The monitoring of the spatiotemporal distribution and movement of brown shrimp (*Crangon crangon* L.) using commercial and scientific research data

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1 SUMMARY

This study aimed at closing important knowledge gaps relevant for the stock assessment of brown shrimp (*Crangon crangon* L.), a species supporting a large fishery with over 500 active vessels, mainly fishing on brown shrimp with annual landings exceeding 30 000 t. The majority of the annual catch is obtained by the Dutch and German fleet mainly operating in Natura 2000 sites of the Wadden Sea, designated for the protection of habitats. Despite the sensitive location of the fishing grounds and the large size of the fleet, the European brown shrimp fishery is currently unmanaged.

However, recently a management strategy has been discussed for the brown shrimp stock as well as for the Natura 2000 sites. A management plan for the brown shrimp stock appears to be necessary since there are indications of growth overfishing. A potential risk for the brown shrimp population exists due to the increasing efficiency of the fleet, which is also reflected in increased mean annual landing volumes of 32 972 t (2000 – 2013), which nearly is twice the amount of the mean landing volume of 16 820 t reached from 1960 – 1999. Therefore, the International Council for the Exploration of the Sea (ICES) in October 2014 advised to implement a management of the brown shrimp stock. Due to the short life span of brown shrimp an annual stock assessment based on scientific surveys and the determination of annual total allowable catches (TACs) are not suitable. Consequently, ICES recommends that the management ought to be based on monthly commercial brown shrimp catches including the monitoring of commercial landings per unit effort (LPUE) and an additional scientific monitoring to obtain independent estimates, for example on biomass.

Unlike the brown shrimp stock management, the management considerations for the Natura 2000 sites focus on spatial protection measures for specific habitats and can therefore be expected to affect the brown shrimp fishery and in consequence also potentially the brown shrimp stock. The Natura 2000 management considerations include the estimation of the degree of degradation or destruction to which those sites are exposed. In order to protect ecologically coherent areas, the establishment of spatial closures for the brown shrimp fishery is suggested.

The suitability and the potential impact of any possible future management option, either for Natura 2000 sites or for the brown shrimp stock can only be discussed if so far unavailable spatiotemporal variations in the brown shrimp abundance are described. Up to now, knowledge on the spatial distribution of brown shrimp is derived from spatially limited annual survey data only. However, commercial data are available, providing information from more than 200 German brown shrimp vessels with a large spatial and temporal coverage. This valuable data source was so far unused despite its potential to provide a comprehensive picture of the spatiotemporal distribution of brown shrimp which is not available from survey data only.

Estimates about the spatiotemporal distribution of brown shrimp from either of the named data sources are obtained from catch rates per unit of time. The same applies to estimates needed for brown shrimp stock assessment, such as the swept area biomass. Thereby the catchability of the gear is assumed to be constant, i.e. it is presumed that always the same amount and composition of abundant brown shrimp is caught. However, this might not be the case and the standardised catch rates may depend on environmental factors, such as depth, daylight or tidal state but also vessel dependent factors, for example power. Such factors could influence the amount of brown shrimp caught as well as the proportions of large, small, egg-carrying and not egg-carrying brown shrimp in the catches.

This study pursued the identification of factors affecting catch rates and the composition in the catches in order to contribute to a sound basis for the calculation of reliable estimates necessary for brown shrimp management. We also aimed to quantify the portion of the brown shrimp stock located pelagically and thus unreachable for the beam trawl, the traditional catching device. Further, this thesis aimed to establish a comprehensive picture of the spatiotemporal patterns in the distribution of the brown shrimp stock.

Factors potentially affecting catchability such as season, depth, tidal state, daylight, sex, reproductive state and size of the shrimps were addressed in **manuscript 1**. To identify the influencing factors, three different German survey data sets were used, covering the years 1997 – 2010. The surveys included data from autumn and winter beam trawl surveys as well as data from a vertically resolving stow net. All the named factors were found to influence the catch rates significantly; especially the composition of the beam trawl catches was strongly influenced by depth. Particularly in winter, females carrying eggs (berried females) were found to disperse more evenly over depths from 12 – 54 m than the brown shrimp without eggs (unberried individuals) which rather accumulated in shallower water. In winter, a significant effect of tidal state was found, suggesting two different survival strategies for the winter months: The "nearshore" brown shrimp stayed close to the coast and used the flood stream to get into shallower water, while the "offshore" brown shrimp used the ebb stream to be transported towards deeper water. Hence, the expected offshore migration of large and berried females was not found in the form of a simple ebb stream transportation.

The most impressive and surprising result of the survey data was obtained from analysing the vertically resolving stow net data, The stow net was employed from April – September in 2005 – 2007 and the results of our analysis show clearly that in these months more than 70% of the brown shrimp are expected to be in pelagic layers of the water column, unreachable for the beam trawl. This finding clearly challenges the assumption of brown shrimp living primarily benthically and already led to an adaption of the swept area biomass estimate.

Overall, the results of the analysis described in **manuscript 1** suggest that for obtaining reliable estimates such as the swept area biomass, survey data need a standardisation of the catch rates and the composition of the catches. This

standardisation should be extended from trawling speed, gear used and haul duration to also include at least season, depth, daylight and tidal state.

Manuscript 2 deals with methodical aspects of using commercial brown shrimp data for spatial estimations of effort and catch. Effort and catch estimations are needed to obtain spatial LPUE estimates, from which, in a further step, the spatiotemporal distribution of brown shrimp can be evaluated. Spatial estimates, either of effort or catch can be obtained, if vessel monitoring system (VMS) data is combined with logbook and landing data. The VMS data include information about the vessels' position ('pings') on a two-hourly basis. It is not recorded, where the vessels were located during a two hourly interval. Prior to this study at least five different methods have been developed to deal with this uncertainty. However, it had remained unclear, to what extent the methods differ in their spatial estimations. Moreover, the spatial estimations from combined commercial data are based on arbitrarily chosen resolutions, which might also influence the results.

To elucidate the performance of the various methods for evaluating the fine-scale spatial distribution of the brown shrimp fishery, in **manuscript 2** raw pings, the straight line interpolation, cubic Hermite splines, ellipses and the amplification method were applied on different resolutions within the range of 0.005° x 0.005° to 1° x 1° (latitude/longitude). Subsequently, a comparison of the methods at different resolutions was performed, contrasting the distribution and spatial extent of the estimated areas fished. Likewise, total effort and catch estimates were compared, which were allocated to differently sized case study areas, located within the German brown shrimp fishing grounds. As case study areas served a small windfarm and three German National parks, all of them entirely designated as Natura 2000 sites, but at present still allowing unmanaged brown shrimp fishing activities.

The results show that the area identified as having been fished differed in its location between the methods even at the very coarse resolution of 1°x1°. Moreover, the spatial distribution of allocated effort and catch within the case study areas was not identical between any of the methods. Further, effort and catch allocated to the case study areas differed by 11 to > 100% between the methods, with especially large differences in areas where only little information about the fishing vessels was available. Hence, the findings of this study elucidate that the estimated fished area varies between methods. They show that effort and catch estimations should be handled cautiously, as they might differ considerably, especially in areas were only few fishing positions are transmitted. The latter becomes relevant if estimations of effort and catch are, for example, used for the calculation of compensations that have to be paid in relation to previously fished areas that were turned into no take zones.

Considering the different tested resolutions, the resolution should from the user's point of view be as small as possible to provide detailed information. At the same time the resolution should prevent artificially allocated unfished areas between consecutive pings, when raw pings are used. The findings of this study show clearly, that for the data of German brown shrimp fishers the very fine resolution of 0.005° x 0.005° would still be too coarse as it still led to an undesirable 'patchy' distribution of pings within a single 0.005° x 0.005° grid cell. A patchy situation implies that within a grid cell non-homogeneous fishing took place. Hence, a uniform allocation of the amount of effort and catch to the whole grid cell leads to a biased picture of the spatial impact of the fishery. Moreover, the usage of non-interpolating methods, e.g. raw pings, leads to areas that are falsely identified as unfished.

For the German brown shrimp fleet it was found that straight line or a spline interpolation enable the usage of the fine resolutions of ≥ 0.01° x 0.01°. This approach ensures that > 80% of the grid cells along possible vessel tracks are identically identified as "fished" by either method. This procedure is a good compromise to minimise the underestimation of the fished area and to remove a maximum of the uncertainty about the vessels' track. Further, it incorporates all information available from the VMS data set, such as direction or speed of the vessel. Hence, preconditioned on two-hourly transmitted fishing positions, this approach leads to best possible spatial estimates for the German brown shrimp fleet. This is of particular relevance for estimations according to future natural conservation measures for specific sites and habitats.

In **manuscript 3** the findings of manuscript 2 were applied to all commercial brown shrimp data available from 2007 - 2013 in order to obtain a comprehensive picture of the spatiotemporal distribution of the brown shrimp stock. In this manuscript, the commercial data were also used to identify areas with high densities of berried females in winter, thereby evaluating previous assumptions on migration patterns of brown shrimp. Brown shrimp had been suggested to migrate onshore in spring to reach their nursery grounds in intertidal zones of the Wadden Sea and to execute a seaward migration towards their spawning grounds in the open sea in late autumn/winter. However, the location of the brown shrimp spawning grounds had still remained unknown.

As the vessels differ in their fishing behaviour and vessel characteristics, e.g. length and power, the obtained LPUE will depend on the individual vessels' efficiency. To attain a proxy for brown shrimp densities, the calculated LPUE were, in **manuscript 3**, standardised to the level of a mean vessel. This approach revealed that the commercial vessels differed on average by about 16% in their efficiency, with the most efficient vessel being more than 4 times as efficient as the least efficient one. Moreover, it was found that efficiency increases with distance to the coast, mostly due to the fact that larger, newer and more powerful vessels fished further offshore. Hence, in this manuscript we demonstrated how commercial data from the brown shrimp fishery can be used for the advancement of biological knowledge. The findings revealed clearly that an unbiased view on the situation of the stock is only possible if the LPUE are standardised.

Previously unavailable maps of the spatiotemporal distribution of brown shrimp of two different size groups (ca. 50 - 73 mm and > 73 mm total length) are provided in this manuscript. The maps provide a quantitative basis for considerations concerning spatial management measures. A density increase in estuaries in spring and low densities in coastal areas in winter largely confirmed the assumed migration patterns

of an onshore migration in spring and an offshore migration in winter. Nevertheless, considerable and unexpected regional differences were found, suggesting that a seaward migration of berried females in winter was most pronounced in Dutch and western German waters but was not present in Danish waters. This implies that an increased fishing effort in deeper areas particularly in the westernmost areas in winter may pose an additional risk for the local brown shrimp spawning stock. Such an effort shift towards deeper areas could be caused if, for example, as currently discussed, certain areas of the Natura 2000 sites were closed for the brown shrimp fishery.

On an overall basis, this thesis indicates a strong need for the standardisation of brown shrimp catch rates, both in the survey and in the commercial data. Using not only scientific research data but also standardised commercial data for biological research is an important step towards a comprehensive picture of the spatial and temporal situation of the brown shrimp stock. The usage of standardised commercial data is an essential need to clarify the effects of potential future management options, either for brown shrimp stock management or for spatial management of Natura 2000 sites.

2 ZUSAMMENFASSUNG

Die vorliegende Studie möchte wichtige Wissenslücken schließen, die relevant sind für die Beurteilung des Krabbenbestandes (*Crangon crangon* L.). Diese Art bildet die Basis für eine große Fischerei mit mehr als 500 aktiven Kuttern, die fast ausschließlich Krabben fischen und Anlandungen von mehr als 30 000 t pro Jahr erreichen. Der Großteil der jährlichen Fangmenge wird dabei von der niederländischen und deutschen Flotte erzielt, die hauptsächlich im Wattenmeer fischen, ein Gebiet, welches als Natura 2000 Gebiet für den Schutz von Lebensräumen ausgewiesen ist. Trotz dieser sensiblen Fischgründe und der großen Flotte unterliegt die europäische Krabbenfischerei aktuell keinem Management.

Neuerdings wird ein Management sowohl für den Krabbenbestand als auch für die Natura 2000 Gebiete diskutiert. Für den Krabbenbestand erscheint ein Management nötig, da es Anzeichen für Wachstumsüberfischung gibt. Ein potentielles Risiko für die Krabbenpopulation besteht darin, dass die nordseeweit operierenden Krabbenkutter effizienter werden. Dies ist auch erkennbar in den ansteigenden mittleren jährlichen Anlandungsmengen, welche von 2000 bis 2013 bei 32 972 t lagen und sich damit, im Vergleich zu den mittleren Anlandungen von 1960 bis 1999 von 16 820 t, fast verdoppelt haben.

Vom internationalen Rat für Meeresforschung (ICES) wurde daher im Oktober 2014 ein Management für den Krabbenbestand empfohlen. Wegen der kurzen Lebensspanne der Krabben ist ein Management basierend auf einer Bestandsbeurteilung anhand jährlicher wissenschaftlicher Forschungsreisen sowie der Bestimmung von jährlichen zulässigen Gesamtfangmengen (total allowable catches – TACs) nicht anwendbar. Folglich wird vom ICES empfohlen, das Management auf monatlichen Fangmengen kommerzieller Krabbenfischer zu basieren. Die Managementempfehlung beinhaltet die Überwachung der kommerziellen Anlandungen pro Stunde (landings per unit effort – LPUE) und die zusätzliche Bestandsüberwachung anhand von wissenschaftlichen Forschungsreisen um unabhängige Abschätzungen, z.B. über die vorhandene Biomasse an Krabben, zu bekommen.

Im Gegensatz zum Management für den Krabbenbestand liegt der Schwerpunkt der Managementüberlegungen für die Natura 2000 Gebiete auf dem Schutz bestimmter Habitate und somit auf räumlichen Managementmaßnahmen. Diese Maßnahmen werden voraussichtlich einen Einfluss auf die Krabbenfischerei und damit potentiell auch auf den Krabbenbestand haben. Für die Natura 2000 Gebiete beinhalten die Managementüberlegungen die Abschätzung des Ausmaßes der Zerstörung, dem diese Gebiete ausgesetzt sind und schlagen die Schließung von Arealen für die Krabbenfischerei vor.

Die Zweckmäßigkeit und die potentiellen Auswirkungen bestimmter Managementoptionen, sei es für Natura 2000 Gebiete oder für den Krabbenbestand kann nur diskutiert werden, wenn bisher unbekannte räumlich-zeitliche Variation in der Krabbenabundanz beschrieben werden können. Das bisherige Wissen über die räumliche Verteilung der Krabben basiert auf räumlich begrenzten Daten, die auf jährlichen Forschungsreisen erhoben wurden. Allerdings sind auch die Daten von mehr als 200 kommerziellen Krabbenfischern verfügbar, die eine große zeitliche und räumliche Abdeckung haben. Obwohl ein flächendeckendes Bild der räumlich-zeitlichen Verteilung des Krabbenbestandes ausschließlich anhand der wissenschaftlich erhobenen Daten nicht möglich ist, wurden die kommerziellen Daten trotz ihres Potentials aber bisher nicht genutzt.

Abschätzungen über die räumlich-zeitliche Verteilung der Krabben werden, unabhängig von den dafür genutzten Daten, anhand von Fangmengen pro Zeiteinheit gemacht. Das gleiche gilt für Schätzwerte, die für Bestandsabschätzungen genutzt werden, wie z.B. Biomasseabschätzungen. Dabei wird von einer konstanten Fängigkeit ausgegangen. Dies bedeutet, dass angenommen wird, dass von den vorhandenen Krabben immer der gleiche Anteil und die gleiche Zusammensetzung gefangen wird. Möglicherweise ist das jedoch nicht der Fall, da Umweltfaktoren wie beispielsweise Tiefe, Tageslicht oder Gezeitenstand und auch schiffsabhängige Faktoren wie etwa die Motorleistung sowohl die Gesamtfangmenge als auch die Anteile an gefangenen großen, kleinen, eitragenden oder nicht-eitragenden Krabben beeinflussen können.

Diese Studie will die Faktoren identifizieren, die die Fangmengen und die Zusammensetzung der Fänge beeinflussen, um so zu einer soliden Basis für die Berechnung von Schätzwerten beizutragen, die für ein Management des Krabbenbestandes nötig ist. Außerdem soll der Anteil der Krabben quantifiziert werden, der sich pelagisch aufhält und somit unerreichbar für das traditionelle Krabbenfanggerät, die Baumkurre, ist. Ein weiteres Ziel der vorliegenden Arbeit ist es, ein flächendeckendes Bild der räumlich zeitlichen Muster der Verteilung des Krabbenbestands zu vermitteln.

In **Manuskript 1** werden Faktoren adressiert, die die Fängigkeit potentiell beeinflussen. Dazu gehören Jahreszeit, Tiefe, Gezeitenstand, Tageslicht, Geschlecht, Reproduktionsstatus und Größe der Krabben. Um die Faktoren, die einen Einfluss auf die Fängigkeit haben zu identifizieren, wurden die Daten dreier verschiedener Forschungsreisen verwendet, die zwischen 1997 und 2010 erhoben wurden. Dazu gehörten jährliche Daten einer Herbst- sowie einer Winterreise, die mit einer Baumkurre erhoben wurden und Daten eines gestaffelten Vertikalhamens. Alle der genannten Faktoren hatten signifikanten Einfluss auf die Fangraten. Insbesondere in den Baumkurrenfängen zeigte sich, dass die Zusammensetzung der Fänge stark von der Tiefe der Probennahme abhing. Gerade im Winter hat sich gezeigt, dass sich eitragende Weibchen gleichmäßiger über alle Tiefen zwischen 12 und 54 m verteilten als nicht eitragende Krabben, die sich eher in flacherem Wasser ansammelten. Zudem war im Winter ein signifikanter Einfluss der Gezeiten vorhanden, der vermuten lässt, dass es zwei verschiedene Überwinterungsstrategien gibt: Die „Nearshore-Krabben“ verbleiben im Winter dicht an der Küste und nutzen die Flut um in flachere Gebiete zu kommen wohingegen die „offshore-Krabben“ die Ebbe zu nutzen scheinen, um in tiefere Gebiete transportiert zu werden. Insofern wurde die erwartete einfache Wintermigration der Krabben mit der Ebbe in tiefere Gebiete nicht gefunden.

Das eindrucksvollste und überraschendste Ergebnis der Forschungsdaten hat sich aus der Auswertung der Daten des gestaffelten Hamens ergeben, die von April bis September 2005 bis 2007 erhoben wurden. Es wurde gezeigt, dass ein Anteil von mehr als 70 % der vorhandenen Krabben in pelagischen Wasserschichten zu erwarten ist, wo sie für eine Baumkurre unerreichbar sind. Dieses Ergebnis tritt der Annahme entgegen, dass Krabben hauptsächlich benthisch leben und hat inzwischen zu einer Anpassung der Biomasseabschätzung geführt.

Insgesamt legen die Resultate der Auswertung, die in **Manuskript 1** beschrieben sind, nahe, dass für glaubwürdige Schätzwerte, wie zum Beispiel die Biomasseabschätzung, eine Standardisierung der Fänge und der Fangzusammensetzung nötig ist. Diese Standardisierung sollte zusätzlich zum genutzten Fanggerät, Holdauer und Schleppgeschwindigkeit zumindest auch Jahreszeit, Tiefe, Tageslicht und Gezeitenstand berücksichtigen.

Manuskript 2 befasst sich mit methodischen Aspekten, wenn Daten der kommerziellen Fischerei für räumliche Abschätzungen von Aufwand und Fangmenge genutzt werden. Aufwand und Fangmengenabschätzungen werden benötigt, um daraus räumliche Abschätzungen für LPUEs berechnen zu können. Aus der zeitlich-räumliche Verteilung der LPUEs kann dann in einem weiteren Schritt auf die Verteilung der Krabben geschlossen werden. Diese räumlichen Abschätzungen werden durch die Kombination von VMS- (vessel monitoring system) mit Logbuch- und Anlandungsdaten möglich. Die VMS-Daten beinhalten zweistündige „Pings“, in denen die Schiffsposition übermittelt wird. Es ist nicht aufgezeichnet, wo die Schiffe im zweistündigen Intervall zwischen zwei aufeinanderfolgenden Pings gewesen sind. Vor Erstellung der vorliegenden Arbeit wurden schon mindestens fünf verschiedene Methoden entwickelt, um mit dieser Unsicherheit umzugehen. Dennoch ist bisher nicht geklärt gewesen, inwieweit sich die verschiedenen Methoden in ihren räumlichen Abschätzungen unterscheiden. Darüber hinaus werden die räumlichen Abschätzungen, die auf der Basis kommerzieller Daten gemacht werden, auf beliebig gewählter Auflösung gemacht. Dies kann ebenfalls zu einer Beeinflussung der Ergebnisse führen.

Um zu klären, wie gut die Performanz der verschiedenen Methoden ist um die detaillierte räumliche Verteilung der Krabbenfischerei zu beschreiben, wurden in **Manuskript 2** rohe Pings, die linearen Interpolation, kubische hermitesche Splines, Ellipsen und die Amplifikationsmethode auf unterschiedlichen Auflösungen zwischen 0.005° x 0.005° und 1° x 1° (lat. /lon.) angewendet. Anschließend wurden die Methoden bei den verschiedenen Auflösungen bezüglich der geschätzten Verteilung und Ausdehnung der befischten Fläche verglichen. In gleicher Weise wurden die Aufwands- und Fangmengenabschätzungen der unterschiedlichen Methoden für unterschiedlich große Fallstudiengebiete innerhalb der Fischgründe der deutschen Krabbenfischer gegenübergestellt. Als Fallstudiengebiete dienten ein kleiner Windpark sowie drei deutsche Nationalparkgebiete, die zwar vollständig als

Natura 2000 Gebiet ausgewiesen sind aber momentan noch nicht gemanagte Krabbenfischerei erlauben.

Die Ergebnisse zeigen, dass sich die als befischt abgeschätzte Fläche sogar bei einer Auflösung von 1°x1° zwischen den Methoden in ihrer Lage unterschied. Darüber hinaus war innerhalb der Fallstudiengebiete auch die räumliche Verteilung des zugewiesenen Aufwandes und der zugewiesenen Fangmenge zwischen den Methoden nicht identisch. Ebenso wichen der zugewiesene Aufwand und die Fangmenge um 11 bis mehr als 100 % voneinander ab, mit besonders großen Unterschieden in Gebieten, in denen nur wenige Informationen über fischende Kutter verfügbar waren. Die Resultate verdeutlichen, dass die als befischt geschätzte Fläche sich zwischen den Methoden unterscheidet und zeigen, dass sowohl Fangmengen- als auch Aufwandsabschätzungen mit Umsicht verwendet werden sollten, insbesondere in Gebieten, in denen nur wenige Pings übermittelt wurden. Letzteres wird relevant, wenn beispielsweise die Höhe von Kompensationszahlungen für zu schließende Flächen berechnet werden soll.

