark (DK), Mecklenburg Bay (MB) and Kiel Bay (KB), the black dots marked samples from the eastern sampling sites around the vicinity of the Island of Rügen.

Inshore spawning areas — In total, the concentrations of 39 elements could be determined in the juvenile otolith samples from the inshore spawning areas. Altogether, 17 elements were used to distinguish the chemical otolith signatures from different sampling sites. The mean element concentrations in juvenile herring otoliths are given in Tab. 2.

All 17 elements of 105 individuals were included in an MDS-plot for visualizing the chemical signature differences in each sampling area (Fig. 3). Otoliths from the western sampling areas (SF and KC) are more similar in their elemental concentrations than otoliths from the eastern

Table 2: Mean otolith element concentrations (µg g^{-1}) of 17 elements in age-0 herring otoliths from four different spawning areas with standard deviation (± SD), median and number of analyzed individuals (n).

Elements	SF				KC				WE				GB			
	Mean	± SD	Median	n	Mean	± SD	Median	n	Mean	± SD	Median	n	Mean	± SD	Median	n
Li	0.037	0.02	0.040	30	0.055	0.02	0.053	30	0.132	0.09	0.125	29	0.086	0.05	0.073	15
B	1.66	0.18	1.63	30	2.62	0.40	2.52	30	3.64	1.13	3.49	30	1.88	0.29	1.81	15
Na	2611.1	141.1	2593.9	30	2841.8	95.3	2841.7	30	3011.4	263.7	2981.8	30	2919.6	179.6	2933.4	15
Mg	57.7	28.9	48.9	30	135.9	108.7	87.1	30	249.8	109.7	257.1	30	173.4	65.7	179.7	15
Si	313.7	25.9	313.7	30	303.8	37.6	300.9	30	269.9	55.5	268.7	30	211.9	41.9	197.3	15
Mn	21.3	22.0	10.6	30	4.38	1.74	4.00	30	6.50	4.67	6.4	30	3.79	2.71	3.30	15
Fe	48.8	2.9	48.6	30	72.3	8.9	71.5	30	60.4	31.2	51.1	30	50.5	4.4	52.9	15
Co	0.035	0.01	0.034	30	0.108	0.06	0.113	28	0.090	0.11	0.048	30	0.034	0.01	0.032	15
Cu	0.060	0.02	0.056	30	0.079	0.04	0.068	30	0.234	0.21	0.130	30	0.173	0.09	0.144	15
Zn	1.29	0.79	1.073	30	2.68	2.38	2.31	30	8.19	7.66	6.29	30	13.5	17.7	8.6	15
Rb	0.094	0.02	0.092	30	0.158	0.05	0.145	30	0.208	0.23	0.122	30	0.168	0.08	0.150	15
Sr	640.4	74.7	640.4	30	651.9	78.9	655.6	30	817.6	149.5	825.9	30	726.8	102.0	732.7	15
Sn	0.028	0.01	0.028	30	0.239	1.13	0.026	30	0.100	0.11	0.050	30	0.029	0.02	0.023	14
Ba	6.9	3.1	6.49	30	12.7	5.1	11.8	30	6.49	2.45	6.46	30	8.93	2.98	9.25	15
Pb	0.003	0.00	0.002	29	0.018	0.04	0.009	29	0.183	0.20	0.098	28	0.043	0.05	0.027	15
Tl	0.005	0.00	0.004	30	0.019	0.01	0.019	30	0.036	0.07	0.003	28	0.010	0.00	0.009	15
U	0.000	0.00	0.000	28	0.001	0.00	0.000	28	0.027	0.07	0.006	29	0.004	0.00	0.002	15

sampling areas (WE and GB). Elemental otolith compositions from WE show a higher variability in individual element concentration. However, a clear separation between the western and eastern located spawning areas is discernible (Fig. 3).
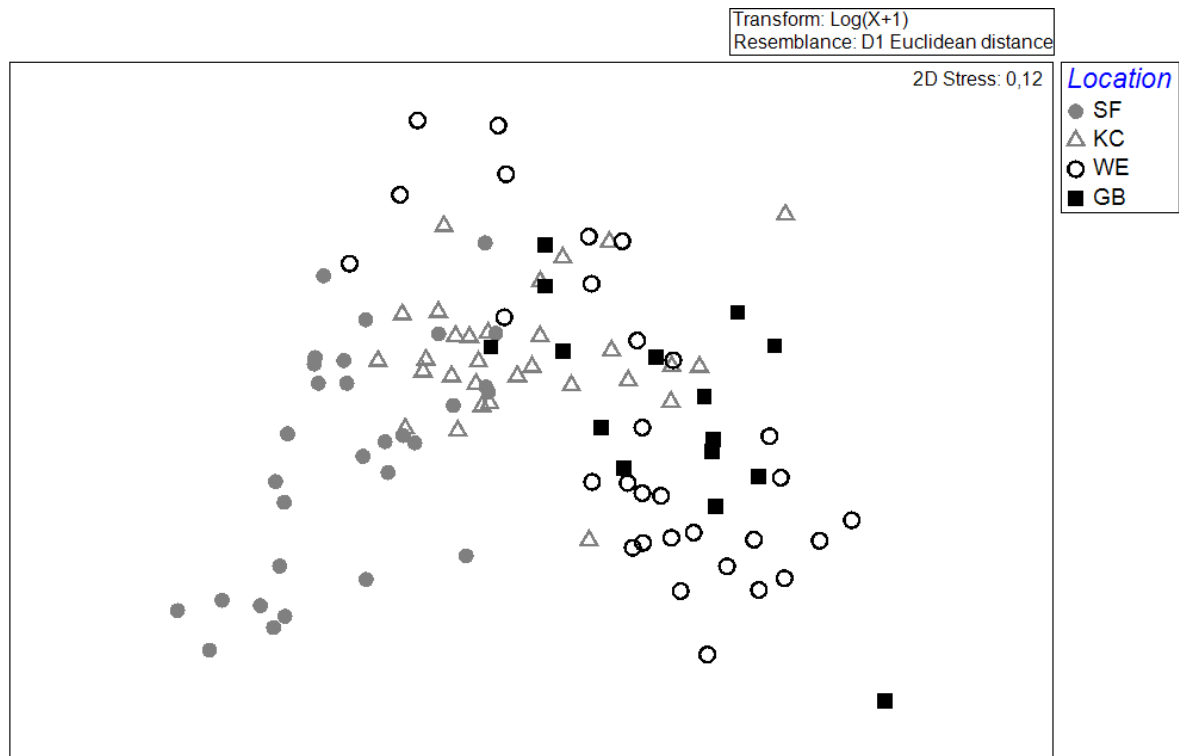
Figure 3: MDS-Plot, using the Euclidean distance to classify groups in juvenile otoliths (based on 17 elements). Data were $\log(x+1)$-transformed for standardization. The filled grey circles (SF) and unfilled grey triangles (KC) originated from the western sampling locations and the unfilled black circles (WE) and filled black quadrats (GB) represent samples from the eastern spawning areas. Each data point represents a single otolith and individual fish, respectively.

Significant differences in elemental compositions — We found continuously high significant differences in element concentrations between all four sampling areas (Tab. 3).

Based on these results we performed a post-hoc test to identify the sampling areas with distinct significant elemental differences and potential habitat-specific elements. Concentrations of Li, Na, Mg, Mn and Rb found in SF otoliths differ significantly to all other sampling areas. B and Ba concentrations in KC samples differ significantly to all three other sampling sites. The element concentration of Si, Pb, B and Mg, found in WE samples, were significantly different to all other three sampling areas. Moreover, Si concentration of GB samples was significantly different between all other three sampling areas (Tab. 4).

Table 3: Results of ANOVA with Welch correction for statistical differences in element concentration between juvenile inshore areas, with degrees of freedom (*df*1 and *df*2), *F*-value and significance level (*p*) for each single element.

	df1	*df2*	*F*	*p*
Li	3	41.22	18.92	< 0.001
B	3	43.43	70.19	< 0.001
Na	3	43.66	27.65	< 0.001
Mg	3	40.56	41.25	< 0.001
Si	3	44.82	26.65	< 0.001
Mn	3	43.29	7.77	< 0.001
Fe	3	43.47	61.25	< 0.001
Co	3	45.00	19.41	< 0.001
Cu	3	39.31	14.91	< 0.001
Zn	3	37.42	12.62	< 0.001
Rb	3	39.57	16.79	< 0.001
Sr	3	45.61	12.98	< 0.001
Sn	3	37.89	4.59	0.008
Ba	3	46.95	12.98	< 0.001
Pb	3	35.28	10.93	< 0.001
Tl	3	52.02	61.11	< 0.001
U	3	35.36	6.87	0.001

Table 4: Games Howell post-hoc test results to show significant differences for site-specific elements with respective significant levels (*p*).

Site	Elements	SF	KC	WE	GB
SF	Li	-	0.001	< 0.001	0.006
	Na	-	< 0.001	< 0.001	< 0.001
	Mg	-	0.003	< 0.001	< 0.001
	Mn	-	0.001	0.006	0.001
	Rb	-	< 0.001	0.046	0.012
KC	B	< 0.001	-	< 0.001	< 0.001
	Ba	< 0.001	-	< 0.001	0.017
WE	B	< 0.001	< 0.001	-	< 0.001
	Mg	< 0.001	0.001	-	0.028
	Si	0.002	0.038	-	0.002
	Pb	< 0.001	0.001	-	0.009
GB	Si	< 0.001	< 0.001	0.002	-

Elemental fingerprinting indices (EFI) — Based on mean standardized elemental concentrations of 17 elements, we visualized the chemical otolith signatures for each inner coastal juvenile area by radar plots (Fig. 4), showing the relative proportion of each element. The results revealed four different fingerprint plots for each sampling area with similarities in the generally dominance of single elements, but clear differences in their relative element ratio (Fig. 4).
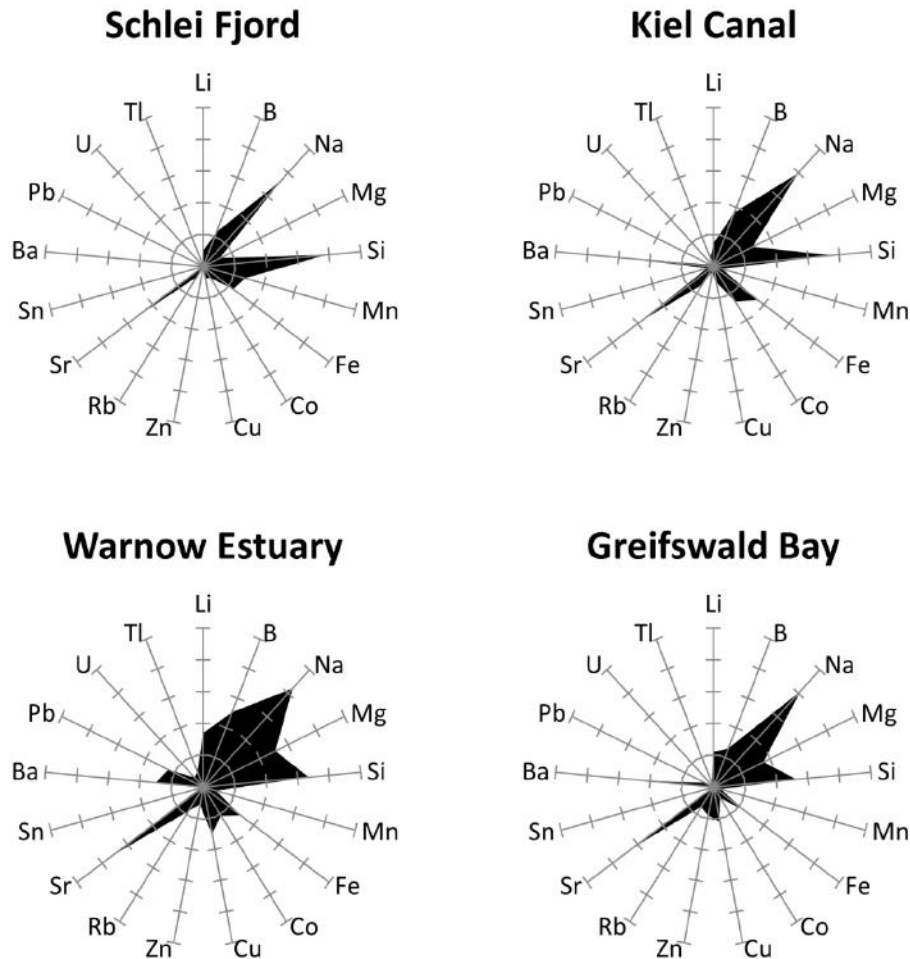
Figure 4: Radar plots with specific elemental fingerprints for each spawning area, based on 17 elements. Data were standardized (the highest concentration of each single element for all measured individuals was set to 1 and all other concentration values were set in relation to 1). Mean concentrations of each single element are shown in a defined order.

We conducted multi-elemental concentration pairwise comparisons for all individuals within one sampling site and pairwise comparisons of all individuals between different sampling sites, using *EFI* to identify similarities within one group and differences in scope of elements concentration between groups. Elemental concentrations of all individuals within one group were quite stable within SF samples, KC samples and within GB samples, whereas WE samples are slightly more variable in their multi-element composition than SF, KC and GB (Tab. 5). Comparisons between all individuals of two sampling groups revealed clear differences with

Table 5: Elemental fingerprinting indices mean *EFI* (with standard deviation $\pm$ SD) and median *EFI* and number of comparisons for each sampling area (upper table) and results of comparisons between respective groups (lower table).

Comparisons within one group			
Area 1		**No. comparisons**	**Mean *EFI* ($\pm$ SD)**	**Median *EFI***
SF		435	0.877 ($\pm$ 0.039)	0.879
KC		435	0.858 ($\pm$ 0.043)	0.861
WE		435	0.755 ($\pm$ 0.074)	0.762
GB		105	0.845 ($\pm$ 0.048)	0.850

Comparisons between two groups				
Area 1	**Area 2**	**No. comparisons**	**Mean *EFI* ($\pm$ SD)**	**Median *EFI***
SF	KC	900	0.799 ($\pm$ 0.048)	0.802
SF	WE	900	0.705 ($\pm$ 0.086)	0.703
SF	GB	450	0.777 ($\pm$ 0.062)	0.784
KC	GB	450	0.792 ($\pm$ 0.046)	0.795
WE	KC	900	0.737 ($\pm$ 0.059)	0.739
WE	GB	450	0.759 ($\pm$ 0.067)	0.764

the lowest conformity found between WE and SF, whereas comparisons between samples SF-KC and KC-GB are most similar in their element signatures (Tab. 5). *EFI* values for SF-GB comparisons, WE-KC comparison and comparison of WE and GB were smaller than *EFI* values of within-group comparison, indicating that elemental concentrations between all four groups are more different than within groups (Tab. 5). Regarding statistical differences between the within group comparisons and between the two group comparisons, the *EFI* values were highly significant different ($p = 0.001$) for almost all comparisons, except for the within group WE and between groups GB-WE comparison ($p = 0.640$). The comparison GB-KC ($p = 0.031$) show significant differences in *EFI* values (Tab. 6).

Discussion

Otolith chemistry research progressed during the last decades and is nowadays an indispensable tool for investigations on migration patterns, especially for diadromous fish species (Rieman et al. 1994, Tzeng & Tsai 1994, Limburg 1998, Secor et al. 2001), for fish stock discrimination analyses (Geffen et al. 2011, Heidemann et al. 2012) and juvenile and adult habitat connectivity studies, which improved the understanding on fish habitat utilization and fish stock dynamics (Thorrold et al. 1998b, Gillanders 2005b, Gahagan et al. 2012). However, the successful outcome of otolith microchemistry studies strongly depends on the spatial variability of elemental concentrations in fish otoliths. There is abundant evidence that fish otoliths from different basins and even sites within basins show spatial variability in their elemental composition

Table 6: Statistical results for the two-group comparisons and post-hoc results for the calculated *EFI*-values with degrees of freedom ($df1$ and $df2$), *F*-value and significance level (*p*).

Comparison between groups	Robust tests of equality of means (Welch test)	post-hoc results (Games Howell test) for calculated *EFIs*	
GB & KC	$df1 = 2$ $df2 = 288.7$ $F = 253.2$ $p < 0.001$	EFI_{GB} & EFI_{GB_KC}	$p < 0.001$
		EFI_{GB} & EFI_{KC}	$p = 0.031$
		EFI_{KC} & EFI_{GB_KC}	$p < 0.001$
GB & WE	$df1 = 2$ $df2 = 345.1$ $F = 144.8$ $p < 0.001$	EFI_{GB} & EFI_{GB_WE}	$p < 0.001$
		EFI_{GB} & EFI_{WE}	$p < 0.001$
		EFI_{WE} & EFI_{GB_WE}	$p = 0.640$
GB & SF	$df1 = 2$ $df2 = 289.1$ $F = 410.8$ $p < 0.001$	EFI_{GB} & EFI_{GB_SF}	$p < 0.001$
		EFI_{GB} & EFI_{SF}	$p = 0.001$
		EFI_{SF} & EFI_{GB_SF}	$p < 0.001$
WE & KC	$df1 = 2$ $df2 = 1767$ $F = 959.5$ $p < 0.001$	EFI_{WE} & EFI_{WE_KC}	$p < 0.001$
		EFI_{WE} & EFI_{KC}	$p = 0.001$
		EFI_{KC} & EFI_{WE_KC}	$p < 0.001$
WE & SF	$df1 = 2$ $df2 = 1013.4$ $F = 1413.6$ $p < 0.001$	EFI_{WE} & EFI_{WE_SF}	$p < 0.001$
		EFI_{WE} & EFI_{SF}	$p = 0.001$
		EFI_{SF} & EFI_{WE_SF}	$p < 0.001$
SF & KC	$df1 = 2$ $df2 = 975.5$ $F = 563.2$ $p < 0.001$	EFI_{SF} & EFI_{SF_KC}	$p < 0.001$
		EFI_{SF} & EFI_{KC}	$p < 0.001$
		EFI_{SF_KC} & EFI_{KC}	$p < 0.001$

(de Pontual et al. 2000, Rooker et al. 2001, Gillanders & Kingsford 2003, Hamer & Jenkins 2007, Yamane et al. 2010). Our results fit well into this broad research results, showing distinct chemical signatures in juvenile herring otoliths from different spawning and juvenile areas. We were able to detect multiple elements in early life stage herring otoliths and by using our unique and interdisciplinary multiple element approach, we were able to find significant differences in elemental composition between all four sampling areas.

Offshore samples

Age-0 herring samples from offshore sampling stations were analyzed with the solution based-ICP-MS approach, where the calcified otolith substance is dissolved in nitric acid and the whole sampling solution is analyzed for concentration of all included elements. The practicability of this method depends on the specific sensibility of the analyzing instrument. In our case, the

minimal sample mass was 1 mg, requiring to pool individual otoliths from a station (average individual otolith weight 0.47 mg ± 0.14 mg), making it impossible to detect individual chemical signatures. Moreover, fish collection was accomplished offshore and the total length of juvenile herring caught during the trawl survey in autumn was 84.9 mm (± 1.1 mm) in average. There are several studies based on chemical differences between coastal waters and the open sea (Thorrold et al. 1998b, Secor et al. 2001, Able 2005), but studies on small scale inner coast -outer coast differences are rather scarce (but see Forrester & Swearer 2002, Gillanders 2005b, Leakey et al. 2009). Forrester and Swearer (2002) investigated trace element concentrations of juvenile California halibut (*Paralichthys californicus*), caught in bays and at the open coast in the same year and found higher Cu and Pb concentrations in bay samples compared to the open coast samples. Although we could not discriminate between inner coastal and offshore water signatures, the pooled sample approach seems appropriate for analyzing spatial variability in elements along the Western Baltic Sea. Our results show a clear spatial variability in elemental signatures of juvenile herring otoliths between western and eastern sampling location in the brackish Western Baltic Sea. The samples from Kiel Bay are considered as outliers with specific otolith elemental composition, similar to the Rügen otolith samples. This result matches well to the results from the two group comparison of inshore otolith samples. The *EFI* value revealed a more similar chemical signature for GB and KC spawning areas, which are in the near vicinity of the offshore sampling areas Rügen and Kiel Bay, assuming that offshore migration of juveniles might took place shortly before sampling and that inshore element signals might dominate the entire chemical signature.

Samples from inshore spawning areas

We found highly significant differences of elemental composition between all four investigated sampling areas. Although we were able to detect concentration values of 39 elements in total with the LA-ICP-MS approach, we had to exclude all rare earth metals and some elements (i.e. Hg or Al), due to a high number of missing values, possibly caused by higher gas blank values or concentration levels below the instrument detection threshold. All together 17 elements were found in suitable concentrations for data analysis, which is still an appreciable element number. In most studies, differences in elemental compositions were mainly based on a few elements (e.g. Ba, Mg, Mn, Sr) (see Thorrold et al. 1998a, Campana et al. 2000, Gillanders 2002a, Hamer & Jenkins 2007) with some exceptions with the focus on other elements (Gillanders & Kingsford 1996, Secor & Zdanowicz 1998, Forrester & Swearer 2002) or with multiple element distinctions > 9 elements (see Edmonds et al. 1991, Dove et al. 1996, Milton et al. 2000, Brown 2003, Leakey

et al. 2009). For our interdisciplinary multiple-element approach, we created the innovative elemental fingerprinting index to describe differences and similarities of otolith chemical signatures, regarding multiple-element patterns. We found highly significant differences for almost every inter-group comparison, except between GB and WE, possibly due to the high variability in individual chemical signatures of WE samples. Sampling in four different areas was performed at the same month in June 2016, but due to site specific growth patterns in distinct sampling areas, we were not able to sample juvenile herring and otoliths of the same size. While juvenile herring from GB and WE were quite small with an average total length (TL) of ~23 mm in June 2016, juvenile herring from SF and KC were more developed at that point of time, showing a mean TL of 37-38 mm. It cannot be excluded, that different otolith sizes might reveal some differences in individual element concentration using the LA-ICP-MS. Brophy et al. (2004) investigated the manganese concentrations in polished otoliths from juvenile Atlantic herring and found differences in Mn concentrations within samples by setting the laser once exactly to the otolith core region and once outside the core region. Due to the otolith preparation by polishing the otoliths with very fine (2,000- and 4,000-grit) Silicone carbide paper, the authors were able to analyze the exact core region of the herring otoliths (Brophy et al. 2004). However, based on the fact that all our samples were collected within their spawning area, it can be assumed that using the LA-ICP-MS for unpolished herring otolith samples from Western Baltic inshore reproduction areas is practicable, since the results revealed clearly significant distinctions of elemental composition between all four sampling areas. Taking all 17 elements into account, the *EFI*, created for samples within one group/sampling area were more similar than *EFI* between different sampling areas, suggesting that variability in the individual chemical signatures were less prominent within a particular area than between individuals from different sampling areas. The possible concentration differences, resulting from different otolith sizes seem to be marginal, because solution-based ICP-MS is an approved and successful method, where the whole otolith is dissolved in acid to analyze otolith chemical signatures (Patterson et al. 1999, Rooker et al. 2001, Secor et al. 2001, Rooker et al. 2003). However, the comparability between different ICP-MS approaches and results on herring otolith chemistry should be tested in future studies.

Element concentrations

Our concentration values of single elements were comparable with other studies, where the LA-ICP-MS approach was used. Our measured Mn concentrations fluctuated from mean values of 3.8 µg g^{-1} (GB), 4.4 µg g^{-1} (KC) and 6.5 µg g^{-1} (WE), which is in the range (1-10 µg g^{-1}) reported

from other studies (Gillanders 2002a, Brophy et al. 2004). Only the Mn concentration of the SF area was higher with 21 µg g^{-1}, but matches the level of Mn concentration (1-35 µg g^{-1}) in juvenile trumpeter (*Pelates sexlineatus*) otoliths from different estuaries and different sites within the estuaries (Gillanders & Kingsford 2000). Brophy et al. (2003) investigated the elemental composition of otolith core regions in larval and juvenile Atlantic herring and found generally higher values in larval otoliths, compared to juvenile otoliths. However, element concentrations found in juvenile herring otoliths show the same range as our measured concentrations, except for the elements Sr and Ba (Brophy et al. 2003). Sr and Ba are some marker elements for salinity with higher Sr concentrations in marine habitats, whereas Ba is higher in freshwater habitats (Kalish 1990, Tzeng & Tsai 1994, Secor et al. 1995, Kafemann et al. 2000, Secor & Rooker 2000, Elsdon & Gillanders 2005, Zimmerman 2005). The concentrations found in our inshore otolith samples were lower in Sr and higher in Ba, reflecting the brackish Baltic Sea ecosystem, with high salinity gradients (from rather marine salinities of ~30 PSU) at their feeding area up North in the Kattegat and Skagerrak to more brackish conditions within the Western Baltic Sea. In addition to the overall Baltic Sea salinity gradient from Southwest to Northeast, there are multiple local inshore-offshore salinity gradients composed by river estuaries or other transitional waters, making it difficult to interpret results, mainly based on these salinity signatures. Hence, we focused on the multiple element approach instead of limiting the focus to Sr and Ba to find differences in elemental composition of herring otolith from different coastal spawning grounds.

Impact of environmental factors

The prevailing elemental concentration in the ambient water, water temperature and salinity are seen to be the three major variables influencing otolith chemistry (Elsdon & Gillanders 2003). Several studies dealing with the impact of these main environmental factors on the incorporation of elements into fish otoliths, but results are rather contradictory, depending on species, i.e. either for salinity (Fowler et al. 1995, Tzeng et al. 1997, Elsdon & Gillanders 2002) or temperature (Martin et al. 2004, Martin & Thorrold 2005, Barnes & Gillanders 2013) or the interaction between both (Yamashita et al. 2000, Elsdon & Gillanders 2002). Of course intrinsic factors like physiology, genetics and growth effects are also able to impact the uptake of elements (Kalish 1989, Sadovy & Severin 1992, 1994). However, elemental uptake by digestion of prey seems to be marginal for some species (Farrell & Campana 1996, Milton & Chenery 2001, Buckel et al. 2004). Regarding the impact of water temperatures, Radtke et al. (1990) and Townsend et al. (1992) found a negative relationship between the Sr:Ca ratio and water temperatures in larval Atlantic herring otoliths.

Potential temporal variability of element concentrations is one important aspect to be considered in future connectivity studies (Milton et al. 1997, Thorrold et al. 1998a, Hamer et al. 2003, Swearer et al. 2003, Elsdon & Gillanders 2006, Arkhipkin et al. 2009). Despite studies showing high temporal and spatial variability in elemental signatures of otoliths, there are also other examples, where inter-annual variability in elemental concentrations was only observed for specific elements (Patterson et al. 1999, Rooker et al. 2001), indicating that variability might be habitat-specific and also depends on the species of interest. Gillanders (2002b) revealed to build up a library of elemental fingerprints over several years for each study area to increase the interpretation success of fingerprint patterns from juvenile fish, regarding contribution estimates of single reproduction areas to the overall fish population. The role of other environmental variables, impacting the incorporation of elements into herring juvenile otoliths remains presently unknown. A future perspective should be to investigate general assumptions concerning temperature effects and other potential factors on elemental composition in otoliths for a better interpretation of future results.

Conclusions

With our new multiple-element approach in combination with the elemental fingerprinting index (*EFI*), we detected significant differences in otolith elemental composition from four different spawning and juvenile areas along the Western Baltic Sea. Our findings are the baseline for further connectivity studies on herring populations to gain new insights of juvenile-adult herring habitat connectivity, extending the knowledge on spawning site fidelity, homing behavior and population dynamics of herring, one of the most ecologically and commercially important fish species in the world. This knowledge could represent a foundation for reliable estimations on individual spawning ground productivity and the contribution of different juvenile habitats to the overall Western Baltic herring population and therefore to a more directed management of important spawning grounds and coastal nurseries in the future.

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Chapter 2

Contribution of an inshore nursery area to the Atlantic herring (*Clupea harengus*) population in the Western Baltic Sea

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Abstract

Coastal waters are highly productive, providing essential spawning and nursery habitats for many fish species worldwide. However, they are also extremely exposed to multiple anthropogenic threats. Atlantic herring (*Clupea harengus*) is an economically and ecologically important component of the North Atlantic ecoregion. In the Baltic Sea, *C. harengus* relies on shallow inner coastal waters (estuaries and lagoons), performing extensive annual migrations for reproduction. In the western Baltic Sea, herring recruitment decreased over the past two decades for widely unknown reasons, but it is assumed that a variable suite of stressors acting on the local scales of important spawning grounds affects population dynamics on the ocean scale. Hence, the estimation of the contribution of single herring spawning areas and juvenile habitats to the total Western Baltic herring population is a crucial step to evaluate their potential function as nurseries and to estimate if local stressors become transported to the level of adult populations. To investigate the contribution of distinct spawning areas to the Western herring population, we used elemental fingerprinting in otolith cores of age-0 herring from different coastal spawning areas and compared these natal chemical signatures with otolith elemental core compositions of the adult population. By using a discriminant analysis, we assigned herring caught in the adult habitats according to their coastal origin. Results indicated in general that the contribution of particular coastal reproduction areas varied among year classes. However, the superior contribution of one single juvenile habitat remained relatively constant. This study emphasizes the importance of single coastal habitats to the overall population, calling for a more sensitive coastal zone management, implementing specific strategies for these transitional coastal waters.

Introduction

Coastal habitats often function as important nursery areas for marine fish species (Heck & Thoman 1984, Forrester & Swearer 2002, Nagelkerken et al. 2002, Vasconcelos et al. 2008), supplying sufficient food and adequate hiding places for early life stages to avoid predation (Orth et al. 1984, Shulman 1985, Levin et al. 1997), which generally leads to high densities of larval and juvenile fish in these specific areas (Heck & Thoman 1984, Vasconcelos et al. 2010). However, species diversity and high densities of juveniles are often the only criteria to determine specific areas as nurseries (Carlson & Straty 1981, Robertson & Duke 1987, Bennett 1989, Nagelkerken et al. 2001, Tse et al. 2008). Postulating the nursery role concept, Beck et al. (2001) approached an alternative definition of the term "nursery area" by introducing certain quantitative criteria. Besides factors, such as juvenile growth, survival and density, this concept is based on the quantitative contribution of distinct juvenile habitats to the adult population on a per-unit area basis, resulting in a better conservation and management of these ecologically important areas (Beck et al. 2001). Accordingly, several publications addressed this nursery habitat issue by estimating the contribution of juvenile fish habitats to the adult population, using elemental composition of fish otoliths (Yamashita et al. 2000, Thorrold et al. 2001, Forrester & Swearer 2002, Gillanders 2002, Brown 2003, Thorisson et al. 2011). Although coastal waters are of utmost significance by contributing the majority of ocean productivity, at the same time they are highly affected by anthropogenic ecosystem alteration. Research on habitat alteration effects on fish recruitment is rather scarce leaving general uncertainties with consequences on fish life history, population dynamics and migration patterns (Able 2005). Those knowledge gaps emphasize the risk to jeopardize fish population resilience. It is consensus that habitat degradation globally led to a decline in marine biodiversity (Jones et al. 2004, Worm et al. 2006), affecting fish reproduction capacity and led to a severe decline in fish abundances (Wolff 2000, Paddack et al. 2009). Despite the superior function of coastal habitats, especially for exploited fish species, the evaluation of fish habitat dependency has rarely been implemented into current coastal zone management plans (Seitz et al. 2014). However, this is crucial to realize adequate conservation concepts and management strategies for threatened coastal habitats, thus warranting a preservation of essential spawning and nursery habitats for ecological and commercial key species. Atlantic herring (*Clupea harengus*) is one of the best studied fishes in the world, but due to its high plasticity (Haegele & Schweigert 1985, Geffen 2009), there is still some uncertainty on general population dynamics and potential habitat dependency of distinct herring populations. Herring is considered to show a distinct homing

behavior (Wheeler & Winters 1984, McQuinn 1997), indicating a strong estuarine dependency. The Western Baltic herring population is considered a metapopulation composed of multiple spawning components (Bekkevold et al. 2005, Gaggiotti et al. 2009). It is established knowledge that *C. harengus* in the Western Baltic Sea performs annual migrations between their summer feeding grounds in the Kattegat/Skagerrak and their overwintering area in the Öresund Strait (Jönsson & Biester 1981, Otterlind 1984, 1987, Poulsen et al. 2000, Nielsen et al. 2001). In spring, herring enter their coastal inshore spawning areas (estuaries, bays and lagoons) for spawning predominately on submerged aquatic vegetation in the shallow littoral zone (Klinkhardt et al. 1985, Scabell 1988, Kanstinger et al. 2016). Nowadays, in the Western Baltic Sea, research on herring early life stages is mainly focused on the particular spawning area Greifswald Bay (Scabell 1988, Kotterba et al. 2017a, Kotterba et al. 2017b, Polte et al. 2017, Moll et al. 2018, von Nordheim et al. 2018). As the annual larval production in Greifswald Bay correlates strongly with the age-1 juveniles recruiting to the population in the overall Western Baltic Sea (Oeberst et al. 2009), it is assumed that this spawning area has an extraordinary contribution to the population dynamics. However, empirical studies on the quantitative contributions of particular coastal juvenile habitats to the adult herring population and their inter-annual contribution consistency are missing. Studies on other coastal spawning habitats are rather scarce (but see Paulsen et al. 2014), with only little or anecdotal information available. Almost all empirical knowledge comes from historical documentation (Nellen 1965, Neb 1970, Weber 1971, Schnack 1974, De Groot 1980, Lupatsch & Nellen 1981) but there is no information on the situation today. As Western Baltic herring recruitment decreased during the last decades for widely unknown reasons and the population is still in a period of low reproduction, there is an increasing need to understand whether regional stressors on the local scale of important spawning grounds become transported to the population level by their superior contribution of recruits. Therefore the identification of nursery areas is essential to understand general habitat connectivity in the Baltic Sea and to evaluate the potential impact of regional stressors on herring recruitment. This is required to implement coastal zone management strategies, counteracting anthropogenic habitat degradation activities. We used the habitat-specific elemental fingerprints of age-0 herring from four historically documented juvenile areas and compared those results with chemical fingerprints in adult herring otolith cores to investigate the contribution of distinct spawning areas to the Western Baltic herring population. We addressed the hypothesis that (i) particular inshore systems, such as Greifswald Bay, have a greater than average contribution to the adult population and that (ii) the relative contribution is consistent between year-classes.
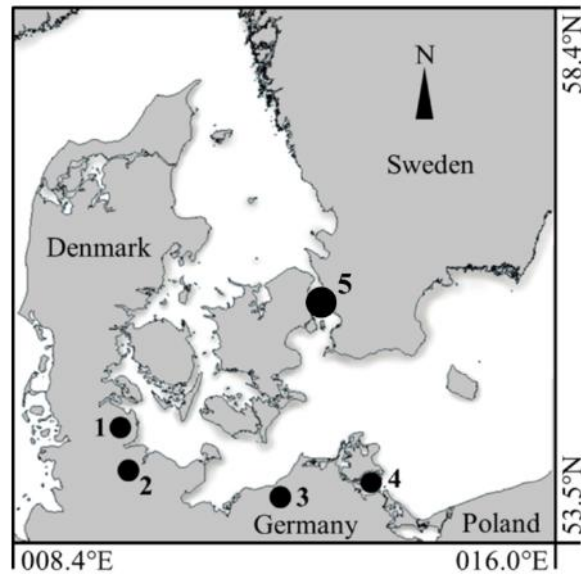
Figure 1: Coastal inshore sampling locations (age-0 herring) in the Western Baltic Sea with the spawning areas Schlei Fjord (**1**), Kiel Canal (**2**), Warnow Estuary (**3**) and Greifswald Bay (**4**). Adult herring were caught in the Öresund Strait (**5**).

Material and Methods

Sampling of age-0 herring

During the early summer 2016, juvenile herring were caught by beach seine sampling in the Schlei Fjord (SF) (beach seine: 7 m opening, 5 mm mesh size, 1.5 m wing height) and by purse seine in Kiel Canal (KC) (purse seine: 40 m length, 3 m height, 4 mm mesh size). Juvenile herring from farther eastern locations (Warnow Estuary (WE) and Greifswald Bay (GB), Fig. 1) were caught with a ring trawl (net opening of 1 m diameter and a mesh size of 1550 µm) onboard a research vessel. Additionally, age-0 herring from GB, which hatched during the spawning season 2015, were caught by beach seine sampling in the shallow littoral shoreline in June 2015 to investigate potential inter-annual variability of chemical habitat signatures. All samples were frozen ($-20°$C) immediately after the catch and stored frozen until later otolith dissection. A sample size of 30 individuals per sampling area was used for chemical analyses, except for GB samples in 2016 (n=15). Information on individual total length (TL mm) and general samples size is summarized in Tab. 1.

Table 1: The mean total length (TL, in mm) with standard deviation ($\pm$ SD) for age-0 herring samples from the four different sampling areas and for age-2 and age-3 adult herring samples from the Öresund Strait with respective sample sizes.

Location		Mean TL mm	Sample size
Schlei Fjord		37.2 ($\pm$ 2.9)	30
Kiel Canal		38.0 ($\pm$ 1.8)	30
Warnow Estuary		23.2 ($\pm$ 3.5)	30
Greifswald Bay	2015	40.9 ($\pm$ 5.6)	30
	2016	22.7 ($\pm$ 2.2)	15
Öresund	age-2	228 ($\pm$ 17.8)	70
	age-3	245 ($\pm$ 17.2)	70

Adult herring sampling

In October 2016, adult herring were caught during trawl fishery within the Öresund Strait, which is considered an overwintering accumulation area for the Western Baltic herring population (Jönsson & Biester 1981, Otterlind 1987) (Fig. 1). We sampled adult herring in post-spawning condition to avoid potential autumn-spawning populations and distributed herring sampling over four hauls to avoid possible effects of school assemblages, approaching a representative sample of the entire population. Herring were frozen for further processing in the laboratory. Sagittal otoliths were dissected for general age determination. We sampled otoliths from age-3 herring (n=70), because on the time scale they represented the closest mature year-class to the age-0 herring sampled in 2016. Furthermore, otoliths from age-2 herring (n=70) were selected for chemical analysis to estimate the potential for inter-annual variability of the quantitative contribution of particular juvenile areas to the adult population. Information on individual total length (TL mm) and samples sizes is given in Tab. 1.

Sample processing

Age-0 otoliths — Prior to otolith dissection, all used equipment (microscope slides, petri dishes, ceramic forceps) were washed in 2% nitric acid (Rotipuran Supra 69%, Carl Roth) and rinsed with ultrapure water. Microscope slides were dried under a flow cabin to keep them clean from dust particles. Right before otolith dissection, double-sided adhesive transparent pads were mounted on clean microscope slides as otolith fixing material. Sagittal otoliths were dissected with non-metallic ceramic forceps under a microscope (Olympus SD 30) to avoid any elemental contamination. Otoliths were rinsed with ultrapure water several times to remove adhesive tissue. After drying, otoliths were transferred and placed on adhesive pads (Fig. 2A).
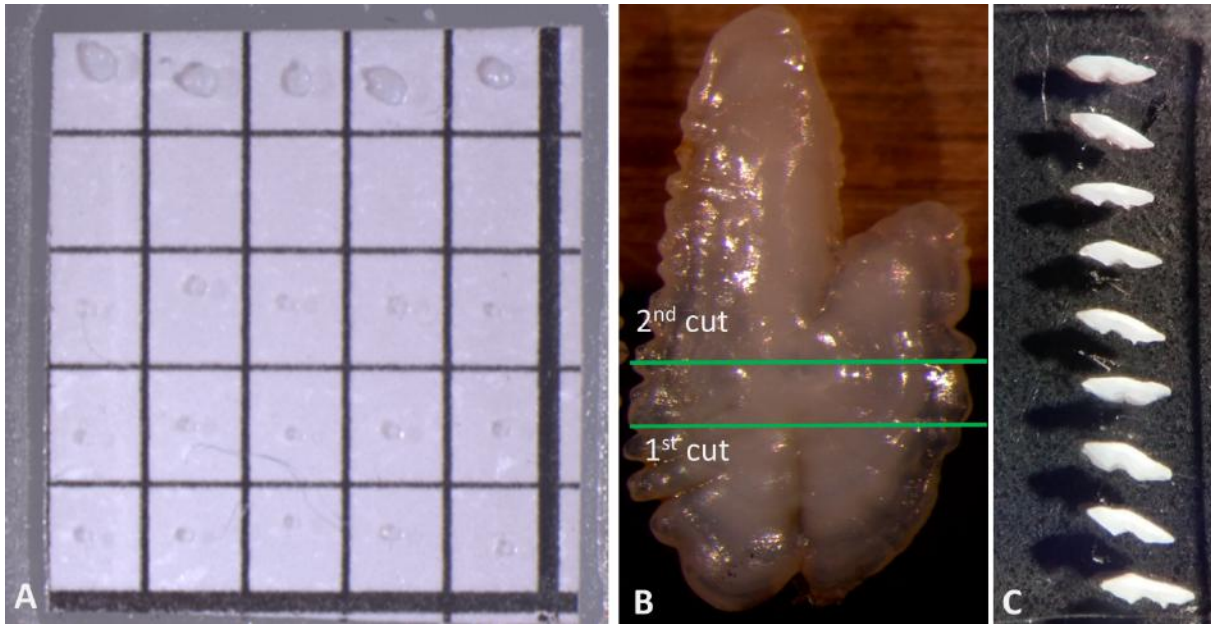
Figure 2: (**A**) Different sizes of age-0 herring otoliths on fixing material, (**B**) Adult herring: Otolith processing steps from the whole otolith to 0.5 mm thick slices through the core region set by two cutting planes (indicated by green lines). (**C**) Otolith slices were mounted core side up, prior to transition into the LA-ICP-MS.

Adult otoliths — Due to the fact that adult herring otoliths were proved too small for the standard procedure (cutting transverse core sections using a double-bladed diamant-saw), otoliths were cut with a high energy laser (in cooperation with the Schweißtechnische Lehr- und Versuchsanstalt (SLV) Mecklenburg-Vorpommern, Rostock, Germany). The operating parameters are shown in Tab. 2.

Table 2: The operating parameters used for the otolith cutting process with the high energy laser Trumpf TrMicro 5X50+GFH GL.5 in cooperation with the SLV with given laser parameters (wavelength, cutting speed and laser energy).

TRUMPF TruMicro 5X50 + GFH GL.5	
Laser wavelength	1030 nm
Scan/Axes speed	2 m s^{-1}
Pulse duration	6 ps
Pulse energy	30-60-80 µJoule
Repetition rate	400 kHz

This approach had two clear advantages: 1) It is a time effective processing technique and 2) potential contamination with embedding resin and metallic saw blades are avoided. In a first step, each otolith rostrum was mounted on a piece of wood with double-adhesive pads. In a second step, the laser cut a 0.5 mm transverse slice, by cutting first beneath the core region and then (with a second cut) directly through the core region (Fig. 2B). Otolith slices were rinsed with ultrapure water, washed in 2% nitric acid (about 5-10 seconds) to clean them from

adhesive tissue and to minimize elemental contamination, potentially caused during dissection with metallic forceps. In case of highly adhesive organic material, 10% nitric acid was used (only for 3 seconds to avoid total solution of otoliths). After nitric acid washing, otolith slices were rinsed again with ultrapure water and dried inside the flow cabin. Five otoliths from the age-3 herring samples were damaged during sample processing and could not be used for further chemical analysis. Each otolith was mounted core side up on double adhesive pads (see Fig. 2C), which were previously mounted on washed microscope glass slides. All microscope slides with attached otoliths were stored in clean plastic vials to warrant a safe transport to the laboratory for Laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) measurements.

Analytical methods

Elemental composition of juvenile and adult otolith core regions was analyzed with the LA-ICP-MS-technique, using a ThermoFinnigan ELEMENT2 ICP-MS with an UP-213 Nd:YAG laser ablation system at the Max Planck Institute of Chemistry in Mainz, Germany. Certified reference material NIST 612 (National Institute of Standards and Technology) and the micro analytical reference material MACS3 (United States Geological Survey) were used for calibration (Jochum et al. 2007, Jochum et al. 2011). The reference materials were analyzed at the beginning of the measurements and the analyses were repeated regularly for quality assurance. Core regions of age-0 herring and adult otoliths were ablated with 80 μm laser spot size at 60% power, a pulse repetition rate of 10 Hz and energy densities of ~10.2 J cm^{-2}. Gas blank count rates were measured for 12 seconds prior to ablation. Otolith samples were measured with dwell durations of 70 seconds, followed by a washed out time of 30 seconds. Dwell durations of age-0 otoliths were generally shorter and operated manually. For further information on the operating parameters for the ELEMENT2 ICP-MS system see (Jochum et al. 2007). In total, 39 elements could be detected in age-0 otoliths during microchemistry analysis, but due to very low element concentrations and some missing values, we considered 15 elements with constantly detected count rates into the further analysis: Li, B, Na, Mg, Si, Mn, Fe, Co, Cu, Rb, Sr, Sn, Ba, Tl, Pb.

Data analyses

All statistical analyses were performed with R Studio (version 3.4.1) (R Development Core Team 2008). Statistical significances of single element concentrations between each juvenile habitat were tested by using one-way analysis of variance (ANOVA) with a significance level of $p < 0.05$.

Data sets were tested for variance homogeneity by Levene's test and were logarithmically transformed $\log(x + 1)$ if necessary to meet the requirements of ANOVA. Post-hoc tests (Games Howell test) were conducted to investigate significant differences between the four sampling sites. A linear discriminant analysis (LDA) was used to classify the chemical signatures of Öresund adult herring (age-2 and age-3 herring) to their respective juvenile habitat signals. The classification estimation was performed using the MASS package in R (Venables & Ripley 2002). Multi-dimension scaling (MDS) plots were illustrated with PRIMER 6 software with the dissimilarity matrix of calculating the Euclidean distances.

Classification model

To ensure a good classification model with suitable predictor elements, we further reduced the number of elements and excluded elements with more than one missing value in the juvenile and adult data sets (e.g. Pb, Co, Tl). Due to a small sample size of GB age-0 herring otoliths in 2016 (n=15) and to deal with possible inter-annual variability within the area, we pooled otolith signatures from 2015 and 2016 as one GB signal. Hence, we only included significantly different elements between the four locations, when these elements concurrently show no significant differences between the two-year sampling in GB to ensure the best element components with adequate classification accuracy (see appendix C2 Tab. A1). Nine remaining elements (Li, B, Na, Mg, Mn, Fe, Rb, Sr, Ba) found in age-0 otoliths were used as a training data set to assess model accuracy using the leave one out cross validation-test, revealing a good fit of the model with high classification accuracies of 0.83 for SF, 0.93 for KC, 0.72 for WE and 0.91 for GB. Adult otolith data were then used to investigate natal origin, resulting in a classification of each adult individual to one habitat with a distinct percentage value. To deal with non-sampling of all potential spawning areas during this investigation, we determined a likelihood threshold of 75% correct assignment of each individual to a respective habitat. All individuals classified below this threshold were sorted to a group of "other areas".

Results

Habitat-specific fingerprints

The mean concentrations for each element per spawning area are shown in Fig. 3. All elements showed high significant differences between the four groups. Detailed ANOVA results and site-specific significant differences in single elemental concentrations are given in Tab. 3.
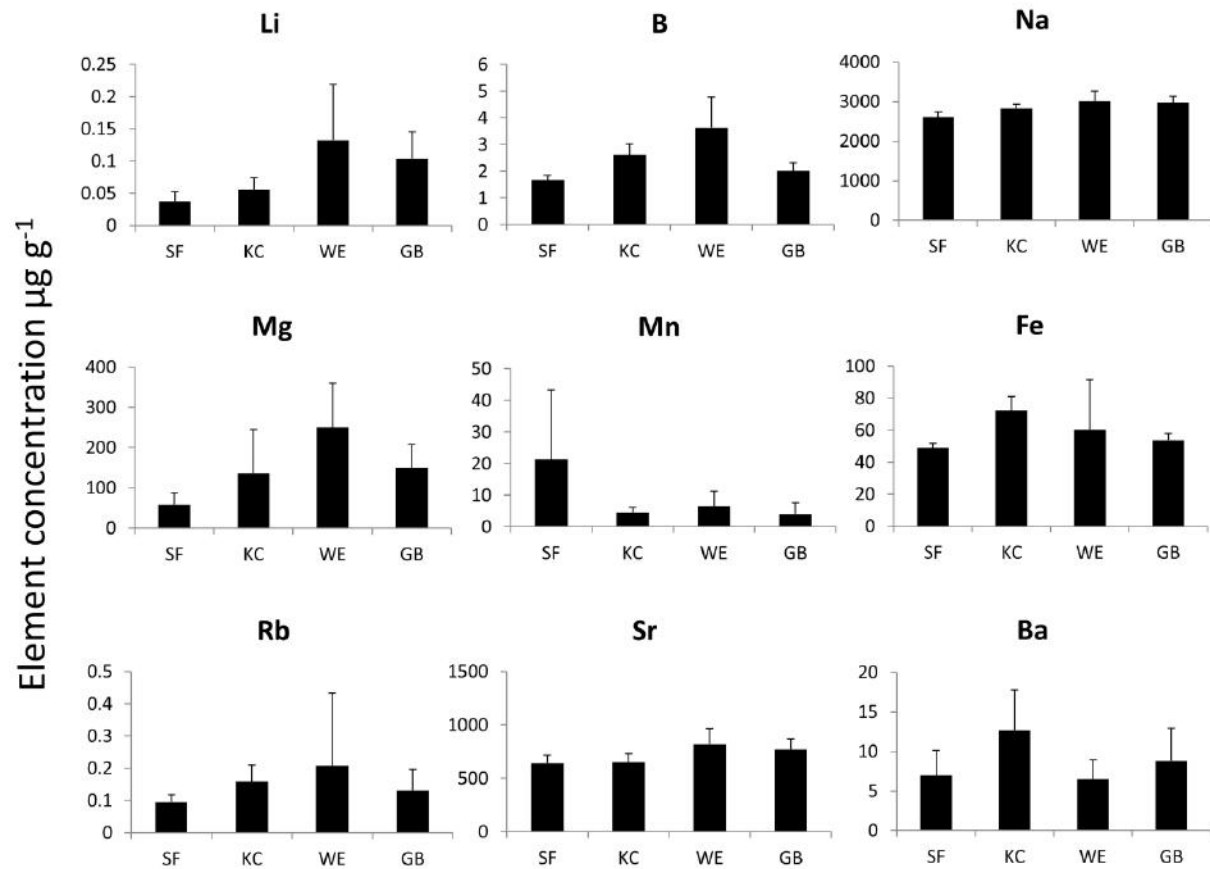

Figure 3: Mean concentrations ($\mu g\ g^{-1}$) with standard deviation of 9 predictor elements for each spawning area Schlei Fjord (SF), Kiel Canal (KC), Warnow Estuary (WE) and Greifswald Bay (GB). Mean concentrations are based on a sample size of n=30, except for GB n=45.

Table 3: Results of ANOVA and Games Howell post-hoc test to identify site-specific significant differences in single elemental concentrations between four sampling areas, with degrees of freedom (df), F-value and significance level (p). GB 2015 and GB 2016 sampling is included to one GB signal, after testing for inter-annual variability.

| Element	df	F	p	Sites	p
				Games Howell post-hoc test	
				SF-KC	0.001
				SF-WE	< 0.001
Li	3	25.3	< 0.001	SF-GB	< 0.001
				KC-WE	< 0.001
				KC-GB	< 0.001
				SF-KC	< 0.001
				SF-WE	< 0.001
B	3	65.88	< 0.001	SF-GB	< 0.001
				KC-WE	< 0.001
				KC-GB	< 0.001
				WE-GB	< 0.001
				SF-KC	< 0.001
				SF-WE	< 0.001
Na	3	35.16	< 0.001	SF-GB	< 0.001
				KC-WE	0.011
				KC-GB	< 0.001
				SF-KC	0.003
				SF-WE	< 0.001
Mg	3	28.28	< 0.001	SF-GB	< 0.001
				KC-WE	0.001
				WE-GB	< 0.001
				SF-KC	0.001
Mn	3	18.38	< 0.001	SF-WE	0.006
				SF-GB	0.001
				SF-KC	< 0.001
Fe	3	13.34	< 0.001	SF-GB	< 0.001
				KC-GB	< 0.001
				SF-KC	< 0.001
Rb	3	5.25	0.002	SF-WE	0.046
				SF-GB	0.007
				SF-WE	< 0.001
Sr	3	22.95	< 0.001	SF-GB	< 0.001
				KC-WE	< 0.001
				KC-GB	< 0.001
				SF-KC	< 0.001
Ba	3	15.78	< 0.001	KC-WE	< 0.001
				KC-GB	0.005
				WE-GB	0.018

The (3-D) MDS-plot showed four distinct juvenile habitat fingerprints based on the 9 predictor elements. The plot revealed that the predictor elements are suitable for further classification analysis of adult herring natal origin (Fig. 4).
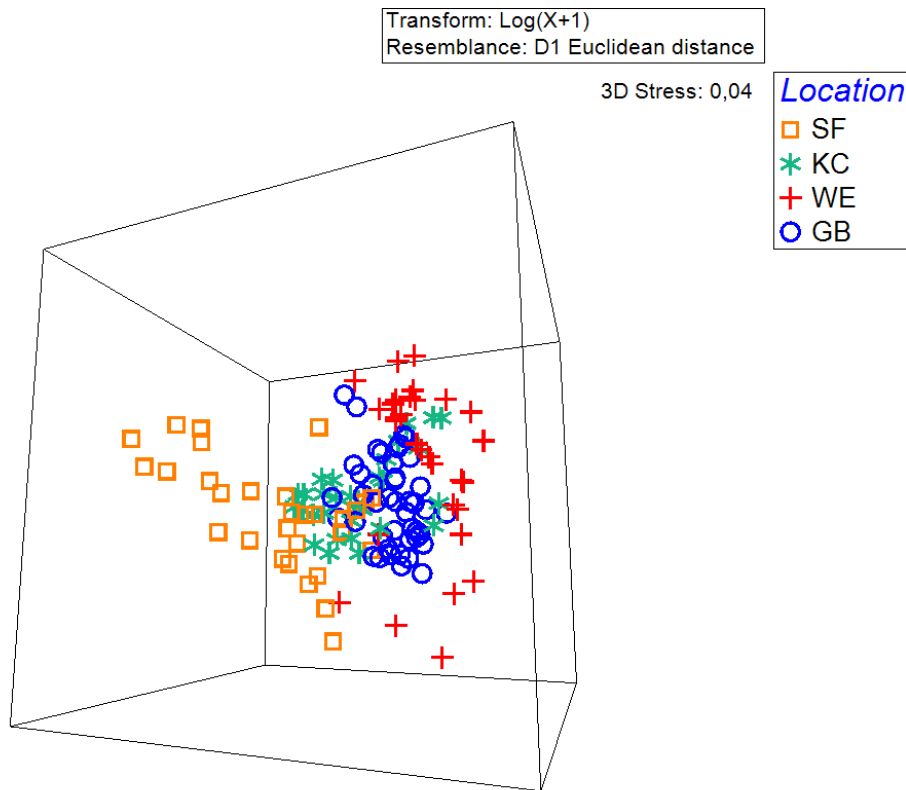
Figure 4: MDS-plot (visualization in 3-D), using the Euclidean distance to classify juvenile otolith fingerprints (based on 9 elements) for the four investigated spawning areas. Data were $\log(x+1)$-transformed for standardization. Color-coding indicates the four areas Schlei Fjord (SF, orange), Kiel Canal (KC, green), Warnow Estuary (WE, red) and Greifswald Bay (GB, blue). Each data point represents a single otolith.

Natal-origin classification

We found different contribution values between the two year-classes. The results revealed that the majority of age-2 adult Öresund herring were classified to GB with 77% (n=54). No single fish could be classified to KC, 4% (n=3) were classified to SF, 3% (n=2) were assigned to WE and 16% (n=11) could not be classified to the four given groups (Fig. 5). Results for age-3 adult herring showed a similar pattern, with GB contributing a great amount to the adult population with 38% (n=25). 11% (n=7) of adult individuals were assigned to SF, 8% (n=5) to KC and 2% (n=1) to WE. 41% (n=27) of adult herring could not be assigned to the four given groups (Fig. 5). Results support the general assumption that Greifswald Bay is an important nursery area for the Western Baltic herring population.

% Contribution to herring population
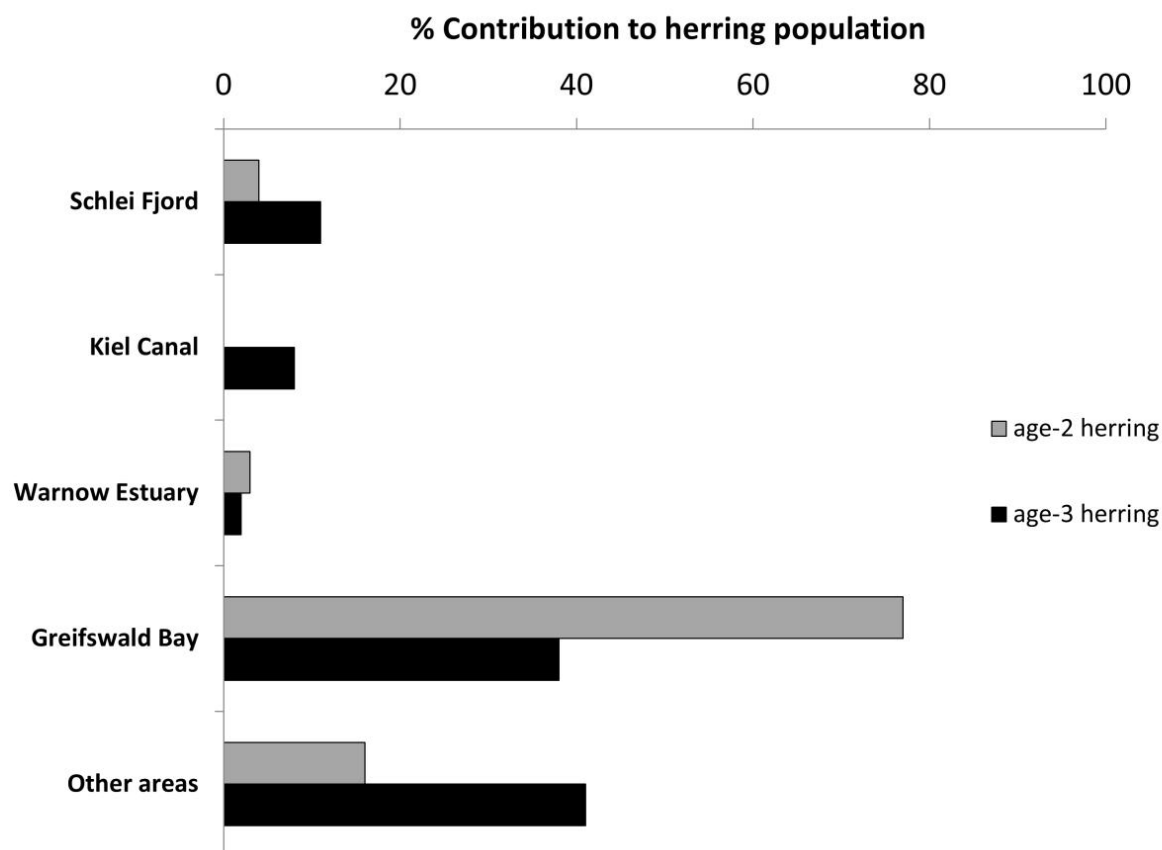
Figure 5: Natal-origin classification estimations of adult herring caught in the overwintering area Öresund Strait, based on chemical signatures in adult otolith core regions. The contribution of individuals to their respective natal habitat (above 75% correct assignment) is given in percent. The group „other areas" indicated all assignments below the respective threshold. Contribution estimates for age-2 herring (n=70) are indicated by grey bars and by black bars for age-3 herring (n=65).

Based on the classification estimates, we analyzed the mean element concentrations of the adult individuals, which were sorted into a certain group by the discriminant analysis to find same patterns of element concentrations in the adult otolith core region and in age-0 otolith signatures. Results are shown in Tab. 4. Although the ratio of elemental concentration between juvenile fish and assigned adults differed in a few elements, the elements B, Na, Mn, Sr and Ba showed similar patterns. Elemental concentrations, found in the adult otolith core region were generally lower compared to juvenile signature concentrations.

Table 4: Model-based results of herring adult otolith elemental core concentrations (mean concentrations in µg g⁻¹, with standard deviation (± SD)), which were prior classified to a distinct group for the two year classes. Since no adult herring (age-2) was classified to KC (upper table), values for KC are missing. The lower table showed results for adult herring of age-3. Due to the fact that only one adult individual was classified to WE, SD is missing.

Age-2 adults

Element	Li	B	Na	Mg	Mn	Fe	Rb	Sr	Ba
conc.	mean (± SD)	mean (± SD)	mean (± SD)	mean (± SD)	mean (± SD)	mean (± SD)	mean (± SD)	mean (± SD)	mean (± SD)
SF	0.08 (± 0.02)	1.67 (± 0.05)	2729.8 (± 66.7)	23.37 (± 3.90)	8.78 (± 10.0)	41.22 (± 1.34)	0.06 (± 0.01)	516.1 (± 24.2)	6.74 (± 0.90)
WE	0.19 (± 0.02)	3.45 (± 0.01)	2769.5 (± 323.8)	31.43 (± 8.94)	5.25 (± 5.89)	43.80 (± 3.58)	0.06 (± 0.01)	1061.5 (± 76.9)	1.72 (± 0.96)
GB	0.53 (± 1.12)	1.89 (± 0.22)	2820.1 (± 97.8)	42.88 (± 19.68)	2.56 (± 1.77)	41.56 (± 2.27)	0.06 (± 0.01)	862.3 (± 212.4)	5.89 (± 4.94)
Other	0.09 (± 0.02)	2.00 (± 0.46)	2736.0 (± 101.2)	31.91 (± 11.45)	3.14 (± 2.31)	42.56 (± 3.63)	0.06 (± 0.01)	756.7 (± 153.5)	8.34 (± 10.67)

Age-3 adults

Element	Li	B	Na	Mg	Mn	Fe	Rb	Sr	Ba
conc.	mean (± SD)	mean (± SD)	mean (± SD)	mean (± SD)	mean (± SD)	mean (± SD)	mean (± SD)	mean (± SD)	mean (± SD)
SF	0.08 (± 0.03)	2.16 (± 0.36)	2654.3 (± 84.2)	22.56 (± 8.38)	2.12 (± 0.90)	45.48 (± 5.01)	0.04 (± 0.01)	604.0 (± 88.6)	4.53 (± 2.15)
KC	0.07 (± 0.02)	2.30 (± 0.18)	2799.7 (± 36.14)	32.40 (± 7.28)	5.38 (± 3.65)	45.42 (± 1.59)	0.06 (± 0.01)	732.9 (± 113.5)	19.36 (± 5.88)
WE	0.24	3.65	2583.3	13.67	0.30	41.51	0.05	675.01	2.23
GB	0.54 (± 1.47)	2.15 (± 0.33)	2806.2 (± 102.9)	27.70 (± 10.24)	4.74 (± 2.60)	44.22 (± 2.72)	0.05 (± 0.01)	873.4 (± 176.9)	5.79 (± 4.97)
Other	0.08 (± 0.04)	2.28 (± 0.48)	2784.6 (± 88.3)	28.62 (± 10.73)	5.27 (± 2.75)	44.28 (± 3.95)	0.05 (± 0.01)	724.5 (± 139.7)	6.94 (± 3.60)

Discussion

Studies on the quantitative contribution of coastal nurseries to the overall population are challenging, but they greatly improve our understanding on fish habitat utilization and fish stock dynamics (Gillanders & Kingsford 1996, Secor et al. 2001, Gahagan et al. 2012). In the North Atlantic ecoregion, investigations on habitat connectivity of commercially important fish species are rather limited and mainly focused on Atlantic cod (*Gadus morhua*) (Gibb et al. 2007, Thorisson et al. 2011, Heidemann et al. 2012), which is a pelagic spawning fish and juvenile habitats are determined by settlement of larvae from offshore spawning grounds. Research on Atlantic herring that display benthic spawning on determined spawning areas is rather scarce (Brophy et al. 2006, Geffen et al. 2011), but generally required due to its high plasticity and ecologic as well as economic value. This study presents the first quantitative evidence of habitat dependency of the Western Baltic Sea herring to a distinct reproduction habitat, indicating that Greifswald Bay contributes a major amount to the overall Western Baltic herring population, hence being an important nursery habitat. This statement corresponds to former assumptions and indications of a strong relationship expressed by strong recurring correlations of larval herring production in GB and the amount of age-1 juveniles in the entire Western Baltic Sea one year later (Oeberst et al. 2009), indicating that early life stage survival in inshore nurseries determines recruitment success of the year-class (Polte et al. 2014).

Natal origin classification

With high classification accuracies (83% for the Schlei region, 93% for Kiel Canal, 91% for Greifswald Bay and 72% for the Warnow Estuary), we constructed a robust classification model resulting in suitable predictor variables. Other studies, concerning the same objective to investigate contribution of fish habitats to the population level, showed partially the same range of accuracy values and received successful results with an average juvenile reclassification success of 82% (Vasconcelos et al. 2008) or an overall reclassification success of 88% (Cuveliers et al. 2010). The Öresund Strait is considered a winter accumulation area of the Western Baltic herring population (Otterlind 1984, 1987, Poulsen et al. 2000, Nielsen et al. 2001). Our results support this assumption, since adult individuals caught in this area could be successfully assigned to particular coastal Western Baltic spawning areas by elemental fingerprinting. To ensure sampling of spring spawning herring exclusively, we specifically sampled post-spawned adult herring individuals. Both selected year-classes showed different contributions to the overall Western Baltic herring population. The observed differences are considered to

reflect natural variability in the productivity of the nursery area. Potential bias introduced by sampling fish from one particular shoal was addressed by distributing herring sampling over four hauls on differing sampling stations to approach a representative sample of the entire population. However, for both year-classes of matured herring, Greifswald Bay contributed most, compared to the other juvenile habitats. Western Baltic herring generally relies on inshore coastal reproduction areas along the Western Baltic Sea (Nellen 1965, Weber 1971, Schnack 1974, Scabell 1988). Due to the various numbers of potential juvenile areas for herring along the Danish, Polish, German and potentially Swedish coasts, we had to focus sampling on historically known juvenile areas. The results reveal a varying amount of recruits from other juvenile areas that could not be assigned to our sampling sites. We carefully addressed this circumstance by defining the additional group („other areas"). The definition is based on individuals with classification accuracies below 75%. The data showed that potential other habitats contributed about 16% and up to 41% to the two different year-classes (Fig. 5). We did not find any comparative strategy or approach with reference values in the literature, dealing with such corrections by including non-sampled habitats to data evaluation. Assuming that we adequately addressed this aspect in our analysis, the result is important since it indicates the presence of unknown but not unimportant juvenile habitats. Future research should attempt to locate as many juvenile areas for this population as possible to uncover the proportion of „other areas", showing a high contribution of 41% for the age-3 herring year-class. The comparisons on element concentration patterns between the age-0 herring otoliths and adult individuals, classified to certain groups, showed rather the same patterns, with some exceptions due to rather small sample sizes of group-specific classification (mainly SF, KC, WE). Some elements, such as Mg, showed different elemental concentrations between the juvenile habitat signatures and classified groups. Woodcock et al. (2012) stated that Mg, although often included into otolith chemistry analyses, is not reliable to distinguish between fish habitats, indicating that Mg might be physiologically regulated. Future studies should focus on the identification of potential inapplicable elements for future fish habitat discrimination analyses.

Temporal variability of chemical signatures

One of the most important aspects concerning the interpretation of general habitat connectivity is the potential temporal variability of elemental concentrations, either on different time scales (weeks, months) within one year (Thorrold et al. 1998, Swearer et al. 2003, Elsdon & Gillanders 2006) or between years (Hamer et al. 2003, Arkhipkin et al. 2009). Few studies showed high inter-annual variability between two sampling years (Milton et al. 1997, Schaffler &

Winkelman 2008), whereas other authors stated inter-annual stability of specific otolith element concentrations over a 2-3 years period (Campana et al. 2000). We addressed potential inter-annual signal variability by including only elements into the analysis, which were significantly different between habitats, but not significantly different between the two successive years to define the Greifswald Bay habitat signal. Our results correspond to other studies, stating inter-annual stability of distinct elements (Patterson et al. 1999, Campana et al. 2000, Rooker et al. 2001). Rooker et al. (2001) revealed that there are significant inter-annual differences over a 3 years period in northern bluefin tuna (*Thunnus orientalis*) otoliths, but this variability was only observed for three elements (Mg, Mn, Ba). Another study on Nassau grouper (*Epinephelus striatus*) showed inter-annual differences only in Ba concentration between two years in one location (Patterson et al. 1999). Although we were not able to investigate potential inter-annual variability in element signatures of the other sampling areas (Kiel Canal, Schlei Fjord, Warnow Estuary), we believe that due to highly significant differences in the entire elemental composition between the four investigated habitats, the temporal variability of single elements would not affect the general patterns observed. This assumption is supported by the study of Cuveliers et al. (2010), who stated that although they found significant differences in elemental concentrations between years in one estuary, the spatial signal was more important than the temporal differences. Regarding the good fit of the model and the general high classification percentages of individuals (> 75%) our results indicate that temporal stability of chemical signals is given in the system, at least within the studied time frame of 3 years. But a future sampling strategy should include a multi-year sampling in all potential spawning areas along the entire Western Baltic coast to proof temporal consistency of habitat-specific fingerprints over time. Since temporal variability of otolith element concentrations is documented to greatly depend on specific study regions and particular fish species, future research is required to understand fish habitat dependency and population migration patterns.

Conclusions

Besides fishery, habitat degradation is a major cause for declining fish populations as demonstrated e.g. by the Zuiderzee herring in the Netherlands in the 1930's (Wolff 2000). At the transition between land and ocean, estuaries, bays and lagoons are subject of multiple environmental alterations, including severe eutrophication by agriculture. In Greifswald Bay eutrophication-induced cascades led to a drastic decline in herring spawning substrates (Klinkhardt et al. 1985, Scabell 1988, Munkes 2005, Kanstinger et al. 2016). Although nutrient

loads could be reduced during the last 20 years, no ecological improvement could be recorded, possibly due to internal loading of accumulated nutrients from the sediment (Munkes 2005). Under the current speed of coastal modification, our findings emphasize the importance of transitional waters for the reproduction of pelagic, ocean-going fish species, highlighting the need for a sensitive regional coastal zone management. Important coastal nursery areas for key species of marine food webs should be identified and become subject of sensitive coastal zone management. Since future climate change scenarios will increase the threats on inshore coastal ecosystems, there is an urgent demand for the implementation of a coastal zone management to maintain fish populations for future generations.

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Chapter 3

First evidence of natal homing behavior of Atlantic herring (*Clupea harengus*) in coastal waters of the Baltic Sea

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Abstract

Annual recurring spawning in a distinct habitat (spawning site fidelity) is a known behavior in diadromous and marine fishes, but some species even show natal homing, returning to their spawning areas of natal origin. This behavioral trait facilitates the utilization of already established and appropriate spawning areas, when habitat conditions are optimal, warranting reproductive success and therefore resilience of populations. Although the understanding of fish migration patterns and population structure is crucial for a successful fishery management, there is still a lack of knowledge on spatial and temporal habitat connectivity of economically important clupeid fish species. This study on Atlantic herring (*Clupea harengus*, L.) showed natal homing to an important Western Baltic inshore spawning area for the first time, providing the first empirical data. Moreover, results revealed herring straying behavior to other spawning habitats, supporting current theory in the literature. With respect to the high anthropogenic impact on coastal inshore waters, these findings highlight the importance and essential function of local spawning habitats to the persistence of herring populations, underlining the need for new coastal zone management strategies.

Introduction

Philopatry is a well-established behavioral trait of animals and subject of common sense for migratory birds with their annual migrations to their breeding and overwintering areas (Greenwood 1980, Greenwood & Harvey 1982, Johns et al. 2005). In the ocean, regular returns to particular reproduction areas are also documented for marine mammals (Oliver et al. 1998, Chilvers & Wilkinson 2008) and sea turtles (Avens et al. 2003, Bowen et al. 2004). This specific homing behavior can also be found in several teleost fishes around the globe, described for coral reef fishes (Marnane 2000) and several high migratory diadromous fish species, which change their environments for reproduction, such as anadromous salmon populations (Youngson et al. 1994, Ogura & Ishida 1995, Dittman & Quinn 1996, Martin et al. 2012), river herring of the genus *Alosa* (Dodson & Leggett 1973, Melvin et al. 1986) and catadromous eel (*Anguilla* spp., Vladykov 1971, Tesch 1975, Parker 1995). Investigations on homing behavior in oceanic fish are rather underrepresented (Robichaud & Rose 2001, Hunter et al. 2003, Florin & Franzén 2010), although the understanding of habitat connectivity and evaluating the relevance of distinct spawning habitats is important from the perspective of effective coastal zone management. Historically homing of migrating fish has been a basis for the establishment of coastal civilizations during past centuries, i.e. the U.S. capital Washington D.C., founded at the Potomac River owing to the annual river herring run to their home stream (Tilp 1978, Roberts 2007) and the establishment of cities along Northern Europe during the hanseatic era with herring, being a vital part of nutrition and therefore a valuable commodity since medieval times. During medieval epochs when ocean going fishery was not an option, people were widely relying on fish annually entering inner coastal waters for spawning. Homing behavior can be distinguished between returning of individuals to their natal origin (natal homing), which is stated for salmonids (Hasler et al. 1978, Dittman & Quinn 1996) or returning of individuals to a certain spawning habitat, but not implicitly to their natal spawning site (repeated homing), as e.g. observed for walleye (*Stizostedion vitreum*) (MacLean & Evans 1981). There are some speculations on the mechanisms behind this behavior regarding olfactory imprinting to natal sites (Dittman & Quinn 1996, Gerlach et al. 2007, Nabi et al. 2014). Olfactory imprinting in salmon is a hormone-linked process, located during the developmental stage of parr-smolt transformation, where the fish is prepared for the physiological and behavioral change from freshwater to the marine environment (Hasler et al. 1978, Dittman & Quinn 1996). Other mechanisms which are discussed are the use of orientation clues, such as the position of the sun and the magnetic field (Hasler et al. 1958,

Lohmann et al. 2008, Mouritsen et al. 2013) or behavioral traits based on social learning (Olson et al. 1978, Brown & Laland 2003). Although herring is one of the best studied fish species in the world, due to its high ecological and economical global relevance, the knowledge on general habitat connectivity and the exact spatial scales on which homing is happening are widely unknown. In general, homing behavior to specific spawning areas and even straying to neighboring areas could be observed for Pacific and Atlantic herring (Wheeler & Winters 1984, Smith & Jamieson 1986, Hay & McKinnell 2002). These behavioral traits are also implied by the adopted-migrant hypothesis (McQuinn 1997), where the author hypothesized that the offspring of a local herring population are not necessarily returning to their natal spawning sites for reproduction. These recruits rather become migrants and recruiting to adopted populations with the same or different spawning season, based on the metapopulation concept (McQuinn 1997). Although natal homing of Atlantic herring is assumed to be a strict determinant of genetic population structure (Bekkevold et al. 2005, Ruzzante et al. 2006, Gaggiotti et al. 2009), no explicit research has so far provided reliable data on homing patterns. Since regional spawning habitats may have an essential function for the persistence of a population (Polte et al. 2014), there is a strong interest to clarify possible natal homing behavior of herring. However, although somewhat speculative because of the lack of pre-impact data, there might be examples that habitat degradation affected herring populations in the past. In the North Sea, economically important populations of spring-spawning herring existed prior to the 1930's, which were a major fishery resource, i.e. in the Netherlands. The so-called "Zuiderzee herring" completely disappeared after the Zuiderzee was closed by a dam, forming what is nowadays the Ijsselmeer (Wolff 2000). At the same time, coastal modifications occurred along the entire Wadden Sea area and the subtidal seagrasses (*Zostera marina*) disappeared in the entire area (Den Hartog & Polderman 1975, Den Hartog 1987, Reise et al. 1989, Giesen et al. 1990). Documentations from Wohlenberg (1935) described that seagrass beds in the Wadden Sea were densely covered by herring eggs before they vanished. There is no evidence, however, if the seagrass decline caused a decrease of spring-spawning herring in the North Sea. However, there are still residuals of this herring population entering the area and spawning on alternative substrates (Polte & Asmus 2006). Available knowledge on homing migration is widely based on former mark-recapture studies providing no possibility to differentiate between homing to their natal origin and repeated homing to a distinct spawning habitat every year (MacLean & Evans 1981, McQuinn 1997). During the last two decades, a new promising method in fishery science arose, using the microchemistry of fish otoliths (Campana et al. 2000) to investigate fish habitat dependency. This method takes advantage of certain fish otolith characteristics, being

metabolic inert and growing continuously without resorption. Otoliths are thought of as life history recorder, incorporating elements into their growing surface and therefore reflecting the physical and chemical characteristics of the ambient water, where the fish is residing during the early ontogeny (Campana & Neilson 1985, Campana 1999). This new technique revealed new opportunities to increase the understanding of fish population dynamics, natal homing behavior and therefore habitat connectivity, which is well- demonstrated for several species (Thorrold et al. 2001, Gillanders 2002, Rooker et al. 2008, Schloesser et al. 2010, Turner & Limburg 2014), except for herring. We hypothesize that (i) spawning migration of Atlantic herring populations in the Baltic Sea is extensively driven by homing behavior and (ii) herring in the Western Baltic Sea home to their natal spawning areas. Moreover we intend to test the adopted-migrant hypothesis (McQuinn 1997), by using empirical data for the first time. Furthermore, we reviewed existing investigations and findings for Atlantic and Pacific herring populations but also for other fish species, summarizing the state of knowledge to underline the importance of the homing subject in marine fish species.

Material and Methods

Coastal inshore spawning areas

Atlantic herring in the Western Baltic Sea is a highly migratory fish, which is considered to perform annual migrations between their summer feeding grounds in the Kattegat/Skagerrak and their overwintering area in the Öresund Strait, relying on inshore coastal waters along the Western Baltic Sea (such as estuaries, lagoons and bays) for spawning during spring time. Four historically known Western Baltic inshore spawning areas were sampled for early herring life stages in the spawning season 2016. Two sampling sites were located in the western part (Schlei Fjord and Kiel Canal) and two sampling sites were located in the eastern part of the German Baltic coast (Warnow Estuary and Greifswald Bay) (Fig. 1). Greifswald Bay is known as a major important spawning area for Western Baltic herring, situated in the vicinity of the Island of Rügen. For that reason, adult herring in spawning mode were sampled within this particular area during the spawning season 2016.

Age-0 herring sampling

During the early summer 2016, age-0 herring was sampled by beach seine (7 m opening, 5 mm mesh size, 1.5 m wing height) in the Schlei Fjord (SF) and by purse seine (40 m length, 3 m height, 4 mm mesh size) in Kiel Canal (KC). Herring samples from the eastern locations
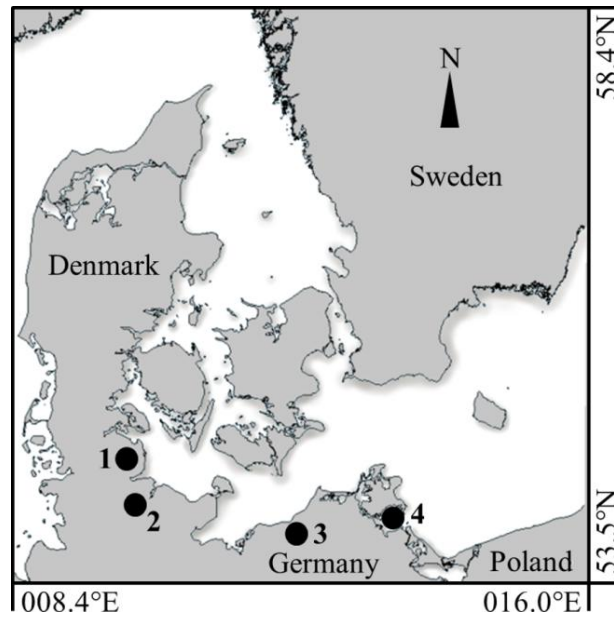
Figure 1: Locations of age-0 herring sampling areas along the coast of the Western Baltic Sea, indicated by black filled circles, Schlei Fjord (**1**), Kiel Canal (**2**), Warnow Estuary (**3**) and Greifswald Bay (**4**). Additionally, adult matured age-3 herring were caught within Greifswald Bay during the spawning season in 2016.

(Warnow Estuary (WE) and Greifswald Bay (GB)) were caught with a ring trawl (net opening of 1 m diameter and a mesh size of 1550 μm) onboard a research vessel. Additionally, age-0 herring was sampled in GB by beach seine during the season 2015. A sample size of 30 individuals per area was used for chemical analysis. In case of consecutive GB sampling, otolith samples from 2015 and 2016 were pooled together (n=45), after the analysis of inter-annual variability of elemental concentrations revealed no significant differences for particular elements (see Appendix, C2 Tab. A1). All samples were frozen right after the catch and were stored frozen until otolith dissection.