Bezüglich der verschiedenen Auflösungen erscheint aus Nutzerperspektive eine möglichst feine Auflösung wünschenswert, um detaillierte Informationen zu bekommen. Gleichzeitig sollte die gewählte Auflösung sicherstellen, dass es nicht zu künstlichen Lücken zwischen aufeinander folgenden Pings in der als befischt bezeichneten Fläche kommt. Die Ergebnisse dieser Studie zeigen deutlich, dass für die kommerziellen Daten der deutschen Krabbenfischer auch die sehr feine Auflösung von 0.005° x 0.005° noch zu grob ist, um zu einer homogenen Verteilung der Pings innerhalb einer 0.005° x 0.005°- Rasterzelle zu führen. Das bedeutet, dass der Fischereiaufwand innerhalb der Rasterzellen in Wirklichkeit inhomogen verteilt ist und dementsprechend eine einheitliche Verteilung von Aufwand und Fangmenge pro Rasterzelle zu einem verzerrten Bild der räumlichen Auswirkungen der Fischerei führt. Überdies hat sich gezeigt, dass die Nutzung von nicht-interpolierenden Methoden, wie z.B. der rohen Pings dazu führte, dass Flächen fälschlicherweise als ‚nicht befischt' bezeichnet wurden.

Für die deutsche Krabbenfischereiflotte hat diese Studie gezeigt, dass die Methode der linearen Interpolation oder die kubisch hermiteschen Splines die Verwendung einer feinen Auflösung von ≥ 0.01° x 0.01° erlauben. Beide Methoden identifizieren Rasterzellen entlang einer möglichen vom Kutter zurückgelegten Route als befischt und bei einer Auflösung von ≥ 0.01° x 0.01° wird sichergestellt, dass mehr als 80 % der identifizierten Routen von beiden Methoden in identischer Art und Weise identifiziert werden. Diese Herangehensweise ist ein guter Kompromiss, um die Unterschätzung der befischten Fläche zu minimieren und ein Maximum der Unsicherheit in der Abschätzung der vom Kutter zurückgelegten Route zu beseitigen. Außerdem kann auf diese Art und Weise auch die ganze Information der VMS-Daten, wie z.B. Geschwindigkeit und Richtung mit berücksichtigt werden. Unter der Voraussetzung von zweistündig gesendeten Pings führt das beschriebene Vorgehen zu bestmöglichen Schätzungen für die deutsche Krabbenflotte, was relevant wird, wenn Abschätzungen für zukünftige Naturschutzmaßnahmen für bestimmte Gebiete und Habitate gemacht werden müssen.

In **Manuskript 3** werden die Ergebnisse von Manuskript 2 auf alle kommerziellen Krabbenfischereidaten von 2007 bis 2013 angewendet, um ein flächendeckendes Bild der zeitlich-räumlichen Verteilung des Krabbenbestandes zu bekommen. In diesem Manuskript werden die kommerziellen Daten auch genutzt, um Gebiete hoher Dichten an eitragenden Weibchen im Winter zu identifizieren und vorhandene Annahmen über das Wanderungsverhalten der Krabben zu überprüfen. Es wird davon ausgegangen, dass Krabben im Frühjahr zu ihren Aufwuchsgebieten in intertidalen Bereichen der Küste wandern und im Herbst/Winter eine Wanderung in seewärts gelegene Gebiete durchführen, um zu ihren Laichgründen zu gelangen. Die genaue Lage der Laichgründe ist allerdings bisher noch unbekannt.

Da sich die Kutter sowohl in ihrem Fischereiverhalten als auch bezüglich ihrer Kuttereigenschaften, wie z.B. Länge und Motorleistung unterscheiden, werden sich auch die erzielten LPUEs entsprechend der individuellen Effizienz der Kutter unterscheiden. Um eine Proxy-Variable für die Dichte der Krabben zu bekommen, wurden die LPUE in **Manuskript 3** auf das Niveau eines mittleren Kutters standardisiert. Bei diesem Vorgehen zeigte sich, dass sich die Kutter im Mittel um 16 % in ihrer Effizienz unterschieden, wobei der effizienteste Kutter mehr als viermal so hohe LPUEs erzielte, wie der am wenigsten effiziente Kutter. Des Weiteren zeigte sich, dass die Effizienz der Kutter mit dem Abstand zur Küste zunahm, was vor allem darauf zurückzuführen ist, dass größere, neuere und leistungsstärkere Kutter weiter offshore fischen. Somit konnte in diesem Manuskript gezeigt werden, wie Daten der kommerziellen Krabbenfischerei zur Erweiterung des biologischen Wissens genutzt werden können. Die Ergebnisse zeigen deutlich, dass ein unverzerrtes Bild des Krabbenbestandes nur möglich ist, wenn die LPUEs standardisiert werden.

In diesem Manuskript werden bisher nicht verfügbare Karten der räumlich-zeitlichen Verteilung von Krabben verschiedener Größenklassen (Gesamtlänge: ca. 50 - 73 mm und > 73 mm) gezeigt. Die Karten schaffen eine quantitative Basis für Überlegungen, die räumliche Managementmaßnahmen betreffen. Ein Anstieg der Krabbendichten im Frühjahr in Estuaren und niedrige Dichten in Küstengebieten im Winter bestätigten weitgehend das vermutete Wanderungsverhalten der Krabben, mit einer Wanderung in Richtung Küste im Frühjahr und einer Abwanderung in seewärts gelegene Gebiete im Winter. Dennoch wurden auch beträchtliche und unerwartete regionale Unterschiede in diesem Muster gefunden, die darauf schließen lassen, dass sich die beschriebene seewärts gerichtete Migration der eitragenden Weibchen im Winter vor allem in niederländischen und den westlichen deutschen Gewässern zeigt, aber vor der dänischen Küste nicht vorhanden ist. Das bedeutet, dass insbesondere in den westlichsten deutschen Küstenabschnitten ein potentielles Risiko für den lokalen Krabbenbestand besteht, wenn sich in offshore-Gebieten der Fischereidruck im Winter erhöhen würde. Dies wäre wahrscheinlich der Fall, wenn z. B. wie momentan diskutiert, bestimmte Bereiche der Natura 2000 Gebiete für die

Krabbenfischerei geschlossen werden würden und es so zu einer Aufwandsverlagerung in tiefere Gebiete käme.

Insgesamt zeigt diese Arbeit deutlich, dass die erzielten Fangmengen der wissenschaftlich wie auch der kommerziell erhobenen Daten standardisiert werden müssen. Die nicht mehr ausschließliche Nutzung wissenschaftlicher Forschungsdaten sondern auch die zusätzliche Verarbeitung der Daten der kommerziellen Fischerei für biologische Forschung ist ein wichtiger Schritt, um ein umfassendes Bild der räumlichen und zeitlichen Verteilung des Krabbenbestands zu bekommen. Die Verwendung standardisierter kommerzieller Fischereidaten ist essentiell um die Auswirkungen potentieller zukünftige Managementoptionen zu verdeutlichen, sei es für das Management des Krabbenbestandes oder für das Management der Natura 2000 Gebiete.

3 OUTLINE OF PUBLICATIONS

The following overview outlines the three publications which are included in this thesis. This outline serves as a clarification of each author's contribution to the respective manuscript.

3.1 MANUSCRIPT 1

3.1.1 Not Easy To Catch: New insights into factors affecting catch rates of partly pelagic brown shrimps (*Crangon crangon* L.)

Schulte, K.F., Temming, A., Hufnagl, M., Dänhardt A., Siegel, V., Neudecker, T., Wosniok, W.

Katharina Schulte processed the data and performed statistical analysis and text writing. Axel Temming and Marc Hufnagl helped with writing and critical reviews of the manuscript. Werner Wosniok provided helpful knowledge for the statistical analysis. Volker Siegel is head of the Crangon working group within the Thünen Institute of Sea fisheries and provided helpful comments on the manuscript. Andreas Dänhardt collected and provided the VSN data and Thomas Neudecker conducted the winter survey.

The manuscript was submitted to the peer reviewed *ICES Journal of Marine Science*. It is reviewed once.

3.2 MANUSCRIPT 2

3.2.1 Interchangeability of different approaches for estimating effort and catch from VMS- and commercial data.

Schulte, K.F., Wosniok, W., Temming, A.

Katharina Schulte did all data processing, analysis and graphical presentations. Writing was done under close cooperation of Werner Wosniok. Axel Temming provided helpful and critical reviews.

The manuscript is ready for submission to the peer reviewed *ICES Journal of Marine Science*.

3.3 MANUSCRIPT 3

3.3.1 Spatial and temporal distribution patterns of brown shrimp (*Crangon crangon* L.) derived from commercial logbook, landing and vessel monitoring data

Schulte, K.F., Siegel, V., Hufnagl, M. , Temming, A.

Katharina Schulte processed and combined the commercial data, did all analysis, graphical presentations and writing. Axel Temming helped to develop the idea for the manuscript. Helpful reviews of the manuscript were performed by Volker Siegel, Axel Temming and Marc Hufnagl.

The manuscript is ready for submission to the peer reviewed *ICES Journal of Marine Science.*

4 GENERAL INTRODUCTION

Brown shrimp (*Crangon crangon* L.) research has received increasing attention in recent years as brown shrimp fishery is a large, currently unmanaged, coastal activity which mainly operates in environmentally protected Natura 2000 areas of the Wadden Sea, an intertidal zone in the south-eastern part of the North Sea.

Brown shrimp belong to the decapod crustacean. They can be found in estuarine and coastal marine areas of Europe, in northern areas such as Iceland (Gunnarsson *et al.*, 2007), but also in the Mediterranean (Campos and van der Veer, 2008), at the coast of the UK (Henderson, 1987) as well as in the Baltic Sea (Dornheim, 1969).

Highest densities of up to 80 individuals $\cdot m^{-2}$ (Boddeke *et al.*, 1986) were found in the Wadden Sea. Not at least due to their great abundance in these areas they support a large multi-national fishery with over 500 active vessels and landings of > 30 000 t annually (ICES, 2014a) in the bordering states of the Wadden Sea. Main contributions to these total annual landings are made in the Netherlands (> 16 000 t) and in Germany (> 13 000 t, ICES, 2012a).

The high abundance of brown shrimp in the Wadden Sea is only possible as they are well adapted to the highly dynamic environmental conditions in these areas, where considerable tidal and seasonal fluctuations in temperatures (van Aken, 2008b) and salinities (van Aken, 2008a) are present. Brown shrimp tolerate temperatures between -1.4°C or even less (Reiser *et al.*, 2014) and > 20°C (Ehrenbaum, 1890; Havinga, 1930) and salinities between 0 and 35‰ (salinity expressed in accordance with Practical Salinity Scale 1978, reviewed in Campos and van der Veer, 2008).

Apart from its importance for the brown shrimp fishery, the Wadden Sea meanwhile is a strongly protected environmental conservation area. It is the largest connected system of intertidal sand and mud flats in the world (WHC, 2009), where 4700 km² emerge during low tide (Kabat *et al.*, 2012). In contrast to other coastal wetlands, the Wadden Sea is rich in biological diversity (WHC, 2009). These were some of the reasons, for the Wadden Sea to be designated as Natura 2000 site (EC, 2011), it has also become a UNESCO World Heritage Site in 2009 (WHC, 2009).

Commercial brown shrimp fishery at its current level is permitted in the National park areas by law (Schleswig-Holstein, 1999; Niedersachsen, 2001). However, the National Park areas are also designated as Natura 2000 sites, and NGOs suggest closing at least 50% of the Natura 2000 sites for fishery and propagate the establishment of ecologically coherent marine protected areas (Ziebarth *et al.*, 2014). In their view these sanctions would ensure the diversity of the constituent ecosystems as suggested by the Marine Strategy Framework Directive (MSFD, EC, 2008). Indeed, for the Natura 2000 sites, a management plan has to be developed within 6 years after their designation (92/43/EEC 4(4), EEC), which has not been provided for any of the Natura 2000 sites yet. The demanded management plan has to include the estimation of the degree of degradation or destruction to which those sites are exposed and could also suggest area closures or a brown shrimp management which reduces bycatch or bottom impact in general. A management plan has not been submitted yet and the lack of environmental protection measures within the designated Natura 2000 sites has meanwhile lead to an action of the NGOs against the Federal Agency for Nature conservation in January 2015 (Anonymus, 2015).

Almost simultaneously to the management considerations concerning the Wadden Sea, the fishers have come under pressure from large retail organisations to apply for the Marine Stewardship Council (MSC) certification. This certification requires a clearly defined management plan for the brown shrimp stock, including the monitoring of stock size.

Furthermore, the previous scientific opinion, that management for the brown shrimp stock was unnecessary because the natural mortality was higher than the fishing mortality (Welleman and Daan, 2001), was revised by Temming and Hufnagl (2014). They found clear indications that the pattern of a high natural and a low fishing mortality is reversed and that nowadays the fishing mortality is up to four times as high as the natural mortality. Temming and Hufnagl (2014) argued that caused by a decrease in the predator stocks (mainly cod and whiting), changes in the distributional range of the predators (ICES, 2012b) and a simultaneous increase of the brown shrimp landings (ICES, 2014a), a management system for brown shrimp would be advantageous.

Temming and Hufnagl (2014) also found indications that brown shrimp are harvested at a too small size, which might be caused by efficiency combination of high effort and small mesh sizes of the fleet (ICES, 2014a). Temming and Hufnagl (2014) reasoned that growth overfishing is therefore probable and an effort reduction (which requires management) would be desirable to achieve the maximum sustainable yield.

From an ecosystem protection point of view management for the brown shrimp stock would also be beneficial, because reduced fishing effort would likewise reduce the catch of undersized and non-target (bycatch)-species, lower the impact on the benthic communities on the seafloor and hence have positive environmental effects.

Typically, a management of fish stocks is based on an annual stock assessment. Commercial catch in numbers by age class and abundance data from research survey data constitute the main data source for the assessment, resulting in an advice given as annual total allowable catch (TAC) or as statement about the sustainability of the current fishing practice. But in contrast to other fish and also long-lived crustacean species, the implementation of a classical management is difficult or does not seem appropriate for brown shrimp.

For long-lived crustacean, for example lobsters (e.g. *Jasus edwardsii* (Saila *et al.*, 1979; Yoshimoto and Clarke, 1993; Breen and Kendrick, 1998), *Panulirus Cygnus, Homarus americanus* and *Jasus novaehollandiae* (Yoshimoto and Clarke, 1993)) and Northern shrimp *Pandalus borealis* (Cadrin, 2000) alternatively biomass dynamics models (or surplus production models) have been applied. This type of model requires reliable biomass estimates, which are difficult to obtain for brown shrimp. Even if the most reliable data series of Dutch (DFS, Tulp *et al.*, 2008) and German survey data (DYFS, Siegel *et al.*, 2005) were used, the depth stratified biomass estimates were not sufficiently similar in areas where both surveys operated in parallel (ICES, 2011; ICES, 2012a; ICES, 2014a). The uncertainties of biomass estimates for brown shrimp are mainly due to the strong dependence on the presumed constant catchability of the gear used. Further, biomass estimate suffers from a high variability due to biological variability, strong seasonality and variable gear efficiency. Consequently, the application of a stock production model to the brown shrimp fishery failed, primarily due to the unreliability of the biomass estimates (van der Hammen and Poos, 2010). Thus, classical assessment methods cannot easily be applied to the brown shrimp stock.

An analytical, age- or size-based assessment, as applied for *Nephrops* (ICES, 2002b), *Pandalus borealis* (ICES, 2002a) and American lobster *Homarus americanus* since 2009 (ASMFC, 2009) is also not applicable for brown shrimp, as it requires age determination and information on the stock recruitment relationship. The age of the brown shrimp caught cannot be determined because they lack permanent hard parts to accumulate annual layers and their variable growth rates depend on temperature and season, with generally higher growth rates at higher temperatures (Hufnagl and Temming, 2011a). Hence, brown shrimp have an almost permanent recruitment and highly variable growth rates (Hufnagl and Temming, 2011b), making cohort tracking impossible. The establishment of a clear stock recruitment-relationship has also not yet been possible (Siegel *et al.*, 2005). Because of the short life span of about one year (Hufnagl and Temming, 2011b), a commonly used annual assessment with catch predictions would also not be appropriate for brown shrimp. This is different from other crustaceans with longer life times, such as the Northern shrimp *Pandalus borealis* (Fu *et al.*, 2001). Although the Northern shrimp also lack any permanent hard body parts from which their age could be determined, age can be derived from length frequency distributions using estimated growth rates (Macdonald and Pitcher, 1979). Moreover, a stock-recruitment relationship can be analysed as the different age classes can be identified in the samples (Fournier *et al.*, 1991).

The very specific conditions in the brown shrimp stock led to an ICES management advice, suggesting a stock management based on a Harvest control rule (HCR) including the monitoring of commercial landings per unit effort (LPUE) based on a monthly basis (ICES, 2014b). The HCR is based on a comparison of the most recent monthly mean LPUE with predefined trigger values. The currently suggested trigger values are, so far, based on observations from earlier years. An effort reduction is demanded as soon as the measured monthly mean LPUE falls below the trigger value. Additionally, further scientific monitoring is advised to obtain independent estimates, for example on biomass (ICES, 2014b).

Commercial data are the only choice for management of the brown shrimp stock, as performing monthly scientific research surveys with a sufficient spatial coverage is unrealistic. Commercial data can reflect and detect within-a-year changes. This is advantageous, as annual reference values, such as TACs would be useless for this short-lived species, and the management of the brown shrimp stock probably needs frequent short-term adjustments. Short-term changes in densities, for example due to changed conditions in fishing effort are not uncommon for brown shrimp. This became particularly evident in 2011, when in spring almost the entire German fleet and large parts of the remaining North Sea fleet (mainly the Netherlands and Denmark) stopped fishing and went on strike for about two weeks. The reduced fishing pressure in combination with the strong 2010/2011-cohort more than doubled the observed LPUE in Germany (nearly 8 kg·horse power-1 ·days at sea-1 in 2011 after the strike in contrast to the average of 3 kg·horse power-1 ·days at sea-1 , in the German fleet, ICES, 2012a). Hence, short term-changes in fishing effort can have an almost immediate effect on the brown shrimp stock. Thus the approach, envisaged in the ICES advice (2014b) seems suitable. However, in order to be able to monitor the stock properly, knowledge on the comparability of catches that are used for monitoring is needed.

Commercial landing data are not standardised and will vary according to the fishers experience and according to vessel and gear characteristics. But even in survey data, which are standardised according to haul duration, trawling speed and gear used (Siegel *et al.*, 2005; Tulp *et al.*, 2008), comparability of catches of different vessels might not be given, but is a prerequisite for obtaining meaningful values on biomass or abundance. Whether vessel and gear characteristics alter the catch rates is analysed in the present study.

Further, the catch rates from survey data and from commercial data can be expected to differ according to the brown shrimp life cycle. For example, size composition in the catches was shown to differ according to depth (Havinga, 1930; Boddeke, 1976; Janssen and Kuipers, 1980). This implies that size distribution of the brown shrimp in the catches depends on sampling depth. As survey data are used to determine the proportion of large brown shrimp, this proportion will depend on sampling depth. The calculated "large shrimp indicator" is used as a measure for fishing pressure (Temming and Hufnagl, 2014) and will of course be biased, if the catches vary in sampling depth. The same difficulty of potential non-comparability applies to the LPUE derived from commercial data. They are only usable as management measure, if comparability between different vessels, regions and times is ensured. Only if based on meaningful, science based values, an effective management is possible. Therefore, the variability of the derived values needs to be well understood. This requires a better understanding of factors influencing catchability of brown shrimp, which in turn implies a better understanding of the brown shrimp behaviour and their life cycle.

The life cycle of brown shrimp can be described as follows: Generally, a massive immigration of the juveniles (10 – 20 mm TL) into the tidal flats is observed in May/June (e.g. Beukema, 1992; Temming and Damm, 2002; Boddeke *et al.*, 1986; Kuipers and Dapper, 1984; del Norte-Campos and Temming, 1998). In these shallow areas the juveniles are protected from many predators and benefit from high food availability (Cattrijsse *et al.*, 1997; Boddeke *et al.*, 1986). Furthermore, in early summer the water temperatures in shallow areas are higher than in deeper water. This, in combination with abundant food resources, enables faster growth of the juveniles. Fast growth is usually associated with lower cumulative mortality (Houde, 1987), especially because it reduces the size-dependent risk of predation (Cattrijsse *et al.*, 1997; Boddeke *et al.*, 1986). Having reached a total length of about 35 mm, the juveniles retreat into subtidal areas of the Wadden Sea (Kuipers and Dapper, 1984), where they grow to adult size. Maturity is reached at different sizes for males and females. Females grow on average 15 – 20 % faster than males (Hufnagl and Temming, 2011b) and grow to larger sizes than males (Havinga, 1930; Tiews, 1970; Tiews, 1954). Females reach maturity at a mean size of 50 – 55 mm (Oh *et al.*, 1999), while males mature at 22 – 43 mm (Campos and van der Veer, 2008). When temperatures decrease (December - March), the mature brown shrimp, and especially females, migrate towards their spawning grounds (Havinga, 1930; Boddeke, 1975; Ehrenbaum, 1890), located in the "open sea" (Boddeke, 1975) where adult brown shrimp can approximately be found down to at least 40 m depth (Siegel *et al.*, 2005). An increase in the share of berried females can already be observed from October onwards (Siegel *et al.*, 2008) and the proportion of berried females then increases over late winter to a maximum between March and end of June (Siegel *et al.*, 2008). The berried females carry their eggs attached to their pleopods until the larvae hatch (Lloyd and Yonge, 1947). As the egg and larval development is temperature dependent, the time until the larvae hatch varies from 18 (at 20 °C) – 45 days (at 10 °C, Campos and van der Veer, 2008). After being released from the berried females in outer coastal waters (Temming and Damm, 2002), larval development lasts 3 (at 18°C) to 7 weeks (at 9°C, Campos and van der Veer, 2008). The larvae pass 5 – 6 planktonic stages (Ehrenbaum, 1890; Criales and Anger, 1986). After these larval stages they have reached a length of about 4.7 mm and become demersal juveniles (Tiews, 1970; Kuipers and Dapper, 1984). The larvae/ juveniles are suggested to be transported by currents from their locations of hatching to the nursery grounds on the tidal flats (Daewel *et al.*, 2011), where the massive immigration in spring can be observed again.

Most studies focussing on the life-cycle of brown shrimp and especially the seasonal immigration and emigration have so far been conducted in shallow areas in depths ≤ 20 m (e.g. Boddeke, 1976; Siegel *et al.*, 2005; Havinga, 1930). Studies that focus on the brown shrimp population structure in deeper areas are lacking. Therefore, assumptions about seasonal migration patterns and the spatial distribution of the stock in deeper areas are currently rather speculative. But both the seasonally differing spatiotemporal distribution of brown shrimp as well as migration behaviour can alter the catch rates and bias the derived estimates. In consequence, conclusions used for management measures would be influenced.

While the spatiotemporal distribution will lead to seasonal and regional different catch rates and the sex and size composition of the catches, also catch rates sampled with one gear at a fixed position may differ according to the brown shrimp behaviour, if a beam trawl, the traditional catching device, is used. A beam trawl has a height of about 0.5 m and hence, does usually not cover the total water column. But the described migration patterns as well as certain brown shrimp behaviour may cause an ascent into pelagic layers of the water column. This ascent may lead to a temporarily reduced accessibility of brown shrimp to beam trawls and thus lead to biased estimates of the brown shrimp abundance and stock biomass. One reason for this ascent into pelagic layers of the water column may be the described migration pattern of a seaward migration of the adults from December to March (Havinga, 1930; Boddeke, 1975) to the spawning grounds and a migration of the juveniles towards coastal nurseries in spring (e.g. Beukema, 1992; Temming and Damm, 2002; Boddeke *et al.*, 1986; Kuipers and Dapper, 1984; Daewel *et al.*, 2011). Most likely it involves the selective usage of tidal currents (selective tidal stream transport, STST, Forward and Tankersley, 2001; Cattrijsse *et al.*, 1997), as shown for blue crabs *Callinectus sapidus* (Forward *et al.*, 2003). The STST can generally be used in regions with significant tidal currents. As brown shrimp adapt their activity according to day-length (Hagerman, 1970) or light intensity (Al-Adhub and Naylor, 1975; Hufnagl *et al.*, 2014) with increased activity during darkness, the beam trawl catch rates and hence, biomass estimates, may also interact with daylight as well as with size and season in times when seasonal migration is performed.

Another factor potentially causing the ascent into the pelagic zone could be the availability of pelagic prey such as mysids (Pihl and Rosenberg, 1984) and copepods (Boddeke *et al.*, 1986; Plagmann, 1939). An ascent for feeding might again be more pronounced during darkness, when brown shrimp preferably feed (Norkko, 1998; Pihl and Rosenberg, 1984). However, an ascent for feeding would, in contrast to STST-usage for migration, probably be present during all times of the year. However, this mechanism would equally lead to a temporal inaccessibility of the animals and influence the conclusions about brown shrimp abundance reached from beam trawl data. Apart from behavioural patterns leading to an ascent into the pelagic zone, brown shrimp of a certain size or reproductive state might behave differently. If brown shrimp behaviour or habitat preferences differ according to their size or reproductive state, this would result in a changed catch composition, not only varying with season but potentially also with other factors, such as region, depth, daylight, or tidal state. In order to achieve comparable catches, the factors affecting catchability need to be understood.

This thesis uses three different types of data sets to evaluate the assumptions about catchability, seasonal distribution and migration patterns: (i) German beam trawl survey data from autumn, conducted in depths between 3 – 13 m and winter survey data covering depths between 12- 54 m, (ii) data from a vertically resolving stow net covering almost the whole water column and employed at fixed positions and (iii) commercial data from German brown shrimp vessels with a large spatiotemporal coverage. These data sets have very different characteristics:

4.1 BEAM TRAWL SURVEY DATA

German brown shrimp survey data are mainly recorded in the demersal young fish survey (DYFS), which was originally implemented to collect data on the prerecruit groups of commercially harvested flat fish species. This survey is conducted since 1974 in September or October (Siegel *et al.*, 2005), but only since 1997 are brown shrimp measured down to millimetres. From 1991 to 2010 a winter shrimp survey, conducted in January or February, was additionally established to estimate the effects of the expanding commercial winter fishery on the shrimp stock (Siegel *et al.*, 2008). These data sources together provide data sampled for one week twice a year. The catches are standardised according to gear dimension (winter survey: 7-m beam trawl, DYFS: 3-m beam trawl, both beam trawls without tickler chain), haul duration (winter survey: 30, DYFS: 15 minutes) and speed (2-4 knots). The survey data include precise haul locations, temperature, water depth, visibility depth, etc.. Moreover, the total catch is weighed, the length of the animals measured and it is also recorded if individuals are berried. Hence, these data provide a very accurate data base and stock estimates such as biomass estimates are based on this data source. In this thesis, this data set was used to identify whether the size and sex composition of catches was influenced by season, depth, tidal state or daylight. If this was the case, an assessment based on the survey catches would need to include the relevant factors to obtain comparable estimates.

4.2 VERTICALLY RESOLVING STOW NET DATA

Another survey was conducted from 2005 to 2007 at two sampling stations: Central Jade Bight (station 1: 53°28 N, 08°12 E, N= 67) and off Minsener Oog (station 2: 53°44 N, 08°02 E, N=23). In this survey, data were obtained from a vertically resolving stow net (VSN). As the data were collected within the scope of a project concerning the vertical distribution of prey fish for diving common terns, samples were taken weekly between May and July, and twice a month in April, August and September (Dänhardt, 2011). The VSN covered almost the whole water column and was divided into 5 vertical net compartments. As brown shrimp were counted per net compartment, it enabled resolving the vertical distribution of shrimps in the water column over a depth range of 7 m. This data set was used to quantify the amount of brown shrimp being located in pelagic layers, unreachable for the beam trawl. Further, it was analysed whether the ascent of brown shrimp depended on season, daylight or tidal state. Temporary inaccessibility of brown shrimp for the beam trawl used in the survey will influence biomass estimates, needed for stock assessment.

4.3 COMMERCIAL DATA

All of the described survey data have the advantage of being as exact as possible, such as exactly known haul locations, the simultaneous collection of environmental variables, concerning weather, tidal state, depth etc. and the precise size of the catches. However, a great disadvantage concerning all of the survey data is their restricted spatial and temporal availability. The survey data can therefore serve as very exact, but also very selective data source.

In contrast, commercial brown shrimp catches for human consumption consist of brown shrimp of at least 6.5 mm carapace width (CW). Hence, mainly adult females are targeted, as this size corresponds to a TL of about 50 mm (Sharawy, 2012), which is the size of female maturity (Oh *et al.*, 1999) and only little less than the usual maximum size of male brown shrimp of about 60 mm (Siegel *et al.*, 2008; Hufnagl *et al.*, 2010). Commercial data include logbook and landing data as well as data from the vessel monitoring system (VMS) for more than 200 German vessels. Within the logbooks, trip and fishing duration is recorded. The catch weight landed per vessel and trip is recorded in the landing data. From these two datasets, data landings per unit effort (LPUE), usually expressed as kilogram·hour^{-1}, can be calculated. Further, logbook and landing data can be combined with the VMS data. The VMS data are transmitted every 2 hours, called "pings", and include coordinates, speed and heading of the vessel. Using this combined data set the catch can be allocated spatially and temporally, according to the transferred positions and the effort made at the different locations.

These data are not recorded for biological purposes but for the monitoring of the fishery. Especially the spatial information is collected for enforcement purposes and not for scientific research (EC, 2002; EC, 2003). Hence, the frequency of the VMS data with its 2-hourly information allows for much speculation what happened between two consecutive pings. Several methods exist to distribute the recorded effort and catch in the area; all usually grid the space into rectangular grid cells. The whole area of a grid cell containing ping positions or parts of tracks is indicated as fished and is assigned a certain amount of catch and/or effort. In this way, areas of high and low effort and catch can be identified. Grid cell size therefore plays a crucial role. Undersized cells underestimate the fished area, oversized cells declare too much unfished area as being fished (Piet and Quirijns, 2009; Dinmore *et al.*, 2003; Hinz *et al.*, 2013) and give an imprecise impression of the fished area's shape. The latter argument has led to the recommendation that an analysis should be performed on the smallest scale possible (Dinmore *et al.*, 2003; Piet *et al.*, 2007).

To distribute the VMS information, some authors use the raw pings as transferred, considering the pings as the only source of verified information (Dinmore *et al.*, 2003; Murawski *et al.*, 2005). The straight line interpolation (Eastwood *et al.*, 2007; Stelzenmueller *et al.*, 2008) acknowledges that the vessel has to cover at least the shortest distance between two consecutive pings. This notion is expanded by using cubic Hermite splines (Hintzen *et al.*, 2010), incorporating speed and heading of the vessel to model the vessel's real track in more detail. Other methods try to account for the uncertainty of the track followed between two consecutive pings in another way, using either ellipses to identify the likely area impacted (Mills *et al.*, 2007) or the amplification method (Fock, 2008). Ellipses are constructed around two consecutive pings using the transmitted speed, while the amplification method deletes the original pings and constructs 4 new pings around the original ping position, depending on previous navigation properties of the vessel.

Thus, results from the combined logbook-, landing- and VMS data will depend on the method used to distribute the spatial information and from the spatial resolution used for the analysis, too. Hence, before using commercial data for brown shrimp research, a comparison of the different methods and different possible resolutions is needed. Further, standardisation of the data is required to eliminate the bias caused by different efficiency of the vessels. Very efficient vessels will probably have higher mean LPUE than less efficient vessels. Hence, high LPUE at certain times or in regions may not reflect high densities but could just be caused by the predominant activity of highly efficient vessels. The same applies for areas and times of low LPUE, which could be caused by the prevailing activity of less efficient vessels. Therefore, only standardised, but not the raw LPUE can be used as proxy for brown shrimp densities. Once these steps are successfully accomplished, commercial data can presumably be used very efficiently to provide information on spatiotemporal patterns of the brown shrimp stock and help to localise spawning grounds. This study proceeds in the described way to analyse the spatiotemporal distribution of the brown shrimp population in the German Bight and to evaluate assumptions on migration patterns and spawning ground locations.

4.4 THESIS OBJECTIVES

Overall, this study aims to identify factors affecting catch rates and the size and sex composition of the catches. Further, this study tries to analyse the spatiotemporal patterns in the distribution of the brown shrimp stock.

Specifically, **manuscript 1** evaluates the influence of season, depth, tidal state, daylight, sex and size of the shrimps on the catch rates by using German brown shrimp survey data, covering the years from 1997 – 2010. Further, based on the vertically resolving stow net data this manuscript aimed to quantify the proportion of brown shrimp being located in the pelagic zone and thus unreachable for a beam trawl, the traditional catching device. It was tested whether this fraction varied, depending on season, daylight and tidal state. Corrections for catch rates are usually made to account for mesh selection effects following Polet (2000), however, a quantification of the amount of brown shrimp being located above the usual beam trawl hauls would contribute substantially to a more reliable basis for the calculation of swept area biomass estimates.

Monitoring and management of the brown shrimp stock requires a clear picture of the spatial and temporal distribution of the stock. The data set with largest spatiotemporal coverage are the combined commercial data. To describe the spatiotemporal distribution of the brown shrimp stock, spatially allocated commercial LPUE values can be used in combination with the VMS data. The derived LPUE patterns, however, might differ between the methods and resolutions used. To elucidate the quality of the various methods for evaluating the fine-scale spatial distribution of the brown shrimp fishery, in **manuscript 2** raw pings, the straight line interpolation, cubic Hermite splines, ellipses and the amplification method are applied on different resolutions within the range of 0.005° x 0.005° to 0.5° x 0.5° (latitude/longitude). Subsequently, a comparison between the methods at the different resolutions is performed, contrasting the distribution and spatial extent of the estimated area fished, and the total values of effort and catch allocated to differently sized case study areas, located within the German brown shrimp fishing grounds. Furthermore, this manuscript aims to identify the best possible method and resolution for the German brown shrimp fishery. The latter is a prerequisite to describe spatiotemporal patterns of the brown shrimp stock in the most reliable form possible. Reliable estimations of the spatial distribution of effort and catch are also of particular relevance for future natural conservation management measures for specific areas and habitats, such as the Natura 2000 sites.

In **manuscript 3** the findings of manuscript 2 are applied to all commercial brown shrimp data available between 2007 and 2013. In order to obtain a comprehensive picture of the spatiotemporal distribution of the brown shrimp stock a standardisation of the LPUEs is performed. In this study, we present maps on the spatiotemporal distribution of the brown shrimp stock in the German Bight. Using this empirical data set, we examined the seasonal distributional range of different sized brown shrimp and evaluated the suggested seasonal migration patterns. Further, we aimed to localise the brown shrimp spawning stock in winter. The latter is of special interest, as in winter growth rates of brown shrimp are low and high fishing impact in areas of high densities of berried females potentially has large effects on the stock.

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5 MANUSCRIPT 1

NOT EASY TO CATCH: NEW INSIGHTS INTO FACTORS AFFECTING CATCH RATES OF PARTLY PELAGIC BROWN SHRIMPS (*CRANGON CRANGON* L.)

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5.1 ABSTRACT

Brown shrimps (*Crangon crangon*) occur in high densities in the southern North Sea and support a large, but so far unmanaged fishery with over 500 active vessels. The stock is only monitored based on catch per unit effort from scientific surveys and commercial landings, since no cohort-based assessment is possible.

For any future management purpose, biomass estimates and factors affecting catch rates and the composition within the catches need to be understood. This paper deals with the effects of season, reproductive state, size, tidal state, daylight and water depth on the numbers of brown shrimps caught. We analyse two independent long-term data sets from scientific surveys, conducted in autumn and winter in the southern North Sea between 1997 and 2010, and a data set from a vertically resolving stow net located at two stations in the German Wadden Sea, conducted from 2005-2007.

To analyse the role of the factors with regard to the catch rates we use log-linear random intercept models. We show that all factors examined factors influence the catch rate, with depth having a strong impact on the composition within the catches. The beam trawl survey data suggest that selective tidal stream transport is employed for migration to preferred depths according to size and reproductive state. From the stow net data we conclude that on average 73% of the brown shrimp are located well above a beam trawl height (ca. 0.5 m).

The results indicate that standardised surveys need to consider the factors mentioned above. Furthermore, stock size estimates, based on beam trawl catches only, strongly underestimate the true density of shrimps per area, and the assumption of brown shrimp living primarily benthically is challenged.

Keywords: Crangon crangon, vertical distribution, depth, daylight, selective tidal stream transport, migration

5.2 INTRODUCTION

Brown shrimps (*Crangon crangon L.*) are among the most abundant macroepibenthos species in the shallow coastal areas of the south eastern North Sea. They attract a large fleet with more than 500 vessels, annually landing about 30,000 t for human consumption at a value of up to € 100 million (ICES, 2011). Despite the economic importance of this fishery, a management of brown shrimp fishing has not been considered relevant so far. This is mainly because the impact of fishing was assumed to be minor in comparison to predation mortality (Welleman and Daan, 2001). This also means that there is no targeted monitoring of this stock. Stock density data are however available from Dutch and German beam trawl surveys designed for the monitoring of 0-group plaice (Neudecker, 2001; van Keeken *et al.*, 2008).

Recently, the main fisheries in the Netherlands and Germany have started a certification process according to the standards of the Marine Stewardship Council (MSC). This certification requires a clearly defined management plan, including monitoring of stock size. The fishermen have subsequently developed a fleet-based monitoring program, which uses the catch per hour (catch per unit effort: CPUE) of commercial vessels as available from log books. The mean CPUE of the most recent month is then compared to pre-established reference values. These are the monthly averages which have been measured over a past period with no reported problems with regard to the stock situation. If the current CPUE falls below 75 % or 50 % of the respective reference value, the management plan triggers effort reductions accordingly. The main problem with this approach is that any increase in vessel efficiency or change in catchability will not be detected, but falsely interpreted as a CPUE increase. Thus, no effort reduction would be triggered, even if it was needed.

This highlights the need for more standardised surveys to monitor brown shrimp stocks. Currently, such fishery-independent scientific survey data are available from a Dutch (Tulp *et al.*, 2012) and a German (Siegel *et al.*, 2005) beam trawl survey targeting 0-group plaice. However, even though these two surveys are carried out in the same season and in partly spatially overlapping regions, the calculated biomass estimates from these two surveys differ substantially from each other (ICES, 2008). Though the different gear size may be partly responsible for this effect, the observed discrepancy has raised questions about other factors influencing catchability of brown shrimps in beam trawls per se.

A better understanding of factors influencing catchability of brown shrimps in beam trawls is also essential for absolute biomass estimates using the swept area method. Such estimates could be related to the amount of total landings to produce an independent estimate of fishing mortality. In such swept area biomass estimates the focus is not on the variability of catchability (Welleman and Daan, 2001), but it is essential to know the magnitude of the escapement of shrimps that are located in the path of the gear. The explanation of both i.e. the relative variability and the amount of catchability, is likely to be found in specific behavioural patterns of brown shrimps: Generally, brown shrimps are bottom dwelling (Berghahn, 1983; Boddeke *et* *al.*, 1986) on sandy or muddy ground (Tiews, 1970; Pinn and Ansell, 1993), but they can also be buried in the sediment (Havinga, 1929). When buried in the sediment, shrimps are less accessible to ground gear (Jeffery, 2002). Brown shrimps are assumed to emerge from the sediment for active feeding on worms, mussels or benthic crustaceans on or near the bottom (Evans, 1983; Havinga, 1930; Pihl and Rosenberg, 1984; del Norte-Campos and Temming, 1994), preferably during darkness (Norkko, 1998; Pihl and Rosenberg, 1984). Typically, brown shrimps are caught with beam trawls, which fish close to the seabed with a maximum height of about 0.5 m. However, during multiannual stow net trials for fish monitoring, Dänhardt (2012) frequently caught brown shrimps pelagically in heights inaccessible to beam trawls.

One reason for this ascent into pelagic layers of the water column, might be the availability of certain food items, such as semi-pelagic mysids (Pihl and Rosenberg, 1984) and pelagic copepods (Boddeke *et al.*, 1986; Plagmann, 1939), which were found in the brown shrimps' stomachs. An alternative theory for this movement of brown shrimps into the pelagic zone relates to a specific migration behaviour, the selective tidal stream transport (STST, Forward and Tankersley, 2001; Cattrijsse *et al.*, 1997). Tidal rhythms have been shown to coincide with brown shrimps' emergence behaviour (Al-Adhub and Naylor, 1975; Hufnagl *et al.*, 2014). In regions with significant tidal currents, shrimps can stay in or on the bottom, when the currents flow in the "wrong" direction and swim into the water column at times when the flow direction transports the animal towards the target regions. Both the ascent for feeding and that for the STST usage could cause a complete inaccessibility of brown shrimps to beam trawls. While the ascent for feeding might be present during all times of the year, the STST usage is suggested to be related to the brown shrimps' life cycle. This cycle includes a seaward migration of adults from December to March (Havinga, 1930; Boddeke, 1975) to spawning grounds and a migration of juveniles towards coastal nurseries in spring (e.g. Beukema, 1992; Temming and Damm, 2002; Boddeke *et al.*, 1986; Kuipers and Dapper, 1984).

In this study we analysed effort-corrected catch rates of beam trawl surveys (a combined total of 1128 hauls from both multi-annual surveys) varying with season (autumn, winter), water depth (as a proxy for location), shrimp size, time of day, tidal and reproductive state. We tested whether the catch rates differed according to tidal states, taking into account different size groups and reproductive states as this might indicate the usage of STST of all brown shrimps or of some subgroups. In winter we expected either higher catch rates during ebb or at least higher catch rates of berried females with increasing depth or, alternatively, highest numbers at a certain depth in winter as a consequence of the seasonal migration. In addition, we analysed effort-corrected catch rates from a vertically-resolving stow net applied in the German Wadden Sea to monitor the depth distribution of forage fish for birds (Dänhardt, 2011). This data set was used to test whether the assumption that brown shrimps are largely demersal is valid, and if not, how catch results of the established surveys and conclusions on stock size derived from them would be affected.

5.3 MATERIAL AND METHODS

5.3.1 Beam trawl surveys

The autumn surveys, ''Demersal Young Fish Survey, DYFS'' (Siegel *et al.*, 2005) were conducted in September or October with the aid of chartered commercial vessels operating with a single 3 x 0.4 m beam trawl with 20 mm mesh size at the cod end (stretched mesh). The sampling is mainly focused on tidal creeks and shallow areas. The autumn data set included 417 hauls between 1997 and 2008 (excluding 1999) covering a depth range from 3–13 m (Figure 5.1). The winter survey was conducted in January and February with the German research vessel Solea and used a larger beam trawl of 7.2 x 0.6 m with the same mesh size of 20 mm at the cod end (stretched mesh). This survey aimed at resolving the winter distribution of adult, especially egg-bearing shrimps, in the German Bight outside the Wadden Sea (Figure 5.1). It included 712 hauls, spanning the years 2003-2010 (excluding 2004) and covering a depth range from 12- 54 m. Both winter and autumn surveys were carried out similarly with regard to analysis procedures and with similar employment of measuring devices and techniques. To compare the numbers of brown shrimps caught during day and night times, only a subset of hauls from both survey data sets were used in our analysis. Data were included if hauls had been conducted at the same depth range and location within the same week during day and night. For all beam trawl survey data the total number, size and reproductive state (egg-carrying or not egg-carrying) of brown shrimps per haul was estimated from a 200 g subsample. The numbers were scaled up to the total catch weight and expressed as numbers per 10000m^3 filtered water (D_{BT}= number of brown shrimps·10000^{-1}·m^{-3}), which will be referred to as "catch rate". Furthermore, time and (mostly) tidal hour were recorded. Missing tidal hours were inserted using a regional solution of the TPXO model provided by the Oregon State University (USA), see Egbert *et al.* (2010). This model calculates tidal hours for given coordinates. The calculated tidal hours were checked by comparing the recorded tidal hours in the survey data set. The total length of the shrimps was measured to the lower mm from the front of the scaphocerite to the tip of the telson. Brown shrimps were separated into brown shrimps carrying eggs (berried females) and brown shrimps without eggs (unberried shrimps). Unberried shrimps can obviously either be males or females. In order to get an impression of the composition of the sexes in the proportion of unberried shrimps, the sex of the brown shrimps was determined in subsamples of 120 hauls (autumn: 33 hauls, winter: 87 hauls) using morphological differences in the endopodits of the second pair of pleopods, see Tiews (1954). It is known that males mature at a smaller size (22-43 mm) than females (33-55 mm, Campos and van der Veer, 2008) and that they usually do not grow as large as females (Tiews, 1954; Tiews, 1970). This was also evident in the decreasing proportion of males in the fraction of unberried brown shrimps with increasing size (Table 5.1).