Adult sampling

Matured adult herring was received from commercial fishery during the spawning season 2016. By counts of annual increments, herring otoliths were selected according to the age-3 year class, since herring at that age are mainly matured, representing the closest fertile year-class to the age-0 herring sampled in 2016. Adult sampling was spread along the season, conducted at the beginning (March) and at the end of the spawning season (May) to ensure a balanced sampling of distinct spawning cohorts, in each case 30 otoliths (total sample size: 60 otoliths). Adult individuals caught in March were slightly larger (mean total length (TL) of 22.6 cm ± 1.5 mm) than adults from the later season (mean TL of 21.3 mm ± 2.0 mm).

Sample processing

Prior to otolith handling, all used glass equipment, microscope slides and ceramic forceps were washed in 2% nitric acid (Rotipuran Supra 69%, Carl Roth), rinsed with ultrapure water and dried under a flow cabin. Age-0 herring otoliths were dissected under a microscope (Olympus SD 30) with non-metallic equipment (ceramic forceps) and were rinsed repeatedly with ultrapure water (TKA-GenPure, 0.2 μm capsule filter, Hartmann GmbH) to remove any adhesive tissue. Cleaned otoliths were dried under flow cabin and were transferred and mounted on the fixing material (double-sided adhesive transparent pads), which were prior placed on the microscope slides. Adult left sagittal otoliths were mounted on a wood piece with double-adhesive pads by attaching only the otolith rostrum, warranting a free space between the fixing material and the otolith core region to avoid potential contamination. Otoliths were cut via high energy laser (Trumpf TrMicro 5X50+GHH GL. 5, 1030 nm wavelength) to ensure an exact cutting through the otolith core. With pulse energies of 30–80 μJoule (depending on otolith thickness), the laser cut a 0.5 mm transverse slice, first cutting beneath the core region and in second step, cutting directly through the core region. Each otolith core slice run through a washing process, starting with ultrapure water, which was continued with 2% nitric acid for 5-10 seconds to clean samples from adhesive tissue and to minimize elemental contamination. In case of highly adhesive organic material, 10% nitric acid was used (only for 2 seconds to avoid total solution of otolith). After nitric acid washing, otolith slices were rinsed again with ultrapure water and dried inside the flow cabin. After the cleaning procedure each otolith slice was mounted core side up on fixing material, which was prior mounted on washed microscope slides. Microscope slides with attached age-0 and adult otolith slices were stored in plastic vials to keep samples free from dust particles and to warrant a safe transport to the laboratory.

Analytical methods

Elemental concentrations of age-0 and adult otolith core region were analyzed with the laser ablation-inductively coupled plasma- mass spectrometry technique (LA-ICP-MS), using a ThermoFinnigan ELEMENT2 ICP-MS with an UP-213 Nd:YAG laser ablation system (213 nm wave length, pulse length of 5 ns). Certified reference material NIST 612 (National Institute of Standards and Technology) and the micro analytical reference material MACS3 (United States Geological Survey) were used for calibration (Jochum et al. 2007, Jochum et al. 2011). Elemental composition of reference materials was measured at the beginning of the measurement and was constantly repeated for quality assurance. Age-0 and adult otolith cores were ablated with

80 μm laser spot size with 60% power, a pulse repetition rate of 10 Hz and an energy density of approximately 10.2 J cm^{-2}. Constantly detected count rates of 15 elements (Li, B, Na, Mg, Si, Mn, Fe, Co, Cu, Rb, Sr, Sn, Ba, Tl, Pb) were considered for the further analysis.

Data analyses

Statistical analyses and linear discriminant analysis (LDA) were performed with R Studio (version 3.4.1) (R Development Core Team 2008). Statistical significances of single element concentrations between different sampling sites were tested by using one-way analysis of variance (ANOVA) with a significance level of $p < 0.05$. Data sets were tested for variance homogeneity by Levene's test and were logarithmically transformed $\log(x + 1)$ if necessary to meet the requirements of ANOVA. Post-hoc test (Games Howell test) was conducted to investigate site-specific differences in element concentrations between the sampling sites. LDA was used to classify chemical signatures of adult herring core regions to the spawning area signals, classification estimations were performed using the MASS package in R (Venables & Ripley 2002).

Identification best predictor elements

The number of detected elements was reduced by excluding elements with more than one missing value to warrant a good classification model with elements of high predictive power. ANOVA results showed high significant differences (except for tin (Sn)) in elemental concentrations between all four age-0 herring sampling areas. Otolith signatures of Greifswald Bay age-0 herring from the consecutive sampling years 2015 and 2016 were combined to get one Greifswald Bay area signal. To deal with possible inter-annual variability, we only include significantly different elements between the four locations sampled in 2016, when these elements concurrently show no significant differences between the two-year sampling in Greifswald Bay to ensure best classification accuracies (see appendix C2, Tab. A1).

Model accuracy

The remaining 9 elements (Li, B, Na, Mg, Mn, Fe, Rb, Sr, Ba) were used as training data set. Results showed high model accuracies for all four sampling areas: SF (0.83), KC (0.93), WE (0.72) and GB (0.91), indicating a good fit of the model. Adult otolith data were then used in the classification model to investigate natal origin, resulting in a classification of each adult individual to one distinct spawning habitat with a distinct percentage value. To deal

with non-sampling of all potential spawning areas during this investigation, we determined a likelihood threshold of 75% correct assignment of each individual to a spawning habitat. All individuals classified below this threshold were sorted to a group of "other areas".

Results

Habitat specific fingerprints

Single mean element concentrations for each predictor element per spawning area and the (3-D) MDS-plot, revealing specific juvenile habitat fingerprints, are shown in Fig. 2.
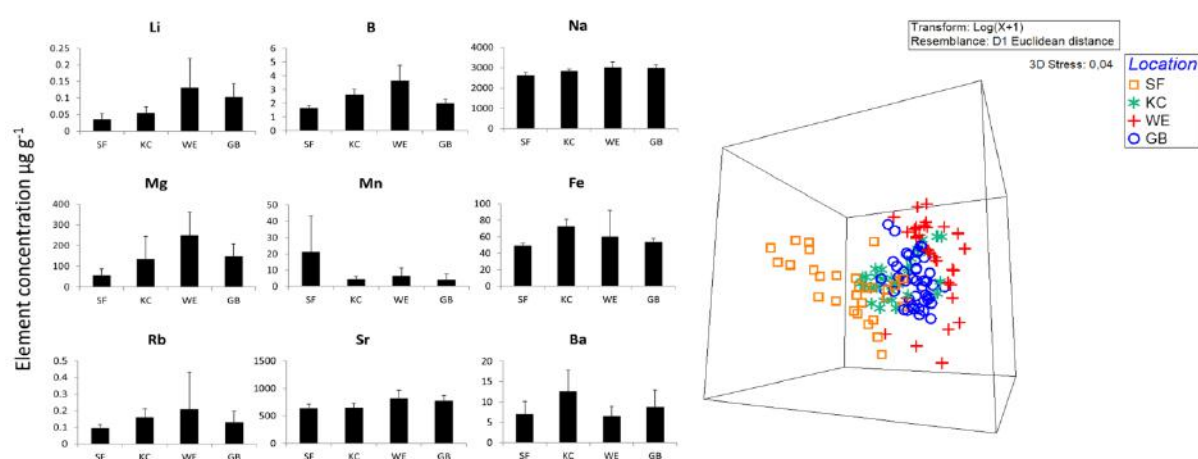
Figure 2: Mean concentrations (µg g^{-1}) with standard deviation of 9 predictor elements for each spawning area Schlei Fjord (SF), Kiel Canal (KC), Warnow Estuary (WE) and Greifswald Bay (GB) are given in the left bar chart. Mean concentrations are based on a sample size of n=30, except for GB n=45. MDS-plot (visualization in 3-D), using the Euclidean distance to classify juvenile otolith fingerprinting (based on 9 elements) for the four investigated spawning areas. Data were $\log(x+1)$-transformed for standardization. Color-coding indicates the four areas Schlei Fjord (SF, orange), Kiel Canal (KC, green), Warnow Estuary (WE, red) and Greifswald Bay (GB, blue). Each data point represents a single otolith. Original figures are shown in the previous chapter (chapter 2, Fig. 3 and Fig. 4).

Natal origin classification

Data explicitly demonstrate natal homing behavior in the Western Baltic Sea herring population (Tab. 1). The classification revealed that the majority of adult herring (56%) were correctly assigned to the GB spawning area, indicating the return of adult herring to their spawning area of natal origin.

34% of adult individuals, caught during spawning activity, could not be classified correctly to a distinct spawning area and 10% were sorted to SF, according to their elemental composition, indicating straying individuals to another spawning area. No single individual was

Table 1: Classification estimations for adult herring caught in GB during the spawning season 2016 based on chemical signatures in adult otolith core regions. The contribution of respective juvenile habitats is based on the 75% threshold of correct assignment. Contribution estimates are given in % with respective individual numbers in parenthesis. The group "other areas" included all assignments below the respective likelihood thresholds.

	SF	KC	WE	GB	Other areas
	% (n)	% (n)	% (n)	% (n)	% (n)
Adult herring Age-3	10 (6)	0 (0)	0 (0)	56 (33)	34 (20)

classified either to KC or WE. Based on the classification estimates, we analyzed the mean element concentrations of the adult individuals, which were sorted into a certain group by the discriminant analysis to find same patterns of element concentrations in the adult otolith core region and age-0 otolith signatures. Results are shown in Tab. 2. Although the ratio of elemental concentrations between juvenile fish and assigned adults differed in a few elements, the elements Na, Sr and Ba showed similar patterns. Elemental concentrations, found in the adult otolith core region were generally lower compared to juvenile signature concentrations.

Review on herring homing behavior

We reviewed existing literature and gathered central findings on herring homing behavior in particular, but also fish homing behavior in general to summarize the actual state of knowledge. Literature research was focused on usage of physical tagging methods and otolith chemistry. Other methods used for homing investigations, such as otolith microstructure patterns in salmons (Quinn et al. 1999) or analysis of morphometric and meristic characters of river herring (Messieh 1977) were excluded. We demonstrated that the majority of existing herring studies is based on tagging-recapture experiments of Pacific herring populations and therefore empirical knowledge on the nature of herring homing behavior (repeated or natal homing) is non-existing (Tab. 3).

Table 2: Model-based results of adult herring otolith elemental core concentrations (mean concentrations in µg g^{-1}, with standard deviation ($\pm$ SD)) from the GB adult herring sampling during the spawning season, which were prior classified to a distinct group of natal origin. Since no adult herring was classified to either KC or WE, values for KC and WE are missing.

Age-3 adults from Greifswald Bay

Element conc.	Li mean ($\pm$ SD)	B mean ($\pm$ SD)	Na mean ($\pm$ SD)	Mg mean ($\pm$ SD)	Mn mean ($\pm$ SD)	Fe mean ($\pm$ SD)	Rb mean ($\pm$ SD)	Sr mean ($\pm$ SD)	Ba mean ($\pm$ SD)
SF	0.07 ($\pm$ 0.04)	1.42 ($\pm$ 0.14)	2670.1 ($\pm$ 144.3)	22.52 ($\pm$ 4.84)	5.82 ($\pm$ 3.83)	35.68 ($\pm$ 4.90)	0.06 ($\pm$ 0.02)	592.4 ($\pm$ 131.1)	5.94 ($\pm$ 2.36)
GB	0.08 ($\pm$ 0.03)	1.41 ($\pm$ 0.16)	2844.5 ($\pm$ 81.2)	25.63 ($\pm$ 6.64)	5.80 ($\pm$ 3.91)	32.88 ($\pm$ 3.35)	0.06 ($\pm$ 0.01)	735.7 ($\pm$ 81.9)	10.98 ($\pm$ 4.08)
Other	0.06 ($\pm$ 0.02)	1.47 ($\pm$ 0.16)	2760.2 ($\pm$ 65.3)	26.17 ($\pm$ 6.81)	6.92 ($\pm$ 5.43)	34.65 ($\pm$ 3.17)	0.06 ($\pm$ 0.01)	696.9 ($\pm$ 59.2)	10.67 ($\pm$ 4.76)

Table 3: Overview of studies with the focus on herring homing in particular and homing behavior of other fish species with separation between repeated homing (including spawning site fidelity) and natal homing with indications on spatial scales, methods and references. The question marks indicate that natal homing is not investigated during the study.

Species	Migration type/Habitat use	Homing		Methods		References
		repeated	natal	Physical tagging	Otolith chemistry	
Clupea harengus	Marine, spawning areas in bays along the coast of Newfoundland, Canada	x	?	x		(Wheeler & Winters 1984)
Clupea harengus	Marine, spawning areas in bays along the coast of Nova Scotia, Canada	x	?	x		(Stobo 1982)
Clupea harengus	Marine, spawning areas around the Isle of Man and Broadhaven Bay, Ireland	x	?	x		(Molloy et al. 1993)
Clupea pallasii	Marine, spawning areas along the coast of British Columbia (B.C.), Canada	x	?	x		(Hourston 1982)
Clupea pallasii	Marine, juveniles and adults from bays and inlets along west Coast of Vancouver Island, Canada	x	?	x		(Hourston 1959)
Clupea pallasii	Marine, spawning areas along the coast of B.C., Canada	x	?	x		(Hay & McKinnell 2002)
Clupea pallasii	Marine, intertidal and shallow subtidal spawning areas along the coast of B.C., Canada	x	?	x		(Hay et al. 2001)
Alosa pseudoharengus *Alosa aestivalis*	Anadromous, coastal watersheds from Canada to Florida, USA	x	x		x	(Turner et al. 2015)
Alosa pseudoharengus *Alosa aestivalis*	Anadromous, rivers along Long Island Sound, USA	x	x		x	(Gahagan et al. 2012)
Alosa sapidissima	Anadromous, rivers from Georgia to New Hampshire, Atlantic Coast, USA	x	x		x	(Walther et al. 2008)
Alosa sapidissima	Anadromous, Connecticut River to Long Island Sound, USA	x	?	x		(Dodson & Leggett 1973)
Alosa sapidissima	Anadromous, fidelity and straying in Annapolis River, Nova Scotia, and in Bay of Fundy, Canada	x	?	x		(Melvin et al. 1986)
Osmerus mordax	Anadromous, adults and juveniles within spawning areas in Placentia and St. Mary's Bay, Coast of Newfoundland, Canada	x	?	x	x	(Bradbury et al. 2008)

Table 3: Continuation overview homing studies

Species	Migration type/Habitat use	Homing		Methods		References
		repeated	natal	Physical tagging	Otolith chemistry	
Anguilla rostrata	Catadromous, adults from rivers along the Northumberland Strait in New Brunswick, Canada	X	?	X		(Vladykov 1971)
Anguilla rostrata	Catadromous, adults from the coast of Maine, USA	X	?	X		(Parker 1995)
Anguilla anguilla	Catadromous, adult sampling in the German Bight, Elbe estuary and Hamburg port area, Germany	X	?	X		(Tesch 1967)
Psetta maxima	Marine, adults from Gotland basin in the central Baltic Sea	X	?	X		(Florin & Franzén 2010)
Pleuronectes platessa	Marine, adult sampling in the central North Sea	X	?	X		(Hunter et al. 2003)
Gadus morhua	Marine, northern Massachusetts Bay, Gulf of Maine, USA	X	?	X		(Zemeckis et al. 2014)
Gadus morhua	Marine, spawning aggregations at the Coast of Norway	X	?	X		(Skjæraasen et al. 2011)
Gadus morhua	Marine, Atlantic ocean, Gilbert Bay, New Foundland/Labrador, Canada	X	?	X		(Green & Wroblewski 2000)
Gadus morhua	Marine, spawning ground in Placentia Bay, Newfoundland, Canada	X	?	X		(Robichaud & Rose 2001)
Cynoscion regalis	Marine, estuary spawning North America, Atlantic Ocean		X		X	(Thorrold et al. 2001)
Stizostedion vitreum	Freshwater, Muskegon river system and bays in Lake Michigan, USA	X	?	X		(Crowe 1962)
Salvelinus namaycush	Freshwater, spawning shoals in the East Arm of Lake Opeongo, Ontario, Canada	X	?	X		(MacLean et al. 1981)

Table 3: Continuation overview homing studies

Species	Migration type/Habitat use	Homing		Methods		References
		repeated	natal	Physical tagging	Otolith chemistry	
Oncorhynchus nerka	Anadromous, adults spawning migrations to Karluk and Brooks Lakes, Alaska, USA	X	?	X		(Hartman & Raleigh 1964)
Oncorhynchus keta *Oncorhynchus kisutch*	Anadromous, juveniles and adults from five rivers in the Norton Sound region, Alaska, USA		X		X	(Zimmerman et al. 2013)
Salmo salar	Anadromous, juveniles and adults at Girnock Burn, River Dee in Scotland, UK		X	X		(Youngson et al. 1994)
Salmo salar	Anadromous, smolts and adults from three rivers in Wales, UK		X	X		(Solomon 1973)
Salmo salar	Anadromous, larvae, juveniles and adults from rivers in the Adour basin, France		X		X	(Martin et al. 2012)
Roccus chrysops	Freshwater, migration from open water of Lake Mendota to spawning grounds, Wisconsin, USA	X	?	X		(Hasler et al. 1969)
Esox lucius	Anadromous, juveniles and adults were caught at the Swedish Coast in the Baltic Sea		X		X	(Engstedt et al. 2014)
Thunnus thynnus	Marine, yearlings and adults from Gulf of Mexico, Gulf of Maine, Gulf of St. Lawrence		X		X	(Rooker et al. 2008)
Thunnus thynnus	Marine, yearlings and adults from Gulf of St. Lawrence and the Mediterranean Sea		X		X	(Schloesser et al. 2010)
Epinephelus tauvina	Marine, Malindi National Marine Park, Kenia, Africa		?	X		(Kaunda-Arara & Rose 2004)
Brachyplatystoma rousseauxii	Freshwater, juveniles and adults from Madeira river, Amazon, South America		X		X	(Duponchelle et al. 2016)

Discussion

Homing is a wide spread phenomenon in diadromous and fresh water species (Parker 1995, Miller et al. 2001, Martin et al. 2012), but also observed in some economically relevant marine fishes (Green & Wroblewski 2000, Robichaud & Rose 2001, Hunter et al. 2003, Florin & Franzén 2010). These investigations are valuable and provide new insights of fish population dynamics, which is a relevant aspect regarding coastal zone management strategies for certain spawning areas. However, studies on high migratory Atlantic and Pacific herring populations (Hourston 1982, Wheeler & Winters 1984, Hay et al. 2001) are rather underrepresented and entirely based on mark-recapture experiments. Those experiments often included an immense effort (in case of herring tagging thousands of individuals) and they provided valuable results that are often the baseline for present migration related fishery management. However, those studies cannot provide information whether the tagged fish actually hatched in the area where it was caught and therefore results are not suitable for the distinction of different homing strategies (repeated or natal homing). This study provided the first empirical data, revealing natal homing behavior for Atlantic herring in the Baltic Sea. Considering the amount of 10% of adults found originating from the Schlei Fjord as straying individuals, the results further support the adopted migrant hypothesis (McQuinn 1997), quantifying the amount of straying fish for a certain year-class, adopted by a different spawning group.

Natal origin classification

We constructed a robust classification model with high classification accuracies (72-93%). Other studies showed the same level of accuracy values and received successful results (Vasconcelos et al. 2008, Cuveliers et al. 2010). The comparison of element concentrations between the juvenile habitat signatures and adult individuals, classified to their natal origin, revealed rather the same patterns for some elements. Other elements showed only little differences in elemental concentrations between the groups of GB and SF (such as Mn) which was identified as a habitat-specific element for the Schlei area. In case of Mn, Brophy et al. (2004) stated that a divergence of laser position of only 50 μm from the exact core region is enough to result in lower Mn concentrations in herring larval otoliths. In case of Mg, Woodcock et al. (2012) stated that Mg concentrations are not reliable to distinguish fish habitats. More research is needed to identify potential inapplicable elements for future fish habitat discrimination analyses.

Herring homing behavior

The ecological relevance of homing was discussed by Leggett (1977), who implied homing to be a mechanism to achieve maximum reproductive success by synchronizing the return of fish when condition in spawning habitats are optimal for successful development of early life stages. Additionally, homing would regulate the number of spawning individuals, avoiding under- or over-utilization of a distinct habitat and finally facilitating the reproductive isolation (Leggett 1977). Herring tagging experiments, conducted by Wheeler and Winters (1984), revealed herring homing behavior with high return rates of approx. 90% for Atlantic herring population along the east Coast of Newfoundland. In this context, the authors defined the term "homing" as returning to the same spawning area in consecutive years (Wheeler and Winters, 1984). The study by Hay et al. (2001) showed homing behavior for Pacific herring, based on several recaptures in one particular region, where tagged herring was once released (Hay et al. 2001). McQuinn (1997) concluded that although tagging data indicate high homing rates for adult herring, there is a need in precise distinctions between natal homing and repeated homing. Although Hourston (1959) tagged juvenile herring in their inshore coastal habitats and investigated the returning rates to their juvenile habitats after maturation, his findings could not be linked to natal homing, since tagged juveniles were already 1-year old and were not necessarily caught in their natal habitat, regarding their behavior of joining adult shoals on their migration to spawning grounds.

In general, two opposing herring population concepts exist in the literature. The "discrete population concept" is based on the view of discrete populations with isolated reproduction cycles and limited gene flow, due to strong natal homing behavior (Iles & Sinclair 1982), whereas the "dynamic balance population concept" is rather based on unstructured population mixing with high gene flow between neighboring populations and less strong homing behavior (Smith & Jamieson 1986). The metapopulation concept after McQuinn (1997) seems to be a unification of both concepts with the main descriptive structures based rather on repeated homing, caused by social learning from repeated spawning adults, associated with significant gene flow.

According to our extensive literature research (see Tab. 3), our study is the first investigation on natal homing behavior of Atlantic herring with empirical data, revealing a returning rate of 56% to the Greifswald Bay spawning area with 10% of straying individuals, originated from the Schlei Fjord. According to the straying individuals, our results seem to support the adopted-migrant hypothesis (McQuinn 1997). However, the high homing rate to the spawning area of natal origin might indicate a direct migration mechanism.

With high classification accuracies for all four sampled juvenile habitats, we constructed a classification model with suitable predictor variables. Other studies showed the same range of accuracy values (Vasconcelos et al. 2008, Cuveliers et al. 2010). However, 34% of individuals could not be assigned to a distinct spawning area. We consider this portion of unknown origin to rather indicate the incomprehensive knowledge on coastal spawning locations rather than deficiencies in the classification model. We assume that an extended sampling of multiple spawning areas in the future will possibly explain the unknown origin of individuals to a great extent, potentially being straying individuals from other spawning areas. Although inter-annual variability of elemental concentrations seems to be an influential factor for origin classification, the effect is supposed to be less significant at broader spatial scales (Turner & Limburg 2014). We pooled age-0 herring from Greifswald Bay from two different years (2015 and 2016), using only elements which were not statistical significant between the consecutive years. Our approach seems applicable, since the study by Rooker et al. (2001) showed inter-annual consistency of specific elemental concentrations. Our results indicate that temporal stability of signals is given in our system, but a sampling strategy in the future should be to follow one year-class from juvenile stage to matured adult herring in a 3-year time frame with an additional multiple-year sampling of all potential spawning areas of this population to proof chemical signature consistencies over a longer period of time and dealing with potential straying from other unknown areas. Otolith chemistry is well-demonstrated tool for investigating natal homing in fish populations (Thorrold et al. 2001, Rooker et al. 2008, Gahagan et al. 2012, Zimmerman et al. 2013) and in this instance, for Atlantic herring population in the Western Baltic Sea.

There is still some ambiguity on the guidance mechanisms driving homing behavior. It is assumed that homing in anadromous salmon populations are driven by a combination of imprinting juveniles to a distinctive odor of natal streams prior to open sea migration (Hasler et al. 1978) and orientation cues, either using the magnetic field that exists when they start their open Sea phase (Lohmann et al. 2008, Putman et al. 2013) or using some sun compass (Hasler et al. 1958, Mouritsen et al. 2013). While salmon, a semelparous strategist with only one single reproduction event, rather recognize their spawning sites by olfactory imprinting (Dodson 1988, McQuinn 1997), herring with an iteroparous reproduction strategy (multiple reproduction cycles) is supposed to find their spawning habitats by social transmitted spatial learning (McQuinn 1997). Hourston's statement (1959), that juvenile Pacific herring show a greater tendency of mixing at the feeding ground and therefore possibly becoming migrants to other neighboring populations (Hourston 1959, McQuinn 1997), underlines the mechanism

of social learning of herring migration routes. Conversely, Brophy et al. (2006) conducted investigations on spawning season fidelity based on otolith microstructure analysis and stated that adult Atlantic herring in the Celtic Sea do home to their natal spawning sites after dispersal to nursery grounds in the Irish Sea. The authors further assumed that larval imprinting is the driving homing factor rather than learning by repeated-spawning individuals (Brophy et al. 2006).

Atlantic herring in the Western Baltic Sea is a high migratory fish, showing some kind of anadromous pattern, migrating from marine conditions to less saline, nearly freshwater habitats for spawning. Although both mechanisms are discussed for herring, we can only speculate on the actual homing mechanisms, demonstrating the requirement of more homing studies with focus on the driving mechanisms.

According to habitat dependency, it is stated that anadromous fish are able to elude on other spawning streams in case of anthropogenic habitat alteration by blocking natal streams or decreased habitat quality (Leider 1989, Pess et al. 2012), but the opposing example of the Zuiderzee herring population (Wolff 2000), which got lost, due to closing the access to their spawning area by a dam construction, demonstrated a diminished capability to migrate to other spawning areas. Hence, herring natal homing behavior, either by social learning or by imprinting, indicates potential problems. If natal spawning habitats are altered by coastal modification (i.e. harbor constructions), pollution or eutrophication and habitat conditions become unfavorable for successful development of early life stages, any further exclusive utilization of these unfavorable habitats might lead to severe impacts on population level. This assumption is underlined by observations on one local Western Baltic spawning component (Warnow herring). Every year, matured adult herring shoals arrive in the Warnow Estuary, highly modified by harbor constructions, in late spring for spawning. Egg deposition on harbor walls, due to lack of vegetation, could be observed (personal observation), but it is unclear whether egg development and reproduction is successful.

Straying behavior

Straying is a well-known behavior, defined as a migration of adult individuals to spawn in other spawning habitats (coastal sites, estuaries, streams) than their natal sites (Quinn 1993), leading to a general genetic flow between local populations. This behavior is documented by Walther et al. (2008), who found 6% of straying shad individuals (*Alosa sapidissima*) of other rivers origin within the study area, but is also observed in other anadromous fish species, such as Pacific salmon (*Oncorhynchus* spp.) (Hartman & Raleigh 1964, Quinn 1993, Sharp et al. 1994, Keefer

& Caudill 2014), showing varying straying rates. Straying behavior in herring was mainly reported for Pacific populations (Hourston 1982, Hay et al. 2001, Stick et al. 2014) and might be a behavioral answer to spatial and temporal changes in habitat quality (Keefer and Caudill 2014), facilitating the discovery of new potential spawning habitats (Stephenson 2006) or even recolonization after reversed habitat alterations, e.g. removing barriers to a distinct stream (Pess et al. 2012), in the end warranting the persistence of fish populations. The population structure of the Western Baltic herring population is considered as a metapopulation, composed by multiple spawning components (Clausen et al. 2007). Hence, these local populations are related to different degrees of gene flow (Wade & McCauley 1988, McQuinn 1997). Studies on herring genetic structure between the North Sea-Kattegat/Skagerrak area and the western Baltic Sea stated genetically distinct populations (Bekkevold et al. 2005, Gaggiotti et al. 2009), but genetic differences on a small spatial scale within the Western Baltic herring metapopulation were not investigated. Although straying to other spawning habitats general leads to a variable gene flow between neighboring local populations, results from other genetic studies indicated some reproductive isolation between genetic separated spawning waves in Greifswald Bay, assuming sympatric divergence (Bekkevold et al. 2005, Jørgensen et al. 2005). Since herring population dynamics are complex, showing a high plasticity of morphology, spawning seasons and locations with genetic mixing and reproductive isolation (Haegele & Schweigert 1985, McQuinn 1997, Jørstad 2004, Bekkevold et al. 2007), future studies should focus on population structure and dynamics of this important Baltic Sea herring population.

Conclusions

Local herring spawning components are highly relevant for small-scale coastal fisheries but also serve the function for the persistence of populations. According to natal homing behavior of Western Baltic herring, the degree of habitat dependency is one essential driving factor for recruitment success. Since important coastal inshore fish reproduction areas are threatened by human-induced habitat alteration and degradation, studies on this important behavioral trait should play an essential role for future research to understand herring habitat connectivity and plasticity of this economically and ecologically important species, resulting in the implementation of new coastal zone management strategies to preserve ecological relevant herring spawning grounds, which are often threatened by anthropogenic impact and coastal modification.

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Chapter 4

Spawning bed selection of Atlantic herring (*Clupea harengus*) in the waters of the Western Baltic Sea

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Abstract

Submerged vegetation is considered a crucial ecosystem engineer for aquatic fauna worldwide. Atlantic herring (*Clupea harengus*) in the Western Baltic Sea strongly depends on the availability of appropriate spawning beds formed by meadows of submerged aquatic vegetation in shallow brackish bays and lagoons. These coastal habitats are subject to multiple anthropogenic alteration and eutrophication impacts. Hypothesizing a distinct function of plant communities as substrate for herring egg deposition along the littoral depth gradient, fixed transects were sampled weekly throughout the herring spawning season in four successive years. Herring spawn concentrations and egg mortalities were quantified and the impact of water temperature fluctuations on spawning intensity and egg mortality was investigated. Our results showed strong inter-annual changes in spawning intensities and revealed years with alarmingly high egg mortalities. Particularly, the results indicated an increase of spawning depth from the shallow to the deeper sites according to the increasing seasonal temperature gradient during spring. This can be interpreted as an adaptation of spawning behavior to avoid unfavorably high water temperatures. Considering the persistent trend in decreasing submerged aquatic vegetation meadows and limited vertical distribution due to eutrophication effects, our results underline the demand for an integrated and sustainable management of shallow coastal spawning grounds.

Introduction

Most fish species in the ocean spawn their pelagic eggs freely into the open water where their fate is largely depending on physical oceanography and predation pressure. As a proxy for reproductive success the drifting eggs of major fishery species are often monitored by plankton surveys (Bunn et al. 2000, Ibaibarriaga et al. 2007) or are subject of oceanographic dispersal models (Petereit et al. 2014). In contrast, relatively little attention is paid to benthic eggs, spawned directly on the seafloor or attached to benthic substrates, although this strategy is performed by some ecologic and economic key species, such as herring (*Clupea* spp.).

One reason for this lack of attention might be the perception that most fish spawn a bulk of eggs subjected to immense natural egg mortality before they can be assessed (Hay & Miller 1982). Hence, instead of egg concentrations, usually larval densities are used to receive some forecasting instrument on herring recruitment (Oeberst et al. 2009). Another reason could be rather related to some kind of survey tradition that is widely focused on vessel-based sea going observations. Spawning grounds in the immediate shore zone, too shallow for research vessels to operate, might present certain "blind spots" for such monitoring programs. Whatever the reasons are, these shallow water spawning grounds certainly deserve attention as they are highly exposed to multiple anthropogenic modifications. Systematic monitoring of herring spawning grounds currently exist only in the North Pacific, globally known for massive herring runs during late winter and early spring, e.g. in the Puget Sound area (US) (Stick et al. 2014) and in British Columbia (CAN) (see review in Schweigert 1993). Since the 1950's, quantitative estimates on herring egg concentrations were the basis for the analysis of population dynamics of Pacific herring (*Clupea pallasii*) stock assessment (Hay & Miller 1982) and diver-based herring egg monitoring programs were an established methodology, which has been improved over the years to adequately record and assess herring spawning for use in stock assessment purposes (Haegele et al. 1979).

In the Atlantic, e.g. North Sea autumn spawning herring (*C. harengus*) mostly spawn on deeper sites with gravel substrate (De Groot 1980) on outer coastal shelf areas and Norwegian spring spawning herring attach their eggs to the sea floor in stony areas deeper than 200 m (Slotte & Fiksen 2000 and citations therein). Although some spring spawning populations also exist in the North Sea, spawning on littoral macrophytes (Polte & Asmus 2006), they are probably only residuals of their former population, as historical documentation describes massive spawning on seagrasses in the Wadden Sea before the drastic seagrass losses occurred during the 1930's (Wohlenberg 1935). However, the local populations in the Baltic Sea show a similar spawning

mode as the Pacific herring, immigrating far inshore to attach their adhesive eggs to benthic vegetation, when available (Rajasilta et al. 1993, Klinkhardt 1996). Besides direct, singular impacts such as oil spills (Hose et al. 1996, Incardona et al. 2011, Rahikainen et al. 2017), predation is considered a main natural cause of egg mortality in benthic spawning fish (Bailey & Houde 1989). Indeed, Kotterba et al. could demonstrate a significant impact of stickleback (*Gasterosteus aculeatus*) predation on herring egg mortality in the western Baltic Sea (Kotterba et al. 2014, Kotterba et al. 2017).

The Western Baltic herring population is considered to rely on inner coastal waters such as bays, lagoons and estuaries for reproduction (Klinkhardt 1984, Scabell 1988, Polte et al. 2017), migrating into their spawning areas in distinct spawning cohorts in spring (Klinkhardt 1996). Although herring spawning habitats are of high ecological importance, their resilience is highly threatened by human impacts. Eutrophication processes, owing to high agricultural land usage in the past, led to a decline of vegetation depth distribution in one major spawning area, called Greifswald Bay (Munkes 2005a, Kanstinger et al. 2016). In this particular system, vegetation cover dropped from 90% (Seifert 1938) to approximately 7% during the past seven decades (Kanstinger et al. 2016). Initial spawning is triggered by prevailing water temperatures (Klinkhardt 1984, 1996). An increase in water temperatures, driven by climate change, could highly impact herring reproduction (Blaxter 1992, Hoegh-Guldberg & Bruno 2010, Peck et al. 2012), especially when macrophyte spawning beds are limited to the shallow littoral zone above 3 m depth, therefore exposing the eggs to rapid spring temperature gradients and strong diurnal fluctuations that would otherwise be buffered in deeper water. Although spawning ecology of coastal spawning herring has been intensively studied in the Baltic Sea region (Aneer et al. 1983, Scabell & Jönsson 1984, Scabell 1988, Aneer 1989, Kääriä et al. 1997, Šaškov et al. 2014), studies on the effects on vertical spawning bed selection and depth-related egg mortality along the season are restricted to Pacific herring (Taylor 1971, Haegele 1981).

A major aim of the present study is to test, if environmental habitat characteristics have an impact on depth-related spawning intensity patterns and herring egg mortality. Moreover, we studied a potential temperature-related change in vertical spawning bed selection along the season, hypothesizing that (i) initial spawning is mainly driven by the spring temperature regime and that (ii) depth-related spawning is based on the prevailing seasonal temperature regime. In addition, we further hypothesize that (iii) egg deposition is related to sufficient biomass of submerged aquatic vegetation and that (iv) egg mortality changes during the spawning season.

Material and Methods

Study sites

The study was performed in Greifswald Bay (N53° 14'; E13° 34'), which is one major spawning area for Western Baltic spring spawning herring population (Klinkhardt 1984, Scabell 1988). During the herring spawning season, this brackish lagoon has a mean salinity of 7.3 PSU (Kell 1989). It is a semi-enclosed highly eutrophic basin with a total size of 514 km^2 and a mean water depth of 5.8 m. Greifswald Bay is located in the vicinity of the Island of Rügen and the German mainland, with a connection to the Baltic Sea via a narrow sound in the West (Strelasund) and a wide, but shallow opening in the East (Fig. 1). These topographic features and the marginal tidal amplitude in the inner Baltic Sea region (< 10 cm) result in a limited water exchange rate ranging between eight times (Stigge 1989) to almost 12 times a year (Schiewer 2008), which is mainly wind driven (Schnese 1973). The water temperatures range from sub 0°C surface waters with closed ice coverage in winter to more than 20°C during summer. The water body is well-oxygenated due to wind-generated mixing events (Schiewer 2008). Due to its limited depth, this water body warms up very quickly in springtime and cools down faster in autumn, compared to the coastal Baltic Sea.

The study site "Gahlkow" is a known herring spawning bed, located at the southern coast of Greifswald Bay (Scabell 1988) (Fig. 1). Gahlkow is characterized by extended beds of submerged aquatic vegetation (SAV), existing in the shallow littoral zone with growth limits at a maximum water depth of approximately 3.5 m (Munkes 2005b, Kanstinger et al. 2016). SAV communities in the shallow littoral zone are stratified by depth and dominated by flowering plants such as pondweeds or seagrass in addition to diverse macroalgal assemblages (Geisel & Messner 1989). The "pondweed" zone is dominated by species of the order Alismatales (pondweeds in the broader sense) with additional filamentous, fast growing algae communities in the very shallow area up to 1 m water depth, followed by an "intermediate" zone, where mixed pondweed and seagrass communities can be found in 1.5 m depth. The subsequent "seagrass" zone, dominated by *Zostera marina* (Zosteraceae) is found in water depths of 2-3 m (Geisel and Messner 1989).
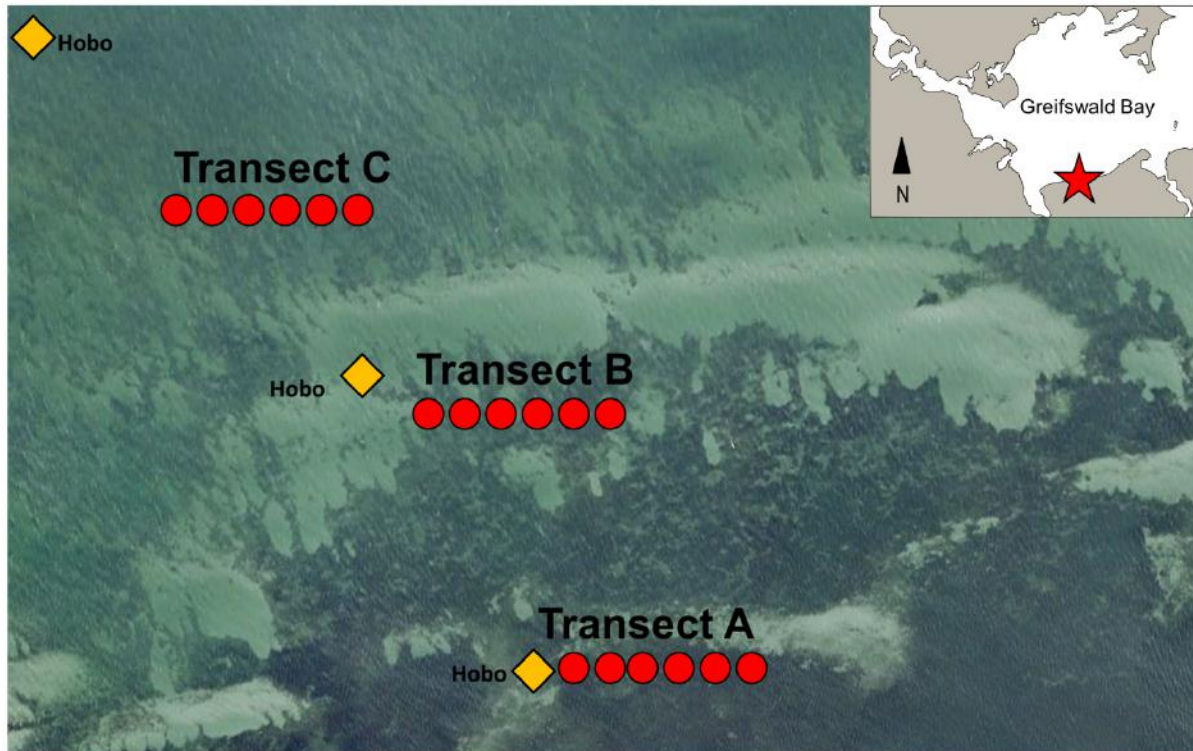
Figure 1: The location of the study site Gahlkow, located at the southern coast of Greifswald Bay (red star, figure in the upper right corner) with six replicates (red dots) on three defined permanent transects in different depth zones (A: 1 m, B: 1.5 m, C. ~2 m). Location of temperature loggers (HOBOS®) are indicated by yellow rhombus.