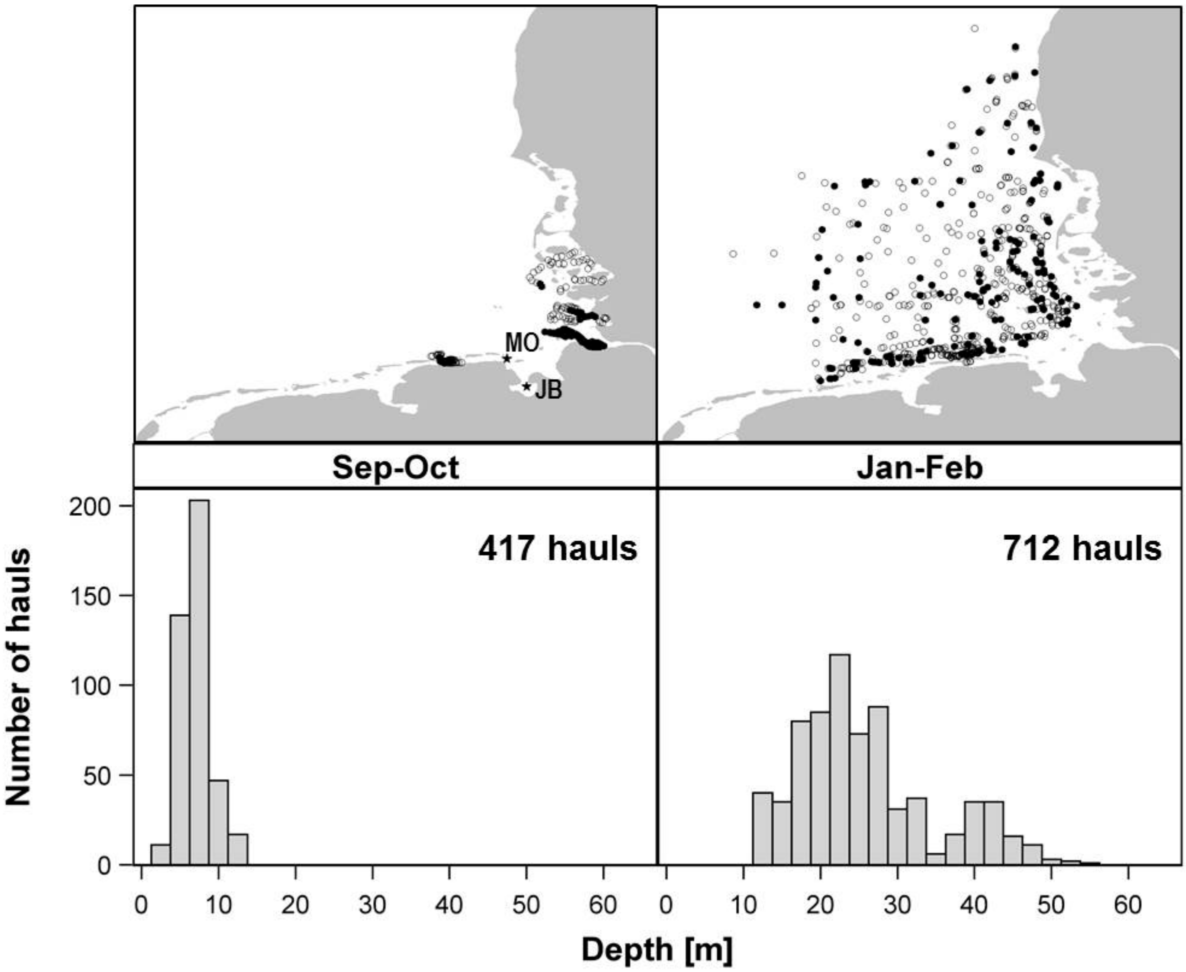

Figure 5.1 Top row: Locations of hauls of the autumn survey data from 1997, 1998, 2000 - 2008 (left column) and winter survey data from 2003, 2005 - 2010 (right column). Each dot represents a single day or night haul (night= filled circles, day= empty circles). Black stars mark locations of the 90 hauls of the VSN trials (MO= Minsener Oog, JB= Jadebusen), conducted from May - September in 2005 to 2007. Bottom row: Number of beam trawl hauls per depth of the autumn (left) and winter survey hauls (right). The total numbers of the beam trawl hauls for both seasons is given in the top right corner of the histograms.

Table 5.1 Mean composition of sexes in the fraction of unberried brown shrimps for different size groups, calculated from 120 sex determined hauls in the beam trawl survey data of autumn (September – October, N= 33 hauls) and winter (January – February, N=87 hauls). Sizes measured refer to total length in mm. Females (ub) = unberried females, unknown= brown shrimps for which sex could not be determined.

Size	fraction	Autumn mean %	Winter mean %
≤ 40	males	34.28	29.71
	females (ub)	31.77	43.53
	unknown	33.94	26.76
> 40 - ≤ 50	males	30.93	26.00
	females (ub)	31.27	43.31
	unknown	37.80	30.68
> 50 - ≤ 60	males	23.72	19.18
	females (ub)	36.17	41.93
	unknown	40.11	38.89
> 60	males	6.03	13.01
	females (ub)	40.83	43.40
	unknown	53.14	43.58

5.3.2 Vertically resolving stow net survey data (VSN)

To analyse the vertical distribution of brown shrimps within the water column, we used a special data set obtained from vertically resolving stow net (VSN) samplings, see Dänhardt (2011). As the data were collected within a project dealing with vertical distribution of prey fish for diving common terns, the top beam of the VSN was fixed at the water surface and the bottom beam of the VSN did not reach the ground. Although the gear was operated for this specific purpose of prey fish sampling, the data contain very valuable information on shrimps occurring in regions above the bottom. At low tide the net also covered water layers very close to the bottom. Obviously, from a brown shrimp researcher's point of view, a position from the seabed to a certain height would have been advantageous; however, the VSN covered almost the whole water column (Figure 5.2). Divided into 5 different net compartments it enabled resolving the vertical distribution of shrimps in the water column over a depth range of 7 m.

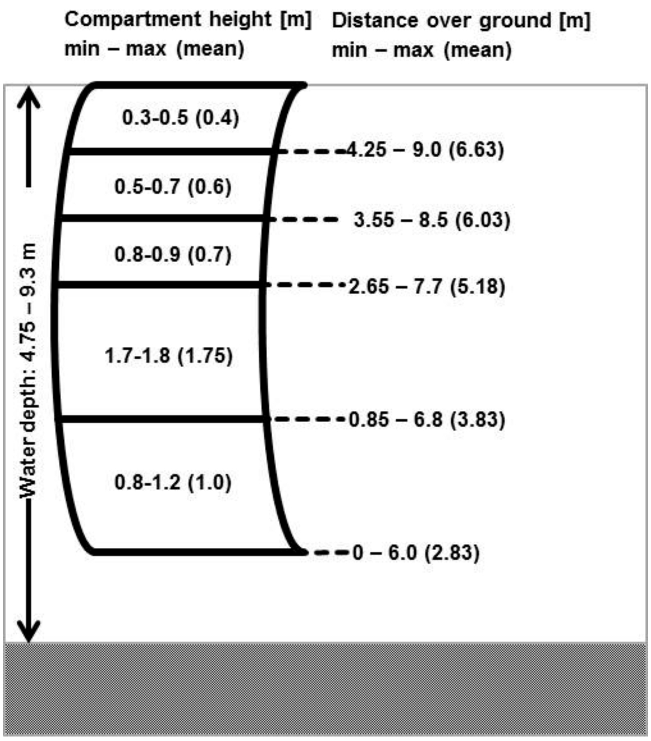

Figure 5.2 Variation in depth of the different compartments of the vertically resolving stow net due to sampling at different times and current velocities.

Using this VSN, a total of 90 hauls was taken from 2005 to 2007 at two sampling stations (Table 5.2): Central Jade Bight (station 1: 53°28 N, 08°12 E, N= 67) and off Minsener Oog (station 2: 53°44 N, 08°02 E, N=23, see Figure 5.1, black stars in top left map). Samples were taken weekly between May and July, and twice a month in April, August and September. During each sampling day 3 to 8 hauls were taken, distributed over both stations. As a current velocity of >0.3 $m \cdot s^{-1}$ is required for stow net fishing, hauls were always conducted 1.5 h after the turn of tide and thus during subsequent cycles of incoming and outgoing tide. Haul duration was 45 ± 5 minutes.

Table 5.2 Dates and locations of vertically–resolving stow net trials

Date	Locations (Number of hauls)
18-08-2005 – 13-10-2005	central Jade Bight (N=11)
19-04-2006 – 06-09-2006	central Jade Bight (N=25) and Minsener Oog (N=16)
24-04-2007 – 10-10-2007	central Jade Bight (N=31) and Minsener Oog (N=7)

The VSN consisted of five vertically stacked compartments of 5 m width. Hanging loosely and without the pressure of the currents, the upper three compartments were each 1 m, the lower two compartments 2 m in height, providing an overall net opening of 5 x 7 m. The stretched mesh size in all net compartments decreased from 40 mm close to the mouth to 10 mm at the cod end. These small meshes generated substantial pressure acting on the net and when in use all of the net compartments were compressed to a certain extent. Hence, while used, the overall net opening was reduced to an average overall opening of 5 x 4.5 m. The VSN was employed in depths between 4.8 to 9.3 m and the lowest edge of the VSN was located between 0 to 6 m above the seabed (Figure 5.2). Date, time, depth and tidal state as well as the number of brown shrimps caught in each of the net compartments were recorded for each haul. The number of brown shrimps in each of the net compartments i (N_{VSNi}) was standardised to numbers per 10000m^3 filtered water volume (catch rate). In order to resolve the factors that potentially influence the vertical distribution of brown shrimps, the mean distance to the ground (*GDist*) of the upper edge of each net compartment was estimated (Figure 5.2) using the recorded depth and the mean height of the net compartments (Dänhardt, 2011). Hence, for each haul and for each compartment, standardised numbers of brown shrimps were available. This number, N_{VSN}, was linked to the distance from ground by using the upper border of the net compartments as height above ground in which the brown shrimps were caught.

5.3.3 General statistical approach

For all our models, the standardised number of brown shrimps caught per 10000 m^3 filtered water (catch rate) served as the response variable. Original catch rates are counts and would usually be modelled by discrete distributions like the Poisson distribution. However, in our data the counts are very large and can therefore be approximated by a logarithmic normal distribution (McCullagh, 1983, p.200). The catch rate might be influenced by the various factors such as depth, tidal state, size group, etc.. On the logarithmic scale the simplest assumption about the random variation in the catch rate is that observed rates vary around the mean catch rate with constant variance under all conditions, while the mean rate may depend on the factors mentioned. This implies that on the linear scale the variance resulting from the log-normal distribution depends on the expected mean. Hence, we fitted log-linear models using the catch rates as response variable for each of the data sets. Model terms were selected in a stepwise manner and an individual model was fitted for each of the data sets, using the same set of model terms and the same categorisation over the data sets, where possible.

All models included daylight and tidal state as main effects. Daylight was categorised into day and night, where night was defined as the time span from 30 minutes after sunset to 30 minutes before sunrise. Tidal state was also categorised into two states (“flood and high tide” and “ebb and low tide”), to ensure full rank of the models.

Not only recorded but also unrecorded variables might have influenced catch rates. Variables such as turbidity (Addison *et al.*, 2003), weather conditions, salinity, temperature, size and sex composition of the shrimps, or power and length of the vessels, for example. To separate those unknown effects from the effects of the recorded variables we were interested in, a random intercept per vessel and date was introduced in all applied models. This term reduces the residual variance, thus improving the possibility to detect effects of the model terms included.

In order to find a model capable of explaining as much data variation as possible with the least model complexity, model fitting for each of the data sets (VSN data, beam trawl data of autumn and winter) was done in two major steps per data set. First, the most detailed data set was used to determine those components that could reasonably be included in a model. Model terms were chosen by forward selection with AIC as optimality criteria. This model, called the "full" model, was smaller than the saturated model, as the data were not generated according to a full factorial design. In a second step, the previously found full model was fitted to the other data sets, as far as this was possible. Due to gaps in the data structure, some terms had to be removed. Eqs. (1) and (2) show the structure of the full models. Starting from the full model, backward selction was used to obtain a parsimonious "final" model (explaining much variance with few parameters) for each of the data sets.

During the backward process non-significant model terms were excluded from the model. Significance was determined with type III tests of fixed effects which are robust against the inclusion order. Furthermore, type III tests aim to reduce the bias caused by an unbalanced design (Pendleton *et al.*, 1986). Main effects that were part of significant interactions were maintained, even if they themselves were not significant. Interaction parameters were also tested with type III tests. Using the parameter estimates of the final model, predictions for the mean catch rates (N_{pred}) were calculated for all depths within the given depth range and constrained to a random effect of zero.
Once the final model was determined, it could be used for the prediction of catch rates with arbitrary explaining variable values inside the data range. This allows prediction for circumstances that had not been seen in the data. Neither in the beam trawl survey data were all combinations of factor levels (e.g. day and night for factor daylight, ebb and flood for factor tidal state, etc.) measured at all different depths within the depth range, nor were all factor levels of all possible model terms available at all different *GDists* in the VSN data set.

To compare catch rate predictions from the different final models, score data sets were created. These included all possible factor levels of the included model terms and all depths within the sampled depth range. By applying the estimated model to the score data sets, predictions for the catch rates were obtained for all available depths. Since the interest focussed on the systematic aspects of shrimp behaviour as described by the model, not on effects caused for example by trawler attributes, only predictions with a random intercept of zero were considered.

The accuracy of the predicted catch rate was ascertained by bootstrapping (Efron, 1994, pp.168-177). Using the final model, Monte-Carlo simulations were done by fitting the model to randomly chosen subsets of the original data set. Those subsets were constrained to contain 80% of the hauls. Subsequently, the absolute differences between the original prediction and the predictions of the bootstrap-samples were calculated for every sampled depth and the upper 5% were dismissed. Minimum and maximum of the remaining 95% bootstrap-predictions are the lower (LCL) and upper (UCL) 95% confidence limit of the predicted catch rate. These confidence limits account for both biological variability and uncertainty in the estimation of model parameters.

About 250 bootstrap replications in the beam trawl survey data and about 500 replications in the VSN data were needed in order to produce stable confidence bands. For safety reasons this number was doubled. Hence, 500 and 1000 replications were completed for the beam trawl survey data and the VSN data, respectively.

5.3.4 Statistical approach for the beam trawl survey data:

The catch rate (N_{BT}) served as the response variable. In addition to the categorical model terms tidal state (flood and high tide, ebb and low tide), daylight (night and day), reproductive state (berried and unberried) and brown shrimp size (very small: ≤ 40mm, small: ≤ 40- 50mm, large: ≤ 50-60mm, very large: > 60mm), the ln-transformed depth as a continuous variable was included as continuous variable. The inclusion of size groups was preferred over the inclusion of size as a continuous variable, because this allows modelling of nonlinear effects in a simple way.

We observed that the variance of the catch rates differed between the shrimps' size groups. In order to consider this heteroscedasticity we allowed the covariance parameter to vary by size group.

The beam trawl survey data sets allowed an elaborate full model. The best full model (lowest AIC) contained two 2-way-interactions between ln(depth) and size group and ln(depth) and tidal state. In addition, the model contained the 3-way-interaction between ln(depth), daylight and reproductive state, which was equivalent to the inclusion of the two 2-way interactions of both daylight and reproductive state with ln(depth). Therefore, the full model for the catch rate in haul *i* from the survey data can be expressed as:

$$
\begin{aligned}
\ln(N_{BT_{i,r}}) = {} & \beta_0 + \beta_r + \beta_{size} \cdot \text{size group}_{size,i,r} + \beta_{dl} \cdot \text{daylight}_{dl,i,r} \\
& + \beta_{egg} \cdot \text{egg}_{egg,i,r} + \beta_{tide} \cdot \text{tide}_{tide,i,r} + \beta_{depth} \cdot \ln(\text{depth})_{i,r} \\
& + \beta_{depth*size} \cdot \ln(\text{depth})_{i,r} \cdot \text{size group}_{size,i,r} + \beta_{depth*tide} \cdot \ln(\text{depth}) \cdot \text{tide}_{tide,i,r} \\
& + \beta_{depth*dl*egg} \cdot \ln(\text{depth}) \cdot \text{daylight}_{dl,i,r} \cdot \text{egg}_{egg,i,r} + \varepsilon_{size}
\end{aligned}
\qquad \textbf{(eq. 5.1)}
$$

with *i*: haul, *size*: size group (1: ≤ 40 mm, 2: ≤ 40 - < 50 mm, 3: ≤ 50- < 60 mm, 4: >60 mm), *dl*: daylight (day, night), *egg*: reproductive state (berried, unberried), *tide*: tidal state (ebb, flood). A random intercept *(r)* for the combination of vessel and date was used in order to account for general differences in the number of brown shrimps caught between different vessels and dates which cannot be explained by the included model terms. The presumed normally distributed random noise was symbolised by ε.

5.3.5 Statistical approach for the VSN data

In order to identify the factors which influence the catch rate (N_{VSN}), the full model included the categorical model terms daylight, tidal state and season (*seas*), the latter categorised as spring (Apr-Jun), summer (Jul-Aug) and autumn (Sep-Oct). The distance to the ground was included as an additional continuous model term. As the

VSN data set was smaller than the beam trawl data sets, categorisation and waiving of interactions was needed, in order to avoid linear dependencies between the model terms. Hence, the full model for the standardised number of brown shrimps in haul *i* as a function of season, daylight, tide and ground distance was:

$$\log_n (N_{VSN_{i,r}}) = \beta_0 + \beta_r + \beta_{seas} \cdot \mathrm{seas}_{seas,i,r} + \beta_{dl} \cdot \mathrm{daylight}_{dl,i,r} + \beta_{tide} \cdot \mathrm{tide}_{tide,i,r} + \beta_{GDist} \cdot \mathrm{GDist}_{GDist,i,r} + \varepsilon_{i,r} \qquad \textbf{(eq. 5.2)}$$

with *seas*: season (spring, summer, autumn), *dl*: daylight (day, night), *tide*: tidal state (ebb, flood), *GDist*: distance from the ground and ε being the random error term. Again a random intercept (*r*) was introduced for each of the *i* hauls, as in previous models. The random error was assumed to be normally distributed on the logarithmic scale with a constant variance.

Linearity of the *GDist* effect was checked by fitting a spline term for *GDist*, which, however, did not reveal a significant effect (p = 0.3147). Therefore the linear term for *GDist* was maintained.

For fixed season, daylight and tidal state the predicted mean catch rate (N_{pred}) within a certain depth stratum is then equal to:

$$N_{pred}(Stratum) = \int_{b_{low}(Stratum)}^{b_{up}(Stratum)} e^{\beta + \beta_{GDist} \cdot GDist} \, \mathrm{d}GDist \qquad \textbf{(eq. 5.3)}$$

with b_{up} and b_{low} as the upper and lower border of the stratum and β and β_{GDist} as the estimated parameters (intercept and factor for *GDist*) of the log-linear model. Confidence limits for the predictions were derived by the delta method (Bishop, 1975, pp. 486-502).

5.4 RESULTS

In order to test the validity of the assumption of brown shrimps living primarily benthically, we analysed multiannual VSN data that covered nearly the whole water column. We tested if the catch rates of certain size groups or reproductive states depend on daylight or tidal state by using German beam trawl survey data.

Catch rates in this data only slightly depended on daylight and only in winter did they depend on tidal state. Catch rates of berried and large females were almost equal over all measured depths or even increased with depth. This was different from the distribution of unberried and small brown shrimps whose catch rates generally decreased with increasing water depth. The VSN data analysis revealed that about 2/3 of the brown shrimps are not bottom dwelling but located above the height of a typically used beam trawl of about 0.5m.

5.4.1 Beam trawl survey data

5.4.1.1 Autumn

As shown in Figure 5.3 the mean catch rates in the autumn survey varied between 1919 and 2502 individuals per 10000m³ filtered water, with highest mean catch rates during nocturnal flood tides. The majority of the hauls was usually composed of unberried brown shrimps of 40 and 50 mm length. Berried females were only present in size groups >40 mm and the mean share of berried females per haul was generally very low (< 5 %).

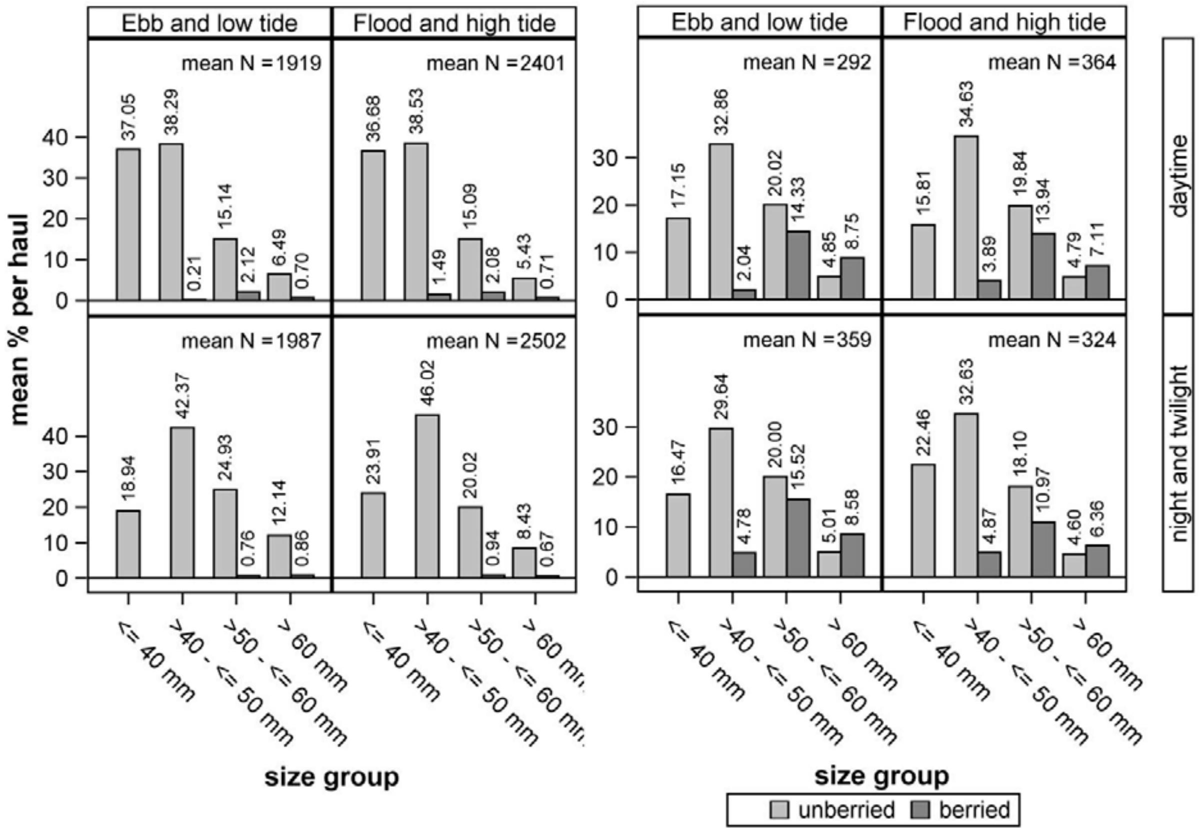

Figure 5.3 Average percentage of brown shrimps caught per beam trawl haul in autumn (left panel) and winter (right panel). Mean N: mean number of brown shrimps per haul standardised on 10000 m³ filtered water.