Herring egg sampling

To investigate patterns of depth-dependent herring spawning and egg mortality, we defined transects located parallel to the shoreline of Gahlkow (Fig. 1). Initially, the entire vertical spawning area from the beach down to a water depth of > 5 m was surveyed by a towed video camera, transmitting real-time images of the sea floor. The entire distribution of the spawning zone was assigned to three transects, randomly placed into the spawning area. The exact position of those transects was tagged by Global Positioning System (GPS), since no physical markers can be placed in this area highly utilized by fishing boats and recreational water sport activities. Transects covered the shallow vegetated littoral zone with distinct vegetated depth zones and corresponding SAV compositions.

Each permanent transect consisted of 6 fixed sampling stations in a row, stretching on a latitudal axis (from West to East) of 125 m total length (distance between sampling stations: 25 m). Prior to each spawning season, a presence-absence-control was conducted to determine the time of initial spawning, warranting that no spawning occurred prior to sampling. Each transect was sampled weekly from March (beginning of the spawning season) to late May/early

Figure 2: Field sampling procedure, using the Van Veen grabber from a zodiac. (**A**) a mesh bag is mounted on the open side of the washing tube (with longitudinal opening on the left), (**B**) the van Veen grabber, held by hand, prior to sampling, (**C**) the van Veen grabber with the plant sample inside the bucket, (**D**) after the grabber content was put into the washing tube, the sample was washed to remove sand particles.

June (end of the spawning season) in four successive years (2012-2015). On each transect, water temperatures were recorded with a hand held field probe (YSI Professional Plus). Additionally temperature loggers (HOBO Water Temp Pro v2) were installed in the immediate vicinity of each transect to record diurnal fluctuations throughout the seasons. Due to technical reasons, the HOBO-logger data are only available for the years 2012 and 2013. Samples were taken from a zodiac with a van Veen grabber (Fig. 2). This sampling method is applicable for soft bottom habitats, which is characteristic for our investigated spawning bed. Sampling procedure is shown in Fig. 2.

In 2012, sampling started on March 14th 2012 and was conducted with a van Veen grabber of a sampling area of 400 cm^2 until May 14th 2012, however for technical reasons all sampling thereafter was conducted using a grabber with a reduced sampling area (250 cm^2). The grab samples consisting of benthic substrate with attached herring eggs were transferred into a specially designed washing tube (Fig. 2). A mesh bag was mounted on the open end of the plastic tube and the hind end of the tube was closed by a lid. The longitudinal side of the tube was cut open to insert the grabber mouth with the sample. Through the tube, the sample could be washed into the labelled mesh bag (mesh size < herring eggs) and after a careful washing procedure to remove sand particles, only vegetation with attached herring eggs was flushed into the mesh bag and assigned with an ID-number. The samples were stored in water filled barrels for transportation to the institute. In the laboratory, samples were fixated in 4% buffered formalin solution for conservation.
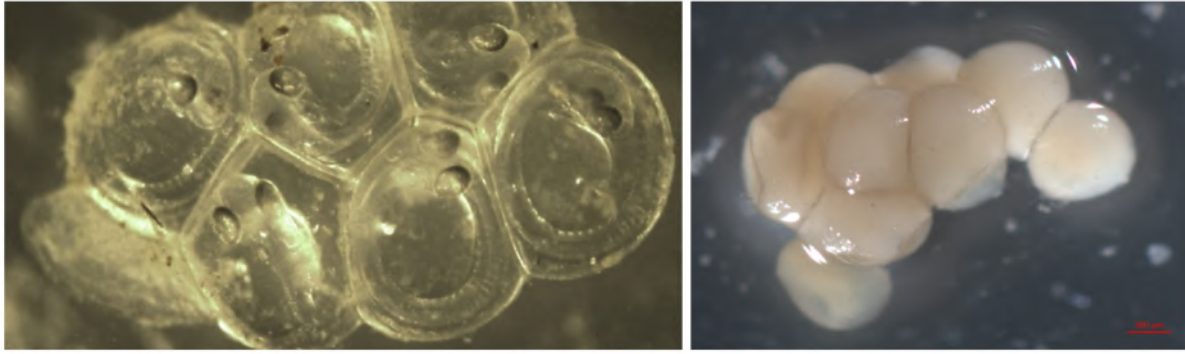
Figure 3: Herring egg quality categories: Alive herring eggs with herring embryos (at a later developmental egg stage) (left) and dead opaque eggs (right).

Sample processing

In the laboratory, samples were rinsed in water (for at least 24 hours) to ensure the removal of the fixative solution. The total plant biomass of each sample (in gram fresh weight (g FW)) was recorded and the percentage of functional plant groups in the total sample was estimated and noted. For egg quantity and egg condition determination, each sample was homogenously spread on a tray and three subsamples of standardized area were taken randomly (see Appendix C4, Fig. A1). Each SAV subsample biomass (g FW) was recorded. Adherent eggs were separated from plant subsamples under a stereo microscope and counted according to different categories "alive" and "dead", since dead (or unfertilized) eggs are easily recognized by their non-transparent opaque color (Fig. 3). Additionally, the biomass (g FW) of total eggs per subsample was recorded using a micro scale (Sartorius MC5).

Afterwards, all plant samples (remaining total sample and subsamples), as well as egg samples, were dried to constant weight at 80°C for at least 48 hours in a compartment drier. After the drying procedure, dry weights (g DW) of plant and egg samples were recorded. To minimize bias due to adherent water, the dry weights were used for later extrapolations of SAV biomasses (g m^{-2}).

Estimation SAV biomass m^{-2} and egg number m^{-2}

To estimate the total dry weight SAV biomass (g DW m^{-2}) per replicate and depth zone, we used the following equations (published in Moll et al. 2018):

$$DW_{SAV} = \left(\frac{DW_{SAVss}}{DW_{(SAV+HE)ss}} \times DW_{RS} + DW_{SAVss} \right) \times x \tag{1}$$

where DW_{SAV} represents the total SAV dry weight per m^2 for each replicate, DW_{SAVss} the

dry weight of SAV in the subsample (summation of all three subsamples) and $DW_{(SAV+HE)ss}$ the dry weight of the entire subsample (including SAV and attached herring eggs), DW_{RS} represents the dry weight of the remaining sample (subsample excluded). x represents the factor needed to extrapolate the sampling area of the grabber to one square meter (e.g. $x = 25$, if the sampling area was 400 cm^2, after the sampling area changed to 250 cm^2, $x = 40$). For calculating the total amount of herring eggs per m^2 for each replicate, we used the following equation:

$$n_{HE} = DW_{SAV} \times \frac{n_{HEss}}{DW_{SAVss}} \tag{2}$$

Where n_{HE} is the number of eggs per m^2, DW_{SAV} represents the total SAV dry weight per m^2, n_{HEss} represents the number of eggs and DW_{SAVss} is the SAV dry weight in the subsample.

Herring larvae sampling

Data for abundance and length frequency of larval herring were received by the annual Rügen herring larvae survey (RHLS), which is conducted weekly throughout the entire herring reproduction period by the Thünen Institute of Baltic Sea Fisheries. This survey includes an intense ichthyoplankton sampling in Greifswald Bay and the adjacent Strelasund. Thirty-five stations are sampled weekly throughout the spawning season (mid-March until end of June) (see Appendix C4, Fig. A2), revealing a high resolution data set of larval distribution throughout the entire spawning area. Sampling is performed with a Bongo net, consisting of two separate nets of different mesh sizes (335 µm and 780 µm). Each haul is towed throughout the entire water body, starting at the water surface (30 seconds towing time) and proceeding depth stepwise tows down to 1 m above the sea ground (see Appendix C4, Fig. A2). Flowmeters, attached at each Bongo frame, ensure the measurement of the filtered water volume, which is necessary to estimate the larval abundance per m^3. Ichthyoplankton samples were fixated in 4% formalin-seawater solution and were transported to the laboratory, where total length (TL) of each herring larvae was measured and recorded (for further details of the laboratory procedures, see Oeberst et al. 2009).

Hatchling abundance data

We used herring larvae abundance data from four selected stations, which were located in the vicinity of Gahlkow (Appendix C4, Fig. A2), assuming that newly hatched larvae of the size class 5-8 mm probably originated from the spawning bed. Hatchling abundance (n m^{-3})

per station was converted into hatchling number per area (n m^{-2}) (abundance per volume m^{-3} * water depth). The average hatchling abundance (n m^{-2}) per survey week was multiplied with the factor 4 to determine the hatchling abundance of all four stations, considering also sampling weeks where not all four stations could be sampled. The hatch date is determined as the first sampling day during the respective survey week. For our calculations, we did not consider diurnal temperature fluctuations. The mean surface water temperature was used to estimate the egg development time (hours to peak hatch) under the respective mean water temperature, using the equation after Peck et al. (2012):

$$HP = 4461.9 \left(\pm 322.4 \times T^{-1.232(\pm 0.031)} \right) \tag{3}$$

Where *HP* represents the time from fertilization to hatch (hours) and *T* represents the water temperature (for further details, see Peck et al. 2012). The resulting hours post-fertilization were converted into days and the number of days was subtracted from hatch date, resulting in an estimated date of spawning.

Statistical Analyses

All statistical analyses were performed with STATISTICA 12 (Statsoft) and R software (car package) (R Development Core Team 2008, Fox & Weisberg 2011). Statistical significance (significance level of $p < 0.05$) was tested by using one-way analysis of variance (ANOVA) and post-hoc test (Tukey's honest significant difference (HSD)-test). Data sets were tested for homogeneity by Levene's test and were logarithmically transformed $\log (x + 1)$, if necessary to meet the requirements of ANOVA.

Results

General spawning patterns: Initial spawning related to temperature

All four spawning seasons (2012-2015) differed in general egg concentrations (n m^{-2}) and seasonal egg deposition patterns (Fig. 4). Since temperature is the most influential factor, triggering herring spawning activity, we combined seasonal egg distributions and prevailing water temperatures to find a particular initial spawning temperature threshold. Initial spawning events were similar in all four spawning seasons. We observed no spawning activity below the threshold of 4°C (Fig. 4).
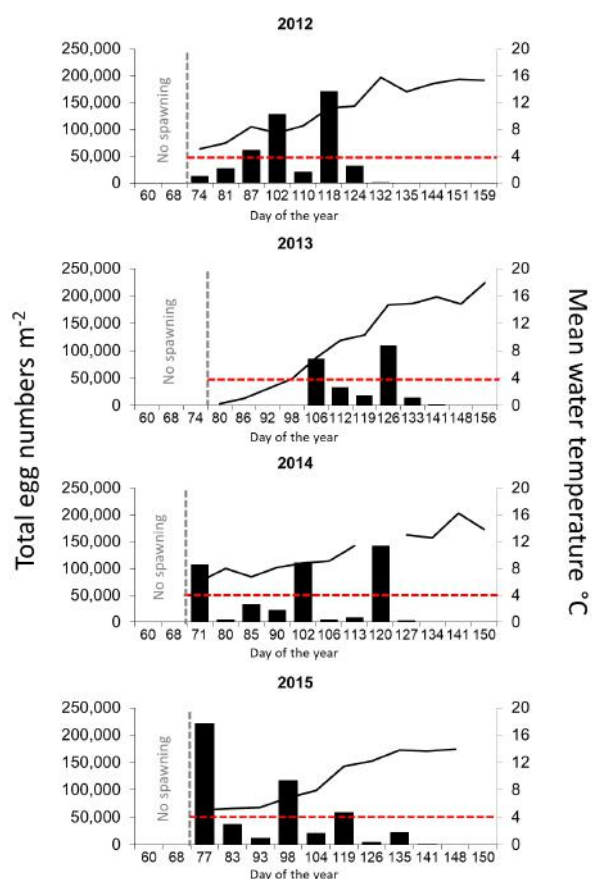
Figure 4: Seasonal egg distribution patterns for all four investigated spawning seasons. Total egg numbers m^{-2} (based on mean egg number m^{-2} per depth, adding up to total egg numbers) are indicated by black bars. The respective mean water temperatures (average of all three depths (1 m (A), 1.5 m (B), and 2 m (C) for each sampling day) is indicated by the black line. The vertical dashed line (grey) indicates the starting point of seasonal egg sampling. Prior this line, presence-absence sampling revealed no spawning activity. Observed 4°C threshold for initial spawning is indicated by a horizontal dashed line (red).

In 2012, first eggs were found on 14th March (day of the year (doy) 74) during mean water temperatures of 5°C. Mean egg numbers per m^2 slowly increased along the season, highest egg concentrations were observed on 27th April (doy 118) with 171,300 eggs per m^2. The season 2013 was special, providing a good example for temperature-related spawning. Compared to the other years, the mean water temperatures were quite low at the beginning of the season (doy 80: 0.2°C; doy 92: 2.4°C). On week prior first egg deposition, mean water temperatures were still low (doy 98: 3.9°C). Initial spawning occurred very late in mid-April (doy 106: 6.9°C) with egg numbers of 85,000 eggs m^{-2}. The highest egg numbers were found on 6th May (doy 126) with a mean number of 108,900 eggs per m^2. We found general lower egg concentrations during the spawning season 2013.

The spawning season in 2014 started relatively early, on 12th March (doy 71) during a mean water temperature of 6.1°C, with high egg numbers of 107,000 eggs m^{-2}, followed by 110,600

eggs m^{-2} on 12th April (doy 102). The highest egg numbers of the entire spawning season (142,000 eggs m^{-2}) were spawned on 30th April (doy 120). In 2015, first eggs were found on 18th March (doy 77) with high numbers of 220,700 eggs per m^2 during a mean water temperature of 5°C. Egg concentrations decreased along the season, with 117,400 per m^2 on 8th April (doy 98) and 58,700 eggs m^{-2} on 29th April (doy 119). All four spawning seasons ended in mid-May/end May (Fig. 4). The spawning days, where highest egg numbers were found along each season, are defined as "spawning peaks" in the following chapter.

Diurnal temperature fluctuations

Data from fixed temperature data loggers (HOBOS$^®$) were used to show diurnal temperature fluctuations in two different water depths, identifying the pre-spawning season temperature regime for the two differing seasons 2012 and 2013 (Fig. 5). Both seasons differed in respective early spring temperature regimes. In 2012, mean daily water temperatures were low in the beginning of the season on doy 53 (22nd February: 0.3°C), then temperature in both depth zones (shallow and deep water) increased within one week (doy 57: 3.0°C), exceeded the 4°C spawning threshold for two days (doy 62: 4.2°C and doy 63: 4.3°C), but then decreased again and remained rather stable (2-3°C), until temperature rose up again to 4°C on doy 72-73. Initial spawning could be observed on doy 74, right after reaching the 4°C for the second time now followed by a progressive, seasonal temperature increase (Fig. 5).

In 2013, the temperature regime showed a completely different pattern. A daily mean water temperature of 0.2°C was recorded on doy 53 and temperatures remained constantly low for both depths (0-2°C) over a period of 37 days (doy 53-90) (Fig. 5). The 4°C-threshold was finally reached on doy 101-102 for both depths. Whereas water temperatures slowly increased in depth C within 2 days (doy 103-105: mean daily slope of approx. 0.6 degrees), the water temperatures in the shallow water rapidly increased (doy 103-105: mean daily slope of 5 degrees), representing a depth-related variation of 5°C between 1 and 2 m water depth prior spawning (A: 10.6°C; C: 5.1°C).

Shift in egg depth distribution

The relative egg numbers (per g DW SAV), referred to the entire spawning season for each depth, showed a general shift in depth-related egg distribution patterns along all spawning seasons (Fig. 6). Regarding only the defined spawning peaks, during the spawning season in 2012, up to 41% of all eggs (100%) spawned in depth C, were deposited in the beginning of the season, compared to only 20% in depth A (doy 87). During the second spawning peak
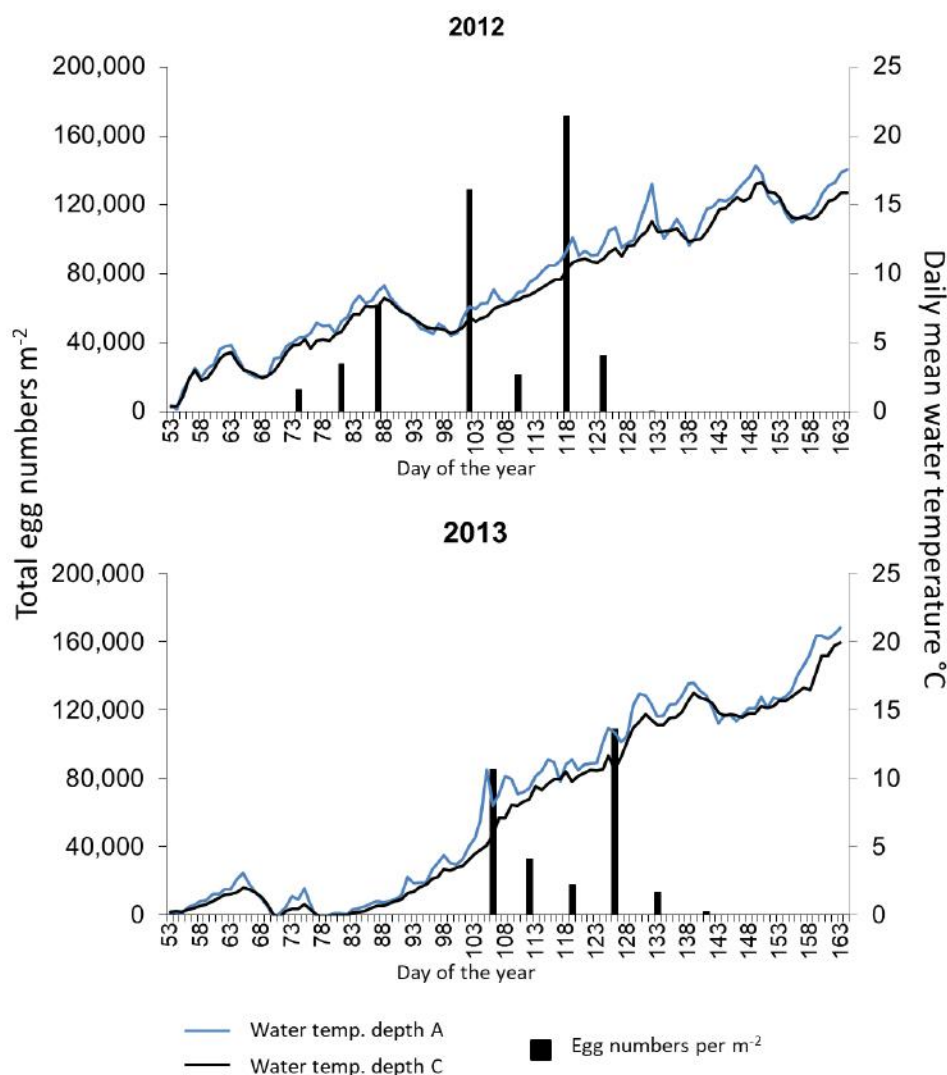
Figure 5: Seasonal egg distribution (n m^{-2}), indicated by black bars, and the respective daily water temperatures (mean values) in shallow water depth A (1 m, blue line) and the deep water C (2 m, black line) for the spawning seasons 2012 and 2013.

(doy 102), more eggs (36%) were deposited in the shallow water, compared to only 9% of all spawned eggs in the deeper zone. This distribution shifted later in the season, when spawning intensity increased again in depth C (28%), but slightly decreased in depth A (29%, doy 118) (Fig. 6).

In 2013, by half of all eggs (55%) were spawned in the shallow depth A during initial spawning (doy 106), 41% of all eggs were deposited in depth C. During the second spawning peak (doy 126), more eggs were spawned in deeper water (B: 63% and C: 28%), compared to the shallow zone A (21%), indicating a temperature-related shift in spawning depth.

In the early season in 2014, seasonal depth-related shift in egg deposition from the shallow water to deeper water was more pronounced (Fig. 6). The shallow water A was more important
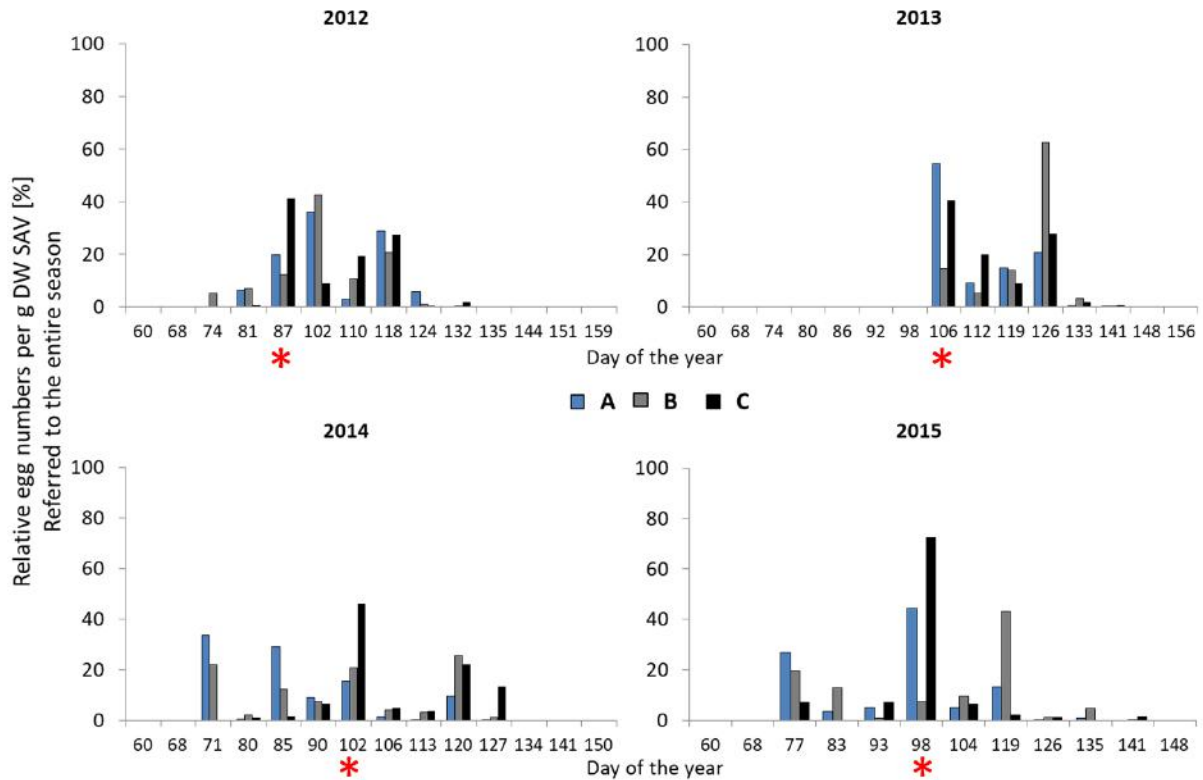
Figure 6: Relative egg numbers per g DW referred to the entire spawning season for all three depth zones (A, B, C) and all four spawning seasons (summing up all percentages for the respective depth zone revealed 100%) Red asterisks indicate the time of observed shift in egg deposition from shallow to deeper waters.

with 34% of total egg deposition at initial spawning activity (doy 71). No eggs were found in depth C. This pattern changed during the second spawning peak, when depth C became more important (46%), whereas relative egg numbers according to the entire season decreased in depth A (16%). At the end of the season (doy 120), the importance of depth A further decreased (10%), as well as for depth C, but still 22% of all eggs were spawned in depth C. The intermediate zone B showed rather stable egg concentrations along the entire season (between 22% and 26%). During initial spawning in 2015, the shallow water was more important (27%) than depth C (8%). The relative egg concentrations in depth A and C increased during the second spawning peak (doy 98), but depth C became more important (73%) than the shallow water zone A (44%). At the end of the season (doy 119), the intermediate depth B showed the highest relative egg numbers (43%), whereas relative egg numbers in depth A (13%) and depth C (2%) decreased. We determined the time, when depth-related shift in egg distribution was observed (indicated by red asterisks in Fig. 6) and checked the respective temperatures during this particular days to investigate the relation of seasonal temperature regimes on egg depth

Table 1: Observed depth-related shift in egg deposition and the respective water temperatures. Mean daily water temperatures (in 1 m) are given for 2012 and 2013 and temperatures for the seasons 2014 and 2015 are based on punctual measurements during sampling.

Spawning season	Depth-related shift in egg deposition (doy)	Water temperatures during observed shift (°C)
2012	87	8.8
2013	106	8.0
2014	90	8.7
2015	98	7.1

Table 2: Correlation coefficients were calculated for the relation between egg concentrations and SAV biomass for all investigated years (2012-2015). Correlations are based on each spawning peak, all depths were included. Respective significance values ($p < 0.05$) are highlighted in bold type, indicating that the relation between egg numbers and SAV biomass is significant different from a non-linear relation ($R^2 = 0$).

Year	Date	Doy	R^2	*p*-value
	Spawning peaks			
2012	27th March	87	0.44	0.003
	11th April	102	0.36	0.009
	27th April	118	0.28	0.025
2013	16th April	106	0.14	0.125
	06th May	126	0.09	0.213
2014	12th March	71	0.33	0.013
	12th April	102	0.76	< 0.001
	30th April	120	0.28	0.025
2015	18th March	77	0.98	< 0.001
	08th April	98	0.00	0.827
	29th April	119	0.11	0.184

distribution (Tab. 1). Due to the steep increase in water temperatures during the spawning season in 2013, where 10°C was reached one day before sampling was conducted and according to the results in Tab. 1, we defined a threshold for the depth-related shift in spawning depth, occurring at water temperatures of approximately 8-10°C.

Relation between SAV biomass and egg numbers

To investigate whether herring egg numbers are generally related to SAV biomass, the SAV biomass g DW m^{-2} and the respective egg numbers m^{-2} were correlated for each year and each spawning peak (including all depths) to test for seasonal patterns (Tab. 2).

A general decreasing seasonal trend could be observed for all four seasons. Correlations between egg numbers and SAV biomass were usually higher at the beginning of the season, compared to the end of the season, except for 2014. In 2012, all correlations are significant different (Tab. 2) with a decreasing trend along the season. In 2013, correlations were weak and differences were not statistically significant, neither at the beginning nor at the end of

the season. In 2014, all three spawning peaks showed significant positive correlations. The strongest correlation was found during the second spawning peak ($R^2 = 0.76, p < 0.001$). In 2015, egg numbers and SAV biomass were highly correlated at the beginning of the season ($R^2 = 0.98, p < 0.001$) with a decreasing trend along the season with no significant differences (Tab. 2). According to different depth zones, depth-related egg distribution (n m^{-2}) and the prevailing SAV biomass distribution for each spawning peak and all four spawning seasons are shown in Fig. 7.
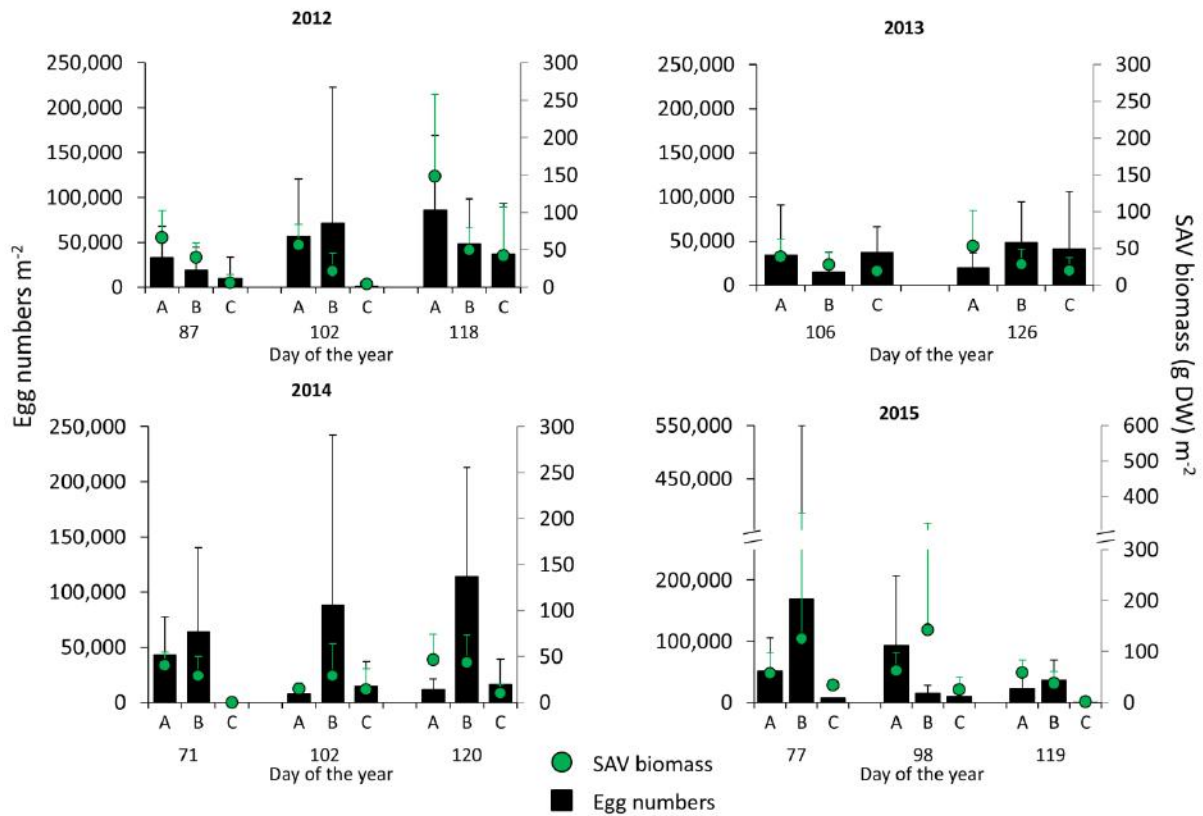
Figure 7: Relation between SAV biomass (g DW m^{-2}) and egg numbers for each year on each depth zone during the distinct spawning peaks. Egg numbers are represented by black bars (with standard deviation, $\pm$ SD) and green dots indicate SAV biomass (with $\pm$ SD) during the defined spawning peaks.

Egg numbers appeared to be not independent from SAV biomass. In 2012, the strongest seasonal increase in SAV biomass was observed for depth A, but seasonal differences were not significant ($F_{(2,15)} = 3.21, p = 0.069$). During initial spawning, SAV biomass significantly differed between all three depth zones ($F_{(2,8.4)} = 12.33, p = 0.003$), with significant lower SAV biomass in depth C ($p_{A-C} = 0.007; p_{B-C} = 0.005$). This pattern was also observed for the second spawning peak ($F_{(2,15)} = 8.04, p = 0.004$), where differences in SAV biomass were highly significant between depth A and C ($p_{A-B} = 0.046; p_{A-C} < 0.001$). The late season showed no significant

differences in depth-related SAV distribution. Regarding seasonal egg concentrations, egg numbers increased along the season with significant higher egg concentrations during the third spawning peak, compared to the beginning of the season ($p_{1-3} = 0.035$). No significant differences in egg concentrations were found along the littoral depth gradient.

In 2013, egg numbers and SAV biomass showed no differences, either in similar depth in a seasonal trend or depth-related differences within the two distinct spawning peaks.

In 2014, we found significant seasonal differences in SAV biomass on depth A ($F_{(2,15)} = 4.97$, $p = 0.022$). SAV biomass was high during the early season, then significantly decreased ($p = 0.003$) and increased again in the late season ($p = 0.021$). Furthermore, SAV biomass was significantly different between different depths during initial spawning ($F_{(2,15)} = 27.24$, $p < 0.001$), with a significant lower biomass in depth C ($p_{A-C} < 0.001$; $p_{B-C} < 0.001$). This pattern was also observed at end of the season ($F_{(2,15)} = 4.25$, $p = 0.035$; $p_{A-C} = 0.012$; $p_{B-C} = 0.025$). Depth-related egg distribution showed highly significant differences in egg numbers during initial spawning ($F_{(2,15)} = 25.38$, $p < 0.001$), being significantly lower in the deep water ($p_{A-C} < 0.001$; $p_{B-C} < 0.001$). Furthermore, we found significant seasonal differences in depth A ($F_{(2,15)} = 4.15$, $p = 0.036$), with high egg numbers at the beginning of the season, showing a significant decreasing seasonal trend ($p_{A1-A2} = 0.029$; $p_{A1-A3} = 0.063$). No significant difference was found regarding the observed seasonal increase in egg numbers on depth C (Fig. 7). In 2015, no significant differences in seasonal and depth-related distribution, either for SAV biomass or egg numbers, could be observed during the first and the second spawning peak. Solely at the end of the season, SAV biomass and egg numbers significantly differed (eggs: ($F_{(2,15)} = 51.59$, $p < 0.001$); SAV biomass: ($F_{(2,15)} = 63.22$, $p < 0.001$)), showing significant higher egg numbers and SAV biomass in depth A and B, compared to depth C (eggs: $p_{A-C} < 0.001$; $p_{B-C} < 0.001$; SAV biomass: $p_{A-C} < 0.001$; $p_{B-C} < 0.001$) (Fig. 7).

Seasonal egg mortality

We focused further results on only two years (2013 and 2014), since both chosen years are representatives of a cold winter (2013) and a warm winter (2014) period, hence, being good examples to analyze seasonal depth related egg mortality. Both years showed high significant differences in seasonal egg mortalities (Fig. 8).

In 2013, egg mortality significantly increased from 6% to 83% along the season ($F_{(1,34)} = 101.1$, $p < 0.001$). In 2014, egg mortality rates significantly differ during the season ($F_{(2,23.8)} = 13.49$, $p < 0.001$) (Fig. 8). Egg mortality significantly increased from 1% to 47% within one month ($p < 0.001$), but then significantly decreased again to 7% ($p < 0.001$). Egg mortality
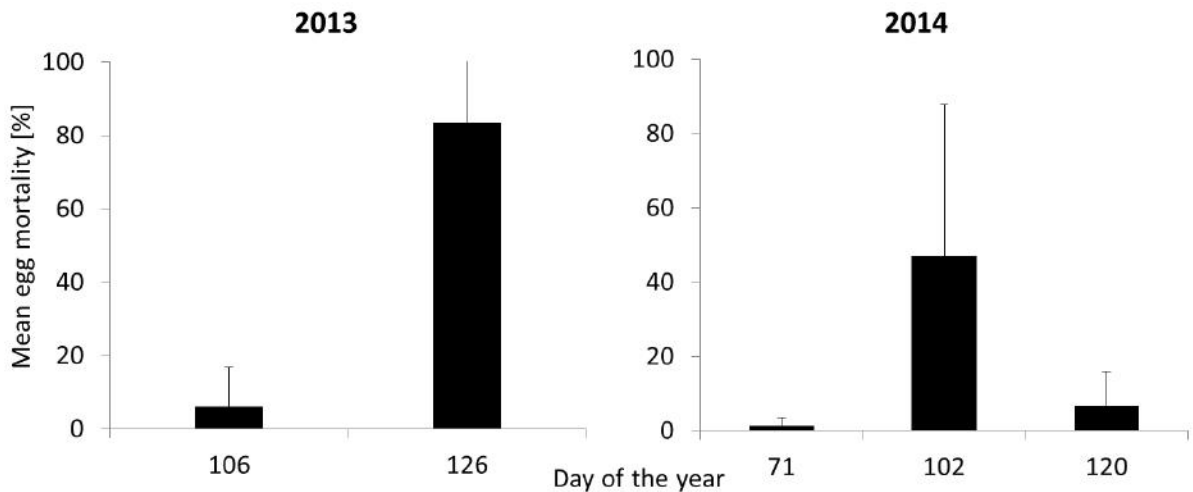
Figure 8: Mean egg mortality rates (with standard deviation) for each spawning peak along the spawning seasons 2013 and 2014.

was slightly higher at the late season, compared to the early season ($p = 0.027$). We further tested, if egg mortality is related to the littoral depth gradient (Fig. 9). In 2013, egg mortalities significantly increased on all investigated water depths (A: $F_{(1,10)} = 298.57, p < 0.001$; B: $F_{(1,10)} = 203.47, p < 0.001$; C: $F_{(1,10)} = 6.61, p = 0.027$). At the end of the season, egg mortality was higher on depth A (97%) and B (96%), compared to depth C (55%), but depth-related differences were not statistically significant ($F_{(2,15)} = 2.97, p = 0.082$).
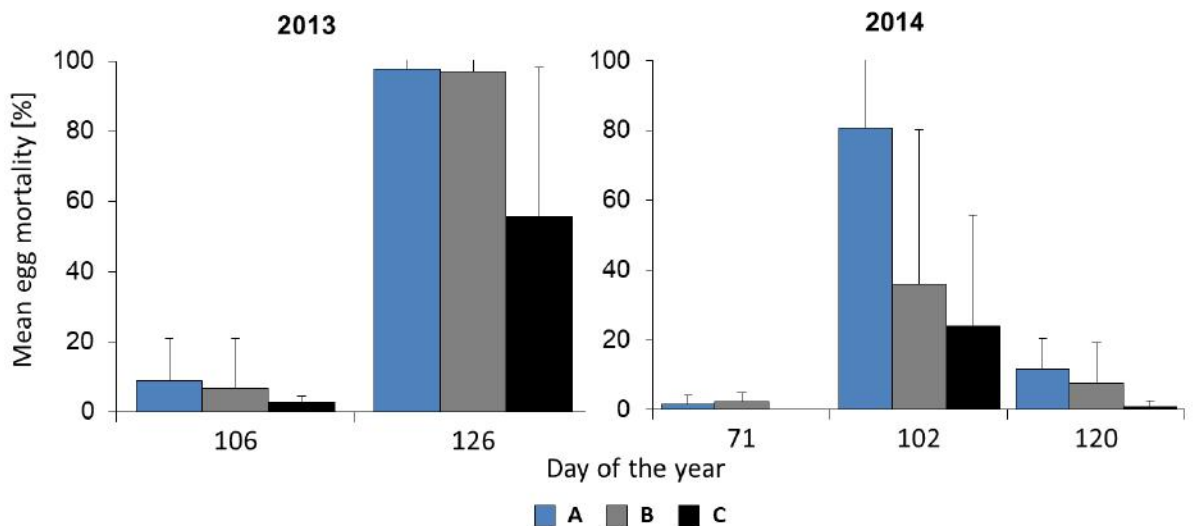
Figure 9: Mean egg mortality rates (with standard deviation) for each spawning peak on all three investigated depths during the spawning season 2013 and 2014.

Spawning season 2014 started with low egg mortalities during the first spawning peak (1-2%) in the shallow water. At that time, no eggs were found in depth C (Fig. 9). Seasonal differences in egg mortality were limited to the shallow water ($F_{(2,15)} = 51.09, p < 0.001$;

$p_{A1-A2} < 0.001$; $p_{A2-A3} < 0.001$; $p_{A1-A3} = 0.026$). During the second spawning peak, herring egg mortality increased up to 80% in depth A. Observed depth-related differences in mortality were significant ($F_{(2,15)} = 4.57$, $p = 0.028$), showing a significant higher egg mortality in depth A, compared to C ($p_{A-C} = 0.005$). At the end of the spawning season, egg mortality on all three depth zones decreased back to moderate values with a significant lower egg mortality on depth C ($p_{A-C} = 0.016$). Results for the spawning seasons 2012 and 2015 are presented in the Appendix (C4, Fig. A3).

Egg numbers and related hatchling abundances

In 2013, less viable eggs were found in the later season, but those eggs resulted in high larval abundances (Fig 10). The observed *in situ* spawning peaks in 2013 perfectly matched with the back-calculated spawning day of the hatchlings, showing two distinct hatching peaks in cw 18 and cw 21 (Fig. 10). In cw 23 (05th June), a third small larvae hatching peak could be observed, which was calculated back to cw 21 (21st May), when only a small number of eggs were found in the spawning bed. Regarding the high egg mortality in the late season, the number of viable eggs in cw 19 (doy 126) is rather low, but this later spawning peak resulted in high hatchling abundances of 140 individuals m⁻² (Fig. 10).

The spawning season in 2014 was longer than in 2013, more eggs were found in the spawning bed, but larvae were less abundant in the early season, being most productive with 87 hatchlings m⁻². We observed three hatching peaks along the season (cw 15, cw 20 and cw 22) (Fig. 10). The back-calculation revealed that eggs were potentially spawned in cw 13, cw 18 and cw 21. The first observed spawning peak (cw 11) did not match to the back-calculated peak. The second spawning peak (cw 15) did not result in any larvae. The second larvae hatching peak (cw 20) were back-calculated to the third observed *in situ* spawning peak (cw 18). The larvae of the third observed hatching peak (cw 22) were back-calculated to be spawned in cw 21. This virtual spawning peak was not confirmed by our field sampling, since observed spawning activity ended in cw 20 and no eggs were found in the spawning bed.