In autumn, tidal state and all interactions with tidal state were dismissed from the final model during the backward selection process. The final model explained 53.02% of the variance and included daylight (p=0.7651), ln(depth) (p=0.0175), size group (p<0.0001), reproductive state (p<0.0001), the 2-way interaction between depth and size group (p<0.0001)) and the 3-way interaction between depth, daylight and reproductive state (p=0.0029, see Table 5.3).

Table 5.3 Type 3 Tests for the final model of the beam trawl surveys of autumn (depth-range 3 – 13 m) and winter (depth-range: 12 - 54.5 m). As in autumn no small berried females during night and flood were caught, size group was not included into the model for the autumn data. This is symbolised by an X at the according position.

Effect	----------- Autumn -------		----------- Winter --------	
	F Value	Pr > F	F Value	Pr > F
Daylight	0.09	0.7651	3.08	0.0795
Reproductive state	15.54	<.0001	35.55	<.0001
Size group	18.98	<.0001	40.23	<.0001
Tidal state			24.93	<.0001
ln(depth)	5.66	0.0175	140.92	<.0001
ln(depth)*Size group	11.97	<.0001	38.07	<.0001
ln(depth)*Tidal state			24.04	<.0001
ln(depth)*Daylight*Reproductive state	4.69	0.0029	13.19	<.0001

Table 5.4 Estimates of the final log-linear random intercept model for autumn survey data from 1997 to 2008 (except 1999). Effect: index of the β-Parameter, Repro. state: Reproductive state, DL: daylight (d=day, n=night), EGG: reproductive state (0=unberried, 1=berried); SG: size group (1: ≤ 40 mm, 2: > 40 - ≤50mm, 3: >50 - ≤ 60 mm, 4: >60 mm); ln(depth): natural logarithm of depth; Est: Estimate; Std Err: Standard Error of the estimate; LCL: Lower confidence limit; UCL: Upper confidence limit.

Effect	DL	EGG	SG	Est	Std Err	Pr > |t|	LCL	UCL
Intercept				3.6327	0.8292	<.0001	1.9592	5.3061
Daylight	d			-0.1751	0.5859	0.7651	-1.3245	0.9742
Daylight	n			0	.	.	.	.
Size group			1	4.7426	0.6560	<.0001	3.4557	6.0294
Size group			2	3.0149	0.5723	<.0001	1.8922	4.1376
Size group			3	2.0300	0.5643	0.0003	0.9230	3.1370
Size group			4	0	.	.	.	.
Reproductive state		0		2.4182	0.6135	<.0001	1.2147	3.6217
Reproductive state		1		0	.	.	.	.
ln(depth)				0.4211	0.4080	0.3022	-0.3793	1.2216
ln(depth)*Size group			1	-2.0000	0.3365	<.0001	-2.6602	-1.3399
ln(depth)*Size group			2	-0.7750	0.2940	0.0085	-1.3517	-0.1983
ln(depth)*Size group			3	-0.5980	0.2884	0.0383	-1.1638	-0.03229
ln(depth)*Size group			4	0	.	.	.	.
ln(depth)*Daylight*Repro. state	d	0		-0.2352	0.4351	0.5888	-1.0887	0.6183
ln(depth)*Daylight*Repro. state	d	1		0.3431	0.2937	0.2429	-0.2331	0.9193
ln(depth)*Daylight*Repro. state	n	0		-0.2040	0.3141	0.5163	-0.8202	0.4123
ln(depth)*Daylight*Repro. state	n	1		0	.	.	.	.

We observed that the general trend of decreasing catch rates with increasing depth levels off or even reverses with increasing size and with change of reproductive state. The predicted catch rates for brown shrimps <40 mm decreased strongly with increasing depth (Figure 5.4). During day their catch rates were significantly lower in 4 m (LCL: N=5052, UCL: N=10383) than in 12 m depth (LCL: N=688, UCL: N=1415). For berried females >60 mm length this trend is different. Their predicted catch rates significantly increased with increasing water depth (at 4 m: LCL: N=126, UCL: N=259; at 12 m: LCL: N = 292, UCL: N =600).

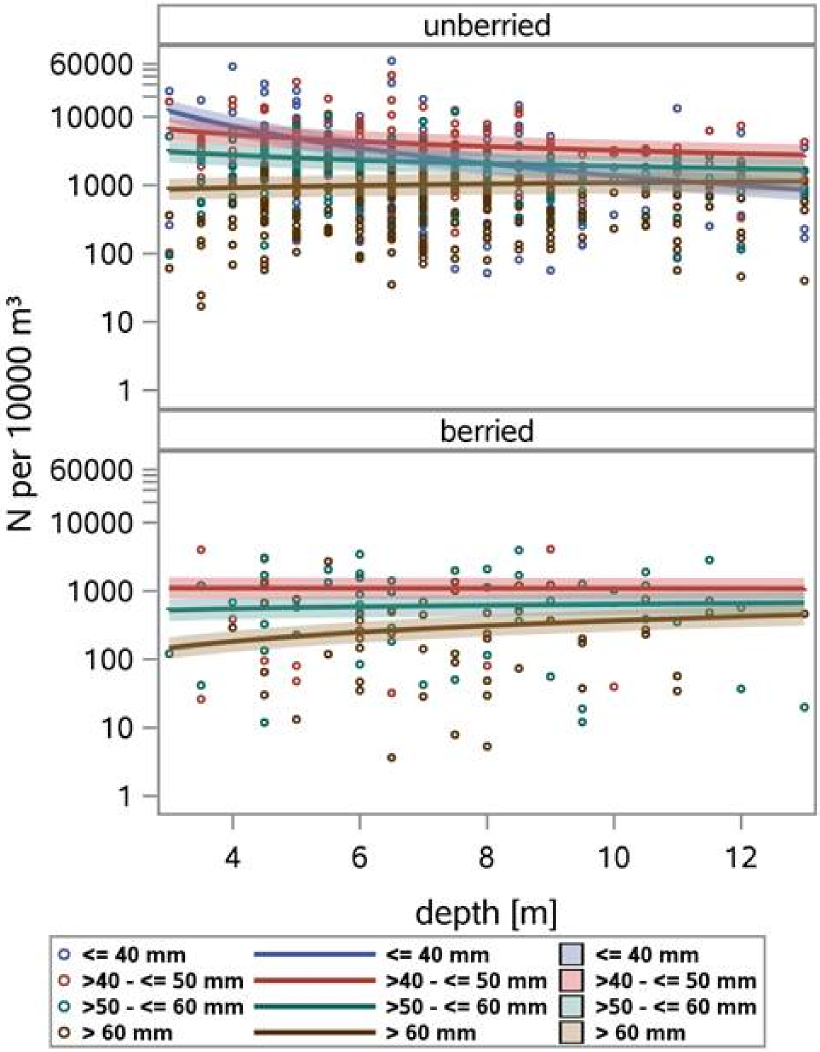

Figure 5.4 Predicted and observed numbers of caught numbers of brown shrimps for different depths in the autumn beam trawl survey data at daylight. The numbers are standardised to 10000 m³ filtered water and the effect of vessels and date was removed. Each haul is symbolised by one circle per size group and reproductive state. Predictions of the log-linear model are represented by the solid lines including their 95% confidence bands (semi-transparent bands) based on 500 bootstrap replications. Tidal state is not shown here as it was not part of the final model for the autumn beam trawl survey data, hence, the predictions would be equal for all tidal states. As no berried females <40mm were caught, we also refrained from predicting their expected numbers over depth.

As listed in Table 5.3 and Table 5.4, daylight was also part of the final model for the autumn data. However, daylight was not significant as a main term (see above) and only kept as main term in the final model due to its contribution to the 3-way interaction. As shown in Table 5.4 none of the estimated differences of the 3-way interaction were significant. However, conventional estimate tables only display differences to the selected “reference group”. Hence, Table 5.4 is only displaying differences to nocturnal catch rates of berried females. This means that not all possible comparisons, i.e. contrasts, of the 3-way interaction are shown. We calculated those contrasts which are not listed in Table 5.4. We found however, that none of those additionally calculated contrasts were significant (not shown). This apparent contradiction is evidence for small single effects which sum up to an improved model fit in general when the interaction is included.

5.4.1.2 Winter

In the winter beam trawl hauls, the mean catch rates were low (Minimum: 292, Maximum: 364, Figure 5.3), with usually highest proportions of unberried brown shrimps of a length between 40 and 50 mm. The portion of berried females comprised around 20% of the haul (Figure 5.3) and all berried females were larger than 40 mm. Highest mean proportions of berried females were found for the size group between 50 and 60 mm total length.

In the analysis for the winter survey data all variables of the full model were kept in the final model. This model explained 43.52% of the variance. Hence, the final model for the winter survey data included the main effects daylight ($p = 0.0795$), reproductive state ($p < 0.0001$), size group ($p < 0.0001$), ln(depth) ($p < 0.0001$), tidal state ($p < 0.0001$), the 2-way interactions between ln(depth) and tidal state ($p < 0.001$) and between ln(depth) and size group ($p < 0.0001$). Furthermore, the 3-way interaction between ln(depth), daylight and reproductive state ($p < 0.0001$, see Table 5.3) was part of the final model in winter.

Though the depth range in the winter survey (12 - 54 m) data was different from the depth range of the autumn survey data (3 - 13 m), the model for the winter survey data identified the same depth-specific trends as in the autumn data set. These trends can be seen most clearly in Figure 5.5 (top left) showing the catch rates of ebb tides during daylight. Here we observed that the predicted catch rates of unberried brown shrimps <40 mm length were significantly higher at 15 m (LCL: N = 396, UCL N = 771) than at 50 m depth (LCL : N = 10, UCL: N = 9) but this trend is reduced with both increasing size and change of reproductive state from unberried to berried (Figure 5.5). Similar to the autumn data the trend reversed for berried females >60 mm length where the predicted catch rates were significantly higher at 50 m depth (LCL: N = 102.3, UCL: N = 198.9) than at 15 m depth (LCL: N = 52.3, UCL: 101.8). Of course, whether the differences between the different depths can be called significant depends on the depths in consideration (here: 15 and 50 m). However, from Figure 5.5 the flattening of the trend of catch rates over depth of the small unberried brown shrimps < 40 mm to the large berried females > 60 mm length is evident.

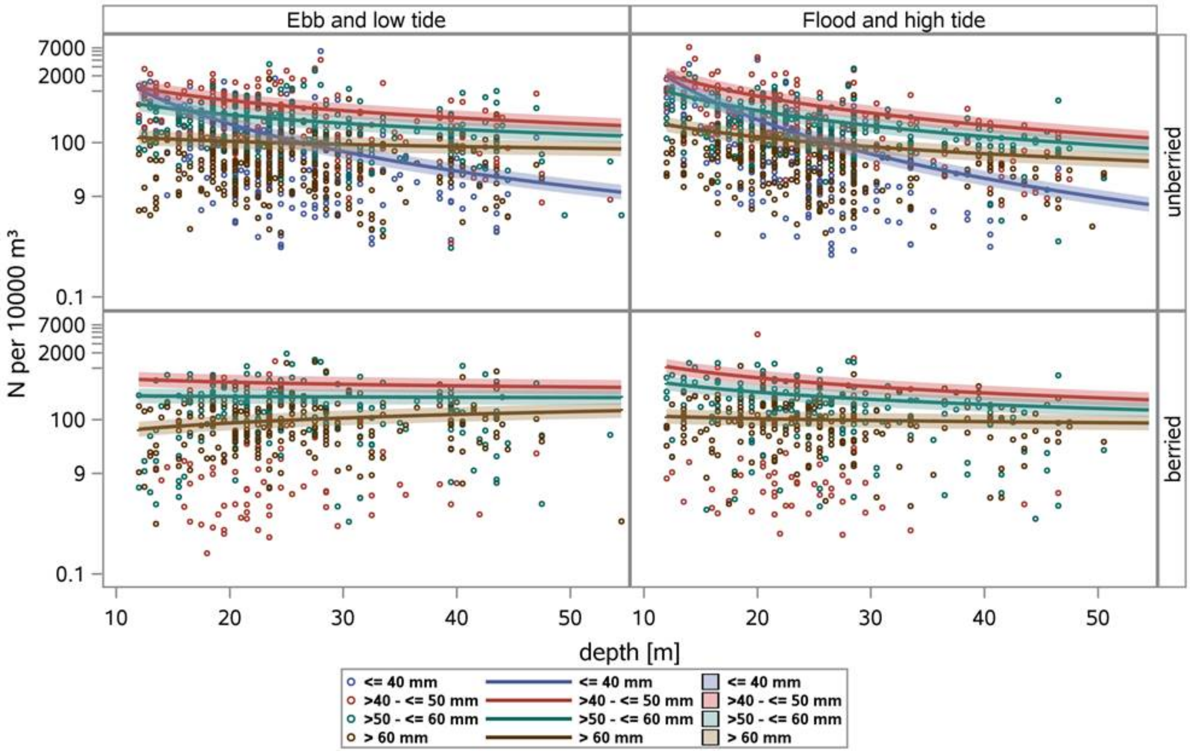

Figure 5.5 Predicted and observed numbers of caught numbers of brown shrimps for different depths in the winter beam trawl data at daylight conditions at different tidal states. Both observed and predicted numbers are standardised to 10000m³ filtered water. Furthermore, the effect of vessels and date was removed. Each haul is symbolised by one circle per size group and reproductive state; the predictions of the log-linear model are represented by the solid lines including their 95% confidence bands (semi-transparent bands) based on 500 bootstrap replications. As no berried females <40mm were caught, we refrained from predicting their expected numbers over depth.

As in autumn, daylight was also part of the final model for the winter survey data and again, daylight as a main term was not significant (p= 0.0795) and was kept in the final model only because of its contribution to the 3-way interaction. However, in contrast to the model for the autumn survey, some of the estimates of the 3-way interaction between day and night were significant (Table 5.5 and Table 5.6). A closer look revealed that the significant contrasts represent differences between unberried and berried females rather than differences between day and night. Table 5.6 shows that the differences in catch rates between berried females during the night and berried females during the day were not significant (p= 0.0978), and neither were the differences between diurnal and nocturnal catch rates of unberried brown shrimps (p=0.0746).

In contrast to the analysis of the autumn survey data, in winter a significant difference in catch rates was found when observing various tidal states. With negative values of $\beta_{\text{tide=ebb}}$ = -2.4289 (Table 5.5), generally lower catch rates are predicted during ebb than during flood and high tide. However, as ebb also contributed positively to the 2-way interaction with depth ($\beta_{\text{depth}\cdot\text{tide=ebb}}$ = 0.7456, Table 5.5), the main effect estimate cannot be interpreted without considering the interaction. The tidal effect in total leads to the following effect: During flood and high tide the predicted catch rates are higher in "shallow" depths, during ebb and low tide the predicted catch rates are higher in "deeper" water. This means for example, that during flood at 15 m depth the predicted catch rates of all brown shrimps (i.e. all sizes, berried and unberried) increase by 50.65% compared to the catch rates during ebb. In contrast, at 50 m depth the catch rates increase during ebb by 64.09% compared to the catch rates during flood and high tide.

Table 5.5 Estimates of the final log-linear random intercept model for the winter survey data from 2003-2010 (except 2004). Effect: index of the β-Parameter, Repro. state: Reproductive state, DL: daylight (d= day, n = night), EGG: reproductive state (0=unberried, 1=berried); SG: size group (1: ≤ 40 mm, 2: > 40 - ≤50mm, 3: >50 - ≤ 60 mm, 4: >60 mm); Tide: tidal state (E= outgoing and low water, F= incoming and high water); ln(depth): natural logarithm of depth; Est: Estimate; Std Err: Standard Error of the estimate; LCL: Lower confidence limit; UCL: Upper confidence limit.

Effect	DL	EGG	SG	Tide	Est	Std Err	Pr > |t|	LCL	UCL
Intercept					5.4499	0.6815	<.0001	4.1008	6.7989
Daylight	d				-0.9717	0.5540	0.0795	-2.0578	0.1144
Daylight	n				0	.	.	.	.
Size group			1		8.4682	0.8037	<.0001	6.8925	10.0439
Size group			2		3.2421	0.7266	<.0001	1.8175	4.6667
Size group			3		3.0029	0.4915	<.0001	2.0392	3.9666
Size group			4		0	.	.	.	.
Tidal state				E	-2.4289	0.4865	<.0001	-3.3827	-1.4750
Tidal state				F	0	.	.	.	.
Reproductive state		0			2.8719	0.4817	<.0001	1.9275	3.8163
Reproductive state		1			0	.	.	.	.
ln(depth)					-0.4809	0.2105	0.0224	-0.8937	-0.06816
ln(depth)*Size group			1		-2.7107	0.2546	<.0001	-3.2099	-2.2115
ln(depth)*Size group			2		-0.7895	0.2276	0.0005	-1.2358	-0.3432
ln(depth)*Size group			3		-0.6027	0.1529	<.0001	-0.9025	-0.3029
ln(depth)*Size group			4		0	.	.	.	.
ln(depth)*Tidal state				E	0.7456	0.1521	<.0001	0.4474	1.0437
ln(depth)*Tidal state				F	0	.	.	.	.
ln(depth)*Daylight*Repro. state	d	0			-0.6013	0.2327	0.0098	-1.0575	-0.1451
ln(depth)*Daylight*Repro. state	d	1			0.2875	0.1736	0.0978	-0.05283	0.6278
ln(depth)*Daylight*Repro. state	n	0			-0.9114	0.1524	<.0001	-1.2102	-0.6125
ln(depth)*Daylight*Repro. state	n	1			0	.	.	.	.

Table 5.6 Differences and p-values of comparisons of different interaction estimates for the winter beam trawl data. Berried= female carrying eggs, unberried= brown shrimp without eggs. (The reference value is tabulated in column-heading; Est= estimate, p= p-value; alpha = 0.05).

		Unberried		Berried	
		Day	Night	Day	Night
Unberried	Day	-	Est = 0.3101 p = 0.0746	Est = -0.8888 p = <.0001	Est = -0.6013 p = 0.0098
	Night	-	-	Est =-1.1988 p =<.0001	Est = -0.9114 p =<.0001
Berried	Day	-	-	-	Est = 0.2875 p = 0.0978
	Night	-	-	-	-

5.4.2 VSN data

The final model of the VSN analysis fitted the data with an R^2-value of 51.71%. The model included daylight (type 3 tests: F-value= 4.19, p= 0.0427) and the distance to ground (type 3 tests: F-value=38.22, $p < 0.001$) while tidal state and season were excluded during the backward selection process.

During the day average catch rates were significantly lower than during the night. Day catch rates are expected to be only ca. 39% (Table 5.7) of nocturnal catch rates.

Table 5.7 Final Estimates of the loglinear random intercept model for the VSN (GDist= Distance from the ground, StdErr= Standard Error of the estimate, LCL= Lower confidence level, UCL= Upper confidence level).

Effect	Daylight	Estimate	Std Err	t Value	Pr > |t|	Lower	Upper
Intercept		7.0319	0.7136	9.85	<.0001	5.5896	8.4742
Daylight	day	-0.9446	0.4614	-2.05	0.0427	-1.8577	-0.03151
Daylight	night	0	.	.	.	.	.
GDist		-0.6624	0.1071	-6.18	<.0001	-0.8744	-0.4503

An increase of the distance to ground by one metre reduces the expected catch rate by about 52% as indicated by the estimate of -0.662 (Table 5.7). The expected proportion of brown shrimps located above the usual beam trawl height is surprisingly high in spite of the reduction of densities with increasing distance from ground (Figure 5.6). Supposing a beam trawl height of 0.6 m, 67.14% of the brown shrimps are predicted to be above the height accessible to the fishing gear (Table 5.8). Assuming a lower beam trawl of 0.4 m, on average 76.68% of all brown shrimps in the water column are predicted to be inaccessible for the beam trawl.

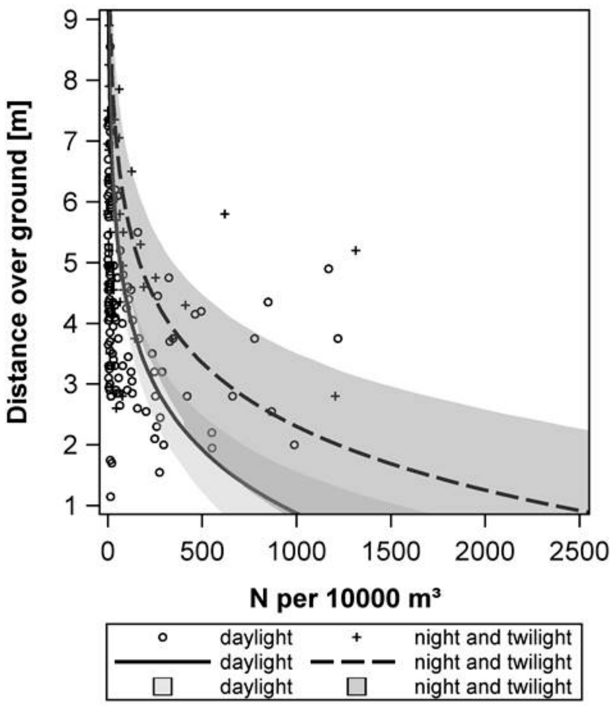

Figure 5.6 Observed and predicted number of brown shrimps for the VSN data during day and night at different distances over ground. The distance over ground indicates the height of the upper border of the 5 different net compartments of the VSN. The empirical observations of 90 hauls in total are shown as symbols during day ("o") and night ("+"). Predictions of the log-linear model are represented by lines including their 95% confidence bands (semi-transparent bands) after 1000 bootstrap replications.

Table 5.8 Predicted ratio of brown shrimps caught within different potential beam trawl heights of 0.4, 0.5 and 0.6 m in a water depth of 9.3 m. GDist: Distance over ground, LCL: Lower 95% confidence limit of the mean , UCL: Upper 95% confidence limit of the mean.

Height	Predicted percentage of brown shrimps	Predicted number of brown shrimps
	Mean (LCL, UCL)	**Mean (LCL, UCL)**
GDist > 0.4 m	76.68 (70.53, 83.20)	3555.41 (3270.25, 3857.72)
GDist ≤ 0.4 m	23.31 (16.80, 29.47)	1080.81 (778.96, 1366.43)
GDist > 0.5 m	71.75 (64.64, 79.45)	3326.82 (2997.15, 3683.84)
GDist ≤ 0.5 m	28.25 (20.55, 35.36)	1309.86 (952.84, 1639.53)
GDist > 0.6 m	67.14 (59.24, 75.87)	3113.07 (2746.77, 3517.85)
GDist ≤ 0.6 m	32.86 (24.13, 40.76)	1523.61 (1118.83, 1889.91)

5.5 DISCUSSION

The first goal of this analysis was to provide arguments whether or not adult brown shrimps use STST. Our findings of berried females being distributed almost equally over all depths in autumn and winter and of unberried and small brown shrimps mainly being located in shallower areas, suggest that brown shrimps use tidal currents to place themselves at a certain, preferred depth. The second aim was to find out, whether the assumption of brown shrimps living primarily benthically is supported by the VSN, which is appropriate to such a study as it covered nearly the whole water column. This study showed that the common assumption of brown shrimps living primarily benthically (Berghahn, 1983; Boddeke *et al.*, 1986) requires rethinking. The validity of quantitative biomass estimates from beam trawl sampling needs questioning, as our results indicate that about 2/3 of the brown shrimps can be found in heights unreachable for beam trawls.

5.5.1 Limitations of this study

The data used in this study are a product of general survey sampling. Information recorded in the data was selected according to the survey purpose, not for the needs of the present study. This means that information which might have been useful for this study is not available. An example is shrimp transport: the survey data gives counts at a given time and location, but no information about the process of shrimps changing their geographic location. The technique of transport used by the shrimps can therefore only be concluded from the locations where they were found. This is a less firm conclusion than inference from direct observation of transport. Also, the factors that are present in the data, only allow conclusions up to a certain extent. Typically for environmental data, only a subset of all possible factor levels and covariate combinations is present in the data set. This restricts the set of main terms and interactions that can be modelled and subsequently assessed, with regard to their relevance. A full analysis of all imaginable model terms requires a factorial sampling design, which is hardly feasible in any environmental study.

The previous considerations give rise to the assumption that observed catch rates will only partially be explainable by the observed factors. Therefore, and observing that catch rates as all environmental quantities are highly variable, an explained variance of about 50% as reached by the present analyses seems quite considerable, even though formally there is room for improvement. As pointed out, many unrecorded variables may have affected the catch rate (e.g. turbidity). The impact of these unavailable variables was incorporated in the present study by introducing a random intercept per vessel and date. This is certainly better than simply ignoring the existence of unknown factors, but also carries some danger that the random intercept takes up a part of the real effect. This problem can only be resolved by introducing empirical data on the so far missing factor levels into the analysis.

Conclusions from the statistical models were reached after a model selection procedure. To rule out that model selection generated a model responding to exotic features of the data, the robustness of the results was investigated in two respects.

Firstly, fitting the final model to bootstrap samples produced fits similar to the fits which were based on the full data set. This is demonstrated in the small confidence band, mostly identifiable in presentations with a logarithmic axis, see Figure 5.4 and Figure 5.5. Secondly, the impact of single data portions contributed per vessel and date was analysed by removing those 5 contributions which had highest impact on the predictions. This removal had no visible impact on the predictions, implying that the global predictions obtained have a more general validity and do not rely on properties of small data portions.

5.5.2 Influence of season

In the beam trawl surveys of autumn and winter, catch rates and the composition within the catches were consistent with the general belief of the brown shrimps' life cycle as described by Hufnagl and Temming (2011). The catch rates in autumn were more than six times higher than in winter. This is consistent with Henderson *et al.* (2006) and Maes *et al.* (1998) and also corresponds to the autumn peak in commercial catches (ICES, 2012).

Main contribution to this autumn abundance peak comes from brown shrimps that hatched in spring of the same year: These shrimp mostly reach commercial size of 50 mm in September and 60 mm in winter (Hufnagl and Temming, 2011). For brown shrimps of length > 60 mm, the probability for females to carry eggs is > 80% (Siegel *et al.*, 2008; Oh *et al.*, 1999). This matches with our beam trawl data, where we found greater proportions of berried females in the catches in winter and only very small fractions of berried females in autumn (see also: Siegel *et al.*, 2008). As the catch rate and catch composition are, hence, strongly influenced by the life cycle of the brown shrimps, standardised catches can only be obtained when hauls are made on a regular basis at predefined times (e.g. months) of the year.

5.5.3 Trends over depth

Our analysis of the beam trawl data provides strong evidence that brown shrimps distribute differently over depth depending on their size and reproductive state. Despite the different depth ranges of 3-13 m in autumn and 4-54 m in winter, in both seasons the catch rates of small brown shrimps are highest in shallower water and their catch rates decreased with increasing depth. With increasing size brown shrimps tend to distribute more equally over depth. As soon as they are berried, the trend towards an even distribution (i.e. almost stable catch rates independent of depth) is stronger and even reverses for very large berried females of length >60 mm. Their predicted catch rates are highest in deep areas. This confirms the observations of Havinga (1930) and Boddeke (1976) of increased numbers of large brown shrimps with increasing depth in late autumn and winter insofar as generally the relative share of large berried females in the catches increased with increasing depth.

As in relation to the composition within the catches the same general depth-dependent trend was found in the autumn and winter beam trawl survey data, it can be suggested that this probably is not simple coincidence, but may rather be the result of active behaviour, such as STST.

A generally low gradient in the catch rates over depth for large berried females and even increasing catch rates with depth during ebb (Figure 5.5 and 5.6) could indicate a strategy to distribute as uniformly as possible and not just be related to temperature as suggested by Boddeke (1976). A maximum dispersal of the starting positions for the drifting larvae into potential juvenile habitats would increase the likelihood of juveniles reaching all beneficial juvenile habitats and might hence increase recruitment. As temperature influences egg-development exponentially (Havinga, 1930; Tiews, 1954; Meredith, 1952), hatching is mainly triggered by the rapid temperature increase in spring. Hatching is therefore largely synchronized leading to a distinct recruitment peak (Temming and Damm, 2002) with very high densities on the tidal flats from June to September, with an average of 60 shrimps per m^{-2} (Beukema, 1992). A uniform distribution of the berried females and a widespread release of their larvae could also help to limit local densities of juveniles in shallow nurseries in spring. This would reduce density dependent food limitation. Consequently, the cumulative mortality of well-fed and hence larger juveniles will be reduced (Cowan *et al.*, 1996; Houde, 1987).

5.5.4 Daylight

Daylight was part of the final models in all three analysed data sets. However, in the beam trawl hauls the effect of daylight was small and, considering the variability in the data, not significant. In the VSN data however, the differences were large and the predicted catch rates at night were more than twice as high as those for the day.

During the backward selection process for the VSN data, season was eliminated from the statistical model. This implies that the catch rates from May to September did not change significantly within this period.

The lack of significance of daylight in the beam trawl sampling and in contrary its strong effect in the VSN data, may be explained by differences in sampling seasons. Highest sampling frequency in the VSN data was reached in summer, which was the same season in which the field studies of Al-Adhub and Naylor (1975) and Addison *et al.* (2003) were conducted. They also found higher nocturnal than diurnal catch rates. Also observations carried out in summer using an underwater camera (Burrows *et al.*, 1994) recorded highest activity peaks around sunrise and sunset (i.e. in our categorisation mostly during night).

However, brown shrimps adapt their activity to day-length (Hagerman, 1970) or light intensity (Al-Adhub and Naylor, 1975; Hufnagl *et al.*, 2014) with increased activity during darkness.

In the autumn and winter beam trawl data set, daylight was still part of the final models and increased the overall model fit. However, the effect on the catch rates was not significant. The light intensities probably differed because of high light intensities during the VSN-sampling (mainly in summer) and lower light intensities in autumn and the winter beam trawl data set. This could explain the significant effect of daylight in the VSN data and its non-significance in the beam trawl data.

Hence, the result of this study in reference to daylight corresponds well with the results of Addison *et al.* (2003). It implies that standardised catches could be obtained by fishing only at fixed light intensities, e.g. during night at a fixed depth. It would nevertheless be advantageous if future VSN experiments were to sample during other times of the year, and include size group and reproductive state in the collected data. This could facilitate the analysis of daylight effects in different seasons and help to identify possible differences in the activity patterns of brown shrimp of different size and reproductive state.

5.5.5 Tidal state

Havinga (1930) described that mature females retreat seawards from December to March in order to release their larvae in deeper waters (15 – 25 m). Consequently, we expected the strongest tidal signal in the winter beam trawl data, which was confirmed by a significant influence of tidal state only in the winter beam trawl data set (Table and Figure 5.5). Drift simulations showed that STST usage during autumn and winter would transport berried females into greater depths, leading to a reasonable spatial distribution of juveniles in spring (Hufnagl *et al.*, 2014). Therefore, we expected a clear ebb signal, transporting the brown shrimps further offshore. This was observed in surface waters during winter by van der Baan (1975). However, contrary to our expectations, we did not find evidence for a simple ebb-stream offshore transportation, i.e. generally higher catch rates during ebb tide. Instead, we found increased catch rates for brown shrimp in shallow (e.g. 15 m) water during flood and high tide, and increased catch rates for brown shrimps in deeper areas (e.g. 40 m) during ebb and low tide. This suggests an onshore transportation of the "coastal shrimps" staying at 15 m depth and an even further offshore transport of the brown shrimps already located offshore to zones as deep as for example 50 m. It can therefore be surmised that there may be two different strategies to cover winter: The "nearshore brown shrimps" staying close to the coast and the more "offshore shrimps" retreating into deep areas.

We were able to include the interaction between tidal state and depth, but it was, unfortunately, impossible to include interactions between tidal state and size group or tidal and reproductive state. The latter would have led to linear dependencies between the different model terms as the data were not of a factorial design. This implies that due to data restrictions all predictions considering tidal state can only be made for all brown shrimps in general. The fitted model does for instance not allow to detect whether certain ebb or flood tides are especially used by berried or large brown shrimp. To resolve this restriction in the analysis, additional data with a predefined sampling scheme including autumn as well as winter data would be necessary.

In the models for the autumn beam trawl data and the VSN data, tidal state was skipped during the backward selection process. Non-relevance of tidal state confirmed the descriptions of Havinga (1930) of an autumn (or better: winter) migration from December to March as neither the autumn beam trawl survey data nor the VSN data were sampled within this period. Nevertheless, our results seem to contradict the findings from the stow net data analysis made in August and October at 5 and 10 m depth by Jansen (2002), who found highest catch rates during night and ebb. As Jansen (2002), we found highest catch rates exactly during those times in our raw data. However, though both main terms daylight and tidal state were included in the starting model for the VSN data, only daylight contributed significantly to explaining catch rates in the VSN, while tidal state did not. This does not contradict the raw data findings that maximal catch rates occurred during nocturnal ebb tides, because the factors that are still present in the model (daylight and *GDist*) were obviously able to predict the same pattern in the catches without using tide as an additional explaining factor.

Given that the catch rates and also the composition within the catches (i.e. the relative proportions of the different sizes and their reproductive states) differ with season, depth and partly also with tidal state and daylight, any standardised surveys, either for research or for management purposes, need to consider these factors. For example monthly survey sampling at a fixed depth may enable correction factors for catch rates and the composition within the catches to be calculated. However, our study reveals that as soon as the depth or light intensity varies, a simple correction factor is not sufficient, but a more sophisticated relation involving at least season, depth, light intensity, size, reproductive and tidal state would be required.

5.5.6 Vertical distribution

Based on the general classification of brown shrimp as a demersal epibenthic species (Boddeke *et al.*, 1986; Berghahn, 1983) we originally expected to find only few brown shrimps above the height of the standard commercial and scientific gear. However, other field studies have shown that brown shrimps can also be caught in heights inaccessible to beam trawls (Dänhardt, 2012; Jansen, 2002; van der Baan, 1975). A modelling study suggested that brown shrimp might ascend higher into the water column to make effective use of currents (Daewel *et al.*, 2011). Our analysis of the VSN data was able to quantify the relative amount of shrimps located above the usual beam trawl height. At a water-depth of 9.3 m, which was the maximal height sampled with the VSN, and beam trawl heights between 0.4 and 0.6 m, on average 67.14% to 76.68% of the brown shrimps were surmised to be located in the water column in heights inaccessible to the gear. In the VSN data set the size of the brown shrimps was not recorded. Hence, we were not able to distinguish between size groups ascending into the water column.

As seen in Figure 5.6, from 0 to about 0.5 m over the ground, VSN data were rarely available. Consequently, the confidence limits for the predictions for this bottom layer are wide, accounting for the small data base. Within the same time period and in the same area three beam trawl hauls were made at times at which the weather was too bad using the VSN. These hauls were conducted on 26th July and 07th and 16th August 2007. The beam trawl had a net opening of 3 x 0.4 m and a stretched mesh size of 10 mm at the cod end and hence, the mesh size at the cod end was comparable to the VSN. During these hauls the water column height varied between 2 and 6.7 metres. In those three hauls on average 240.94 brown shrimps (minimum=

103.84, maximum= 2617.97) were caught per 10000 m^3 water. The mean predicted number of the VSN accounted for 1080.81 brown shrimps within the beam trawl height (Table 5.8), which was higher than the average of the three beam trawl hauls. However, considering minimum and maximum of the beam trawl hauls the comparison shows that the model predictions are within a reasonable magnitude. Furthermore, the estimates of the VSN might actually even overestimate the number of brown shrimps accessible for beam trawls.

According to the general expectation, the catch rate actually decreased with increasing distance from ground which explains the usage of beam trawls for brown shrimp fishing. Nevertheless the cumulative numbers of brown shrimps above the tested beam trawl heights were substantially larger than those close to the bottom. This has two implications: Firstly, even if we assume that the mean proportion of shrimps was at the lower confidence limit of the 0.6 m beam trawl of 59.24% this would still be a considerable amount and might explain how shrimp production can be high although benthic production might not be sufficient to fuel the production of shrimps as indicated by Kuipers and Dapper (1981). Secondly, in biomass estimations the proportion of brown shrimps located above the covered beam trawl height has to be considered. This was not done by Welleman and Daan (2001) who assumed that all available brown shrimps greater than 40 mm are caught with the beam trawl. We showed that biomass estimates based on beam trawl survey data need to at least double the biomass caught. Meanwhile, a new biomass estimate is developed. Correction factors for a size based mesh selectivity and the results of this study have to be taken into account to obtain a more realistic estimate (ICES, 2012).

5.6 CONCLUSION

Our results suggest that simple conversion factors for a standardisation of survey catches will only be appropriate when fishing takes place in the same season, at same tidal states and light intensities, depth and probably location. If any of these factors differ, a simple conversion factor will probably be insufficient, as the patterns found were rather more complex and the composition in the catches varied. Hence, management considerations such as the harvest control rule, which is based on CPUE only, will not be sufficient to detect changes in the population structure as only the total amount of brown shrimps in kg is taken into account. They might also be biased in the sense that the amount of large shrimps might be increased when fishing mainly at night, leaving the harbour during ebb tide, etc. Hence, for the sake of standardisation, fixed locations and times and, if possible, even the separation of the catches by size and reproductive state would be required.

Our study gives evidence that at a water depth of about 9 m ca. 2/3 of the brown shrimp population can be found in the water column at heights inaccessible to a beam trawl. This implies that biomass estimations based on survey data need to correct their amount of catches by a correction factor of at least 2. To improve swept area biomass estimates we recommend a repetition of the stow net surveys with the gear being operated from the bottom upwards.

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6 MANUSCRIPT 2

INTERCHANGEABILITY OF DIFFERENT APPROACHES FOR ESTIMATING EFFORT AND CATCH FROM VMS- AND COMMERCIAL DATA.

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6.1 ABSTRACT

For management purposes, regional fishing impact needs to be quantified. Vessel monitoring system (VMS) data combined with logbook data seem to provide the best available information about location, size and utilisation of affected areas. Different approaches exist to deal with the unknown track between two-hourly transmitted positions (pings). We compare the use of raw pings, straight line interpolation, cubic Hermite splines (Hintzen *et al.*, 2010), ellipses (Mills *et al.*, 2007) and the amplification method (Fock, 2008) at different resolutions based on C-Squares (Rees, 2003) from 1x1° to 0.005°x0.005°. Using German brown shrimp fleet data, we analyse the extent to which spatially resolved estimates of effort, catch and affected area differ by method, either generally or when applied to selected areas. Moreover, we identify the most adequate method and resolution to be used for the German brown shrimp fishery.

Differences between methods have been found in all aspects. The area identified as fished differed in size even at a large resolution of 1°x1°. It was observed that catch and effort estimations varied largely, sometimes by >160%, over areas of different sizes. Heavily fished places have been identified by all methods, but the distribution of effort and catch within study areas differed without any consistent pattern. For the coastal German brown shrimp fleet, a resolution ≥0.01°x0.01° and the usage of straight lines or spline interpolation, seems the most appropriate solution at this current time. This approach ensures comparatively low patchiness, covers most of the possible tracks between consecutive pings and avoids the occurrence of artificial gaps on the vessel's track. The development of a method to bound tracks away from permanently or temporarily unfishable land positions is recommended, as well as the introduction of higher ping rates to improve the reconstruction of vessel tracks.

Keywords: fishing activity, spatial distribution, vessel monitoring systems, VMS, track interpolation, high resolution

6.2 INTRODUCTION

Fisheries compete for marine space with a wide range of other industries or uses, e.g. wind farms, mining or nature conservation. Current fishery management is not only concerned with the protection of the target species but increasingly also with the ecosystem effect of fishing, especially in relation to bottom impact of ground gear on benthic communities (Rijnsdorp *et al.*, 1998; Dinmore *et al.*, 2003). Hence, information on the spatial distribution of effort and catch is needed to assess the impact of management actions such as area closures on local benthic communities, lost catches and effort displacement. On the European level, the Natura 2000 network defines habitats of special importance for nature protection, which include the Wadden Sea (EC, 2011). According to the Directive of the Council of the European Union (92/43/EEC 4(4), 1992), a management plan has to be prepared within 6 years after the designation of a Natura 2000 site. It has to include the estimation of the degree of degradation or destruction to which those sites are exposed. This requires information about past fishing effort and catches in a high spatial resolution, but has not been submitted to date (Anonymus, 2015).

For a long time the exposure to fishing effort could only be done based on ICES statistical rectangles of 30x30 nm (55.56 km²) as recorded in the logbooks. Fortunately, spatial effort estimations can meanwhile be calculated on a smaller scale by using satellite-based vessel monitoring system (VMS) data. These data are legally required to be recorded since 2005 and all vessels longer than 15 m fishing in European waters are monitored (EC, 2003). The VMS information provides comprehensive data on vessel activity including position, heading and speed, with a temporal resolution of one signal (ping) approximately every two hours. The VMS data can be combined with logbook and landings data (e.g. Pedersen *et al.*, 2009; Bastardie *et al.*, 2010; Lee *et al.*, 2010; Gerritsen and Lordan, 2011), which include species caught, trip duration, fishing periods, landings and revenue per trip.

Regarding the presumed impact of fishing on a certain area, typically two main questions are asked:

(i) How great is the total impact within a certain area, i.e. how much catch was taken and how much effort was exerted in total within a certain area?

(ii) How is the fishing impact distributed within the considered area? Are there places that have not been fished at all?

Though VMS data, especially in combination with logbook data, seem to be the best available information source for impact assessment, some problems remain. The temporal resolution of VMS data requires speculating about what happened between pings. For example, for brown shrimp fishers who usually trawl at about 3.5 knots, 2-hourly pings imply that during gear operation a ping is transmitted approximately every 6.4 km. For vessels steaming or when fishing at higher speed, the distance is even greater. VMS data give no information about the track between two consecutive ping positions. Such information is relevant. Examples are: the analysis on small-scale spatial variation of species distribution, e.g. for prawns (Deng *et al.*, 2005), the assessment of the bottom impact of trawling in certain restricted areas (Rijnsdorp *et al.*, 1998), and the analysis of local variation in density measured as commercial catch per unit effort (Deng *et al.*, 2005).

Different approaches exist for processing the information contained in VMS pings. Some studies consider the pings as the only source of verified information and only use raw pings as transmitted (Dinmore *et al.*, 2003; Murawski *et al.*, 2005). Straight line interpolation (Eastwood *et al.*, 2007; Stelzenmueller *et al.*, 2008) acknowledges that the vessel has to cover at least the shortest distance between two consecutive pings. This notion is expanded by using cubic Hermite splines (Hintzen *et al.*, 2010), incorporating speed and heading of the vessel to model the vessel's real track in more detail. Other methods used, to account for the uncertainty of the track followed between two consecutive pings, include the use of either ellipses to identify the likely area impacted (Mills *et al.*, 2007) or the amplification method (Fock, 2008). Ellipses are constructed around two consecutive pings using the transmitted speed, while the amplification method deletes the original pings and constructs four new pings around the original ping position, depending on previous navigation properties of the vessel.

There are two main principles behind these approaches. The first is to use as few assumptions as possible beyond the raw data. The second is to respond to the fact that using the ping positions alone produces a strong underestimation of the truly impacted area. This is obvious, because on the way to the next ping position, a vessel moves along a certain track. Positions on the track are not seen in the ping data set. Such additional positions may have been visited even if two consecutive pings were issued at the same position. The simplest assumption to account for the vessel's movement is to assume that the vessel moved around the ping position within some simple geometrical structure, e.g. a square centred at the ping position. This approach is only reasonable, if the squares are so large that at trawling speed no gaps arise between two consecutive ping positions. This requirement defines a lower bound to the sensible size of such squares. Squares, however, are not realistic geometrical shapes for the totality of tracks that a vessel may follow between pings. More realistic is assuming an elliptic shape with focal points at ping positions and axes lengths such that the points on the contour can just be reached by a vessel moving between the first ping position to the ellipse circumference and from there to the second ping position. The use of ellipses also implies that the vessel had a constant speed over two hours and hence all points within the ellipse have the same probability of being reached. This scenario seems more appropriate than the squares approach, but it still includes somewhat strange tracks. Straight lines between ping positions seem more plausible tracks, but they imply course changes only at ping positions which may also contradict the course information transferred. The amplification method joins the square assumption with vessel specific navigation properties but ignores the speed information. Splines try to reconstruct the vessel's track by a smooth line, thereby including all available information. A radical counterpart to all attempts of constructing the vessel's track is using ping positions only, arguing that the totality of all pings from all vessels should give a sufficient picture of where fishing took place and where not. However, taking this literally implies that the fished area is always zero, no matter how many pings there are, because a point has area zero. Relaxing the point approach by using squares instead of points, results in the squares method discussed above.