Discussion

Since coastal spawning grounds are subject to multiple anthropogenic alterations, investigations on the importance of appropriate spawning substrates for herring, the selection of spawning beds along the littoral depth gradient and the resulting egg mortality are urgently required to evaluate the impact of eutrophication-induced cascade effects and increasing temperatures
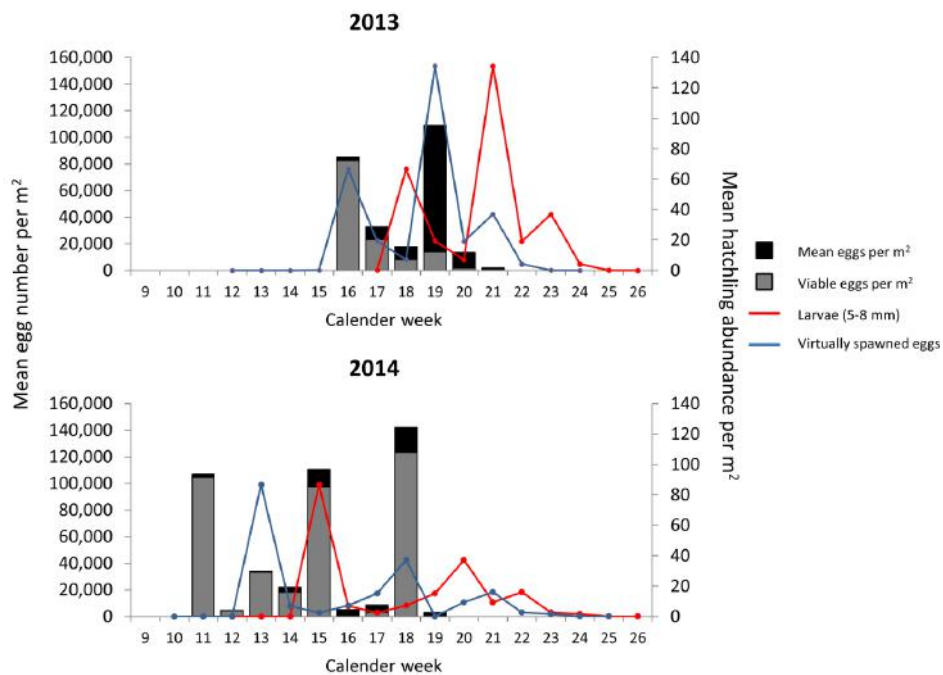
Figure 10: Seasonal egg concentrations (n m^{-2}) are divided in mean egg number (black) and mean viable eggs (grey) for the spawning seasons 2013 and 2014 (x-axis represents calender weeks). Larval abundance (n m^{-2}) of 5-8 mm total length, found on four stations in the vicinity of the investigated spawning bed, is indicated by the red line. The blue line indicates the number of virtually spawned eggs, resulting from a temperature-based back-calculation-model after Peck et al. (2012).

on herring reproduction success. Our study on spawning bed selection of Western Baltic spring spawning herring provided a unique data set of four consecutive spawning years with a week-based fine temporal resolution of egg quality and quantity and a depth-related egg distribution sampling. Results demonstrated the importance of the vegetated littoral zone for benthic spawning herring and the impact of spring temperature regimes on spawning phenology, driving seasonal spawning patterns. We observed a temperature-related change in vertical spawning bed selection. According to that, we further observed a seasonal and depth-related increase in egg mortality, emphasizing that anthropogenic habitat degradations and future climate change scenarios have the potential to highly impact herring reproduction success.

General spawning patterns: Initial spawning related to temperature

We found no spawning activity below water temperatures of 4°C, indicating temperature-related spawning activity. According to the literature, this temperature-based threshold is documented for initial spawning of Western Baltic herring (Klinkhardt 1984, Scabell 1988,

Klinkhardt 1996). Initial spawning temperatures were summarized for several Atlantic herring populations, according to their spawning time (Haegele & Schweigert 1985a). Whereas White Sea herring initially spawn at low temperatures of ~0°C (April/May, see Soin 1971), the initial spawning of Norwegian herring and Baltic Sea herring is reported to be at ~5°C (Runnström 1941, Ojaveer 1981). Baltic herring spawning in the Archipelago Sea (Finland) started in May at approximately 5°C (Rajasilta et al. 1993), which corresponds to our observations. Although we did not record water temperatures prior to our first egg sampling, we can exclude prior spawning activity, due to presence-absence-controls before initial spawning was observed in all four years.

The mean egg concentrations (n m^{-2}) differed within and between spawning seasons. Herring fecundity is related to fish age and depends on female body length (Anwand 1962) and is very variable between different fish populations (Kändler & Dutt 1958, Haegele & Schweigert 1985a). Western Baltic herring showed general lower egg concentrations compared to the Pacific and Atlantic herring populations, where generally higher egg concentrations with multi-layer depositions could be observed (Haegele & Schweigert 1985b, Aneer 1989). Our observed egg numbers correspond to results of other Baltic herring egg surveys (Scabell & Jönsson 1984, Rajasilta et al. 1993). Multiple egg layers were not found during our investigation, as reported by other authors (Scabell, 1988; Klinkhardt, 1996; Kanstinger et al. 2016). Herring spawns in distinct spawning waves, starting with larger adult individuals while the later spawning herring is usually smaller and younger (Horrall 1981, Hay 1985). Generally, two-three spawning waves could be observed within one spawning season (Lambert 1987) and time between distinct spawning waves is variable, ranging between one and four weeks (Haegele & Schweigert 1985a, Hay 1985, Lambert 1987). The time between our observed spawning peaks was roughly between 16 days and 30 days and fits the range of the former references.

Shift in egg depth distribution

Whereas Pacific herring spawns in the inter and subtidal zone along the West coast of the United States (US) and British Columbia coast (CAN), down to about 10 m depth (Haegele et al. 1981, Haegele & Schweigert 1985b, Stick et al. 2014), Atlantic herring prefers a wider range of spawning depths (Norwegian herring: 5-150 m (Runnström 1941), Firth of Clyde herring: 13-24 m (Parrish et al. 1959); North Sea herring: ~40 m (Hempel & Schubert 1968)). Baltic herring populations spawn in shallow waters (1-4 m) (Aneer et al. 1983, Scabell 1988, Rajasilta et al. 1989), with some exceptions, where egg deposition was also observed in deeper waters (11 m, Aneer & Nellbring 1982). We found a relation between seasonal increasing water

temperatures and decreasing spawning depth. Herring preferred spawning in shallow water during the early season, while shifting their egg deposition to deeper water in the late season. This depth-related spawning pattern is also described in other studies (see Aneer & Nellbring 1982, Sjöblom 1963, Ojaveer & Simm 1975), where herring started spawning in shallow water, but then moved into deeper water, probably due to increased water temperatures. Moreover, Rannak (1971) indicated a shallow spawning depth of 3 m at the beginning of the season with a shift down to 10-12 m for the eastern Baltic Sea. According to these observations, we assume that herring might avoid increasing temperatures during the season by selecting deeper spawning beds. We further defined a temperature-based threshold of approximately 10°C, where a shift in spawning depth was observed. According to the literature, this threshold is confirmed by a study of Sjöblom (1963), where the author observed a movement to deeper waters at temperatures of 11-13°C, indicating the validity of our defined 10°C-threshold to determine the change to deeper spawning depth.

Relation of SAV Biomass and egg numbers

According to a towed camera survey, the location of our permanent three transects were carefully determined and were defined to the vegetated littoral zone, consisting of distinct vegetation zones. Our findings revealed substrate-related egg deposition, with no herring eggs to be found on soft sediment, which is confirmed by results of Aneer (1989). Egg numbers appeared to be related to SAV biomass. Relations between egg numbers and SAV biomass showed a general decreasing trend, being high in the early season and became less related at the end of the season. This pattern is explained due to seasonal succession of the vegetation period of aquatic plants, showing an opposite course (increasing biomass during the season) compared to the period of spawning activity (decreasing egg numbers during the season). Our data further revealed that SAV biomass was higher in the shallow water, compared to the deeper beds in 2 m, possibly due to general depth-related decline in vegetation biomass caused by eutrophication-induced reduction of light availability (Duarte 1991) and general patchiness of vegetation.

Seasonal egg mortality

Spawning in such shallow waters involves several risks, impacting successful reproduction. Besides the fact that high water temperatures can negatively affect herring egg development and egg survival (Blaxter 1992), spawning in shallow waters increases the vulnerability of herring eggs to storm-induced hydrodynamics (Hay & Miller 1982, Rooper 1996, Moll et al.

2018). Furthermore, increased solar radiation (UV-A and UV-B) might have detrimental effects on early life stages of fish, damaging molecules such as DNA, RNA and proteins and causes oxidative stress to cells and tissues (Zagarese & Williamson 2001). Herring egg predation, either by birds (Haegele & Schweigert 1989, Rooper et al. 1999), reported for Pacific herring populations, or by the local predator community, i.e. sticklebacks (*Gasterosteus aculeatus*) (see Kotterba et al. 2014, Kotterba et al. 2017) is another threat for herring egg survival, acting on a small local scale of important herring spawning grounds.

Besides salinity and oxygen supply, water temperature is considered to be one of the most influential factors for successful egg development, driving spawning phenology, controlling growth rates and various biochemical reactions and determining the duration until hatching (Blaxter 1956, Laurence & Howell 1981). Egg mortality rates in both years increased along the season. According to prevailing water temperatures in 2013, egg mortality was general higher in 1 m depth, compared to 2-3 m depth, where diurnal fluctuations and seasonal increase were less strong. Prior and during the second peak, the observed water temperatures were ~12-13°C, hence, at the edge of the viable hatch window, which is defined between 7°C and 13°C (Peck et al. 2012). Regarding mortality rates, found during the late season in 2013, we assume that high diurnal temperature fluctuations might be the reason for these high egg mortality rates. In 2014, we observed the same depth-related difference in egg mortality rates during the second spawning peak. At the end of the season, egg mortality decreased to moderate levels. During the spawning season, we found high biomass of filamentous algae (*Pilayella littoralis*) in our study area. Algal exudates of this fast-growing brown algae caused high natural mortality of Baltic herring eggs (Aneer 1987), this massive occurrence of *P. littoralis* in 2014 might have contributed to the observed egg mortality. It should be mentioned that observed egg mortalities in 2015 (not represented in the results, see Appendix C4 Fig. A3) were extremely high (up to 100% in all depth zones) throughout the entire spawning season. According to our temperature measurements during the sampling, the probability of temperature extremes causing the observed high egg mortalities is low. However, we cannot exclude potential effects of diurnal fluctuations, since no temperature logger data were available. Although herring early life stages are known to show a broad thermal tolerance (Peck et al. 2012), we found no study concerning the impact of high diurnal temperature fluctuations on herring egg mortality. This should be examined in future studies.

Egg numbers and related hatchling abundances

The *in situ* spawning peaks in 2013 perfectly matched with our virtual (back-calculated) spawning peaks, indicating that observed hatchlings resulted mainly from viable eggs, spawned in the deeper water. However, the back-calculations for 2014 revealed some time shift between virtually spawned eggs and observed spawning peaks. It is well-known that the duration of egg development is related to water temperature (for herring eggs: at ~10°C approx. 12 days (Klinkhardt 1984)). Increasing water temperatures resulted in a decreased incubation time (see Peck et al. 2012) and even small fluctuations in temperature (of 2°C) can result in a reduction of incubation time of a few days (Klinkhardt 1996; Peck et al. 2012). Regarding potential diurnal temperature fluctuations in 2014 and the lack of determining the developmental stage of eggs, we expected time shifts in the calculations. Furthermore we only used mean temperatures to roughly calculate the spawning day of hatchlings, using the back-calculation formula after Peck et al. (2012). Daily temperature measurements and the determination of particular egg developmental stages should be taken into account for future back-calculations on spawning time of herring larvae.

Conclusions

Research on ecological characteristics of certain herring spawning habitats and behavioral spawning bed selection are essential aspects to understand recruitment variability of *C. harengus*, one of the most commercially important benthic spawning fish species in the northern hemisphere. Our results underpin the hypothesis that submerged aquatic vegetation represents an important factor for successful recruitment. Regarding the fact that Greifswald Bay is still a eutrophic water body and that eutrophication is still causing limited depth distribution of vegetation to the shallow shore zone, we should expend effort to reduce nutrients inflow. Climate change will lead to higher temperatures with more frequently storm events in the future, affecting these shallow littoral waters and increasing the vulnerability to multiple threats. We should be aware of these anthropogenic ecosystem alterations and should start re-considering current natural conservation programs to implement alternative management strategies. Moreover, further research is needed to increase understanding of the impacts of stressor cascades resulting in recruitment failure of the Western Baltic herring population.

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Chapter 5

Storm-induced Atlantic herring (*Clupea harengus*) egg mortality in Baltic Sea inshore spawning areas

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Abstract

During their spring migration Atlantic herring (*Clupea harengus*) populations in the Baltic Sea rely on shallow transitional waters, such as estuaries, bays and lagoons for spawning. Such inshore spawning grounds are ecologically important by providing suitable substrates for demersal egg deposition. These habitats are often highly impacted by multiple anthropogenic threats. Decades of eutrophication have caused a decline in depth distribution of submerged aquatic vegetation, the main herring spawning substrate in the Baltic Sea. Nowadays spawning beds are limited to the shallow littoral zone ($\leqslant$ 3 m depth). Accordingly, macrophytes are increasingly exposed to mechanic forcing due to storm-induced wave action. Generally, reproductive success and year class strength of the Western Baltic herring population is strongly determined by the survival of early life stages such as eggs and larvae in local nursery areas. However, explicit mechanisms by which local stressors might affect overall recruitment are currently not well understood. Hypothesizing that aquatic vegetation limited by water depth causes high herring egg mortality due to increased exposure to storm-induced hydrodynamics, we performed a combination of field studies investigating the impact of storm events on herring egg loss. Results of an egg loss experiment revealed a total egg loss of 29% in one single spawning bed during a storm event within the spawning season and the quantification of eggs attached to macrophyte litter on the shoreline emphasize the potential for regional weather extremes such as storm events to act as influential stressors for herring reproduction.

Introduction

A wide-spread reproduction strategy among fish species in marine and fresh water habitats is to spawn immense numbers of eggs to compensate for high mortality rates in the early life stages (McGurk 1986; Morrison et al. 1991).

The Atlantic herring (*Clupea harengus*, Linnaeus 1758) is probably one of the best studied fish species in the world and of high economically (FAO 2014) and ecologically importance (Cardinale and Arrhenius 2000, Casini et al. 2004, Möllmann et al. 2004, Overholtz and Link 2007). *C. harengus* follows this strategy by releasing large number of eggs in a short period of time during each breeding season (Murua and Saborido-Rey 2003, Wootton 1990). Additionally, herring is a "bet-hedging" strategist, where spawning stocks spread spawning activity in waves over time, increasing the chances of successful reproduction (Lambert 1990, Lambert and Ware 1984). This reproductive effort is required to ensure recruitment and therefore the survival of populations (Duarte and Alcaraz 1989).

C. harengus is a litho-phytophilous spawner (Balon 1975), attaching adhesive eggs either in deeper zones on outer coastal shelf gravel beds (North Sea populations) (Hempel 1971, Hempel and Schubert 1968) or to submerged aquatic vegetation (SAV) in the near shore zone (Baltic Sea population) (Aneer 1989, Aneer et al. 1983, Kanstinger et al. 2016, Klinkhardt 1986, Kotterba et al. 2014, Rajasilta et al. 1989, Scabell 1988). In contrast, other economically important fish species in the Baltic Sea region, such as Atlantic cod (*Gadus morhua*, L. 1758) and sprat (*Sprattus sprattus*, L. 1758) spawn pelagic eggs. While embryonic development and hatching success of passively floating, pelagic eggs is mainly dependent on hydrodynamic drift patterns, hydrographical conditions and the physical properties of the eggs (Nissling et al. 2003, Petereit et al. 2014, Sundby 1991), the development of stationary benthic eggs is subject to local climate variability and spawning site specific drivers and stressors. Since Johan Hjort's "critical period" hypothesis postulated that the year class strength of a population is determined in the early larval stage during the transition between yolk consumption and active feeding (Hjort 1914), most research on herring early life stage ecology has basically focused on survival bottlenecks in the larval stage (Gröger et al. 2010, Urho 1999). However, quantitative studies on ecological drivers of egg mortality in natural spawning beds are scarce and limited to the effect of toxic exudates of algae species (Aneer 1987, Rajasilta et al. 2006) and physico-chemical variables such as changes in water temperatures and salinity (Alderdice and Velsen 1971, Blaxter 1956, Peck et al. 2012). Furthermore oxygen depletion (Braum 1973, Klinkhardt 1986) and pollutants (Kinne and Rosenthal 1967, Ojaveer et al. 1980, Rosenthal and Sperling 1974, von Westernhagen

et al. 1979) show that these external stressors can highly affect herring egg mortality.

Even though high egg mortalities can be a natural consequence of excessive spawning, there is evidence that increased egg mortality can affect population dynamics, e.g. through egg predation by other fish species (Kotterba et al. 2014, Richardson et al. 2011) or by seabirds (Haegele 1993, Haegele and Schweigert, 1989, Rooper et al. 1999). Although recent studies from the Pacific and Atlantic region provide the hypotheses that herring recruitment occurs mainly during the juvenile life stage (Bishop et al. 2015, Foy and Paul, 1999, Sætre et al. 2002), there is ample evidence for Western Baltic herring recruitment bottlenecks predominantly located in the early life stages previous to metamorphosis (Cushing 1975, Hjort 1914, Houde 2008, Oeberst et al. 2009, Polte et al. 2014). Egg survival and even recruitment of populations often seem to be determined on the regional scale of important spawning grounds. Thereby actual impacts of regional drivers depend on the timing and coincidence with critical developmental periods of earlier herring stages. Polte et al. (2014) reported distinct hatching peaks along the season with differing contributions to the recruitment of the Western Baltic spring spawning herring stock and indicated differing cohort specific, early stage survival bottlenecks. They considered egg mortality as a potential driver of the particular cohort that correlated the most strongly with recruitment success.

Besides changes in environmental factors and predation effects, storm events and related effects in hydrodynamic forcing, can potentially lead to high egg mortalities. However, there is limited information on the subject of herring egg loss due to wind-induced hydrodynamics (Haegele and Schweigert 1989, Hart and Tester 1934, Hay and Miller 1982, Rooper 1996, Tester and Stevenson 1948). Most of the existing studies have been conducted in the vicinity of Vancouver Island, British Columbia, Canada, where Pacific herring (*Clupea pallasii*) deposit demersal eggs on eelgrass (*Zostera marina*), rockweed (*Fucus evanescens*) and other brown algae (Taylor 1964) and therefore shows a similar spawning mode to spring spawning *C. harengus* in the Baltic Sea. The above studies in the coastal Pacific have indicated a high impact of storm activity on herring egg mortality causing egg losses of up to 25% of the total amount of eggs in the study area, corresponding to a spawning capacity loss of 576 tons (Hay and Miller 1982).

Since the middle of the last century, eutrophication processes have severely affected the depth distribution of SAV in the inner coastal waters of the Baltic Sea by increased water turbidity, and the correspondingly reduced light availability for aquatic macrophytes (Kanstinger 2014, Messner and von Oertzen 1990, Munkes 2005b). Consequently, depth distribution of SAV, the main spawning substrate for Baltic herring populations, has decreased significantly and is nowadays limited to the shallow near shore zone (Geisel 1986, Messner and von Oertzen 1991,

Schiewer 2001). Hence, these remaining beds of suitable spawning substrate are increasingly exposed to hydrodynamic forcing. Noting that climate change science forecasts overall increased storm frequency and intensity (Coumou and Rahmstorf 2012, Woth et al. 2006), it is important to know the impact of single storm events on herring egg mortality.

To investigate the impact of local storm events on herring egg mortality, we combined field experiments in an important herring spawning ground with quantitative herring egg sampling and estimated consequences of egg loss on herring recruitment. The present study addresses the hypotheses that (i) depth distribution of eggs on different vegetated spawning zones affects the magnitude of storm-induced egg mortality and (ii) local storm events significantly affect herring egg mortality.

Methods

Study area

The study area Greifswald Bay is a semi-enclosed brackish and eutrophic lagoon (514 km^2) with a mean salinity of 7.3 PSU (Kell 1989). The bay is formed by the island of Rügen northwards and the German mainland in the south. Greifswald Bay is known as a major spawning area for Western Baltic spring spawning herring (Klinkhardt 1984, Scabell 1988). It is a shallow water body with a mean water depth of 5.8 m (with max. depth of 13.5 m), connected with the Baltic Sea by a narrow sound (Strelasund) westward and a wide, but shallow opening in eastern direction (Fig. 1).

The specific topography of the lagoon results in a semi-enclosed basin structure leading to a restricted water exchange with the adjacent waters with a water exchange rate ranges from eight times (Stigge 1989) to almost 12 times a year (Schiewer 2008). Since tides are rather marginal, sea level amplitudes and water exchange processes are mainly wind driven (Schnese 1973). The water body is generally well-oxygenated due to wind mixing events (Schiewer 2008) and seasonal fluctuation in water temperatures is highly influenced by atmospheric temperature regimes.

The study site "Gahlkower Haken" is an important spawning ground for herring (Scabell 1988), located at the southern coast of Greifswald Bay (Fig. 1). The area is characterized by extended beds of SAV. These spawning beds are located in the shallow littoral zone and are stratified by depth with growth limits at a maximum water depth of approximately 3.5 m for Spermatophytes, due to an eutrophication-induced increase in water turbidity (Kanstinger 2014, Munkes 2005a). The "pondweed" zone in the very shallow area comprises flowering
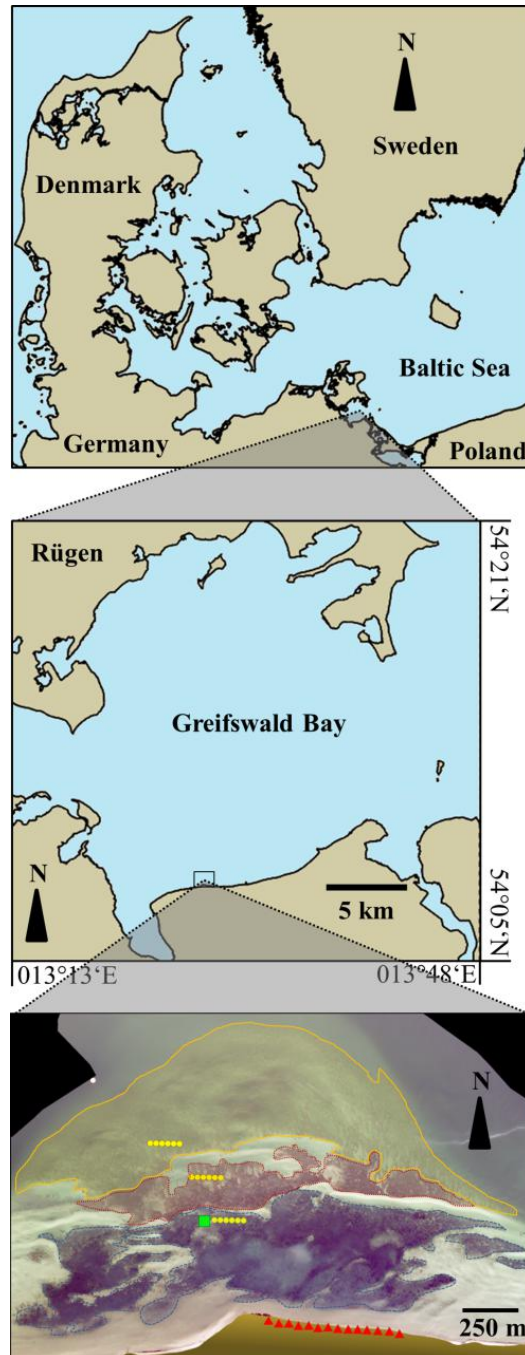
Figure 1: The investigated herring spawning site in Greifswald Bay (middle) and its location within the Western Baltic Sea (top). Dots in the aerial image of the spawning bed (lower map) indicate the location of fixed transects used for the monitoring of depth-dependent spawning intensity. The square represents the area used for the storm impact experiment while the triangles on the beach indicate the sampling points for the examination of storm-induced SAV litter. The broken line defines the area that represents spawning zone "A", the dotted line limits the spawning zone "B" while spawning zone "C" is indicated by the solid line. Black areas on the upper corner of the aerial image indicate SAV-free zones with water depth of more than 5 meters.

plants of the families Potamogetonaceae and Ruppiaceae, in addition to a diverse community of other flowering plants and filamentous algae. The subsequent seagrass zone is dominated by *Zostera marina* (Geisel and Messner 1989).

Field sampling

Herring egg and SAV sampling — To investigate herring egg depth distribution and SAV composition, we defined three permanent transects located parallel to the shoreline of the spawning area "Gahlkower Haken" covering distinct depth zones with corresponding differing SAV compositions. Transect "A" (Fig. 1) is characterized by 1 m water depth comprising the pondweed zone, transect "B" is a transitional zone with mixed stands of pondweed and seagrass (depth ca. 1.5 m) and transect "C" is characterized as the seagrass zone, about 2-3 m deep (Fig. 1). Each transect consisted of 6 sampling stations in a row (distance between neighboring stations: 25 m, total transect length: 125 m). Herring spawning activity started in mid-March and lasted until the middle of May in 2012. To investigate herring egg concentrations during the entire spawning season, weekly egg sampling was conducted at the six stations on each transect. The samples were taken with a small van Veen grabber (sampling area = 400 cm^2) which has performed well on the soft bottom of the spawning bed in previous trials and provided comparability of results to earlier studies (e.g. Kotterba 2015).

The pre-impact/post-impact experiment — To quantify the storm-induced loss of SAV biomass and equivalent herring egg loss, we conducted a field experiment on the particular depth strata of transect A (1 m depth, Fig. 1), where significant egg depositions were observed in earlier years. Experimental units included defined spots homogeneously covered with SAV that were marked with 6 tags on the sea bottom to compensate for potentially high data variability of egg concentrations on natural spawning beds according to SAV patchiness. Prior to and after a predicted storm event (end of March – early April) experimental plots were sampled with a directed Van Veen grab led by a snorkeler on differing sides of the tag.

Characterization of storm events — Hourly wind data of the weather station 'Greifswalder Oie' (N 54.249043°, E 013.923850°) was provided by the Federal Meteorological Service of Germany (DWD). The daily maximum wind speeds (m s^{-1}) and the corresponding wind directions during the spawning period were extracted from the time series of weather recordings for the study area.

Post-storm beach litter sampling — After a multiple-day storm event, a 571 m long beach section on the lee side of the spawning ground (Fig. 1) was sampled for SAV litter with attached herring eggs. This was performed to identify the spawning zones most affected by the storm according to SAV composition and to verify numbers of herring eggs exported out of the system. The total washed up SAV biomass in gram fresh weight (g FW) was determined on 0.5 m wide transects spanning the entire beach width (delineated from edge of dune vegetation landward to the water level). Sixteen of those transects were sampled approximately every 40 m (more details in Online Resource 1), and after recording the total g FW of SAV per transect a random subsample of approximately 1 liter of SAV litter was fixed with a 4% formalin-seawater solution and transferred to the laboratory to analyze SAV composition, to count the number of herring eggs and to determine their condition.

Sample processing

In the laboratory, fixed samples were rinsed for at least 24 hours in cold water to remove the fixative. The total plant biomass in gram fresh weight (g FW) of each sample was recorded and percentage of taxonomic plant composition was identified on the family level. For exact analyses of egg quantity and egg condition, each sample was spread on a tray, three subsamples of standardized area were taken randomly (Online Resource 2) and SAV subsample biomass (g FW) was recorded. Then eggs were separated from the plants under a stereo microscope. Eggs were counted according to different categories (alive and dead, more details in Online Resource 3) and biomass (g FW) of all eggs was recorded using a micro scale. Afterwards, all plant and egg samples were dried at 80°C for at least 48 hours in a compartment drier for recording dry weight. SAV biomass in gram dry weight (g DW) and the number of eggs on the three different depth zones were extrapolated to m^{-2} and were quantified for the entire spawning period in 2012.

Determination of total spawning zone surface area — A Geographic Information System (ArcGIS, 2013 Esri, Arc Map version 10.2) was used to determine the total area of each vegetation covered spawning zone at the study site "Gahlkower Haken". Area definition was performed by manually delineating the vegetated zones, using an aerial image analysis and the GIS tool to measure distance (Fig. 1).

Data analyses

Estimation of total SAV biomass m⁻² and total egg number m⁻² — To cope for high fluctuations in fresh weights (g FW), we used dry weights (g DW) to extrapolate the SAV biomass (g m⁻²) for all samples according to the following equation:

$$DW_{SAV} = \left(\frac{DW_{SAVss}}{DW_{(SAV+HE)ss}} \times DW_{RS} + DW_{SAVss} \right) \times x \tag{1}$$

where DW_{SAV} represents the total SAV dry weight per m² for each replicate, DW_{SAVss} the dry weight of SAV in the subsample and $DW_{(SAV+HE)\,ss}$ the dry weight of the entire subsample (including SAV and attached herring eggs), DW_{RS} the dry weight of the remaining sample (subsample excluded). x represents the factor needed to extrapolate the sampling area of the grabber to m² (e.g. $x = 25$, if the sampling area was 400 cm²). For calculating the total amount of herring eggs per m² for each replicate, we used the following equation,

$$n_{HE} = DW_{SAV} \times \frac{n_{HEss}}{DW_{SAVss}} \tag{2}$$

where n_{HE} is the number of eggs per m², DW_{SAV} represents the total SAV dry weight per m², n_{HEss} represents the number of eggs and DW_{SAVss} is the SAV dry weight in the subsample.

Calculation of egg numbers per spawning zone — The egg numbers per m² (n_{HE}) were multiplied with the surface area of each spawning zone A_{SZ} to estimate the mean number of eggs for each spawning zone ($\overline{n_{HESZ}}$):

$$\overline{n_{HESZ}} = n_{HE} \times A_{SZ} \tag{3}$$

Loss of eggs as shown by the pre-impact/post-impact experiment — We analyzed the storm-induced observed egg loss per m² (EL_{Obs}) on each experimental unit subtracting the egg number after the storm (n_{HEa}) from the egg number prior to storm (n_{HEp}). The EL_{Obs} is interpreted as the maximum egg loss occurring during the storm event:

$$EL_{Obs} = \left(n_{HEp} - n_{HEa} \right) \tag{4}$$

Following the assumption that adherent herring egg abundances correlate strongly to the suitable spawning substrate (Kanstinger et al. 2016) we assumed that any loss of SAV (e.g. due to storm events) directly results in a loss of adherent herring eggs, considering this as

the minimum egg loss. We conducted a pairwise pre-storm/post-storm comparison for each replicate to determine the minimum egg loss EL_{SAV}, using the following equation:

$$EL_{SAV} = \left(\frac{DW_{SAVa}}{DW_{SAVp}} \right) \times n_{HEp} \qquad (5)$$

where $n_{HE\,p}$ is the egg number at the time prior to the storm (p), $DW_{SAV\,p}$ is the dry weight of SAV prior and $DW_{SAV\,a}$ the dry weight SAV after the storm event.

Extrapolation of SAV litter biomass — The SAV biomass (g DW) found on 1 m beach width (DW_{Beach}) was extrapolated using the following equation:

$$DW_{SAV} = \left(\frac{DW_{SAVss}}{DW_{(SAV+HE)ss}} \times DW_{RS} + DW_{SAVss} \right) \times f \times 2 \qquad (6)$$

where f represents the factor needed to extrapolate the sample to the total biomass of SAV litter on the corresponding beach section of each transect (total fresh weight of SAV litter per transect divided by the fresh weight of the corresponding subsample), DW_{SAVss} represents the dry weight of vegetation found in the subsample and $DW_{(SAV+HE)ss}$ the dry weight of the entire subsample (including SAV and attached herring eggs), DW_{RS} represents the dry weight SAV of the remaining part of the sample (exclusive subsample). The factor 2 was used to calculate the SAV biomass found on 0.5 m width beach transect to 1 m beach width.

Estimating the number of eggs in the washed SAV litter — The number of eggs found on a beach width of 1 m was estimated using equation (2). Mean egg number on 1 m beach stretch was then multiplied with the length of the investigated beach section (571 m) to extrapolate the number of eggs washed ashore in the investigated beach section.

Estimating the impact of storm events during the spawning season 2012 — Wind data provided by the DWD were used to identify distinct storm events during the herring spawning season in 2012. Using field observations on herring egg concentrations and SAV biomass during these periods, we calculated the observed maximum egg loss (EL_{Obs}) and the minimum egg loss (EL_{SAV}) for each storm event using the equations (4) and (5). The cumulative egg loss during the spawning season in 2012 was then correlated to the adult spawners by estimating the corresponding reproductive equivalent RE (number of adult spawners needed to produce the number of lost herring eggs). Assuming that a female spawner carries approximately 45,500 eggs (Anwand 1962, Kändler and Dutt 1958), RE was calculated using the following equation:

$$RE = \left(\left(\frac{EL_{2012}}{45500} \right) * 2 \right) \qquad (7)$$

where EL_{2012} represents the cumulative egg loss during the spawning season in 2012 and the factor 2 was used to extrapolate the total number of spawners assuming a balanced gender ratio. The calculation was done twice: first using the observed (maximum) egg loss ($EL_{2012} = \sum EL_{Obs}$) and in a second run using the minimum egg loss ($EL_{2012} = \sum EL_{SAV}$).

Statistical analyses

All statistical analyses were performed with STATISTICA 12 (Statsoft). Statistical significance was tested by using a one-way analysis of variance (ANOVA) with a significance level of $p < 0.05$. Data sets were tested for homoscedasticity by Levene's-test and were logarithmically transformed $\log(x + 1)$ if necessary to meet the requirements of ANOVA.

Results

Herring egg concentrations from different spawning zones

With an area of 1.84 km^2, the largest spawning zone is located in 2-3 m depth (C), followed by the shallow zone in 1 m depth (A = 1.77 km^2) and the spawning zone in 1.5 m (B = 0.55 km^2). For determining the importance of different spawning zones, we estimated the mean egg number per spawning zone for the three different depth zones (Fig. 2), based on egg number and SAV biomass data per m^2 (Online Resource 4). Prior to the storm event, spawning zone A was the most important spawning zone with the highest herring egg concentration in comparison to the other two spawning zones B and C. Although the spawning zone C includes the largest surface area on the spawning ground, the highest egg numbers were found in the shallow spawning zone A (Fig. 2).

However, due to the high patchiness of egg distribution the observed differences in egg concentrations were not statistically significant (ANOVA, $F_{(2,15)} = 3.13, p = 0.073$).

Analysis of beach litter composition

SAV composition from the different transects in the distinct spawning zones were compared with the SAV composition found as litter on the lee side of the beach section immediately after the storm event (Tab. 1).
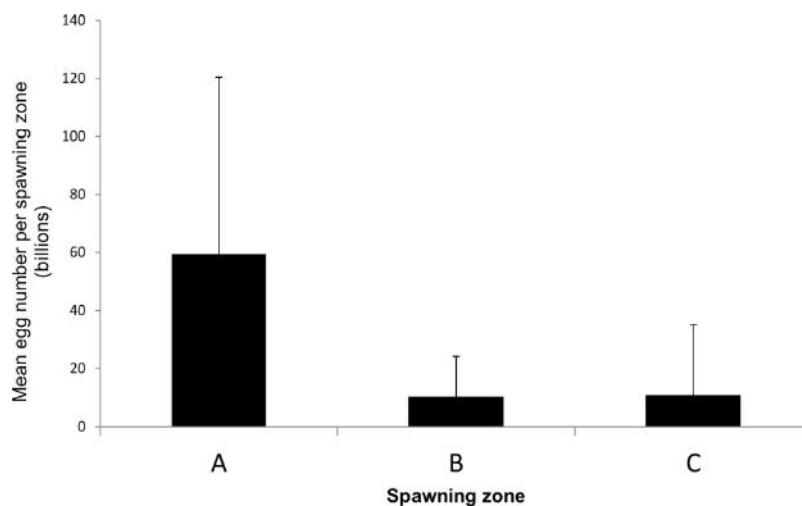
Figure 2: Herring egg distribution from three different spawning zones (A: 1 m depth, B: 1.5 m depth, C: 2 m depth) prior to the storm, based on calculated mean eggs numbers per spawning zone (n=6). Standard deviations are indicated by error bars.

Table 1: SAV composition in percent on transects A (1 m depth), B (1.5 m depth) and C (2 m depth) (prior to storm, 27th of March 2012) and composition of beach litter, found after a storm event (5th of April 2012) on a beach section located at the lee site of one important spawning ground in Greifswald Bay.

Genus	Litter	A	B	C
Zostera spp.	5	0	27	100
Stuckenia sp./*Ruppia* sp.	93	85	73	0
Ceratophyllum sp.	2	10	0	0
Filamentous brown algae	0	5	0	0

Table 2: Pre-impact/post-impact experiment mean and median values of SAV biomass g DW m^{-2} (Standard deviation ($\pm$ SD)), egg number per g DW SAV ($\pm$ SD) and egg number m^{-2} ($\pm$ SD) are given before/after a multiple day storm event in spring 2012 (28th March – 4th April 2012). Asterisk indicates significant differences in egg numbers m^{-2} (ANOVA, $F_{(1,10)} = 5.55, p = 0.040$).

		Prior to storm	**After storm**
g DW SAV m^{-2}	Mean ($\pm$ SD)	101.9 (40.7)	81.8 (31.6)
	Median	106.3	71.0
eggs per g DW SAV	Mean ($\pm$ SD)	393 (408)	44 (77)
	Median	350	0
eggs m^{-2}	Mean ($\pm$ SD)	46533 (45197)	2841* (4652)
	Median	41394	0

It is supposed that most of the SAV litter originated from spawning zone A because the SAV biomass found on the beach consisted mainly of pondweed (Potamogetonaceae, Ruppiaceae) (93%) with a small amount of *Ceratophyllum* sp. (2%), resembling the composition of aquatic plants from that depth zone. Additionally, a small quantity of *Zostera* spp. was found in the beach litter, probably originating from the deeper spawning zones. We estimated that 63.6 million herring eggs were washed ashore along the investigated beach section with a length of 571 m.

Storm-induced egg loss in the pre-impact/post-impact experiment

Results revealed a reduction in SAV biomass and egg numbers after the storm event (Tab. 2), but the observed differences between the SAV biomass g DW m^{-2} (ANOVA, $F_{(1,10)} = 1.51, p = 0.247$) and the mean egg number per g DW SAV (ANOVA, $F_{(1,10)} = 4.03, p = 0.072$) were not statistically significant.

However, mean egg numbers m^{-2} significantly differed prior to and after the storm (ANOVA, $F_{(1,10)} = 5.55, p = 0.040$). We observed a total egg reduction of 43,692 herring eggs, which corresponds to an egg loss of 94% (max. egg loss). The minimum egg loss (EL_{SAV}) was 29%, corresponding to a reduction of 13,724 eggs in total. Considering these two egg losses for the entire spawning area A, the estimated egg loss during the first storm event ranged from 17.2 (min.) to 55.7 billion eggs (max.). These calculated egg loss numbers for the shallow spawning zone A are equivalent to a reproductive potential loss of 756,000 adult herring (min.) and 2,448,000 adult herring (max.) respectively.

Storm-induced egg loss during the spawning season 2012

Based on daily maximum wind speeds [m s^{-1}] with respective wind directions affecting the spawning ground, we identified four storm events during the spawning season 2012 (Fig. 3).
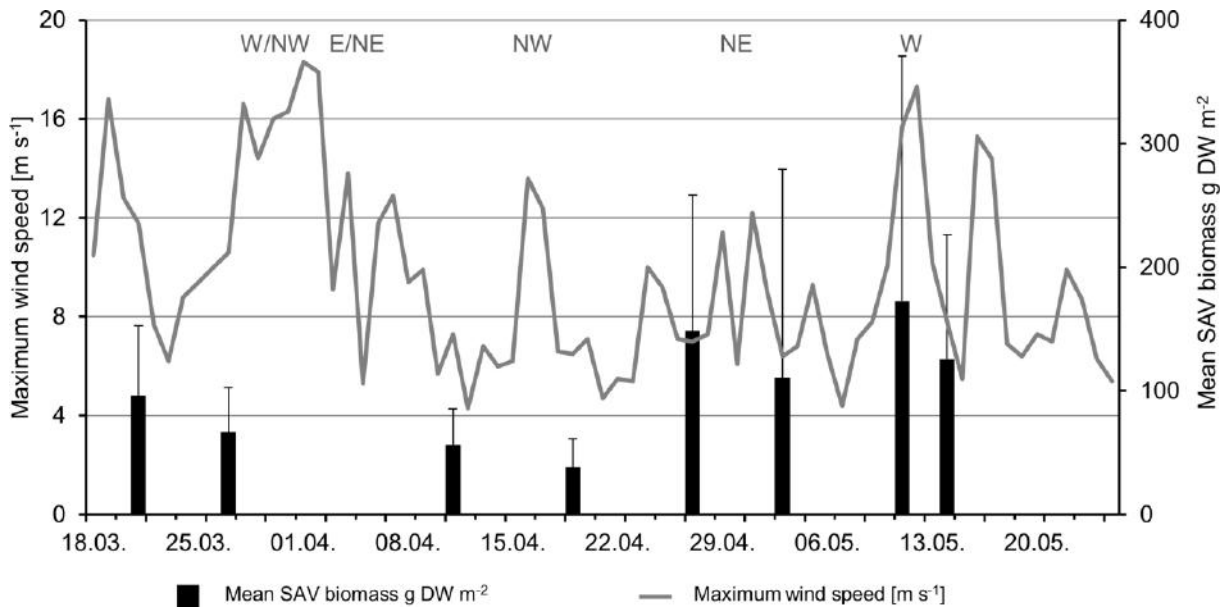
Figure 3: Mean SAV biomass g DW m^{-2} (bars) with standard deviation along the spawning season 2012. The grey line represents the daily maximum wind speed [m s^{-1}] and prevailing wind directions during four storm events are given in abbreviation. The first storm event end of March was characterized by changing wind regimes (north-westerly to north-easterly).