6.2.1 The consequences of using different track estimation methods

All outlined methods produce spatial estimations of the fished area and consequently of the spatial distribution of effort, catch and revenue. However, without further information none of the methods can identify with certainty the true track of the vessel. Depending on the chosen method, estimates can differ (i) in the total area estimated as fished, (ii) in the absolute estimated values of effort and catch made in a restricted area, and also (iii) in the spatial distribution of catch and effort.

Differences in the spatial allocation of effort and catch can become relevant in the context of spatial management, if e.g. compensations are to be paid in relation to previously fished areas that were turned into no take zones. Systematic differences between estimates could also lead to a certain method being most advantageous for a certain stakeholder (e.g. the party obliged to provide compensatory payments), while another method might be favourable for another group of stakeholders (e.g. the recipient of compensatory payments).

The different approaches are likely to differ in their estimates, but the extent of the differences is so far largely unknown. To quantify the differences in the estimates caused by using different methods and grid sizes, a systematic comparison of the different approaches was performed.

6.2.2 The gap between pings

Independent of the method used, most spatial analyses use a rectangular grid to describe the fished area, regions of high effort or high catches. The whole area of a grid cell containing ping positions or parts of tracks is indicated as fished. Grid cell size therefore plays a crucial role. Cells which are too small underestimate the fished area whereas cells which are too large declare too much unfished area as being fished (Piet and Quirijns, 2009; Dinmore *et al.*, 2003; Hinz *et al.*, 2013) and give an imprecise impression of the shape of the fished area. The latter argument has led to the recommendation that an analysis should be performed on the smallest scale possible (Rijnsdorp *et al.*, 1998; Dinmore *et al.*, 2003; Piet *et al.*, 2007; but see also: Lambert *et al.*, 2012). Following the recommendation of Rijnsdorp *et al.* (1998), Dinmore *et al.* (2003) and Piet *et al.* (2007) leads to maps with the highest resolution possible, which is desirable from the user's perspective. However, when comparing VMS interpolation methods, using a very fine resolution might exclude those methods from the comparison which do not interpolate tracks from ping positions, because under a fine resolution the cells containing ping positions will become isolated cells, which generate "artificial" gaps in a vessel's track. Artificial gaps denote the situation that the track between two consecutive pings is not covered in any way, even though the vessel naturally had to bridge the distance between those two pings somehow. Grid cells on this way are falsely labelled as unfished. Therefore, the grid size must be carefully selected with the aim of avoiding gaps.

6.2.3 Why brown shrimp fishery is relevant

For the comparison of the effects of the different methods of VMS data, data from the German brown shrimp fishery were chosen. For this bottom contact fishery there is particular interest in spatial information at different and especially small scales. The main fishing ground for the brown shrimp fishery is the Wadden Sea (ICES, 2011) which is almost entirely part of the marine Natura 2000 area in Dutch and German waters (EC, 2011). In addition, parts of those Natura 2000 sites have been designated a World Heritage Site in June 2009 (WHC, 2009). The fishery cannot relocate to alternative areas because the Wadden Sea is the core distribution area of its target species brown shrimp.(ICES,2013b). In recent years, total landings from the North Sea from all nations were always >30 000 tons, with the Netherlands and Germany accounting together for >80% of the landings (ICES, 2013b). Though the brown shrimp fishery is currently allowed to operate within the established Natura 2000 areas (Schleswig-Holstein, 1999; Niedersachsen, 2001), the closure of at least parts of the Wadden Sea within Natura 2000 sites for bottom contact gear was repeatedly discussed (ICES, 2013b; Ziebarth *et al.*, 2014; Anonymus, 2015), in order to fulfil requirements of National park and Natura 2000 regulations. While the requirements for Natura 2000 sites include the submission of a management plan the German federal law on nature protection concerning the protective status of a national park even requests that a preponderant part of the national park should already exist, or in future be, in a state of being very slightly or not at all influenced by humans (§24 (1 and 2), BNatSchG, 2009; Anonymus, 2015).

Brown shrimp fishery is characterised by small mesh sizes of about 20 mm (stretched mesh) and may hence also affect species other than its target species. Fish and invertebrate by catch rates amount to about 20% of the total catch, with some year-to-year variation (Neudecker and Damm, 2010) and highest rates occuring in spring and summer (Aviat *et al.*, 2011). Though the brown shrimp beam trawl gear is relatively light and operates without tickler chains (different to gear used in the flatfish fishery, Stock *et al.*, 1996) brown shrimp trawling may affect benthic communities (Reiss *et al.*, 2009). Some studies consider beam trawls to damage *Sabellaria spinulosa* reefs (Riesen and Reise, 1982; Holt and Hartnoll, 1995). In contrary, a study of Vorberg (2000) indicated that neither rollers nor shoes of the brown shrimp trawls caused lasting damage to the reefs and that changes in the distribution and occurrence of these reefs was rather due to changes in water currents.

For every management purpose within the Natura 2000 sites the extent of exposure to degradation needs to be estimated (EEC, 1992). Reduction of the fished area is one possible management option. In the Netherlands, several small areas from ca. 20 - 55 km² within the Wadden Sea were already closed to brown shrimp fishery (Ministry of Economic Affairs, 2011).

The complex topographical structures of the Wadden Sea, as well as the influence of the tide, add more aspects to the discussion of track estimation methods. Some tidal creeks and flats are only passable during high tide while other areas in the Wadden Sea are never passable. All discussed interpolation methods assume that the whole area is passable at all times. Therefore, interpolation methods (except the raw ping method) are likely to distribute effort and catch at occasionally or generally unfishable positions, and coarse resolutions cannot represent the true spatial distribution of the fleet which follows tidal creeks before reaching open water.

We tested the extent to which raw pings, straight lines, splines, ellipses and the amplification method differed in their estimates of effort, catch and area impacted, if differently sized parts of the Natura 2000 sites in the German Wadden Sea were closed at the start of the high season to the brown shrimp fleet. We considered three National Parks (two of them with more than 3000 km² each and one with 137.5 km²), a harbour porpoise protection area of 1240 km² and a very small wind farm of area 3.5 km². We used differently sized case study areas, as specific suggestions of the spatial location of area closures within the National parks are still lacking. The main focus of this study was the identification of differences between the estimates by different methods. We also compared estimates for the most drastic form of nature conservation. This would be the 100% closure of the case study areas for brown shrimp fishing.

For all five case study areas we calculated the estimated amount of effort and catch by each of the five methods and quantified the differences between the methods. Further target quantities were the size of the area estimated as fished and its exact location. Moreover, we analysed whether systematic differences between methods were present with regard to the distribution of effort and catch within the selected case study areas. To identify the role of resolution in the method comparison we used different grid cell sizes from a very fine grid of 0.005°x0.005° to the coarse resolution of 1°x1°. Finally we investigated which resolution would be most suitable for the German brown shrimp fleet in accordance with current available data.

6.3 MATERIAL AND METHODS

6.3.1 Data

To compare the different methods we used all German brown shrimp vessels operating in September 2010, for which logbook-, landing- and VMS-data were available (175 vessels). 2010 was a comparatively strong year of brown shrimp landings (ICES, 2013a), and September is the beginning of the high season for brown shrimps. This implies that catches were already relatively high and most of the active vessels (ca. 200) could be assumed to be fishing.

The landing data included the landed weight of the catch for which the fishers received revenue. A trip was included in the analysis if at least two pings were transmitted and if all consecutive pings of that trip were less than three hours apart.

German brown shrimp fishers record fishing start- and end times in their logbooks, though according to the regulation (EU) No 404/2011 it is still an optional record (EU, 2011). Only these recorded fishing periods were used for analysis, whereas the steaming times were excluded. Also, trips that included pings with speed greater than 6.4 knots during the stated fishing periods, or with difference > 3 hours between two consecutive pings, were excluded from analysis. The cleaned dataset included 157 vessels and 765 trips with a total of 7410 pings transmitted. 11423 hours of effort were spent with fishing in September 2010 and the total of 858890 kg catch was used for analysis.

6.3.2 Case study areas

Case study areas of different size were analysed to test how their size influenced the differences in total amount and the spatial distribution of estimated effort and catch as estimated with the different methods. All of the areas are located within the 12 nm zone of the German coast (Figure 6.1).

1. The National park "Wattenmeer Schleswig-Holstein" (NTP-SH) was the largest case study area with about 4410 km²; 2418 pings were transmitted in September 2010 within its borders.
2. The National park "Niedersächsisches Wattenmeer" (NTP-LS) was slightly smaller with about 3460 km² but had a slightly higher density of pings with a total of 2737 pings.
3. A marine protected area (MPA) established to protect an important breeding area of harbour porpoises (*Phocoena phocoena*). It is located within the NTP-SH. It has a size of 1240 km² and 152 pings of the 2418 pings within the NTP-SH were transmitted from within its boundaries.
4. The National park "Hamburgisches Wattenmeer" (NTP-HH) with a size of 137.5 km² and a total of only 18 pings was transmitted from within this area, as in 95% of the area fishing is prohibited (Nehls *et al.*, 2009).
5. The wind farm Nordergründe (WF), the fourth case study area, with a size of only 3.5 km². The construction was permitted in 2008 (ML, 2008). It is located about 15 km north-east of Wangerooge and 30 km north of Wilhelmshaven. Construction was scheduled to start in 2012/2013 (http://www.ofw-online.de/projekte/nordergruende.html). From this area 37 pings were transmitted.

Brown shrimp fishing was generally allowed within the area of the planned windfarm and in the selected nature conservation areas (Hamburg, 1990; Schleswig-Holstein, 1999; Niedersachsen, 2001) and limited only in the National park "Hamburgisches Wattenmeer" (Nehls *et al.*, 2009).

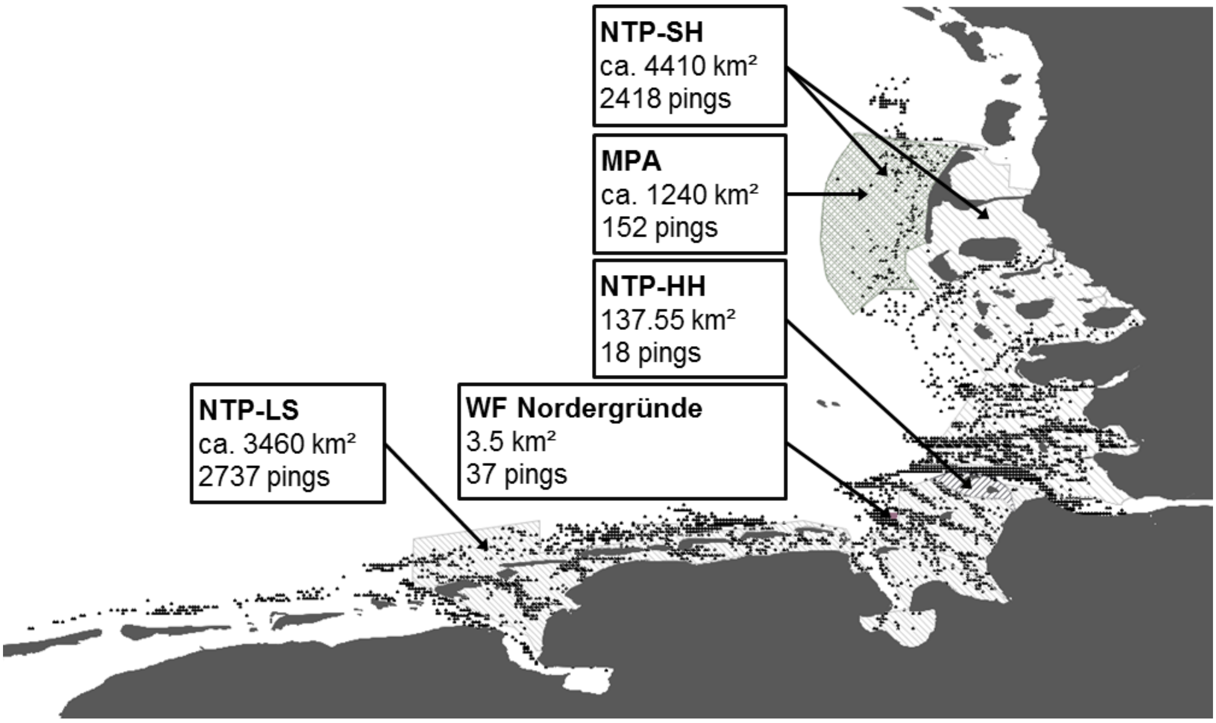

Figure 6.1 Originally transmitted pings in September 2010 and location of the case study areas. In the boxes, the name of the case study areas, their area in km² and the number of pings transmitted within the area is given. NTP-LS: National park Niedersächsisches Wattenmeer, NTP-HH: National park Hamburgisches Wattenmeer, NTP-SH: Nationalpark Wadden Sea Schleswig-Holstein, part of NTP-SH is also the MPA Porpoise: Marine protected area for porpoises. WF Nordergründe: Windfarm Nordergründe.

6.3.3 Grid

All analyses and methods were applied on different grid resolutions of 1°x1°, 0.5°x0.5°, 0.1°x0.1°, 0.05°x0.05°, 0.01°x0.01° and 0.005°x0.005° using C-Squares (concise spatial query and representation system, Rees, 2003). The defined grid cells have fixed locations and are based on latitude and longitude. The borders of the case study areas do not exactly match the borders of the C-Squares. In this analysis only pings located within the exact borders of the case study areas were used.

6.3.4 Methods used for comparison of estimations

6.3.4.1 Raw pings (Raw)

The raw pings method uses the original pings only (Figure 6.2). It neither considers speed nor headings transmitted. The time of fishing effort as recorded in the logbook was summarised per trip and distributed equally on all pings of the related trip. The same was done with the weight of landed shrimp. In the following step the distributed hours of effort and catch weight of the pings were summarised over all pings per grid cell.

6.3.4.2 Straight lines (SL)

Straight line interpolation joins consecutive pings by straight lines. These were represented for analysis by additional way points set in time intervals of one time second between the original pings. The straight lines do also not use the transferred information of speed and heading. Trip effort and catch was allocated evenly on all pings and way points of that trip and then summarised per grid cell.

6.3.4.3 Splines (SPL)
Cubic Hermite splines were generated according to Hintzen *et al.* (2010). We used the standard parameterisation given in the R-package vmstools 0.63. The splines are constructed by using the time difference between two successive pings as well as heading and speed transferred. From one original ping to the subsequent one additional way points were set every time second. As in the straight lines method, trip effort and catch was distributed evenly among all pings and additional way points of the trip and then summarised per grid cell.

6.3.4.4 Ellipses (E)
The ellipses were constructed according to Mills *et al.* (2007) using the position and speed of the vessel. A maximal distance that the vessel could have travelled between the two pings was calculated using the mean speed at two consecutive pings and the time difference between them.

Two cases are distinguished when constructing the ellipses. The measured distance between two successive pings is either less than the distance that the vessel was assumed to travel, or the real distance between two consecutive pings was longer than this distance.

In the first case the vessel could have trawled a longer distance than only the direct way between two subsequent pings. An ellipse is then constructed with the ping positions as focal points and axes lengths such that the points on the contour could just be reached by the vessel when moving from the first to the second ping position and running at constant speed between two consecutive positions, with all tracks having the same probability. The fished area is represented by the area of the ellipse. Within the ellipses a fixed number of additional way points were established. The number and hence the distance between these additional way points was based on a basic setting of one way point every 250 m, but weighted with the maximal distance that vessel could have covered. The distance between the way points therefore increased with increasing size of the ellipse. This weighting was needed to consider the fact that in large ellipses the probability to meet a vessel is smaller than in small ellipses. Effort and catch per grid cell was calculated by summation, as described for straight lines and splines. In the second case, where the distance between two successive pings was greater than or equal to the estimated maximal travel distance, a straight line interpolation was performed.

6.3.4.5 Amplification (A)
The amplification method was programmed as used in Fock (2008). This method uses both the transmitted heading of the vessel and the information of the angle between consecutive positions. The amplification method assumes that fishers have an individual pattern of navigation behaviour. Using the differences between the headings of subsequent pings the ‘usual deviation’ from the original direction heading was calculated and expressed in proportions for each of the geographic

directions (North, East, West and South). This implies that the vessel has a usual angle of deviation from its original course, for example: in 30% of all trips the vessel steers 15° further eastward than before, in 20% it steers 30° further northward, etc. Subsequently, this 'usual deviation' in each of the geographic directions, as well as the time difference between two consecutive pings and the mean speed were used to calculate the location of four new way points that replace the original ping positions (Figure 6.2). The distance of the new way points from the original pings ranged from 0 to 21.16 km. Trip effort and catch was then distributed evenly on all way points of that trip. In a final step, the allocated effort and catch per way point were summarised per grid cell. Though Fock (2008) intentionally chose the resolution of 3 x 3 nm (≈ 0.0854°lon x 0.0501°lat) in order to avoid unfished grid cells (gaps) between consecutive pings, we used this method (as well as all other presented methods) at all resolutions from 1°x1° to 0.005°x0.005° to be able to provide a systematic comparison.

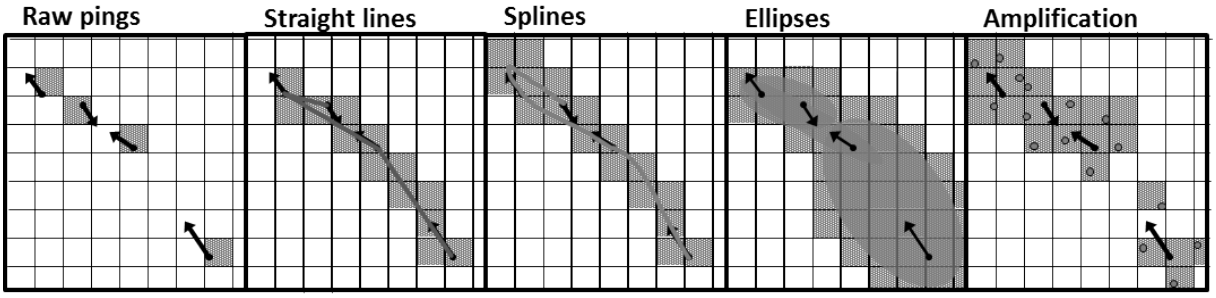

Figure 6.2 Visualisation of different estimation methods which can be applied on VMS data.

6.3.5 Analysis of the differences in the estimates of the different methods

Three types of differences between the methods were compared:

(i) The estimated amount of effort and catch made in the different case study areas

(ii) The size and differences in the location of the area identified as fished ("*fished area*") within the different case study areas

(iii) The distribution of catch and effort within the different case study areas

The estimated amount of catch weight and hours of effort obtained by different methods for the case study areas were compared in two ways: Firstly, the total amount of effort and catch in all areas made in September 2010 by all 175 brown shrimp vessels was considered. Secondly, estimations by using all methods were compared separately per case study area. The latter was done to highlight the role of area size. If the total amount of effort and catch alone were compared, different contributions of effort and catch estimations of the different methods would remain undetected in small areas with low effort and catch estimations.

Size of the fished area was compared between the different methods using the proportion of each case study area which was identified as fished by the different methods at all considered C-Square resolutions (see above). Differences in the locations of the fished area between the different methods were identified in pair-wise comparisons. For this purpose the number of overlapping C-Squares was counted and divided by the total number of C-Squares estimated as fished. Hence, an overlap of 100% indicated that the estimates of the fished area by two different methods were identical. If the fished area identified by one method was completely located inside the area of the other method, but not identical, this resulted in less than 100% overlap.

In order to quantify the local differences in the distribution of effort and catch in the different case study areas at the different resolutions, we firstly used the absolute differences of estimated hours of effort and kilogram catch estimations per C-Square. This implies that in small areas, such as the WF, where the allocated effort or catch is low, the differences will also be small. Compared to the total effort and catch made in September 2010 of 858890 kg, the proportional differences will be small especially in small areas and it may therefore not make a great difference whether, for example 20 kg or 500 kg are allocated to a certain C-Square. The distribution of absolute effort and catch within a case study area, however, may prove interesting, when effort and catch estimations are needed for management purposes. If several areas were in question to be closed an area which yields < 0.5% of the monthly catch might be more attractive to potential closing than areas of higher effort and catch. Also for the individual fisher, the absolute values will also probably be important as it may make a great difference if his estimated catch per month within an area of interest was about 20 kg (≈50 €) or 500 kg (≈1250 €).

To get a general statement about the differences between the methods, independently of the size of the case study area we secondly expressed the local differences in the allocated effort and catch also on a relative scale and considered the different amounts of effort and catch allocated in the case study areas by the different methods each as 100%. Subsequently, this 100% was distributed proportionally among the C-Squares of the different areas according to the allocated absolute estimated effort and catch values per C-Square. Then, the maximal differences that occurred locally due to the different distribution of effort and catch were calculated on the relative scale and expressed in percentage points.

The relative scale was also used to test the differences in the spatial allocation of effort and catch within the different case study areas. For this purpose, the C-Squares were ordered consecutively and cumulative curves, of the proportional effort and catch per C-Square involved, were used. The proportional estimated effort and catch had the advantage of being identical between two methods if the distribution of effort/catch within a case study area was identical, even if they differed in the estimated total amount of catch and effort made in the case study area. Using relative proportions we were able to find out whether the methods allocated the same proportion of effort and catch in identical C-Squares.

6.3.6 Choosing a suitable resolution for German brown shrimp data

The comparison of methods should be done by employing a common grid which is suitable for all methods. From the user's view, the resolution should be as small as possible to provide detailed information but should at the same time also prevent artificial gaps, when raw pings are used.