We examined the egg loss per m^2 for each storm event to evaluate the cumulative storm impact during the entire spawning season, based on data from natural spawning bed transects. The estimated egg numbers for each storm event and the resulting total egg loss for season 2012 are presented in Tab. 3. The strongest storm event occurred between 28th March and 4th April 2012, when the egg loss experiment was conducted. This first storm included circulating wind directions, starting with north-westerly winds (290°) with maximum speeds of 16.6 m s^{-1} on March 28th. Wind speed increased up to 18.3 m s^{-1} on 1st April. During this initial storm, wind directions shifted from north-westerly to north-easterly winds (70°) of 13.8 m s^{-1} on April 4th. The dominant wind directions and wind speeds for Greifswald Bay between March 15th and May 25th 2012 are given in Fig. 4 (additional data are given in Online Resource 5).

We combined these data with our data on SAV biomass (g DW m^{-2}) at the shallow transect and defined storm action by a minimum wind speed of 12 m s^{-1}. We found a slight reduction in SAV biomass after the first storm event (end of March) in this shallow area. There were subsequent SAV biomass losses after the following three consecutive storm events. The minimum and maximum egg loss numbers for the first storm event are the values calculated from the experiment units. The estimated egg loss for the entire spawning season 2012 was 53.2 billion (min.) and 260.5 billion eggs (max.).

Table 3: Estimated egg loss of the each storm event in the season 2012. The storm-induced observed egg loss numbers are indicated by maximum egg loss. Following the assumption that any loss of SAV directly results in a loss of adherent herring eggs, this calculated egg loss numbers are indicated as the minimum egg loss on the shallow spawning zone A (1 m depth). Minimum and maximum values for the first storm event are based on results from the experiment, the other egg loss values are based on transect egg concentration data, taken along the entire spawning season 2012.

	Egg loss in billions	
Storm event	Min.	Max.
28th March – 04th April	17.2	55.7
11th April – 19th April	32.7	94.7
27th April – 03rd May	3.3	110.1
11th May – 14th May	0	0
Estimated egg loss per spawning zone A (1 m depth) in 2012	**53.2**	**260.5**
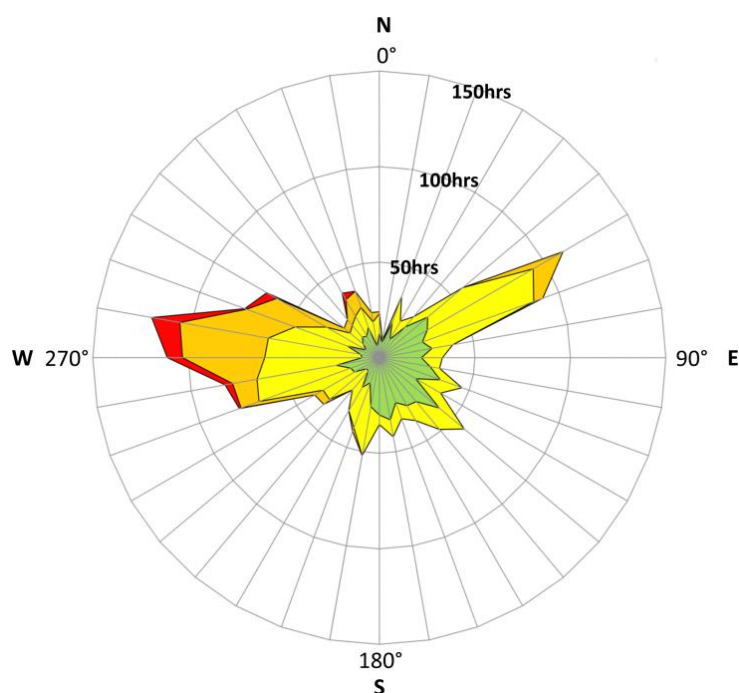
Figure 4: Dominant wind directions and wind speeds for Greifswald Bay between March 15th and May 25th 2012 based on hourly measurements provided by Germany's National Meteorological Service (DWD). Wind speeds are given in distinct categories (green indicates hours with a measured wind speed of $\leqslant 5$ m s^{-1}; yellow indicates hours with a wind speed between 5 and 10 m s^{-1}, orange indicates a wind speed between 10 and 15 m s^{-1} and red a wind speed of > 15 m s^{-1}).

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Discussion

This study revealed a substantial impact of storm-induced wave action on herring egg mortality. During a multiple day storm event we observed an egg loss which ranged between 29 and 94%. According to the observation that adherent herring egg abundances are strongly related to SAV, rather than to hard substrates (Kanstinger et al. 2016), heavy storms can damage and uproot aquatic vegetation and cause considerable loss in plant canopies (Cruz-Palacios and van Tussenbroek 2005, Mataraza et al. 1999) and consequently leading to the loss of attached fish eggs. We found a total of 63.6 million eggs on vegetation washed ashore along a 571 m long stretch of the leeward shore of the spawning ground.

Considering the similar composition of plant taxa in the SAV litter on the beach and the macrophyte community found in the shallower spawning areas (mainly zone A), we conclude that the majority of the egg loss occurred in the spawning beds in the immediate proximity to the shore line. Furthermore, the hydrodynamic effects of waves on SAV are probably more pronounced in the shallower areas, however we cannot exclude that deeper areas were also affected as indicated by a minor proportion of seagrass in the SAV litter washed ashore.

Prevailing wind directions during the storm implied that the vegetation washed ashore probably originated from the spawning ground "Gahlkower Haken". We did not find any loose eggs detached from the vegetation washed up on the beach. Concerning the quantification of egg numbers found on the beach site, we assume that estimated egg numbers found on SAV litter most likely are an underestimation of the entire egg loss. This is due to the observation of high amounts of vegetation retrieved from the beach caused by wave action during the storm before sampling could be performed (Online Resource 6). Hourston and Rosenthal (1967) described that after a series of storms high numbers of detached eggs were found in the intertidal zone during low tide. Survival analyses in the laboratory indicated that eggs attached to vegetation showed an overall higher hatching rate than the un-adhered eggs. Compared to the Pacific Ocean, lunar tides are marginal in the Baltic Sea. Therefore air exposure time is the influencing factor for egg survival, causing hypoxia and desiccation and air exposure of washed up fish eggs depend on irregular wave forcing (Jones 1972). According to our observations (unpublished) most of the eggs washed back into the water did not survive but accumulated at the sea bottom in sheltered waters creating thick layers consisting of decaying SAV and eggs.

Our estimated numbers of herring eggs per m^2 detached and exported from the spawning ground by storm action was equivalent to 94% of the initial egg number (Tab. 2). Since this egg loss might at least be partially influenced by other factors such as hatching or predation, we

consider the 94% to be the uppermost limit of storm-induced egg loss. Based on SAV reduction in experimental units, we estimated a mean minimum egg loss of 29% (based on pairwise comparisons). Since this value does not include those eggs that are detached from the plants but only eggs that are still attached and lost through the removal of plants, we consider the 29% to be the lowermost limit of storm-induced egg loss. This storm effect and loss of eggs which occurred at the end of March most likely is an underestimation of the de facto storm-induced loss, yet a 29% minimum egg loss represents a considerable extent of total spawning capacity. However, extrapolating these effects to the total spawning area of Greifswald Bay or the total population remains difficult since storm effects must be considered to be strongly site- and habitat specific.

Considering both the minimum (EL_{SAV}) and maximum value (EL_{Obs}), the estimated egg loss for the entire shallow spawning zone in the investigation area during the storm event at the end of March ranged between 17.2 and 55.7 billion herring eggs. The average number of eggs per female of western Baltic herring is 45,500 (Anwand 1962, Kändler and Dutt 1958). Our projection revealed that the storm-induced loss of eggs found during our experiment would result in a minimum equivalent of the reproductive loss of approximately 756,000 adult individuals (129.3 tons). With a magnitude of approximately 0.15% the proportion of this reproductive capacity loss in relation to the total number of reproductive 3+ group herring in the Western Baltic Sea (506 million individuals, 74.0 kilotons) estimated for the particular year 2012 (ICES 2015) seems marginal, but represents only the absolute storm-induced egg loss on a small single spawning bed. For Pacific herring in British Columbia, Canada, Hay and Miller (1982) indicated a 576 ton loss of reproductive capacity caused by storms. Although our findings in the Baltic Sea indicate only about a fourth of this amount, such loss in reproductive capacity is a remarkable number considering that our results represent only one storm event out of many storm events in only one out of multiple spawning areas. Regarding the entire spawning season 2012 with four consecutive storm events, we calculated a total egg loss of 53.2 and 260.5 billion eggs in the shallow spawning zone. These additive results would have led to a minimum reproductive capacity loss of 2.3 million individuals (393 tons) and a maximum capacity loss of 11.4 million individuals (1.9 kilotons) revealing a total loss of 0.5–2.3% of total matured 3+ group herring individuals.

Since vegetation cover and seasonal succession is generally dynamic due to varying temperatures and light regimes (Blümel et al. 2002, Dennison 1987, Munkes 2005a), spatial extension of spawning zones in 2012 might have slightly differed from conditions during the herring spawning season 2009 where aerial images of SAV distribution were obtained (Kanstinger et

al. 2016). However, the overall impact of local storm events on the reproductive capacity of inshore spawning herring in the Baltic Sea is most probably underestimated by our findings, but regarding cumulative effects of multiple storm events in different spawning areas and the overall multiple stressors, acting on the local scale of spawning grounds, it can be assumed that all these stressors unquestionably have a negative impact on population level. Furthermore hydrodynamic forces might also affect the condition and development of herring eggs and should be considered in further research.

This is supported by findings of the annual larval herring monitoring in Greifswald Bay which samples larval abundance during the reproduction period on a weekly basis to provide an annual recruitment index for stock assessment of the Western Baltic spring spawning herring (Oeberst et al. 2009, Polte et al. 2014). Greifswald Bay is considered a major spawning ground for the Western Baltic population because the larval herring production in the basin regularly correlates strongly with the number of 1-group juveniles in the overall Western Baltic Sea (Oeberst et al. 2009, Polte et al. 2014). In 2012, the total number of larval herring produced in the system was one of the lowest in two decades of larvae monitoring (ICES 2013). Furthermore the number of 1-group juveniles one year later was correspondingly low (ICES 2014). Although there is no solid evidence for a causal relation between this cascade of recruitment failure and local storm events, there is a strong potential that high storm-induced egg mortality has largely contributed to the multiple stressors and interactions leading to minor recruitment in 2012. Although, the comparably low larval herring numbers found during the season 2012 cannot be directly proven to be linked to storm-induced egg mortality, it is unlikely that the low numbers of newly hatched larvae was due to reduced spawning activity for two reasons: i) the initial egg numbers found on the spawning bed was similar to other years (D. Moll unpublished) and ii) herring fishery on the spawning grounds took its quota in a relatively short period compared to the previous year, indicating massive herring runs.

Our results reveal a substantial storm impact on herring egg mortality, noting that we only investigated one out of multiple spawning grounds. The cumulative effects of multiple storms in different spawning areas should be considered in further storm impact investigations. Wind events in general can also have positive effects on population dynamics, e.g. providing a well-oxygenated water body (Munkes, 2005b, Schoknecht, 1973) and improving herring egg development or better feeding conditions for herring larvae (e.g. Ojaveer, 1998). However, considering scientific forecasts of increasing storm intensities and frequency (Coumou and Rahmstorf 2012, Woth et al. 2006), this study has highlighted the fact that different anthropogenic stressors (e.g. eutrophication and climate change) can act as hazardous stressors for herring reproduction success.

Conclusions

The results of the study indicate that depth distribution of vegetated spawning zones and related egg concentrations affect the magnitude of herring egg mortality caused by storm events during the reproduction period. Anthropogenic impacts in the Baltic Sea have already resulted in a limited depth distribution of submerged aquatic vegetation leading to an increased exposure of herring spawning beds to storm-induced wave action. We conclude that regional storm events are crucial stressors on the reproduction of inshore spawning herring and potentially other fish species. In addition to other local stressors, such as coastal modification and predation by the local estuarine fish community (Kotterba et al. 2014), synergistic impacts of eutrophication and increasing storm frequencies (Coumou and Rahmstorf 2012, Woth et al. 2006) might pose a threat to herring egg survival in inner coastal waters. Regional coastal zone management should consider these types of ecological cascades and implement appropriate strategies to maintain crucial habitats for early life stages of fish populations since local stressors negatively affect the population dynamics at higher spatial scales.

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Chapter 6

Ontogenetic loops in habitat use highlight the importance of littoral habitats for early life-stages of oceanic fishes in temperate waters

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Abstract

General concepts of larval fish ecology in temperate oceans predominantly associate dispersal and survival to exogenous mechanisms such as passive drift along ocean currents. However, for tropical reef fish larvae and species in inland freshwater systems behavioural aspects of habitat selection are evidently important components of dispersal. This study is focused on larval Atlantic herring (*Clupea harengus*) distribution in a Baltic Sea retention area, free of lunar tides and directed current regimes, considered as a natural mesocosm. A Lorenz curve originally applied in socio-economics to describe demographic income distribution was adapted to a 20 year time-series of weekly larval herring distribution, revealing size-dependent spatial homogeneity. Additional quantitative sampling of distinct larval development stages across pelagic and littoral areas uncovered a loop in habitat use during larval ontogeny, revealing a key role of shallow littoral waters. With increasing rates of coastal change, our findings emphasize the importance of the littoral zone when considering reproduction of pelagic, ocean-going fish species; highlighting a need for more sensitive management of regional coastal zones.

Introduction

Understanding dispersal mechanisms of larval fish is vitally important in determining whether fish during early life stages can grow and survive in marine habitats, a prerequisite to the successful recruitment of a population. For temperate waters, some general concepts or paradigms postulated decades ago set the direction of modern fishery science. Dispersal and survival of larval fish has been widely attributed to: passive drift along prevailing wind and current regimes (aberrant drift hypothesis, Hjort 1926; stable retention hypothesis, Iles & Sinclair 1982), accumulation of larvae due to thermoclines and haloclines in stratified water bodies (stable ocean hypothesis, Lasker 1978), resulting in spatial and temporal overlap with suitable planktonic prey (match-mismatch hypothesis, Cushing 1975, 1990), particularly at the transition between yolk consumption and exogenous feeding (critical period hypothesis, Hjort 1914). Most of these principal concepts were developed based on the early life history ecology of small pelagic fishes, such as the clupeid species with a rather cryptic, translucent larval morphology. Studies have rarely discriminated between larval development stages although mobility and physico-chemical tolerance ranges can differ significantly in the early stages of life (Sogard 1997, Moyano et al. 2016). Although behavioural traits and active habitat selection are important drivers of larval settlement for many tropical reef fish (Paris & Cowen 2004, Leis 2010) and are increasingly implemented in coastal zone management (Hughes et al. 2005), these behavioural aspects are not often considered as mechanisms of larval dispersal in temperate waters (Houde 2008). However, in riverine systems including those with significant current velocities, larval dispersal appears to be not entirely passive but has an active, behavioural component (Schludermann et al. 2012). According to the distinct morphology of consecutive development stages it can be assumed that active habitat selection becomes increasingly pronounced along the early ontogeny and laboratory experiments have shown a significant increase of mobility in successive stages of larval Atlantic herring (*Clupea harengus*) (Moyano et al. 2016). If active habitat selection is involved in larval dispersal of major fishery species such as herring, this would have significant impact on the interpretation and application of each of the paradigms outlined above. The overlap of larval distribution with suitable planktonic prey fields might not be exclusively determined by large scale oceanography but would also be influenced by the directed movement of larvae. A potential shift from passive to active dispersal at an advanced larval stage prior to metamorphosis to the juvenile fish would render dispersal models, integrated over the entire larval phase, imprecise to an unknown extent. However, the incorporation of behavioural aspects would potentially improve parameterization

of such models. In the Northeast Atlantic Ocean many commercially important fish species, such as plaice (*Pleuronectes platessa*) and Atlantic cod (*Gadus morhua*), recruit from pelagic eggs and larvae, moving towards coastal nursery grounds as post-larval juveniles (Gibson 1994, Linehan et al. 2001, Gibson et al. 2002). For herring that spawn benthic eggs in coastal areas, a reverse dispersal of hatched larvae from inshore and coastal shelf bank spawning grounds towards offshore habitats has been documented (e.g. Heath & Rankine 1988, Bartsch 1993). This unidirectional habitat shift might be contradicted by active habitat selection when i.e. larval fish frequent littoral zones for retention as is known from riverine fish larvae (Schiemer et al. 2001). Although current velocities and hydrodynamic forcing in rivers can be at magnitudes higher than in the ocean, limnetic fish larvae do not necessarily display linear unidirectional habitat use following the direction of the flow but primarily forage in sheltered retention zones in the littoral zone of river beds (Flore & Keckeis 1998, Schludermann et al. 2012). In freshwater systems, inshore retention areas and specifically the littoral zone with sheltered hydrodynamic conditions and macrophyte cover allows for better foraging (Flore & Keckeis 1998, Schludermann et al. 2012), increased prey density (e.g. Mavuti 1990, Meerhoff et al. 2007) and decreased exposure to predators (MacRae & Jackson 2001, Okun & Mehner 2005). The function of habitats located in the upper littoral zone for larvae of ocean-going species such as herring was reported on by Urho and Hildén (1990) 25 years ago. They attributed a decrease in abundance of larval herring in the outer coastal waters of the Baltic Sea to inshore migration rather than to mortality and suggested that knowledge of the spatial distribution of herring larvae must be broadened to understand the drivers of year-class strength.

The present study investigated habitat use of larval Atlantic herring in the Baltic Sea where the relative calm hydrology of retention areas provides a suitable model system to study stage-dependent habitat selection of differing larval development stages independent from large-scale physico-chemical stratification or the impact of major current regimes.

We adapted demographic distribution analysis from socio-economics to a 20 year time series of weekly larval distribution supplemented by field studies of stage-specific larval abundance in littoral and pelagic habitats. The objectives of the study were to test the hypotheses that i) spatial homogeneity of distribution is stage-specific, ii) vertical stratification of herring larvae occurring in shallow, well mixed water bodies point to an active positioning of larvae in the water column and iii) stage-specific shifts in habitat use are not unidirectional on the inshore-offshore gradient but the littoral zone is an important retention area for advanced larval stages.

Methods

Stage-specific spatial distribution homogeneity

The distribution of herring larvae was studied in the Greifswald Bay (N54°14′, E013°34′), a major spawning ground and retention area for Atlantic herring in the Western Baltic Sea (see supporting information and Fig. S1 for more details). The 'Rügen Herring Larvae Survey' (RHLS) is an ongoing complex stock assessment process where herring larvae are quantitatively sampled weekly at 36 stations in the bay and adjacent waters between March and July (Oeberst et al. 2009) (see SI and Fig, S2A for details). Thirty stations from the RHLS were included in the present study. Stations located in the adjacent sound with a different hydrology and were excluded from the analysis. For the investigation of the spatial distribution of different herring size classes (Fig. S1), data from the years 1992 to 2014 were used to initially visualize the relative distribution during the calendar weeks of the highest abundances of each length group and each year using the Esri® Geographic Information System ArcMap™ version 10.2 (see SI for further information on the selection process). The homogeneity of spatial dispersal of the larvae was then further characterized in detail by plotting the data into a Lorenz curve (Lorenz 1905). We then calculated the area below the curve as a measure of data homogeneity:

$$A = \sum_{i=1}^{30} \left(\frac{(y_i - y_{i-1}) \times (x_i - x_{i-1})}{2} + y_{i-1} \times (x_i - x_{i-1}) \right) \tag{1}$$

Where A is the area below the Lorenz curve in relative dimensions, y represents the cumulative proportion of larvae abundance ($0 \leqslant y \leqslant 1$) and is the cumulative proportion of sampling stations ($x = \frac{1}{30}; \frac{2}{30}; \frac{3}{30}; ...; 1$). We used a Kruskal-Wallis test and corresponding post-hoc tests (Games-Howell test) to examine the differences between the larvae sizes.

Assigning larval size classes to specific development stages

Larval herring size classes (mm TL) were assigned to particular life stage categories according to literature on western Baltic herring (Moyano et al. 2016) and central Baltic herring (Arula et al. 2016). The transition between stages ranges between multiple millimeters in growth and differences in critical morphological traits (e.g. development of fin rays) could potentially affect larval distribution patterns. Therefore it was necessary to select size categories with definite stage classification and discard intermediate length classes to investigate stage specific habitat selection. Accordingly, larvae between 5 and 9 mm were categorized as yolk-sac-bearing hatchlings not yet feeding actively, while larvae between 14 and 18 mm were classified as

having already passed the critical period of first feeding (shift from endogenous to exogenous nutrition). Larvae between 24 and 28 mm were classified as having already passed the main structuring bottlenecks of larval survival since their abundance relates linearly to the resulting numbers of juvenile fish caught in consecutive years (Oeberst et al. 2009). We used a Kruskal-Wallis test and corresponding post-hoc tests (Games-Howell test) to compare the means of the distinct groups.

Larval herring sampling in the littoral zone

Every second week between April and June in 2011, herring larvae abundances in the shallow littoral zone of the Greifswald Bay were investigated, using a plankton net mounted on an epibenthos sledge (see details in SI and Fig. S2B). The data were normalized against the volume of filtered water and then compared to simultaneous RHLS catches of larvae from the pelagial of the bay.

Vertical distribution in the pelagic zone

In April 2012, the vertical distribution of herring larvae was investigated with standardized plankton samples at three distinct depths strata on three different stations within the Greifswald Bay (Fig. S1). Sampling was repeated six times at each depth stratum at every station and larvae abundance was calculated by the volume of water filtered by the plankton net (see details in SI and Fig. S2C). Larvae abundance from each depth strata from the stations were compared by ANOVA and corresponding post-hoc tests (Tukey's HSD test). As the level of cloudiness might affect depth stratification of the larval fish, weather data, derived from the federal meteorological service of Germany (DWD) were used to analyze the cloudiness during the depth-stratified sampling. For each sampling time, the mean hourly cloudiness ($n = 9$) was compared and an ANOVA was performed to test for significant differences in cloud cover. Furthermore, water probe profiles measuring conductivity, temperature and oxygen content of the water (CTD) were recorded to analyze the level of mixing in the water column. A total of 40 CTD profiles were recorded in the bay during the sampling period. We compared surface and bottom values of salinity, temperature and oxygen in order to identify possible stratification events of water masses.

Sampling of advanced larval stages

Between March and June 2015 an additional sampling was performed weekly, specifically targeting herring larvae in advanced growth stages prior to metamorphosis. Sampling of larvae in the pelagial of the bay was conducted with a ring trawl equipped with a 1.5 mm mesh plankton net (see SI and Fig. S2D for detailed information). Sampling in the shallow littoral zone was conducted with a beach seine (mouth opening 7m, mesh size 5 mm (Fig. S2E), towed over a distance of 100 m. The exact area fished by beach seine hauls was determined by Global Positioning System. Principle environmental parameters such as sea temperature, salinity, oxygen saturation and weather data were recorded at the same time as the field sampling. All field samplings of larval fish were conducted under current licenses for wild fish sampling according to Mecklenburg-West Pomeranian (Germany) fishery law (§ 11 LFischG, Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei, Mecklenburg- Vorpommern).

Results

Size-specific larvae distribution

We found strong size-dependent differences in the spatial distribution of herring larvae in the study area (Fig. 1). Weekly distribution data of each larval length group (mm TL) were used to visualize the level of distribution homogeneity by a Lorenz curve (Fig. 2A). The size classes assigned to certain larval development stages based on information from the literature (Arula et al. 2015, Moyano et al. 2016) were found clearly reflected by the post-hoc test (Games-Howell test) of Lorenz curve areas of each mm size class (see Table S5 for details). Therefore, shifts in distribution homogeneity could be assigned to particular size classes which translate to developmental stage with sufficient certainty. Fig. 2B reflects this pattern by showing aggregated measures of homogeneity for the years 1992 to 2014 represented by the mean areas below the corresponding Lorenz curves. Kruskal-Wallis test confirmed highly significant differences in spatial distribution homogeneity of distinct length classes ($\chi^2 = 477,447, df = 29, p < 0.001$). While there was a gradual increase of distribution homogeneity observed for the larvae prior to the first feeding stage (5-9 mm), larger larvae can be assigned to sharply delimited groups along their homogeneity of spatial distribution (Fig. 2B, Table S5). Life-stage associated groups of length classes were also significantly different (Fig. 2C; $\chi^2 = 140,704, df = 2, p < 0.001$).
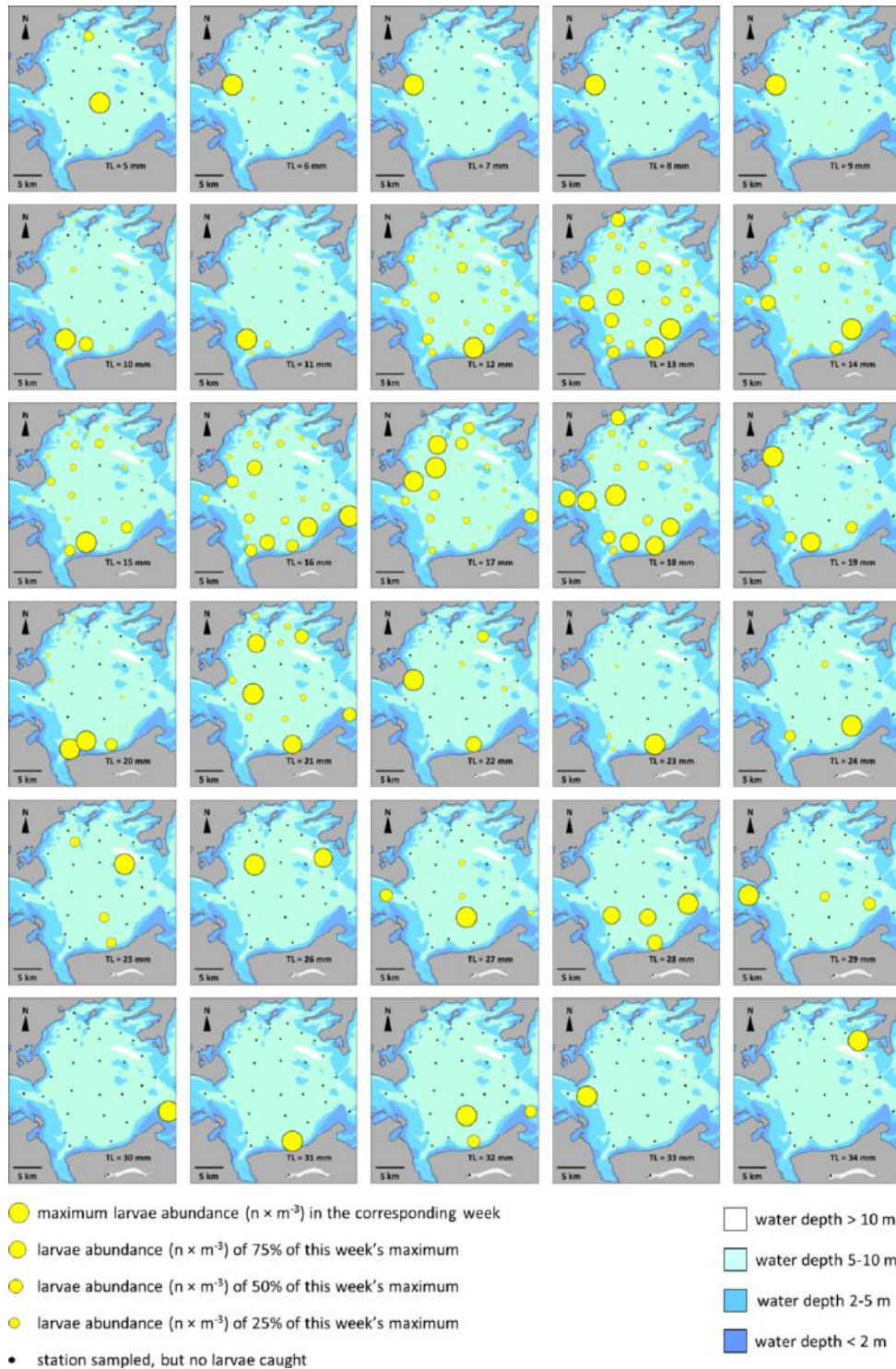
Figure 1: Relative distribution of larval herring size classes (mm total length) during weeks of their maximum absolute abundance in 2011. Data are based on the number of larvae per m³ filtered water. Size of yellow circles reflects the relative proportion of maximum abundance observed in the particular week. Source of elevation data: Federal Maritime and Hydrographic Agency (BSH), Germany.
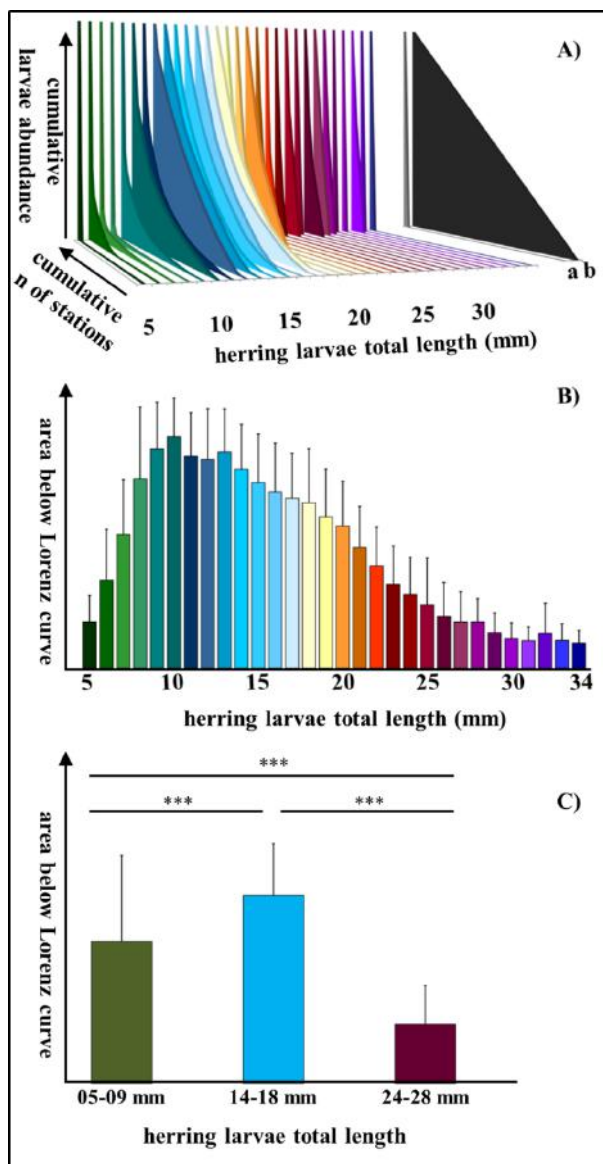
Figure 2: Size-specific spatial distribution homogeneity of larval herring. A) Spatial homogeneity of herring larvae of different size classes (5-34 mm) plotted in a Lorenz curve design (exemplarily shown for 2011): "a" and "b" represent theoretical curves for maximum heterogeneity and homogeneity, respectively. B) Mean Homogeneity of larval distribution for each 1 mm length class aggregated for the years 1992-2014. Bars represent arithmetic means, error bars represent standard deviations. C) Mean area (and standard deviations) below Lorenz curve for selected larvae length groups. Horizontal bars with asterisks indicate significant differences (*** represents a significance level of $p \leqslant 0.001$).

Larval size classes from 5-9 mm (yolk-sac) all occurred on a single patch resulting in a very heterogeneous spatial distribution over the entire sampling area. The intermediate stages represented by the size class of 14-18 mm (flexion stage) were distributed homogenously throughout the bay. The advanced stages of larvae in size class 24-28 mm (post-flexion) stage showed a high spatial heterogeneity.

Larval habitat utilization

Quantitative sampling of larval herring in the pelagic zone and the respective littoral zones of the bay resulted in comparable numbers in both habitats (Fig. 3).
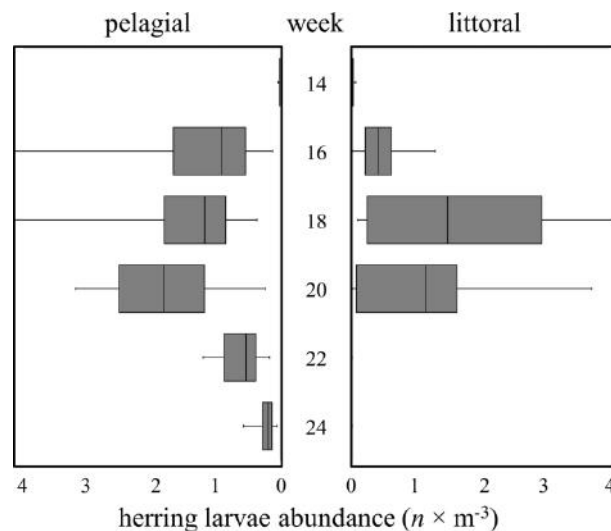
Figure 3: Herring larvae abundances in the pelagic zone of Greifswald Bay (left panel) during selected weeks in 2011 compared with larvae abundances in the littoral zone (right panel) in corresponding weeks. Data are presented in boxplots with boxes reaching from the 0.25 quantile to 0.75 quantile (containing the median – given as horizontal line). Whiskers represent the absolute maximum and minimum values, respectively.

However, the size distribution differed slightly (Fig. SI 6). The majority of larvae found in the littoral zone during the sampling season (calendar week 14-24, 2011) was composed of yolk sac larvae (mean length 8.1 mm, SD = 2.3 mm). Throughout the season the abundance in the littoral zone (Fig. 3) peaked about two weeks earlier (calendar week 18) than in the pelagic zone (calendar week 20). With the passing of the season growing numbers of pre-flexion larvae (size 10-14 mm) could be observed in the littoral habitat but with increasing size their distribution shifted towards the pelagic zone. The mean size of larvae found in the pelagic zone during the sampling duration was 9.9 mm (SD = 3.4 mm).

Vertical distribution

Pre-flexion and flexion stages (14-18 mm) of herring larvae were relatively homogeneously distributed within the bay but exhibited a significantly differentiated vertical distribution even in very shallow areas of the bay (Fig. 4). However, the orientation of vertical distribution patterns was not consistent for all stations: While larvae seemed to aggregate in bottom waters at two stations (Fig. 4A and 4B), the pattern was reversed in the third station (Fig. 4C). The cloudiness differed significantly (ANOVA: $F_{(1,16)} = 6.938$; $p = 0.018$) between the sampling times of the first two stations ($\frac{2}{8} \pm \frac{3}{8}$) compared to the conditions at the third station ($\frac{5}{8} \pm \frac{2}{8}$). CTD profiles recorded in Greifswald Bay during the period of vertically explicit larvae sampling revealed no physico-chemical stratification of the water column and mean differences of surface and bottom temperatures, salinity and dissolved oxygen were marginal (Table S7).

Distribution of post-flexion larvae

Advanced herring larvae of > 20 mm were found to form large shoals in the very shallow littoral (< 0.5 m depth) of Greifswald Bay during spring 2011. Beach seine sampling in spring 2015 revealed high abundances of larvae (up to a maximum of 0.84 larvae m^{-3}) in the littoral zone (Fig. 5). However, simultaneous ring trawl catches in the adjacent pelagic zone did not result in comparably high abundances (up to a maximum of 0.04 larvae $\times$ m^{-3}; Fig. 5).

Discussion

The Lorenz curve applied to the multi-decadal time series of weekly larval herring abundance revealed significant size-specific patterns in the spatial distribution of the herring larvae. Attributing larval size classes to development stages (e.g. Arula et al. 2015, Moyano et al. 2016), hatchlings (yolk sac stage) and advanced larvae (post-flexion) prior to metamorphosis showed high distribution heterogeneity, whereas the pre-flexion and flexion stage larvae were distributed more homogenously within the bay. In fish ecology, habitat requirements are generally assigned to ontogenetic levels (i.e. egg, larvae, juvenile, adult) rather than to development stages on a specific ontogenetic level. However, major fishery species in the Baltic Sea, such as cod, sprat (*Sprattus sprattus*) and herring all have complex life cycles including several larval stages that differ significantly in morphology and motility traits (Guan et al. 2008, Moyano et al. 2016). It is obvious that morphological and ecological differences can be more pronounced between successive larval development stages than between respective
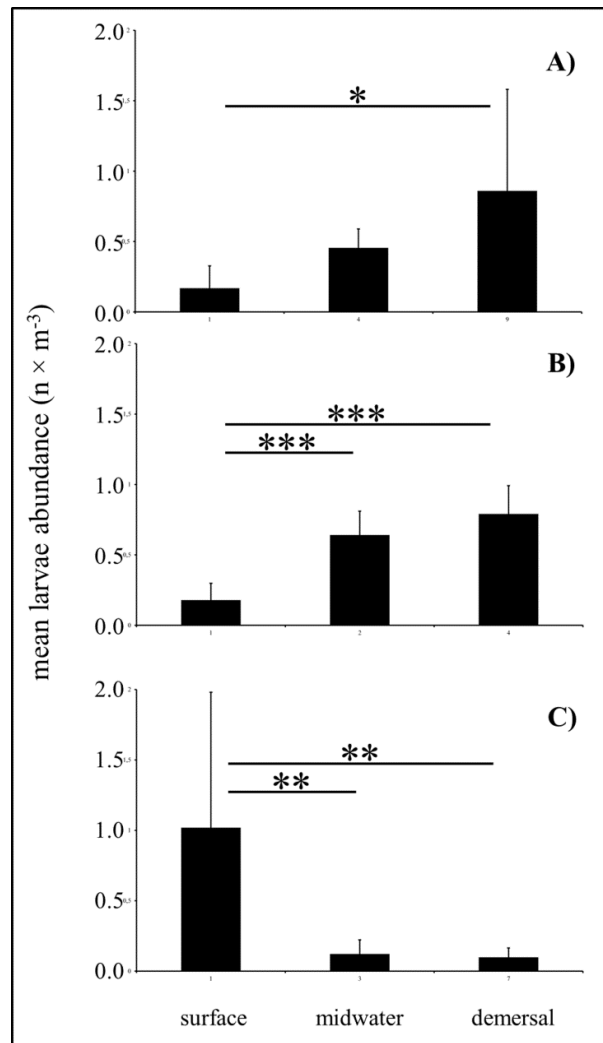
Figure 4: Depth distribution of herring larvae (14-18 mm TL) on different sampling stations in the study area Bars represent mean values while the standard deviation is given by error bars (n=6 hauls for each group). 'Surface' indicates larvae abundance close to the sea surface, 'demersal' refers to the sampling depth of 1 m above the sea bottom and midwater to the sampling in between. A) Northwestern station located in the narrow sound between the Island of Rügen and the mainland (maximum sampling depth = 9 m). B) Station located at the western edge of Greifswald Bay (maximum sampling depth = 4 m). C) Station at the southern coast of the bay (maximum sampling depth = 7 m). Horizontal bars with asterisks indicate significant differences based on a one-way ANOVA and corresponding post-hoc tests (Tukey HSD-test; significance levels are given as: * $p \leqslant 0.05$; ** $p \leqslant 0.01$, *** $p \leqslant 0.001$).
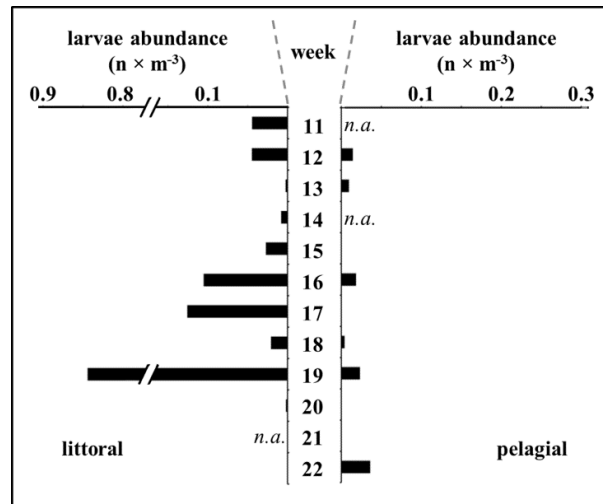
Figure 5: Depth dependent abundance of advanced herring larvae (> 20 mm) in Greifswald Bay. Left panel shows results of weekly beach seine samples in 2015 (littoral zone), while the right panel shows the abundances derived from ring trawl catches in corresponding weeks (pelagic zone). N.a. = not analyzed and sample not taken, respectively. Note the fracture of the y-axis for the littoral data.

post-metamorphosis juvenile and adult stages.

Along the early herring ontogeny our results indicate a selective habitat use according to larval development stage including upper littoral and pelagic habitats of the system. After hatching, larvae in the yolk sac stage left the shore zone and moved towards pelagic habitats of the basin. However, they remained aggregated in the vicinity of the spawning beds. Larvae in the intermediate development stage (pre-flexion, flexion) were found to be increasingly dispersed throughout the pelagic zone of the bay. In contrast, fish in the advanced stages (post-flexion) were found abundant in the upper littoral zone while almost absent in the pelagic zone.

For technical reasons, differing sampling gear had to be used in the pelagic and littoral habitats. Because of potential bias introduced by gear type no direct statistical comparison of larval abundance in both habitats could be achieved but we demonstrated relative abundances of post-flexion larvae caught by the respective gear. As the ring trawl is standard gear to sample ichthyoplankton (e.g. McClatchie 2013), it can be suggested that the low larval numbers caught in the pelagic zone generally are a consequence of selective habitat use. Larvae at different developmental stages which have been observed repeatedly in the shore zones indicates a certain loop in habitat use (Fig. 6) that, to our best knowledge, has not yet been documented even for an otherwise intensively studied fishery species such as herring.

This habitat loop is even more surprising as most studies on larval dispersal commonly describe a rather unidirectional succession of habitats during the ontogeny of young fish. Generally, larval fish movement towards near shore habitats by either passive or active dispersal mecha-
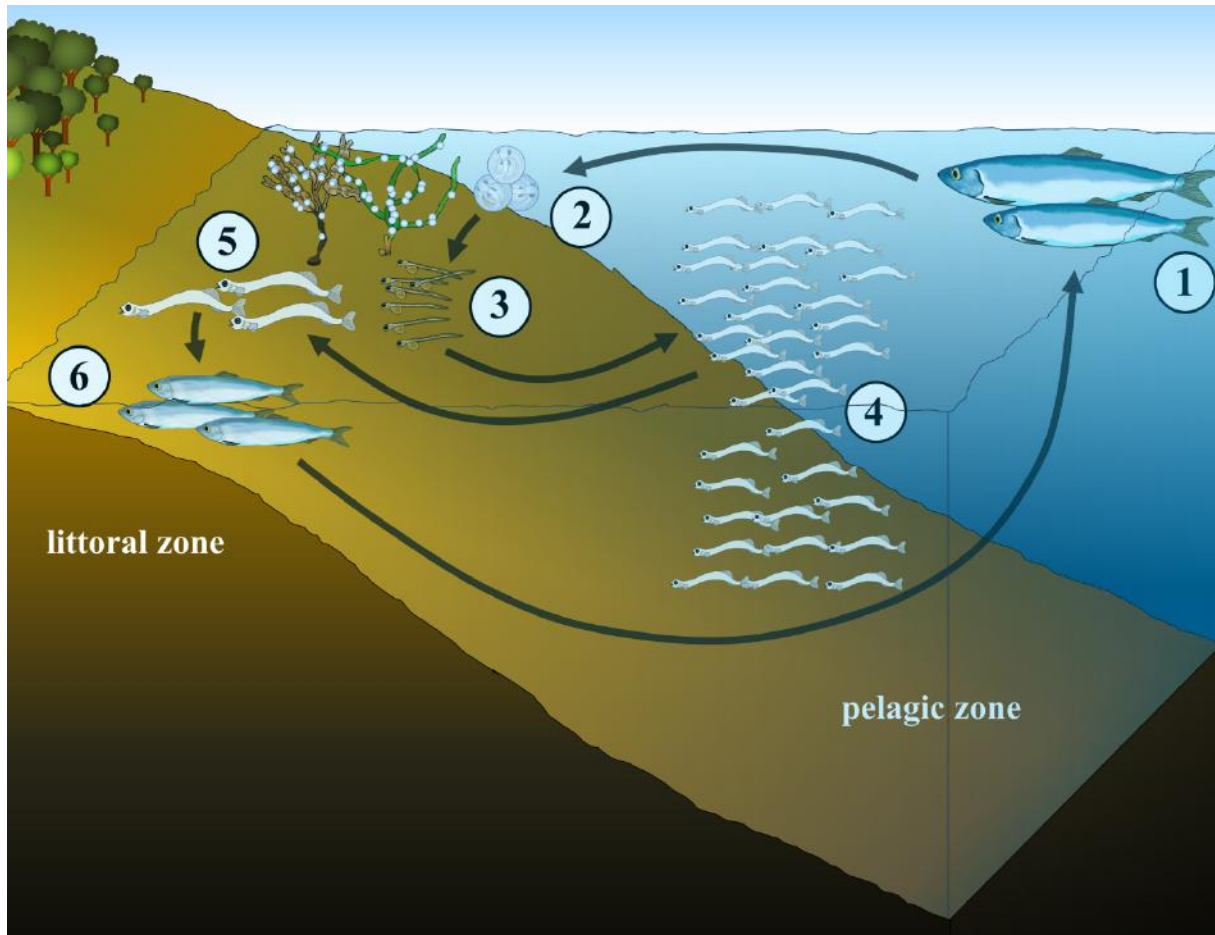
Figure 6: Ontogenetic habitat loop of herring in the Baltic Sea. Adult herring (**1**) migrate from the offshore pelagial into inshore waters to spawn their adhesive eggs on littoral substrates such as macrophytes (**2**). Yolk-bearing hatchlings (**3**) appear concentrated in the vicinity of the spawning beds, while medium sized larvae (**4**) are rather well horizontally distributed in the pelagic area of the bay; however their vertical distribution in the water column is significantly heterogeneous. Advanced larvae (**5**) return to shallow littoral areas where they remain until after their metamorphosis to the juvenile fish (**6**). Growing juveniles migrate to offshore areas along their development and usually recruit to the spawning group after 2-3 years.

nisms has been widely described for ocean spawning fish (Leggett 1984, Drake & Arias 1991). However, "near shore" often refers to the open water body of estuaries, bays and lagoons but rarely includes the shore zone gradient encompassing the upper littoral zone just below the low tide mark.

In the Northeast Atlantic Ocean, many fishery species recruit from pelagic eggs and larvae. Species such as plaice and Atlantic cod are thought to disperse towards coastal nursery grounds as juveniles (Daan et al. 1990, Elliott et al. 1990, Pihl & Van der Veer 1992, Wennhage et al. 2007). For herring that spawn benthic eggs in the inner coastal areas, a reverse dispersal of hatched larvae towards outer coastal zones is generally assumed (e.g. Stevenson 1962, Bartsch 1993). Hence the majority of larval herring surveys conducted for stock assessment purposes are performed in outer coastal waters which substantially neglects the potential larvae habitats in the shore zones. This might represent a somewhat reversed scaling issue by ignoring the contribution of small scale habitats with significant ecological function but with limited geographic extension to overall system productivity. However, stressors to larval survival in inshore retention areas e.g. by altered habitat conditions would explain the discrepancies observed in classic analyses of stock recruitment relationships (e.g. Rothschild & Fogarty 1989, Iles 1994) and would help to clarify the stock-recruitment dilemma.

The example of the Western Baltic herring stock illustrates how local stressors on early life stage survival in spawning grounds and larval retention areas can affect entire population dynamics (Polte et al. 2014). In a system without significant tidal forcing or large scale current regimes, such as the Baltic Sea, behavioural traits might be important mechanisms of larval dispersal. As littoral habitats in temperate waters are underrepresented as important habitats for larval fish by coastal zone management, there remains a potential risk that important fish resources are being affected by habitat degradation before fishes grow into size classes relevant for current stock assessment models. Our case study on the Western Baltic herring could be considered a prime example of this problem because fishery mortality of the stock was drastically decreased during the past decade due to strict quota driven fishery restrictions. However recruitment also continuously decreased during that period, driven by mortality during the early life stages (ICES 2015).

Even in well-mixed waters of the lagoon without pronounced thermoclines or haloclines, fish in the pre-flexion and flexion larval stages were not homogeneously distributed within the vertical water body. Despite site- and day-specific vertical zonation, the overall findings that larvae have shown a distinct distribution hints at the potential of these fish in the larval stages to be capable of active vertical positioning. According to Schnack (1974) the site- and date-

specific differences in larval zonation patterns might be due to differing degrees of cloud cover where larvae are found closer to the surface on an overcast day. At station "C" at an intermediate depth (7 m), larvae were accumulated at the surface whereas at the other two stations they were found in mid-water or close to the sea bed. However station "C" was sampled about one week later when cloud cover was significantly higher. This distribution difference would reflect the documented observation that vertical migration is driven by light levels (e.g. Blaxter 1975, Munk et al. 1989). Vertical migration is an important means of dispersal as ichthyoplankton might use certain vertical current regimes for dispersal (Laprise & Dodson 1989). Hence, behavioural traits should be considered in parameterizing spatial dispersal models for larval herring. The distinct larval distribution hints at an active habitat selection according to life stage. This suggests that transitional waters might offer important retention areas in the developmental stages of early herring until metamorphosis to the juvenile stage.

Since Johan Hjort (1914) postulated his critical period hypothesis it has been commonly accepted in fishery science that recruitment of fish stocks is often determined early in the larval stage of a species. The mechanisms causing most larval fish mortality are assumed to be predominantly linked with predation (Bailey & Houde 1989) and food availability for early larvae (Hjort 1914, Cushing 1975). Habitat-specific mortality could potentially result in inhomogeneous distribution in the early life stages. Major mortality e.g. by starving after yolk consumption, occurs over a period from 6 to 8 days (McGurk 1986). Due to the high sampling frequency it is unlikely that we missed major mortality events related to habitat type. Concerning top-down control, earlier studies have shown that predation on herring larvae is of minor importance in the system (Kotterba 2015). Interpreting the different stage-specific patterns of distribution as being a consequence of active habitat selection, this study indicates that habitat requirements might vary according to the stage of larval development. This could introduce an undocumented suite of survival bottlenecks related to availability and connectivity of differing juvenile habitats. In addition to fishery impacts on the adult populations, coastal modification and habitat degradation might introduce significant stressors to important fish resources. An appropriate quantity of spawning stock biomass (SSB) is clearly necessary to sustain a population; however this alone does not guarantee solid recruitment. It must also be considered that variability or a decrease in recruitment is widely structured by environmental conditions including biotic factors such as predation and competition as well as variation in the physico-chemical environment (e.g. Sparholt 1996, Begg & Marteinsdottir 2002). Many of the general theories and paradigms in larval fish ecology were developed by studying the clupeid

species. The commonly accepted general concepts such as the stable ocean hypothesis (Lasker 1978) or the stable retention hypothesis (Iles & Sinclair 1982) are broadly based on the impact of the physical environment on larval dispersal. Leis (Leis 2010) questioned whether the role of behavioural patterns are important for larval dispersal and concluded that behavioural aspects are more pronounced in tropical species compared to species inhabiting colder waters, due to extrinsic physical and intrinsic physiological reasons. However, in the shallow retention areas of the Baltic Sea, our study indicates that even the fragile and cryptic clupeid larvae are able to actively select their habitats.

The ecological value of shallow temperate systems in general (e.g. Chícharo et al. 2012) and of littoral habitats in particular for larval fish have been only rarely incorporated in both scientific and marine policy plans, although 25 years ago Urho and Hildén (1990) described the importance of these considerations for Baltic Sea herring stocks. This gap is increasingly problematic as particularly shallow coastal habitats are exposed to the growing threat of drastically changing coastlines caused by human activity as well as numerous major environmental factors such as sea surface warming. Although the habitat function of shallow upper littoral zones as nurseries for fish communities has been broadly acknowledged in marine and freshwater systems (e.g. Werner et al. 1977, Beck et al. 2001), their role in the larval period of "wasp waist" (Bakun 2006) species in coastal food webs in temperate waters is not well understood. The findings of this study should not only provide a strong further impetus for investigation of the ecological functions and value of shore zones for early life stages of oceanic fish species, but will also encourage the implementation of these findings into current management of coastal zones.

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General Discussion

Local stressors on herring reproduction

Understanding fish recruitment variability is a major research task for fishery scientists world-wide since the early 20th century. By that time Johan Hjort postulated his "critical period hypothesis", hypothesizing that year-class strength of fish recruits is determined in the early larval stage during the critical change from endogenous yolk consumption to exogenous plankton feeding (Hjort 1914, 1926). This hypothesis paved the way for many general concepts on larval survival, regarding the temporal and spatial co-occurrence of suitable prey items during the larval phase (Sinclair & Tremblay 1984, Cushing 1990) and passive larval dispersal along ocean currents (Hjort 1926, Parrish et al. 1981, Iles & Sinclair 1982, Lasker 1985). Although many existing studies on factors driving recruitment variability are focused on the early larval stages, another critical process is considered the dispersal of pelagic eggs to favorable habitats with suitable growth conditions for larvae (Parrish et al. 1981), applicable for some clupeid fish in the Atlantic ocean, such as sardine (*Sardina pilchardus*) and anchovy (*Engraulis capensis*) (Shelton & Hutchings 1982, Santos et al. 2007). But research on benthic eggs and the possible impact of spawning-site specific drivers and stressors and local climate variability on their development is rather scarce, although one of the most economic relevant clupeid fish, the Atlantic herring (*Clupea harengus*), is a representative of a demersal spawning fish. However, there is general evidence that herring egg predation by predatory fish can affect herring population dynamics (Richardson et al. 2011, Kotterba et al. 2014, Kotterba et al. 2017) and even avian egg predation has the potential to impact reproduction success of Pacific herring (*Clupea pallasii*) (Rooper et al. 1999, Bishop & Green 2001). Moreover, studies on the ecological consequences of oil spills, such as in Prince William Sound, Alaska in 1989 or in San Francisco Bay in 2007 demonstrated disastrous effects on herring egg survival and larval development with significant morphological deformities and cytogenetic abnormalities, leading to high mortality rates (Hose et al. 1996, Norcross et al. 1996, Incardona et al. 2011). Some scientists even assumed that the Exxon Valdez oil spill from 1989 caused the collapse

of the William Sound Pacific herring population in 1993 (Carls et al. 2002, Thorne & Thomas 2008). Hence, herring egg survival and recruitment of populations might be determined on a regional scale of important spawning areas and regional environmental threats have a crucial impact on herring egg and larval development. However, regarding the fact that Western Baltic herring recruitment is assumed to be determined by the second larval cohort with bottlenecks located at the egg stage (Polte et al. 2014), the impact of direct and indirect environmental cascade effects on egg survival are rarely examined *in situ*.

Eutrophication induced cascade effects on herring egg survival

Transitional waters, connecting terrestrial systems with the open Sea, have an important buffering and filter function (Schiewer 2001), as they are subject to increased anthropogenic utilization (e.g. eutrophication, harbor constructions, tourism), which exhausted their natural capacity during the last decades (Schiewer & Schernewski 2002). Eutrophication is defined as a condition, where high nutrient concentrations stimulate the excessive growth of algae, leading to an imbalanced function of the ecosystem (HELCOM 2005) and therefore have serious consequences for the aquatic environment (Smith et al. 1999). The study area Greifswald Bay is a eutrophic ecosystem (Bachor 2005). Although nutrient input in this important herring spawning area could be reduced during the last decades, a recovery of submerged vegetation from spatial limitation is not discernable, possibly due to several diffuse nutrient discharges and a problem of internal nutrient loading from sediment resuspension (Munkes 2005b). In general, nutrients are essential for the growth of phytoplankton, needed as primary producers in aquatic systems. However, high nutrient loads result in massive growth of phytoplankton, which lead to high abundances of zooplankton (Fig. 1).

This massive phyto- and zooplankton growth causes increased water turbidity, which consequently leads to a deterioration of light conditions for submerged aquatic vegetation (Fig. 1). As a consequence, eutrophication negatively affected the vertical depth distribution of vegetation in Greifswald Bay and led to a severe decline in vegetation biomass of about 80% during the past decades (Seifert 1938, Messner & von Oertzen 1990, Bartels & Klüber 1999). Whereas vegetation was found in depths of 6 m in the past, herring spawning substrate is nowadays restricted to the shallow littoral zone with growth limits of 3.5 m (Fig. 2) (Messner & von Oertzen 1991, Kanstinger et al. 2016). This limitation to the shallow littoral zone predisposes submerged vegetation and herring eggs to multiple stressors to an unknown extent, since research on the identification of drivers and stressors and their impact on herring egg survival are rather scarce in this system.
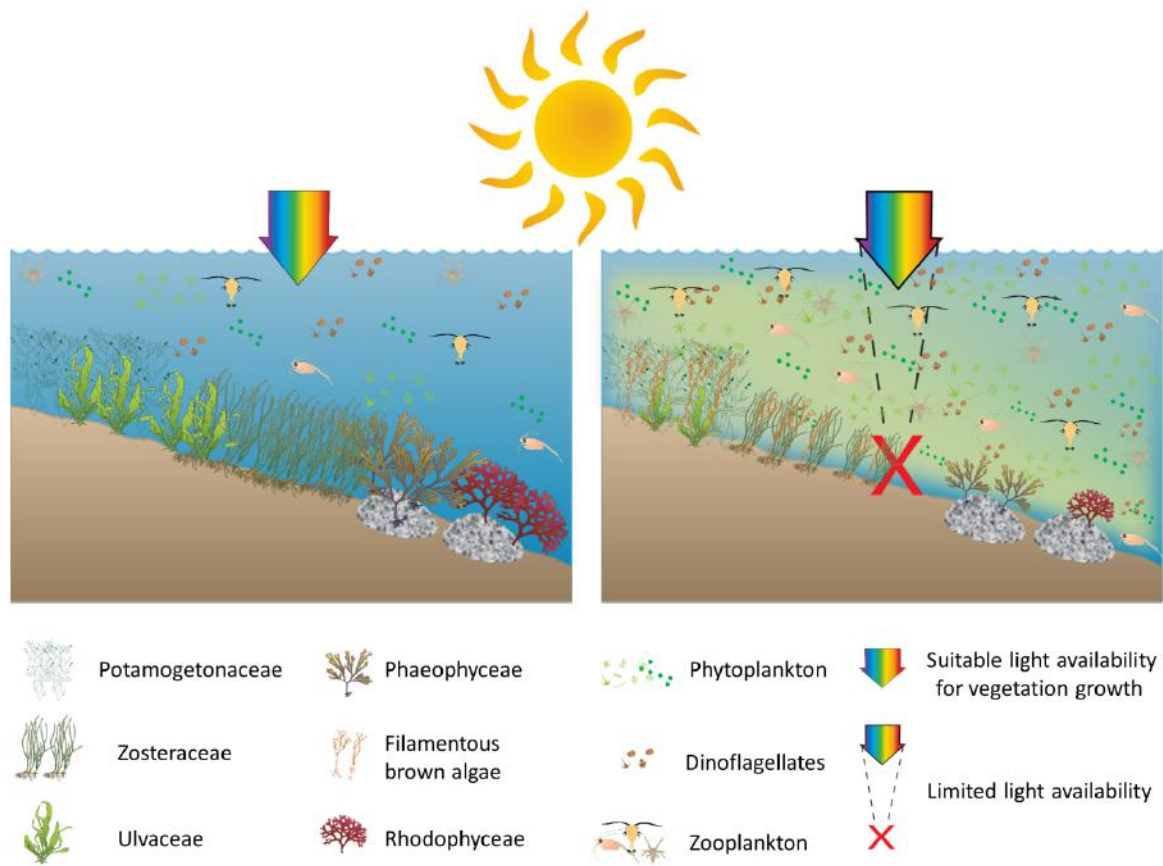
Figure 1: Comparison between oligotrophic (left) and eutrophic (right) ecosystems with respect to indirect cascade effects, such as increased turbidity and resulting decline in light availability for macrophytes in the coastal littoral zone, which leads to a shift in depth distribution to very shallow water. Symbols for this diagram are courtesy of the Integration and Application Network (ian.umces.edu/symbols).
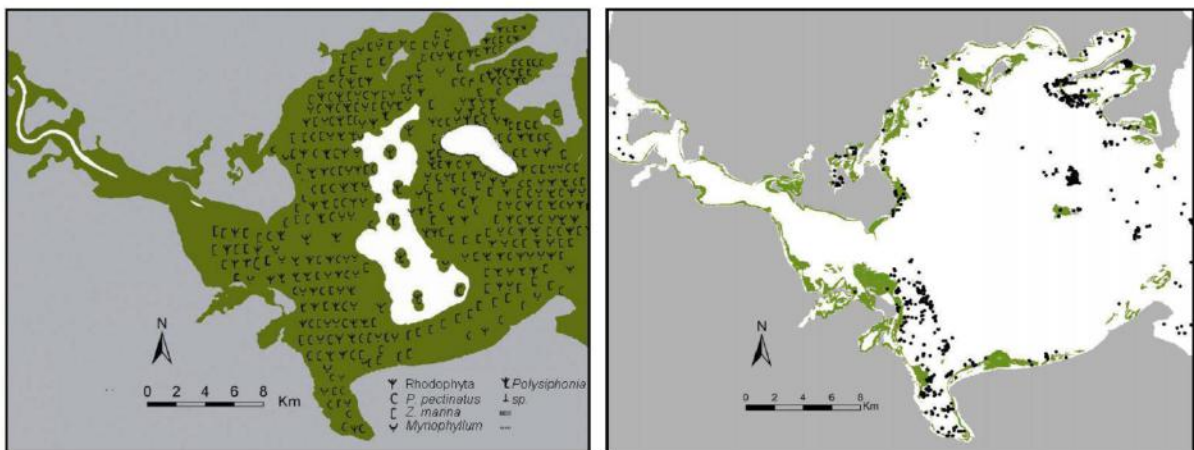
Figure 2: Historical coverage of submerged aquatic vegetation in Greifswald Bay (left, 1940's (after Seifert 1938, Subklew 1955) and status quo (right, after Kanstinger et al. 2016).

There are studies on coastal spawning ecology of Pacific herring populations, revealing informative data on spawning ground utilization, providing egg concentrations and egg depth distribution patterns (Haegele et al. 1981, Haegele & Schweigert 1985, Hay & Kronlund 1987), some studies were also conducted in Atlantic herring spawning areas in the Baltic Sea (Klinkhardt et al. 1985, Scabell 1988, Rajasilta et al. 1989, Kääriä et al. 1997). Due to strong anthropogenic pressure on these dynamic coastal systems within the last decades, it was necessary to examine and evaluate the current ecological status of Greifswald Bay as an important spawning area for the Western Baltic herring population.

In the framework of this thesis, we conducted a systematic, small-scale herring egg sampling in multiple years to investigate general herring spawning patterns and egg survival in one important spawning bed located in southern Greifswald Bay (chapter 4). The results of the study showed that vegetated spawning beds are situated in very shallow water, being stratified mainly by pondweed (*Stuckenia* spec.) and filamentous green- and brown algae in 1 m, a transitional zone with mixed stands of pondweed and seagrass (*Zostera marina*) (1.5 m) and a seagrass zone in 2-3 m depth (Fig. 3).
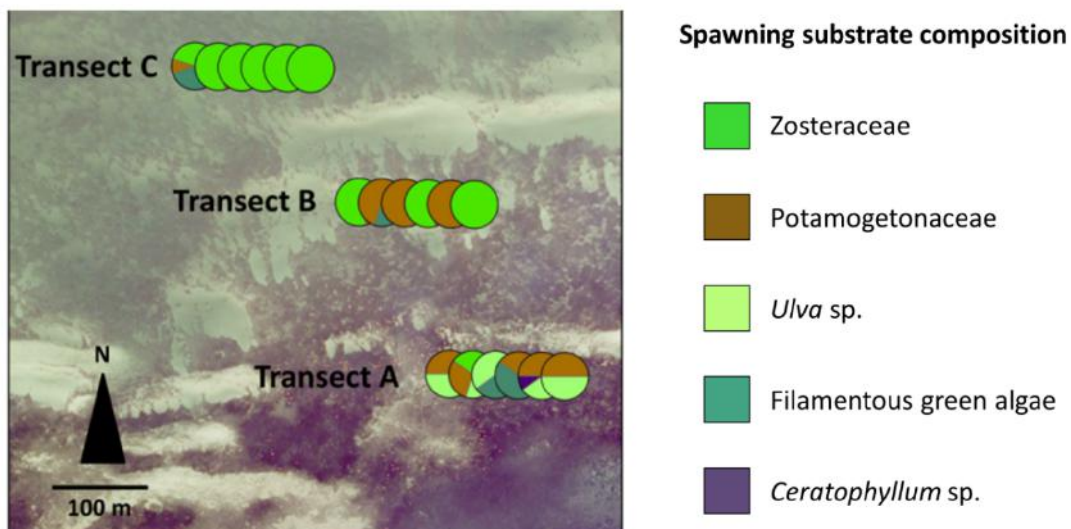
Figure 3: Snap shot of the vertical depth distribution of aquatic vegetation in the littoral zone in one important spawning bed (Gahlkow) within Greifswald Bay. Whereas pondweed and green algae are located in 1 m depth (transect A), transect B is a transitional zone with mixed stand of pondweed and seagrass in 1.5 m and mainly seagrass is found in 2-3 m depth (transect C). Figure was created by P. Kotterba and was slightly modified.

Seasonal shift of spawning depth

The results from the multiple-year spawning investigation (chapter 4) further indicated a shift of spawning depth along the spawning season from shallow water (1 m) at the beginning of the season to deeper water at the end of the spawning season, despite the fact that seagrass biomass in 2-3 m depth was quite minor during the entire season and during all investigated years. *Zostera marina* historically occurred down to 8 m depth (Schories et al. 2009) and the present limit is mainly attributable to eutrophication-induced reduction of light availability (Duarte 1991, Cardoso et al. 2004, Burkholder et al. 2007). According to the results, herring might perform some kind of avoidance behavior against extreme temperature regimes or against high temperature fluctuations in the shallow littoral zone. This behavior could also be observed for other Baltic Sea herring populations (Sjöblom 1963, Ojaveer & Simm 1975). Sjöblom described that Baltic herring in the archipelago of Finland spawn right up the coastline early in spring, avoiding the colder bottom water, whereas shoals in the later season spawn further away from the coast after temperatures increased, avoiding the relatively warm waters in the shallow littoral zone (Sjöblom 1963). Regarding future climate change scenarios, spawning substrates in deeper water could become more important again, compensating the potential threat of extreme water temperatures in the very shallow coastal zone. Another possible compensation strategy for rising water temperatures could be an increased spawning activity on seagrass beds at the outer coastline. Personal observations confirmed spawning at the outer coast of Mecklenburg Western-Pomerania during the winter (February) 2018. This outer coastal spawning is not documented scientifically to date, but might become more relevant in the future and should be taken into account in future studies, particularly in relation to larval growth and survival in outer coastal waters, but also in the scope of habitat conservation and coastal zone management.

Phenology

Another important aspect related to climate change is the temporal shift of the annual recurring life cycle events of plants and animals, i.e. phenology (Cleland et al. 2007). Since phenology is a biological response to climate, changes in phenology demonstrate direct climate change impacts to species and ecosystems (Cleland et al. 2007). This could also have crucial consequences for marine trophic interactions and food web structures (Beaugrand et al. 2002, Edwards & Richardson 2004). Fish reproduction phenology, resulting in a seasonal shift of larval appearance could significantly impact annual fish recruitment (Genner et al. 2010), according to a potential mismatch with their prey (match-mismatch hypothesis, Cushing 1990).

By the current state of scientific knowledge herring spawning activity is related to distinct water temperatures, starting at 3.5-4°C (Klinkhardt 1984). This initial spawning temperature could be confirmed during our investigations (chapter 4). Moreover, a temporal shift of initial egg deposition could be observed regarding the prevailing warmer water temperatures during the investigated years. The spawning season in 2013 started very late, due to hart winter conditions 2012/2013 with long ice cover periods and water temperatures of 0°C until mid of April (doy 106, 16th April 2013). On the contrary, spawning season in 2014 started one month earlier and first eggs were already found at doy 71 (12th March 2014). The general recruitment index was low for the warmer season in 2014 and recruitment index was good in 2013. With respect to climate change and future increase in temperature, the shift in spawning phenology is an important aspect, which should be considered in future studies of coastal fish ecology.

Storm impact

In accordance with our findings, observations from Pacific herring spawning areas pointed out high herring egg loss rates due to storm-induced wave action (Hart & Tester 1934, Hay & Miller 1982, Haegele & Schweigert 1989, Rooper 1996). Although *C. pallasii* shows a similar spawning mode as the Western Baltic herring, quantitative egg loss studies and evaluations of the impact of storm-induced hydrodynamics on herring recruitment are non-existing for Baltic Sea herring populations. With special regards to the vulnerability of vegetated spawning beds in the shallow littoral to storm-induced hydrodynamics, we estimated the egg loss rates in one important herring spawning ground after a multiple-day storm event in spring (chapter 5). At the beginning of the spawning season, most of the herring eggs were deposited in the shallow pondweed zone prior to a multiple-day storm event, indicating an increased exposition to hydrodynamic wave action. Results revealed high egg loss rates (29-94%) for Atlantic herring in the Western Baltic Sea after the storm event in late March-early April. The macrophyte litter found on the shoreline mainly consisted of *Stuckenia* spec. and demonstrated evidently the effect of wave action on the shallow water depth, where *Stuckenia* was most prominent. The quantification of eggs attached to macrophyte litter revealed high numbers of dead eggs (Fig. 4). It is noteworthy to mention that our estimated egg numbers might be an underestimation of the respective storm impact, since a great amount of macrophyte litter was washed back into the water before sampling was conducted (Fig. 4) and herring eggs are not assumed to survive due to possible dehydration stress at the beach or increased solar radiation and the resulting temperature stress, while floating at the water surface.

Figure 4: High biomass of macrophyte litter washed to the shoreline of „Gahlkow" (left) during a multiple-day spring storm event (28th March -04th April 2012), one day later during sampling (05th April 2012, right), a great amount of macrophyte litter was already washed back into the system. Source: P. Kotterba.

Regarding the fact that the shallow spawning zone in 1 m depth was hit by three storm events in total during the entire spawning season 2012, causing estimated total egg losses of 53.2 to 260.5 billion eggs, this study underlined the tremendous impact of hydrodynamic forces on herring egg survival on local spawning grounds. Further observations on a heavy spring storm event three years later during the spawning season 2015 revealed again a high vegetation biomass and attached herring eggs on the beach (Fig. 5 A-D) with a large batch of dead eggs washed to the beach (Fig. 5E).

Figure 5: High amount of macrophyte litter at the beach of „Gahlkow" after a spring storm event in 2015 (**A**), vegetation biomass is layered partly several cm thick (**B**, **C**) with attached herring eggs (**D**). Large batch of multiple dead eggs was found at the shoreline (**E**). Source: D. Moll

This study demonstrated the negative impact of eutrophication-induced indirect cascade effects on herring egg survival and identified storm-induced hydrodynamics to be a local stressor for herring reproduction success. Although spring storm events might not represent a "new" stressor to egg survival, the impact of eutrophication on vertical depth distribution of aquatic plants in combination with a potentially increased storm frequency, due to a changing climate regime is considered an increasing hazard to herring reproduction success.

Other cascade effects

Eutrophication does not only affect vertical depth distribution of submerged aquatic vegetation (Fig. 6). Nutrient enrichment also leads to other severe ecosystem responses, such as a decline in general vegetation diversity (Kautsky 1991, Kanstinger et al. 2016), although species diversity in Greifswald Bay is generally low due to its mesohaline character (Messner & von Oertzen 1991). Munkes (2005a) stated a phase shift in Greifswald Bay from a macrophyte-dominated to a phytoplankton-dominated ecosystem. This decline in diversity might also lead to a decline in spawning substrate complexity. High complexity of spawning substrates is positive related to herring egg survival, since more homogeneous egg disposal on high structural substrates warrants a better oxygen supply and gas exchange between developing eggs and the surrounding water (von Nordheim et al. 2018). Since egg deposition is related to vegetation biomass (chapter 4), substrates of low complexity or even a lack of sufficient spawning substrate during early seasonal spawning activity can cause multi-layer egg deposition, leading to increased egg mortality due to density-dependent hypoxia (Messieh & Rosenthal 1989, Klinkhardt 1996). Furthermore, increased epiphyte growth can be observed in eutrophic ecosystems, leading to a reduced photosynthetic rate of macrophytes (Sand-Jensen 1977, 1990). Eutrophication-triggered occurrence of filamentous algae cloaked together in lumps or thick mats (Bonsdorff 1992, Pihl et al. 1995, Pihl et al. 1999) could also be observed in our spawning area. Some authors even concluded that algal exudates of fast-growing brown algae negatively affected herring egg survival (Aneer 1985, 1987) (Fig. 6).

Increased agglomerations of filamentous brown algae (e.g. *Pylaiella littoralis*) on the spawning grounds are able to decrease oxygen availability for herring eggs (Aneer 1987). Strong phytoplankton blooms, triggered by eutrophication, and subsequent decomposition and sedimentation of organic matter on the egg surface can impede or prevent egg metabolism and gas exchange, possibly leading to a decreased oxygen supply (Braum 1985, Klinkhardt 1996). Western Baltic herring is highly dependent on inshore coastal ecosystems for successful reproduction. Hence, habitat deterioration does not only affect general spawning substrates or herring egg mortality, but might also negatively impact larval survival.
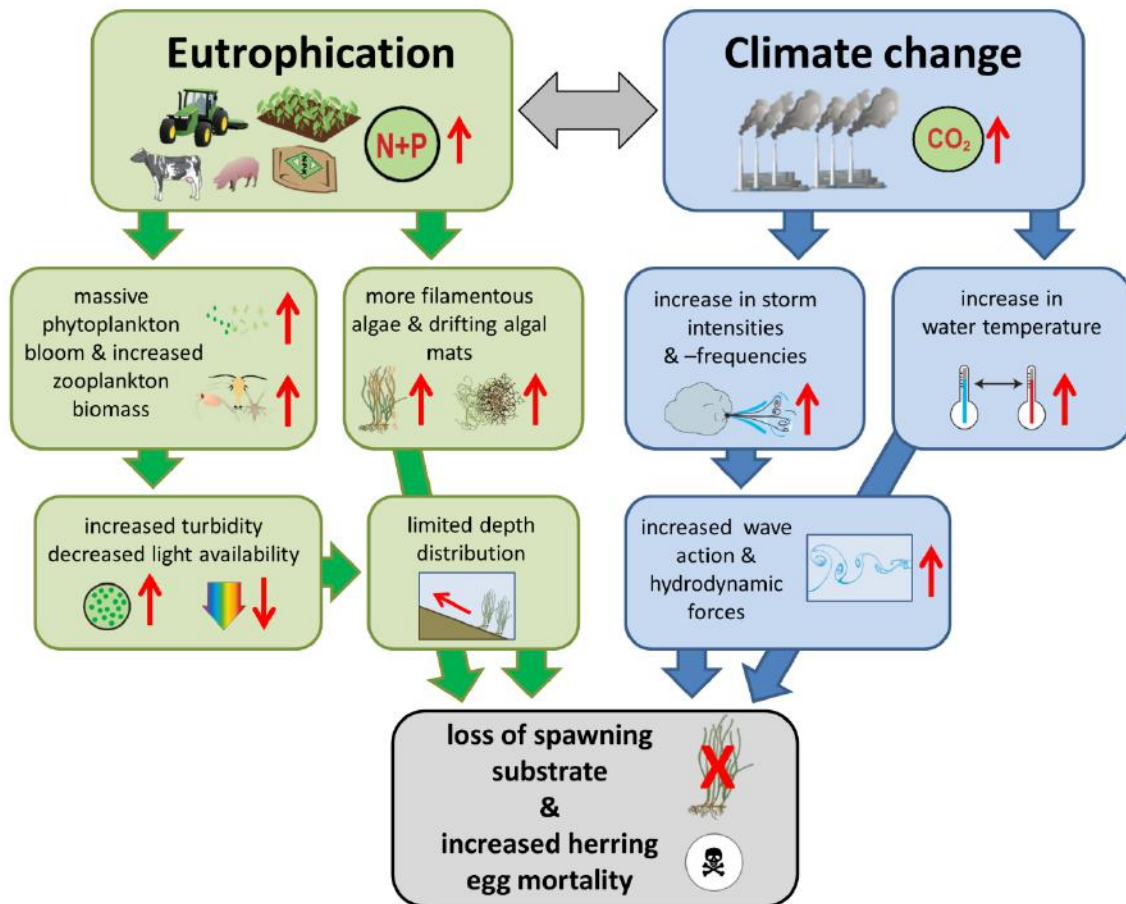
Figure 6: Conceptual diagram of eutrophication-induced cascade effects in synergy with climate change effects on herring spawning substrate loss and herring egg mortality, modified after (Rönnberg & Bonsdorff 2004). Symbols for this diagram are courtesy of the Integration and Application Network (ian.umces.edu/symbols).

Habitat use

In general, herring larvae of all developmental stages are considered as ichthyoplankton, implying that they are dispersed passively through the water column, showing no ability of active movement. Although active habitat selection was already observed for early life stages in coral reef fish (Dudley et al. 2000, Paris & Cowen 2004) and an active component in larval dispersal was observed in larval nase carp (*Chondrostoma nasus*) in high dynamic river systems (Schludermann et al. 2012), studies on this capability are still rather unnoticed. The results presented in chapter 6 indicate that the assumption of all larvae stages being passive drifting particles can be disproved (Fig. 7). Results showed that advanced stages of herring larvae are able to actively influence their distribution, moving to the shallow vegetated littoral zone, hence highlighting the importance of these littoral habitats in temperate waters for Western Baltic herring recruitment (Polte et al. 2017).
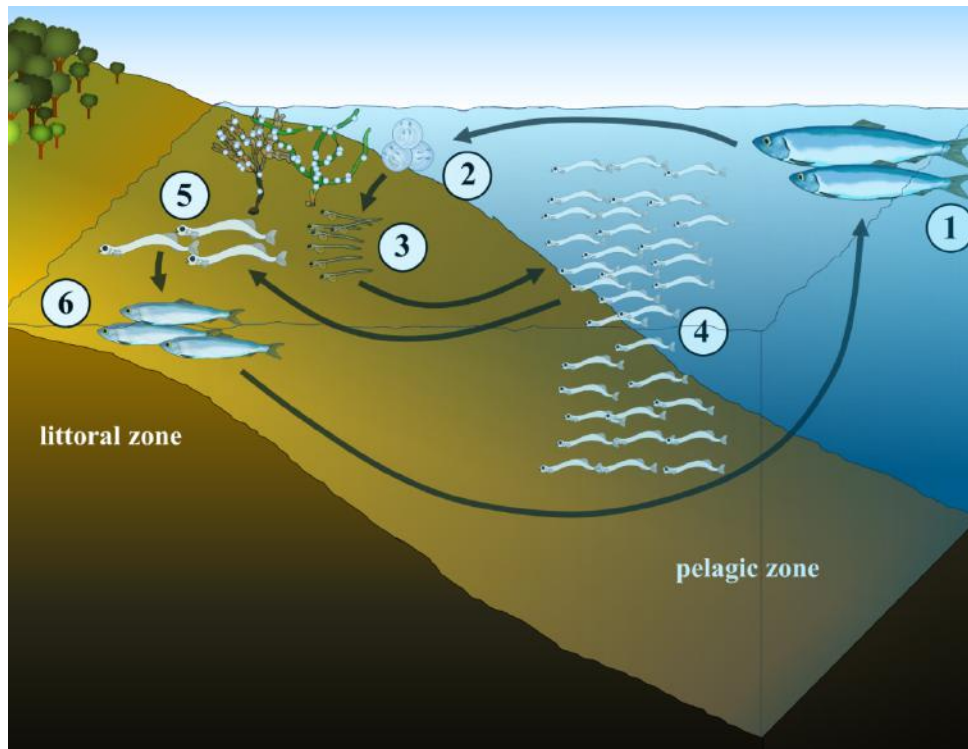
Figure 7: Ontogenetic habitat loop of herring in the Baltic Sea. Adult herring (**1**) migrate from the offshore pelagial into inshore waters to spawn their adhesive eggs on littoral substrates such as macrophytes (**2**). Yolk-bearing hatchlings (**3**) appear concentrated in the vicinity of the spawning beds, while medium sized larvae (**4**) are rather well horizontally distributed in the pelagic area of the bay; however their vertical distribution in the water column is significantly heterogeneous. Advanced larvae (**5**) return to shallow littoral areas where they remain until after their metamorphosis to the juvenile fish (**6**). Growing juveniles migrate to offshore areas along their development and usually recruit to the spawning group after 2-3 years (Source: Polte et al. 2017).

Houde (1969) investigated the swimming ability of yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) larvae in the Oneida Lake in New York, USA, and found differences in spatial distributions. Whereas yellow perch larvae were widely dispersed in the lake, walleye larvae were able to accumulate in bays, assuming better swimming abilities due to larger size at hatch (7.5 mm), greater amount of yolk and a higher number of postanal myomeres (Houde 1969). A recent study on larval herring swimming capabilities revealed an increased swimming ability according to developmental stage and temperatures (Moyano et al. 2016), showing an increased swimming capability with the onset of notochord at 14 mm body length, indicating that herring larvae are able to actively select their habitat at size classes of 24-28 mm (post-flexion stage). More research is needed to draw attention to the observed ability of herring larvae to actively select their habitat to reconsider the general assumption that larvae are passive drifting particles. This chapter demonstrated the essential role of the shallow vegetated littoral zone for herring recruitment success, emphasizing the implementation of coastal zone management strategies.

Distinct survival bottlenecks

Herring recruitment in the Western Baltic Sea continuously decreased since the year 2000 and reached its lowest level in 2016 (ICES Advice 2017). The reasons for this decline are still unclear, but it is assumed that multiple local drivers and stressors are acting on important spawning grounds, impacting herring reproduction success and recruitment. The impact of distinct local drivers and stressors might become even more important for future recruitment success and population dynamics, since Polte et al. (2014) stated two distinct larval cohorts with different survival bottlenecks along the season (Fig. 8). Along the time series of larval herring monitoring in Greifswald Bay from 1992-2011, the later larval cohorts were found to correlate stronger with recruitment strength than earlier cohorts (Polte et al. 2014). The bottlenecks for the second cohort are rather located on the egg stage and include, besides direct temperature stress and storm events, other biological stressors such as predation by sticklebacks (*Gasterosteus aculeatus*) (Kotterba et al. 2014, Kotterba et al. 2017) and lethal effects of filamentous algae (Ectocarpidae) (von Nordheim et al. unpublished).
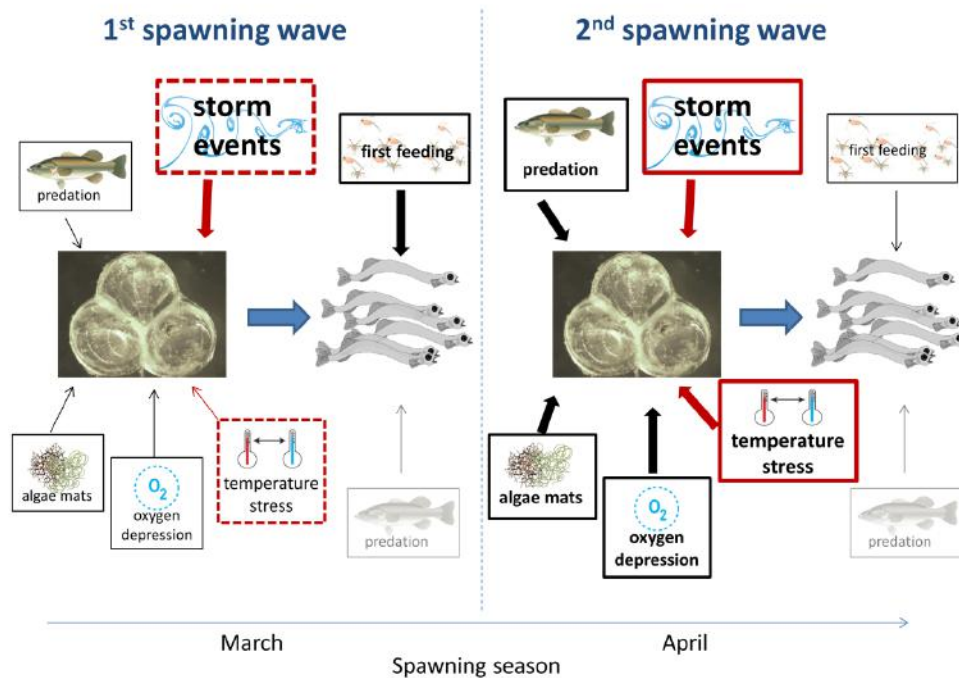
Figure 8: Conceptual diagram on distinct herring cohort bottlenecks, regarding future climate scenarios with an increase in storm frequencies and storm intensities. Red dashed local stressors might become more important in the future, where storm events are able to affect both cohorts and even higher temperature during the early spawning season are able to negatively affect herring recruitment. Symbols for this diagram are courtesy of the Integration and Application Network (ian.umces.edu/symbols).

Although nutrient inputs were reduced during the past 20 years, eutrophication is still a major issue in this important herring spawning area. Scientific forecasts of climate change, resulting in increased storm intensities and -frequencies (Woth et al. 2006, Coumou & Rahmstorf 2012) could mean a future increase of storm-induced herring egg mortality to an unknown extent. Regarding future climate change scenarios and the observed temporal shift in spawning phenology of Western Baltic herring, some bottlenecks and local stressors, normally occurring in the later season, might already negatively affect the first cohort and will become more disastrous for the later cohort by an increasing impact throughout the season (Fig. 8), having a dramatic consequences on future herring recruitment success.

The first part of this thesis revealed that herring reproduction on one important Western Baltic spawning ground is highly affected by local stressors. Since eutrophication-induced indirect cascade effects resulted in multiple drivers and stressors, acting on a local scale of important spawning grounds, it is necessary to evaluate the actual contribution of single spawning areas to the Western Baltic herring population to underline the potential of local ecosystem threats to be transported to the population level. The second part of this thesis deals with contribution estimates of different juvenile habitats to the overall Western Baltic herring population.

Consequences of regional stressors for general population dynamics

Atlantic herring in the Western Baltic Sea undertakes long distance migrations between their summer feeding grounds in the Kattegat/Skagerrak, their overwintering area in the Öresund Strait and their inshore coastal reproduction areas along the Western Baltic Sea (Otterlind 1987, Scabell 1988, Poulsen et al. 2000, Nielsen et al. 2001) (Fig. 9). Whereas Greifswald Bay is a well-described and essential spawning area for the Western Baltic herring population (Klinkhardt 1984, Scabell 1988, Oeberst et al. 2009, Polte et al. 2014), information on other herring spawning areas are rather scarce, descriptive or even anecdotal (but see Altnöder 1929, Nellen 1965, 1968, Neb 1970, Weber 1971, Schnack 1974).

Although correlations between the larval herring N20-index and abundance data of age-1 and age-2 herring in the overall Western Baltic Sea suggest that herring recruitment is not independent from the larval production in Greifswald Bay (Oeberst et al. 2009), quantitative studies on the contributions of single coastal juvenile habitats to the adult herring population and their consistency over time are currently missing but are essential to understand and evaluate the impact of regional stressors on overall stock recruitment. In addition, investigations on Western Baltic herring homing behavior are not yet available, but information on which
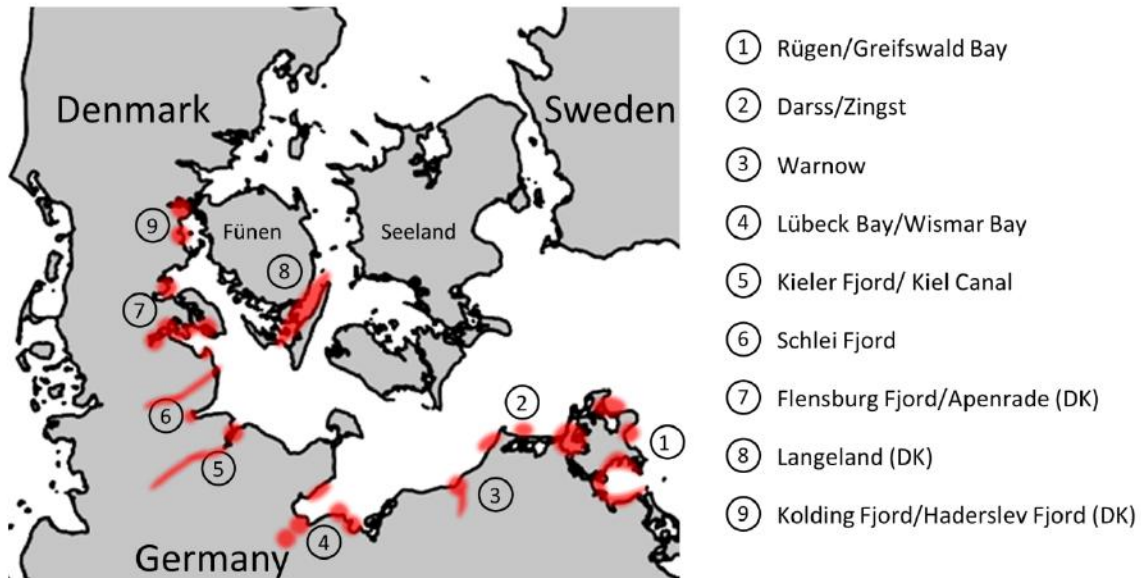
Figure 9: Historically known spawning areas for the Western Baltic herring population along the Western Baltic Sea from the Danish coast and the coast of Schleswig-Holstein, Germany, to the eastern spawning areas along the coast of Mecklenburg Western-Pomerania. Potential spawning areas along the Polish coast are not represented. Figure is modified after Weber (1971).

spatial scales homing is happening, either to the general south-western Baltic coast or to certain spawning areas or even to a particular spawning ground, is crucial for the evaluation of habitat dependence and therefore the relevance of single habitats for the adult population. The following studies (chapter 1 and 2) presented the first empirically compiled data on the contribution of differing (historically known) juvenile areas to the adult population. The results revealed that recruits originating from Greifswald Bay indeed contributed most to the adult herring population. This confirms a superior function of the bay as an important nursery area for the Western Baltic herring population (chapter 2). Moreover, our data showed that herring homing occurs on a quite small spatial scale, indicating the first evidence of natal homing of *C. harengus* in the Western Baltic Sea, where herring adopt some straying individuals from other juvenile habitats (chapter 3), thereby promoting the "adopted migrant" hypothesis postulated by McQuinn (1997).

Habitat connectivity

Otolith microchemistry analyses of juvenile herring otoliths, collected from different spawning areas along the Western Baltic coast, revealed clear habitat-specific elemental fingerprints (chapter 1), which were used as chemical habitat signature baseline for the habitat contribution analysis. By analyzing the chemical compositions of adult herring otolith core regions, we
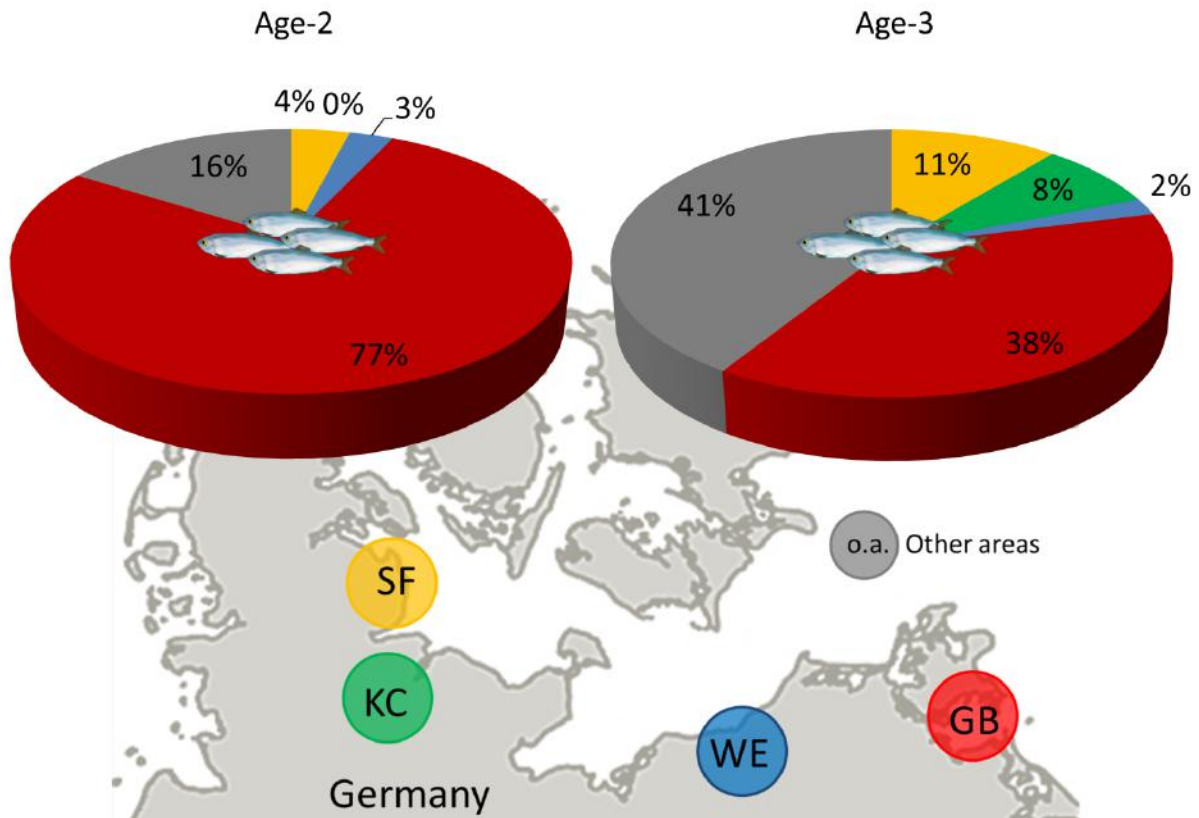
Figure 10: Results from the contribution estimations of four different spawning areas (Schlei Fjord (SF, yellow), Kiel Canal (KC, green), Warnow Estuary (WE, blue), Greifswald Bay (GB, red) and other areas (o.a., grey)) to the overall Western Baltic herring population. Pie charts indicate percentage of contribution of distinct areas to the adult between the two investigated year classes.

were able to assign individual adult herring from a winter accumulation area to their distinct natal spawning areas (chapter 2). Classification results revealed that offspring from Greifswald Bay contribute the most to the adult population regarding herring of age-2 (77%), but varied between the years (38% for age-3 herring) (Fig. 10).

Since not all juvenile areas of the population are known along the Western Baltic Sea, we carefully addressed this circumstance by defining an additional group ("other areas"), based on individuals with classification likelihoods below 75%. The data showed that potential other habitats contributed about 16% to the adult herring population (age-2 individuals) and up to 41% to age-3 herring (Fig. 10). Regarding the good fit of the model and the generally high percentages of assignable adults (above the 75% threshold) our results indicate that a certain stability of chemical signals across years is given in the system. We did not find any contradicting strategy/approach in the literature, dealing with the contribution estimations of non-sampled habitats, nevertheless, our approach is assumed to represent the potential proportion of non-sampled juvenile habitats. The recent outcomes on herring habitat connectivity and homing behavior are reliable and valid, since the general sample sizes of

juvenile and adult otoliths were carefully chosen after an adequate inquiry of sample sizes from otolith microchemistry studies (Gillanders & Kingsford 1996, Rooker et al. 2001, Gillanders 2002, Cuveliers et al. 2010).

Maternal effects are reported to potentially impact the chemical composition of juvenile otoliths (Volk et al. 2000, Thorrold et al. 2006), possibly due to increased maternal investment, such as egg size (Ruttenberg et al. 2005). However, we do not consider our results affected by maternal impacts, due to the fact that otolith formation usually starts at the late embryonal development (Geffen 1982, Campana et al. 1987, Morales-Nin 2000), when spawned eggs are not anymore in contact with the maternal metabolism but in direct exchange with the surrounding water. Despite transmission of maternal effects to eggs (yolk deposition) during maturation (Volk et al. 2000), otolith material, which could be affected is rather small, regarding otolith size at yolk-sac absorption of about 10.8-11.7 µm (Geffen 1982). By choosing a laser spot size of 80 µm (based on Geffen et al. 2011), it can be assumed that measured herring otolith elemental signatures are rather reflecting inshore habitat-specific signals than being biased by maternal effects (Volk et al. 2000, Thorrold et al. 2006).

Although it is reported that inter-annual variability of elemental concentrations are able to influence classification results, the effect is supposed to be less significant at broader spatial scales (Turner & Limburg 2014) and we carefully addressed this topic by using only elements, which were not present in significantly different concentrations between two consecutive years to define the Greifswald Bay habitat signal. This approach seems applicable, since Rooker et al. (2001) showed inter-annual consistency of specific elemental concentrations.

Although there is a strong correlation between the annual larval production in Greifswald Bay and the age-1 juveniles in the overall Western Baltic Sea recruiting to the population over a 25 year time series (Polte & Gröhsler 2018), there is some annual variability in this relation. From this variability it might be derived that in some years other areas provide the majority of recruits. This is in line with our findings that the numerical contribution of recruits from Greifswald Bay differs between year-classes. We consider our sampling of the adult population from the Öresund Strait as relatively robust against e.g. patchiness effects of schooling fish since we sampled fish from four different stations. The Öresund Strait is considered the main overwintering area for the population (Otterlind 1984, Nielsen et al. 2001) and therefore sampling in this area during October is probably the best setting to receive a representative sample of the adult population.

Future contribution studies should seek for sufficient and homogeneous adult sampling of all potential stations/locations. A future sampling strategy should consider all potential spawning areas along the Western Baltic Sea (including habitats at the Polish, Danish and Swedish

coastlines) to increase the level of assignment of the proportion of "other areas". Furthermore, broad sampling should be conducted in a 3-year time frame to sample age-0 herring and proof the consistency of habitat-specific chemical signatures over time, following the cohort until maturation.

Although it is well-established that otolith chemistry generally reflects the physical and chemical characteristics of the ambient water, where the fish is residing throughout its life (Campana & Neilson 1985, Campana 1999) other environmental variables, such as temperatures and salinity (Elsdon & Gillanders 2002, Elsdon & Gillanders 2003) or endogenous drivers on physiology (e.g. growth and stress) can affect elemental incorporation into otoliths (Kalish 1989, Hamer & Jenkins 2007, Walther et al. 2010, Sturrock et al. 2014). Regarding future perspectives, much more effort should be taken in investigating additional drivers affecting herring otolith chemistry. For example, some studies include contrasting statements on the impact of food composition on otolith elemental incorporation (Limburg 1995, Walther & Thorrold 2006). Future studies should imply validation experiments on existing exogenous and endogenous factors affecting herring otolith chemistry. Moreover, according to Gillanders (2002), a library of elemental fingerprints over several years for each juvenile habitat should be build up to increase the interpretation success of fingerprint patterns. With regards to observations on spawning activity in seagrass beds located on the outer coastline of Mecklenburg Western-Pomerania, sampling should be extended to take all possible spawning habitats into account for future investigations.

The results of the nursery area identification (chapter 2) broaden the understanding of habitat connectivity between inshore coastal spawning areas in the Western Baltic Sea and the adult herring population, indicating that Greifswald Bay contributes a major amount to the overall Western Baltic herring population in both studied year-classes, compared to other investigated habitats. This underlines the former assumptions and indications of a strong relationship between Greifswald Bay larval production and age-1 and age-2 herring (Oeberst et al. 2009), identifying Greifswald Bay as a Western Baltic herring nursery area, according to the nursery concept after (Beck et al. 2001). Our findings support the conclusion that local stressors have the potential to be transported to the population level.

Homing

In respect of Atlantic and Pacific herring homing studies, which are mainly based on physical mark-recapture methods (Wheeler & Winters 1984, Hay & McKinnell 2002), statements on natal homing are quite difficult. With our homing study based on otolith chemistry (chapter 3), we demonstrated herring homing behavior to their spawning areas of natal-origin for the

first time, a known behavioral trait rather observed in salmonids (Hasler et al. 1978, Dittman & Quinn 1996). We further observed some straying individuals originated from the Schlei Fjord (10%), making it difficult to speculate on the general homing mechanisms. According to the adopted-migrant hypothesis after McQuinn (1997), herring homing behavior is mainly driven by social learning, where recruiting juveniles learn their migration routes from repeated homing adults (McQuinn 1997). Hourston (1959) further reported that juvenile herring show a greater tendency of mixing at the feeding grounds and consequently juveniles might become strayers, joining other populations (Hourston 1959), which supports McQuinn's social learning theory. On the other hand, (Brophy et al. 2006) stated natal homing behavior of Atlantic herring in the Celtic Sea, assuming that larval imprinting to their natal spawning areas is more likely the driving mechanism rather than social learning by repeated individuals (Brophy et al. 2006). Our results support McQuinn's hypothesis to the effect that some individuals stray to another spawning areas, but our findings on herring natal homing seems to be contrary to his main assumptions, supporting rather the theory after Brophy et al. (2006). We can only speculate that either herring do home to their natal area by some olfactory imprinting, as described for salmonids (Hasler et al. 1978), but are more attracted by natal or non-natal migration schools during the open sea phase, thus some individuals got lost at population mixing areas and migrating with non-natal populations or natal homing is a random event, based on juveniles occurring along the outer coast at their first year (near their spawning areas) and while repeated spawning adults are more stable in their migration routes (McQuinn 1997), juveniles join adult schools to their natal spawning areas in spring and migrating together to the feeding grounds, where mixing events facilitate straying to other migration groups. The scientific controversy on homing mechanisms demonstrate the great demand of further research on herring homing behavior, regarding other local spawning populations and homing mechanisms with focus on olfactory recognition of natal habitats.

Conclusions

This thesis demonstrated that Greifswald Bay is an important nursery habitat for the Western Baltic herring population. This inshore nursery area is of high ecological and economical relevance, since all herring life stages (from the egg stage to the adult herring) showed a high habitat dependency (Fig. 11).

This thesis further presented that local stressors, acting on a regional scale of important spawning grounds, have the potential to be transported to the adult herring population level, since contribution estimations revealed a major importance of Greifswald Bay, consequently
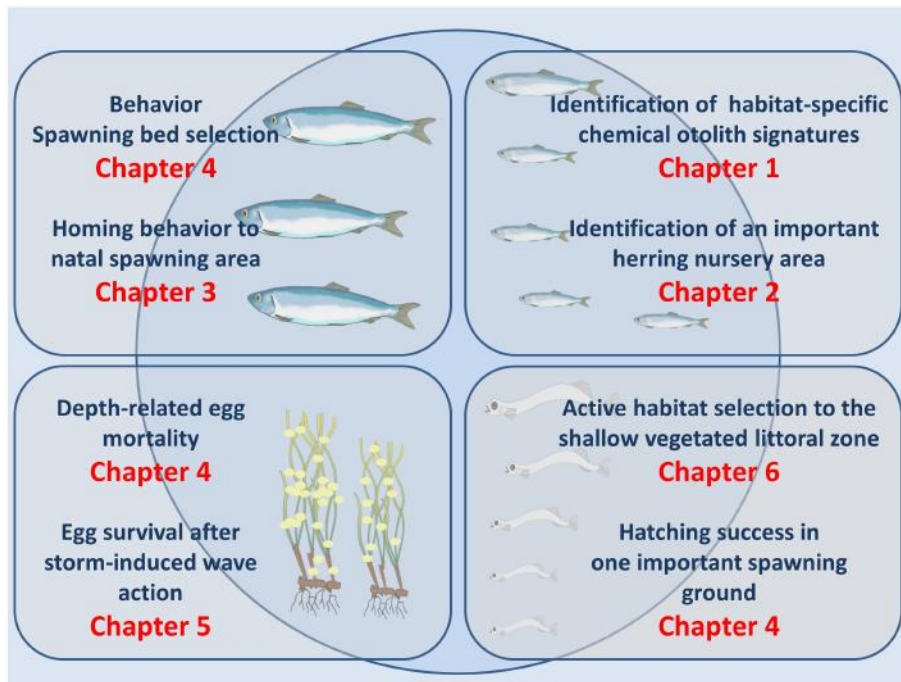
Figure 11: Conceptual diagram on the strong habitat dependency of Western Baltic herring to the inshore coastal spawning grounds. All life stages are highly depended on the shallow littoral zone within the important nursery area Greifswald Bay. Matured adult herring showed strong habitat dependence to their reproduction areas, returning to their spawning areas of natal origin. Symbols for diagrams courtesy of the Integration and Application Network (ian.umces.edu/symbols) and symbols of herring larvae and adult herring are created by Paul Kotterba.

being vital for the resilience of the overall herring population. This is further underlined by the identification of herring homing behavior to their natal spawning areas on a quite small spatial scale, reaffirming the immense ecological relevance of single spawning areas to the resilience of this economically stressed fish species, contributing a high amount to the worldwide human nutrition. Future climate scenarios and forecasts of increasing weather extremes will result in an even more distinctive temporal shift of spawning phenology, which is supposed to highly stress herring recruitment in the future. Since these findings are generally applicable also for other commercially and ecologically important demersal spawning fish species, we should be distinctly aware of anthropogenic-caused cascade effects and their effects on fish population persistence. This thesis highlighted the need for a coastal zone management with the future key tasks to reduce coastal habitat alterations and construction purposes and to improve the ecological status of these ecosystems, reducing eutrophication and subsequent induced cascade effects to preserve fish as crucial natural resources for future generations.

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Declaration on oath

I hereby declare, on oath, that I have written the present dissertation:

„Contribution of coastal nursery areas to the spring-spawning population of Atlantic herring (*Clupea harengus*) in the Western Baltic Sea"

by my own and have not used other than the acknowledged resources and aids.

Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift mit dem Titel:

„Contribution of coastal nursery areas to the spring-spawning population of Atlantic herring (*Clupea harengus*) in the Western Baltic Sea"

selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Rostock, den 21.08.2018   Dorothee Moll

Declaration of authors' contributions to the manuscripts included within this thesis:

The chapters of this thesis are partly published or in preparation to be published in scientific journals with multiple authorships. The list below serves as a clarification of my personal contributions to each manuscript/publication.

Chapter 1

Using elemental fingerprinting in Western Baltic juvenile herring (*Clupea harengus*) otoliths to distinguish different juvenile habitats

Dorothee Moll, Paul Kotterba, Klaus Peter Jochum, Daniel Pröfrock, Lena von Nordheim and Patrick Polte

Manuscript, not published yet

I planned the study in agreement with the Co-authors. I conducted the sampling. I was also responsible for the sample selection and for laboratory processing. Sample preparation, measurements with the LA-ICP-MS, calculations and data digitalization were conducted by me. Data analyses and statistical analyses were mainly done by me, with support of the Co-authors. I wrote the manuscript, the Co-authors revised the manuscript.

Chapter 2

Contribution of an inshore nursery area to the Atlantic herring (*Clupea harengus*) population in the Western Baltic Sea

Dorothee Moll, Klaus Peter Jochum, Paul Kotterba, Lena von Nordheim, Tomas Gröhsler and Patrick Polte

Manuscript, not published yet

I planned the study in agreement with the Co-authors. I was also responsible for the sample selection and for laboratory processing. Sample preparation, measurements with the LA-ICP-MS, calculations and data digitalization were conducted by me. Data analyses and statistical analyses were mainly done by me, with support of the Co-authors. I wrote the manuscript, the Co-authors revised the manuscript.

Chapter 3

First evidence of natal homing behavior of Atlantic herring (*Clupea harengus*) in coastal waters of the Baltic Sea

Dorothee Moll, Klaus Peter Jochum, Paul Kotterba, Lena von Nordheim, Tomas Gröhsler and Patrick Polte

Manuscript, not published yet

I planned the study in agreement with the Co-authors. I was also responsible for the sample selection and for laboratory processing. Sample preparation, measurements with the LA-ICP-MS, calculations and data digitalization were conducted by me. Data analyses and statistical analyses were mainly done by me, with support of the Co-authors. I wrote the manuscript, the Co-authors revised the manuscript.

Chapter 4

Spawning bed selection of Atlantic herring (*Clupea harengus*) in the waters of the Western Baltic Sea

Dorothee Moll, Paul Kotterba, Lena von Nordheim and Patrick Polte

Manuscript, not published yet

I conducted the sampling with the support of the Co-authors. I was also responsible for the laboratory processing, data collection and data digitalization. Data analyses and statistical analyses were mainly done by me, with support of the Co-authors. I wrote the manuscript, the Co-authors revised the manuscript.

Chapter 5

Storm-induced Atlantic herring (*Clupea harengus*) egg mortality in Baltic Sea inshore spawning areas

Dorothee Moll, Paul Kotterba, Lena von Nordheim and Patrick Polte

This chapter has already been published in Estuaries and Coasts:

Moll, D., P. Kotterba, L. von Nordheim, P. Polte 2018. Storm-induce Atlantic herring (*Clupea harengus*) egg mortality in Baltic Sea inshore Spawning Areas. Estuaries and Coasts 41:1-12.

I partly conducted the sampling with the support of the Co-authors. I was also responsible for the laboratory processing, data collection and data digitalization. Data analyses and statistical analyses were mainly done by me, with support of the Co-authors. I wrote the manuscript, the Co-authors revised the manuscript.

Chapter 6

Ontogenetic loops in habitat use highlight the importance of littoral habitats for early life-stages of oceanic fishes in temperate waters

Patrick Polte, Paul Kotterba, Dorothee Moll and Lena von Nordheim

This chapter has already been published in Scientific Reports:

Polte, P., P. Kotterba, D. Moll and L. von Nordheim. 2017. Ontogenetic loops in habitat use highlight the importance of littoral habitats for early life-stages of oceanic fishes in temperate waters. Scientific Reports 7:42709 (publication date: 16 February 2017)

Patrick Polte (P.P.) and Paul Kotterba (P.K.) designed and performed research; Dorothee Moll (D.M.) contributed methods and data; D.M. and Lena von Nordheim (L.v.N.) analyzed data, participated in conceptualizing the study and revised the manuscript. P.P. and P.K. wrote the manuscript.

Further Publications (not included in this thesis):

Kotterba, P., D. Moll, C. Hammer, MA Peck, D. Oesterwind and P. Polte. 2017. Predation on Atlantic herring (*Clupea harengus*) eggs by the resident predator community in coastal transitional waters. Limnology and Oceanography 62:2616-2628.

Kotterba, P., D. Moll, L. von Nordheim, MA Peck, D. Oesterwind and P. Polte. 2017. Predation on larval Atlantic herring (*Clupea harengus*) in inshore waters of the Baltic Sea. Estuarine, Coastal and Shelf Science 198:1-11.

Von Nordheim, L., P. Kotterba, D. Moll and P. Polte. 2018. Impact of Spawning Substrate Complexity on Egg Survival of Atlantic herring (*Clupea harengus* L.) in the Baltic Sea. Estuaries and Coasts 41:549-559.

Hereby, I confirm the accuracy of the statements above,

Dorothee Moll	Dr. Patrick Polte
(Doctoral candidate)	(On behalf of the supervisors)

Appendix

C1: Using elemental fingerprinting in Western Baltic juvenile herring (*Clupea harengus*) otoliths to distinguish different juvenile habitats

Table A1: Technical information about the laser ablation system and the operating parameters of the ICP-MS which was used for trace element analysis of juvenile otoliths (Jochum et al. 2007).

New Wave laser ablation system	
Wave length/nm	213
Pulse length/ns	5
Energy density/ J cm^{-2}	7-10
Irradiance at sample/GW cm^{-2}	1.4-2.0
Spot size/µm	5-160
Pulse repetition rate/Hz	1-20
Operating parameters	
rf power/W	1270
Cool gas flow rate/l min^{-1}	15
Auxiliary gas flow rate/l min^{-1}	1
Carrier gas (Ar) flow rate/l min^{-1}	0.8
Carrier gas (He) flow rate/l min^{-1}	0.7

Table A2: Otolith element concentrations (µg g^{-1}) of 44 elements in age-0 herring otoliths from Western Baltic outer coastal sampling sites in Denmark (DK), Mecklenburg Bay (MB), Kiel Bay (KB) and sampling sites around the vicinity of the Island of Rügen (R1, R2, R3). Elemental concentrations were analyzed with the solution based-ICP-MS and for each sampling site, two to five otoliths were pooled together.

	Outer coastal sampling sites					
Elements	DK	KB	MB	R1	R2	R3
Li	0.406	0.078	0.385	0.000	0.000	0.000
Be	0.002	0.002	0.000	0.002	0.002	0.001
B	7.341	0.000	8.366	0.000	0.000	0.000
Mg	63.6	64.7	67.4	49.7	47.8	46.4
Al	2.15	4.70	2.39	2.34	2.19	2.45
Sc	0.011	0.021	0.017	0.019	0.020	0.024
Ti	0.026	0.071	0.030	0.107	0.036	0.180
Mn	1.94	3.34	4.51	2.34	2.31	2.64
Fe	1.07	3.04	4.49	1.71	1.46	1.69
Co	0.015	0.025	0.023	0.027	0.016	0.013
Ni	0.000	0.000	0.005	0.000	0.077	0.000
Cu	0.000	0.000	0.000	0.616	0.081	0.025
Zn	2.51	3.93	4.05	3.36	3.49	2.22
Ga	0.000	0.150	0.124	0.185	0.208	0.343
Se	0.142	0.193	0.182	0.135	0.151	0.207
Rb	0.094	0.155	0.174	0.173	0.096	0.101
Sr	829.4	767.9	835.3	686.3	659.6	975.3
Y	0.005	0.007	0.004	0.006	0.004	0.005
Zr	0.077	0.094	0.000	0.003	0.008	0.000
As	0.012	0.046	0.034	0.005	0.010	0.011
Mo	0.002	0.011	0.006	0.006	0.005	0.004
Ru	0.000	0.003	0.003	0.002	0.001	0.003
Pd	0.243	0.222	0.245	0.212	0.240	0.298
Ag	0.000	0.001	0.000	0.000	0.001	0.001
Cd	0.004	0.005	0.004	0.024	0.007	0.030
Te	0.003	0.000	0.003	0.000	0.000	0.000
Cs	0.001	0.001	0.001	0.000	0.001	0.000
Ba	0.77	3.77	3.02	3.89	4.64	7.39
La	0.000	0.000	0.000	0.002	0.000	0.000
Ce	0.000	0.001	0.000	0.003	0.000	0.000
Pr	0.000	0.000	0.000	0.001	0.000	0.000
Nd	0.001	0.000	0.000	0.003	0.000	0.000
Sm	0.000	0.000	0.000	0.001	0.000	0.000
Eu	0.000	0.000	0.000	0.000	0.000	0.001
Dy	0.000	0.001	0.000	0.001	0.000	0.001
Tm	0.000	0.001	0.000	0.000	0.000	0.000
W	0.002	0.006	0.003	0.001	0.007	0.001
Pt	0.041	0.043	0.023	0.019	0.017	0.029
Au	0.026	0.072	0.003	0.002	0.009	0.007
Hg	0.058	0.145	0.044	0.025	0.033	0.048
Tl	0.014	0.027	0.004	0.005	0.006	0.007
Pb	0.008	0.015	0.006	0.033	0.010	0.015
Th	0.003	0.015	0.000	0.000	0.000	0.001
U	0.001	0.000	0.000	0.001	0.000	0.001

C2: Contribution of an inshore nursery area to the Atlantic herring (*Clupea harengus*) population in the Western Baltic Sea

Table A1: Results of ANOVA to identify significant differences between the four sampling areas, including GB samples from 2015 and 2016 as two separated groups, with degrees of freedom (df), F-value and significance level (p). Post-hoc test (Games Howell test) revealed no significant differences in elements between the two-year sampling in GB ($p > 0.05$), except for Fe ($p_{GB2015\_GB2016} = 0.006$).

| Element	df	F	p
Li	4	19.99	< 0.001
B	4	49.71	< 0.001
Na	4	27.48	< 0.001
Mg	4	21.87	< 0.001
Mn	4	13.68	< 0.001
Fe	4	10.25	< 0.001
Rb	4	4.56	0.001
Sr	4	18.74	< 0.001
Ba	4	11.75	< 0.001

C4: Spawning bed selection of Atlantic herring (*Clupea harengus*) in the waters of the Western Baltic Sea

Figure A1: Subsampling method of SAV biomass sample (left), three subsamples of a standardized area (right).
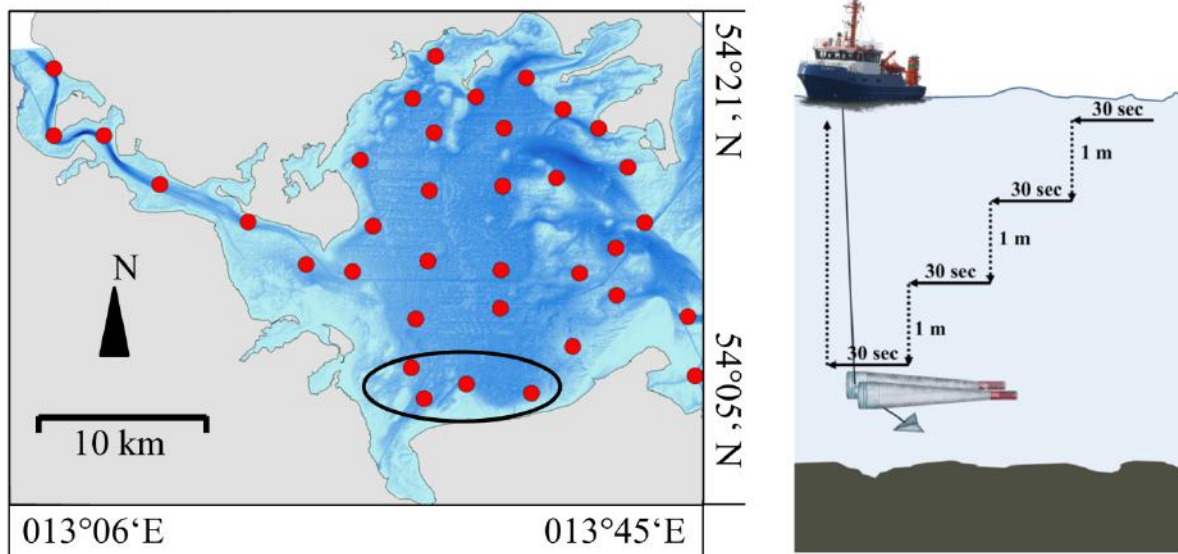
Figure A2: The sampling station grid (35 stations) for the RHLS ichthyoplankton sampling in the spawning area Greifswald Bay (left) with the four selected stations for the hatchling abundance analysis, indicated by the black frame. On the right side, the schematic illustration on Bongo net hauls by towing the net stepwise from the surface to 1 m above the sea ground (modified from Polte et al. 2017).
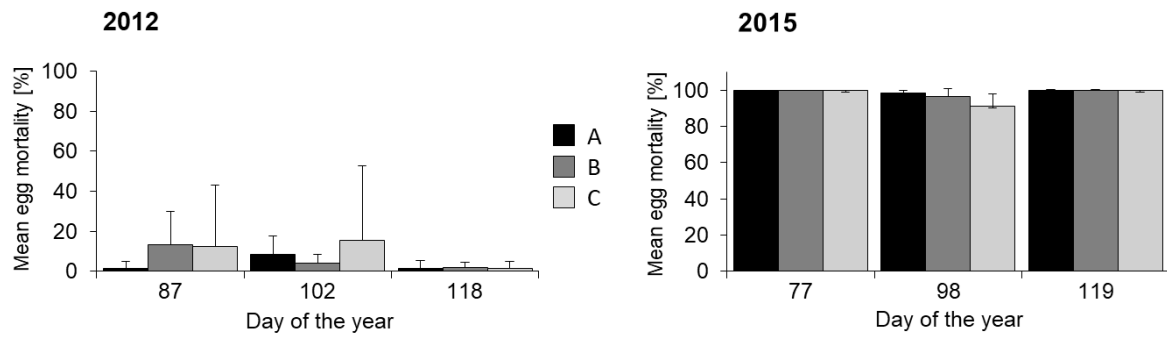
Figure A3: Depth-related mean egg mortality rates (with standard deviation) for each spawning peak along the spawning seasons 2012 and 2015