The finest possible resolution suitable for raw pings can be calculated using the maximal time difference between two consecutive pings and the assumed mean trawling speed. In our data set the maximal accepted time difference between two consecutive pings was 3 hours and the maximal allowed fishing speed was 6.4 knots. Hence, the maximal distance possible to be covered within this time added up to $6.4 \cdot 1.852 \cdot 3 = 35.56$ km. Converted to decimal degrees this would, in Northern Germany, be 0.547° longitude and 0.32° latitude. Based on the pre-defined resolutions of C-Squares a resolution of at least 1°x1° would therefore ensure that no artificial gaps between consecutive pings arise. However, this calculation is based on a single vessel and generally it is argued that the higher the number of pings that are included in the data set, then the rarer the occurrence of these artificial gaps. In order to check whether this latter assumption holds, we used the whole data set to calculate the risk for gaps at different resolutions compared to the risk obtained with a resolution of 1°x1°. As our data set includes data from a month at the beginning of the high season of brown shrimp fishing, this is a good example for this investigation. With 765 trips from 175 vessels, it provides a good illustration of the ping distribution transmitted during fishing periods within a single month. To describe the seasonal distribution of effort and catch, monthly considerations are not uncommon. To calculate the risk of occurrence of artificial gaps in the whole data set, we used the straight line approach for track estimation as a reference method. Straight lines are the most straightforward method that excludes gaps between two consecutive pings. We calculated the proportion of correctly identified fished grid cells (the sensitivity) at the different resolutions, assuming that the straight lines method identified the fished grid cells correctly, as $Sens = \frac{a}{a+c}$, where a = number of C-Squares identified as fished by both approaches and c = number of fished grid cells identified by straight lines only. $Sens = 1$ means that all C-Squares that were covered by straight lines were also identified as fished when using raw pings. A value of $Sens = 0.5$ symbolises that 50% of the grid cells were identified as fished when using straight lines, but not when raw pings were used.

Though generally the usage of the smallest resolution possible is suggested, a coarse resolution of even 1°x1° would also be appropriate to describe the fished area and the distribution of effort and catch, if within one grid cell the pings are distributed homogeneously. This can be checked by starting from very fine resolutions and increasing the grid cell size gradually. In this approach more and more cells are joined together. If the cells to be joined have point densities that vary around the same mean, these larger grid cells are named as having "randomly distributed" densities by some authors ("uniformly distributed" in standard statistical terminology) and it is acceptable to use even coarser resolutions for analysis. A joined set of small cells not having point densities varying around the same mean is called "patchy". This terminology is then also used for single (larger) grid cells.

To test whether pings within the grid cells follow a patchy distribution, two main approaches exist: one based on the assumption that pings counts are Poisson distributed (Rijnsdorp *et al.*, 1998), the other based on the mean distance between a point and its next neighbours (Gerritsen *et al.*, 2013). We followed the approach of Rijnsdorp *et al.* (1998) which is motivated by the fact that, if points are uniformly distributed over an area, then the number of points in equal-sized sub-areas (cells) has a Poisson distribution. The converse does not necessarily hold true. Patchiness is calculated as $C = s^2 / m$, where m symbolises the mean number of raw pings per grid cell and s^2 the variance of the ping counts over all cells. A value of C>1 indicates a patchy distribution. A C-value = 1 indicates that the number of pings per cell has a Poisson distribution and C = 0 shows that each cell has the same number of pings. Obviously an area with inaccessible regions is patchy. Therefore patchiness was checked only for regions that were not already patchy for structural reasons. The area west of 8.562°E and between 54.024°N and 54.308°N contains no tidal creeks or other conditions preventing fishing. This area was used for the examination of patchiness.

Instead of using raw pings with a resolution avoiding artificial gaps, track estimations can be used. As the true track is unknown, it is desirable to choose a resolution that covers the majority of all possible tracks between two consecutive positions. In order to test at which resolution this would be the case, we compared splines, (the most advanced method tested and including all information transmitted), with the robust claim of the straight line approach. Very fine resolutions might result in "unfished" C-Squares between the reconstructed tracks of the straight line and splines. Coarse resolutions will include all possible tracks of the vessels but will not have the geographical accuracy needed to describe this small-scale fishery. We calculated the distance between the possible vessel tracks of straight lines and splines. On the basis of this distance we determined the resolution that would be needed to cover a fixed proportion of the tracks identified by straight lines and the splines within a single grid cell. The proportions were expressed as quantiles, symbolising the proportion of grid cells that were identically identified by straight lines and splines. As in the German Bight, 1° longitude is about 65 km long while 1° latitude corresponds to 111 km, the minimally required distances expressed in decimal degrees differed between latitude and longitude. The quantiles were, hence, adjusted to the predefined resolutions of C-Squares.

All programming was done using SAS 9.4 (SAS Institute, Cary NC).

6.4 RESULTS

6.4.1 Estimated amount of effort and catch allocated in the different case study areas

For each of the case study areas we only used pings and way points located within the exact borders of the areas. In general, none of the methods utilised across all of the case study areas yielded to highest or lowest estimations of effort or catch in all case study areas. Furthermore there was no tendency of one of the methods to always produce high or low effort or catch estimations. Using the total September catch of 858.89 t as a reference value, the estimations of the different methods differed maximally by 4.38% (NTP-LS), though in absolute values some large differences were observed. For example, when using ellipses, the estimated catch weight in the relatively small NTP-HH of 137.5 km² including 18 pings was about 5 times as high as the estimated value when using splines. Generally, the differences in the absolute estimations were larger in smaller areas where fewer pings were received. If the mean estimated catch rather than the total catch of September for the different case study areas was taken as 100% reference (Table 6.1), the estimations deviated by 3.6% in the NTP-SH, by 10.9% in the NTP-LS, by 3.74% in the MPA, by 180.61% in the NTP-HH and by 164.60% in the WF (Figure 6.3).

The estimated amount of effort allocated to a case study area differed less between the different methods than the allocated catch weight. Using the total effort in September of 11423 h as 100% reference, the estimations of effort made in the different case study areas differed maximally by 3.13% (NTP-LS). If the mean effort allocation of all methods per area was used as reference, the estimations deviated by 4.9% in the NTP-SH, by 9.92% in the NTP-LS, by 5.69% in the MPA, by 188.2% in the NTP-HH and by 162.49% in the WF (Figure 6.3). In the WF particularly, where the mean estimated effort was low (5.45 h, Table 6.1), the methods differed strongly with the ellipse method allocating 8.39 hours to the WF area while raw pings only indicated a value of 0.52 hours.

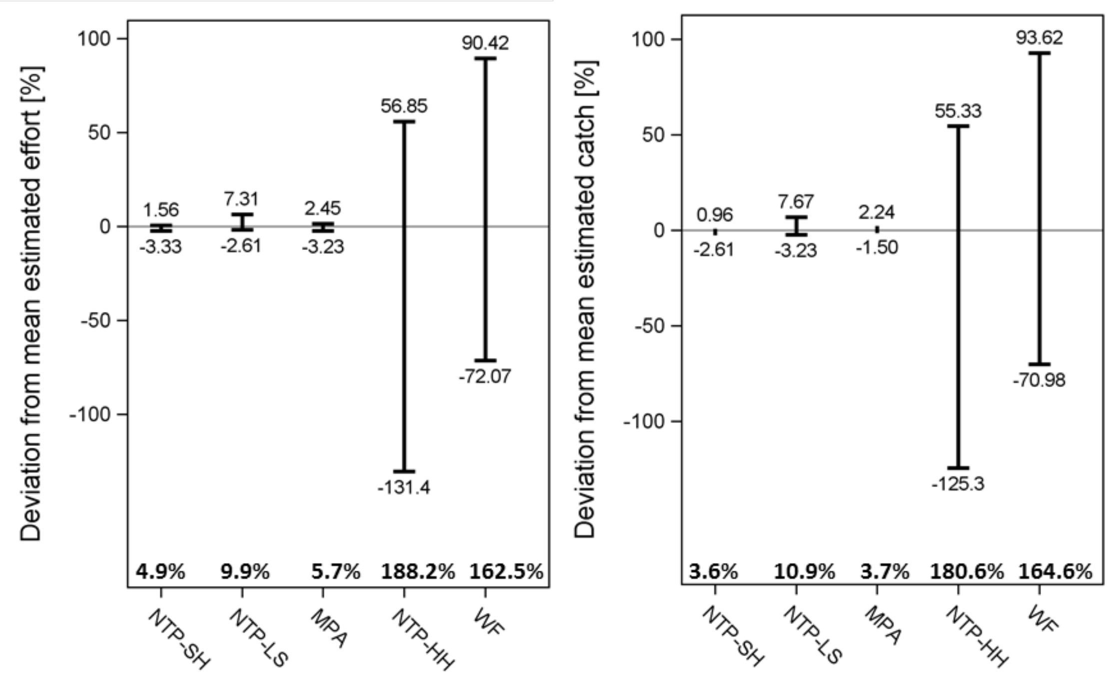

Figure 6.3 Proportional deviation from mean estimated effort (left panel) and catch (right panel). In the bottom of the panels the range between the estimations of the different methods (Raw pings, straight lines, splines, ellipses, amplification) is given in bold numbers, also as percentage of the mean estimated value of effort (left) and catch (right). NTP-SH: National park "Wattenmeer Schleswig-Holstein" (ca. 4410 km²), NTP-LS: National park "Niedersächsisches Wattenmeer" (ca. 3460 km²), MPA: Marine protected area for porpoises (ca. 1240 km²), NTP-HH: National Park Hamburg (137.5 km²), WF: Windfarm Nordergründe (3.5 km²).

Table 6.1 Effort and catch estimations by method and case study area. Given are absolute values and, in brackets, the proportion of the total effort and catch made by the German brown shrimp vessels in September 2010. NTP-SH: National park "Wattenmeer Schleswig-Holstein" (ca. 4410 km²), NTP-LS: National park "Niedersächsisches Wattenmeer" (ca. 3460 km²), MPA: Marine protected area for porpoises (ca. 1240 km²), NTP-HH: National Park Hamburg (137.5 km²), WF: Windfarm Nordergründe (3.5 km²).

		NTP-SH	NTP-LS	MPA	NTP-HH	WF
Mean Estimation of catch [kg]		220768.01 (25.70%)	345375.56 (40.21%)	7303.24 (0.85%)	5359.59 (0.62%)	309.71 (0.04%)
KG	Raw	220071.29 (25.62%)	355496.64 (41.39%)	7139.67 (0.83%)	2477.77 (0.29%)	19.75 (0.00%)
	Straight lines	219049.23 (25.50%)	352492.20 (41.04%)	7250.34 (0.84%)	2986.25 (0.35%)	86.84 (0.01%)
	Splines	218645.71 (25.46%)	356534.56 (41.51%)	7412.51 (0.86%)	2394.09 (0.28%)	492.68 (0.06%)
	Amplification	219545.64 (25.56%)	318899.00 (37.13%)	7307.02 (0.85%)	6865.66 (0.80%)	419.76 (0.05%)
	Ellipses	226528.15 (26.37%)	343455.42 (39.99%)	7406.68 (0.86%)	12074.17 (1.41%)	529.54 (0.06%)
Mean Estimation of effort [h]		3238.11 (28.35%)	3610.77 (31.61%)	260.37 (2.28%)	75.34 (0.66%)	5.45 (0.048)
Hours	Raw	3215.93 (28.15%)	3696.05 (32.35%)	254.46 (2.23%)	32.76 (0.29%)	0.52 (0.00%)
	Straight lines	3198.36 (28.00%)	3685.52 (32.26%)	260.80 (2.28%)	38.89 (0.34%)	1.16 (0.01%)
	Splines	3187.47 (27.90%)	3705.12 (32.43%)	268.79 (2.35%)	32.51 (0.28%)	9.38 (0.08%)
	Amplification	3242.99 (28.39%)	3346.87 (29.30%)	253.98 (2.22%)	98.24 (0.86%)	7.81 (0.07%)
	Ellipses	3345.82 (29.29%)	3620.29 (31.69%)	263.82 (2.31%)	174.30 (1.53%)	8.39 (0.07%)

6.4.2 Consideration of the performance of the different methods within case study areas

In cases where the different methods estimated the same or a similar area size as fished, the question remains if identical grid cells were also assessed as fished. However, this was not the case (Figure 6.4). An identical identification of grid cells by all methods at a resolution of 1°x1°was only found in the very small WF, which only covered a single 1°x1° C-Square. Hence, already at a resolution of 1°x1° the area identified as fished depended on the chosen method. As shown in Figure 6.5 (middle row the largest overlap in the grid cells identified as fished was found mostly for straight lines and splines. Smallest overlaps were found between ellipses and raw pings. It was evident that the finer the resolution used, the smaller the overlap found. Hence, at the smallest resolution of 0.005°x0.005° the largest overlap amounted to 68.42% (overlap of splines and straight lines in the WF) and the smallest overlap of 1.25% was found between raw pings and ellipses in NTP-HH.

Consequently also the proportion identified as fished within the case study areas differed between the methods. We found that for most case study areas at least a resolution ≤ 0.05°x0.05° was needed in order to have a fished area that was, at least for one of the methods, smaller than the case study area itself (Figure 6.5, top row).). For the largest case study area (NTP-SH) the estimations started to differ already at a resolution of 0.1°x0.1°, for the WF the size of a single grid cell needed to become smaller than 3.5 km^2 (size of the WF itself) before less than 100% of the area was classified as fished. This was the case at a resolution of 0.01°x0.01° and at all resolutions ≤ 0.01°x0.01° the estimations varied. In all areas and resolutions at which variation in the estimations was present, the indicated fished area was largest when ellipses were applied for the estimation of the fished area, and smallest when raw pings were used.

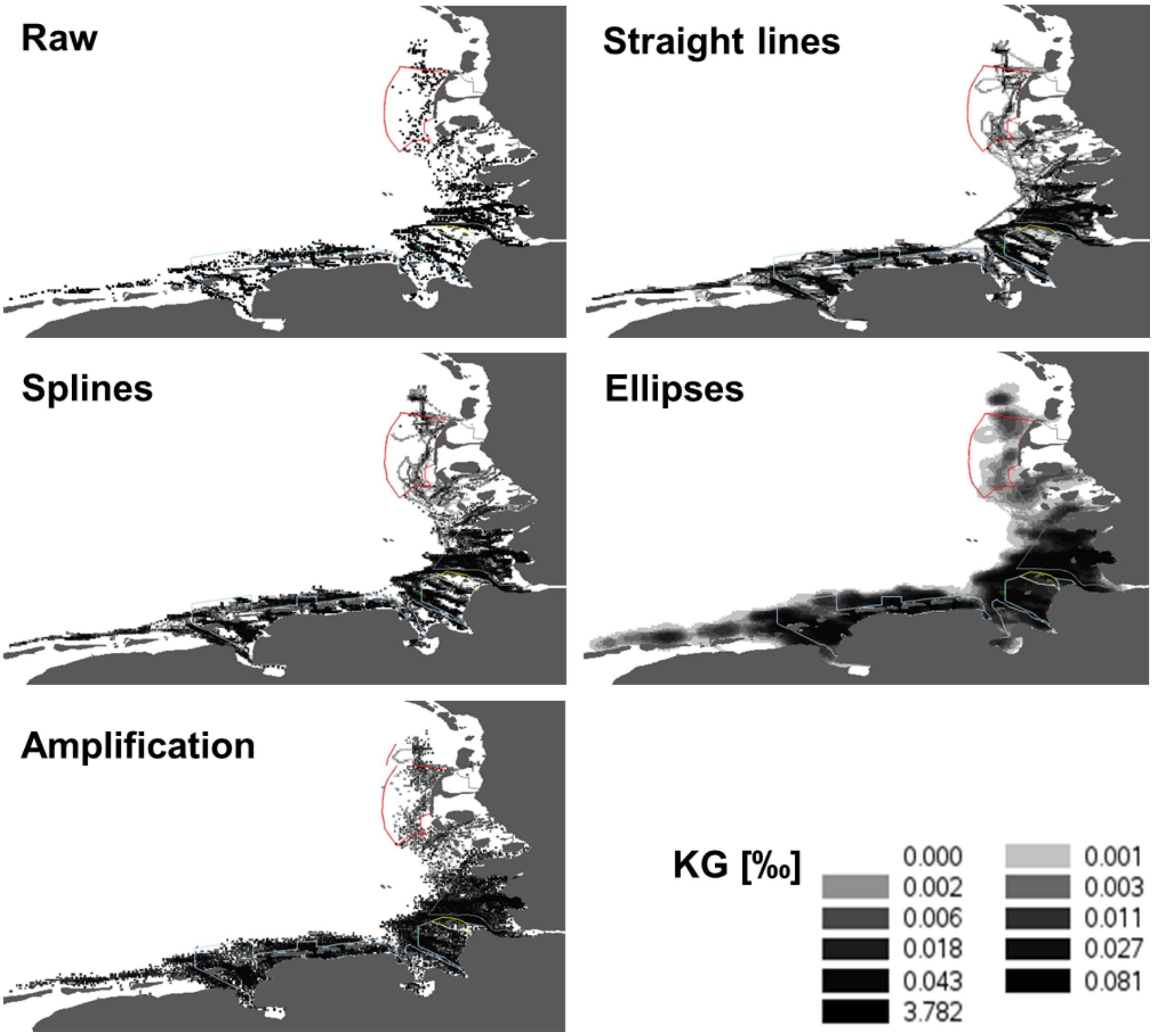

Figure 6.4 Distribution of catch of the German brown shrimp fishers in September 2010 using the different methods at a resolution of 0.005°x0.005°. Colouring is based on the quantiles of the distribution of the catch and given as one tenth of a per cent of the total catch weight obtained in September 2010. Case study areas are surrounded by lines. Green: National park "Wattenmeer Schleswig-Holstein", blue: National park "Niedersächsisches Wattenmeer", red: Marine protected area for porpoises, yellow: National Park Hamburg, orange: Windfarm Nordergründe.

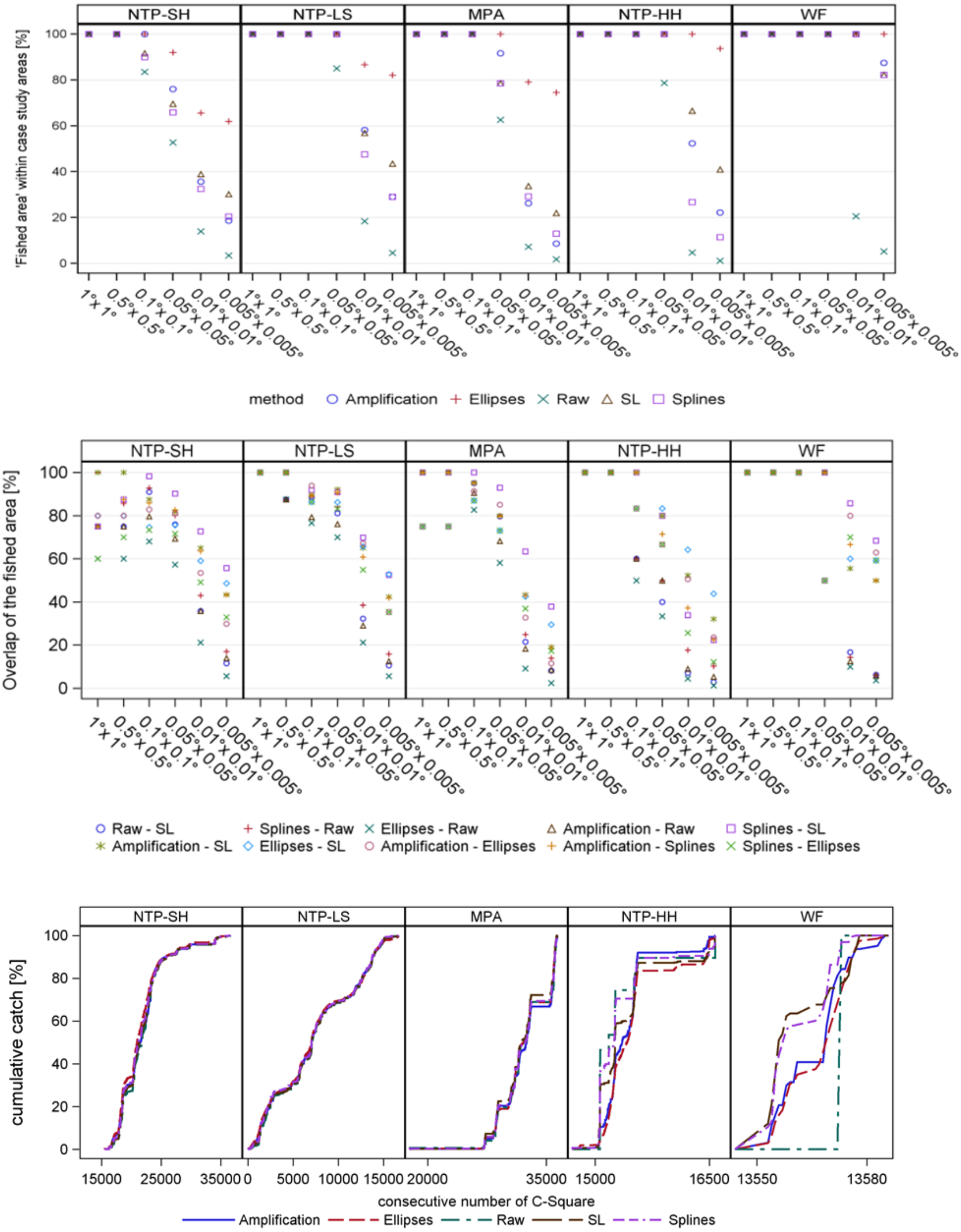

Figure 6.5 Top Row: Overlap of the fished area in the different case study areas using the different methods. The calculation of overlap was based on the set union of the C-Squares identified as fished by both of the methods. Middle Row: Proportion of the case study areas identified as fished at different resolutions. Bottom Row: Cumulative proportional distribution of catch in the different case study areas. This figure assumes that all of the methods distributed 100% effort and catch in the different case study areas, though the absolute values differed, of course. On the x-axis, the C-Squares are numbered consecutively from beginning to end. NTP-SH: National park "Wattenmeer Schleswig-Holstein" (ca. 4410 km²), NTP-LS: National park "Niedersächsisches Wattenmeer" (ca. 3460 km²), MPA: Marine protected area for porpoises (ca. 1240 km²), NTP-HH: National Park Hamburg (137.5 km²), WF: Windfarm Nordergründe (3.5 km²).

The methods differed clearly in their estimations of the area sizes identified as fished (Figure 6.5, middle row). Ellipses led in all case study areas to fished areas that covered at least 61% of the case study areas (minimum reached at 0.005°x0.005° in the NTP-SH) while minimal estimations of raw pings identified only 1.17% of the NTP-HH area as fished at 0.005°x0.005°. The differences between the maximal and minimal estimates of fished areas generally increased with decreasing size of the case study area and finer resolution: The proportion of the fished area differed by minimal 16.52% in the NTP-SH at 0.1°x0.1° and by a maximal value of 89.72% in the WF at 0.005°x0.005°. Only 5.14% of the WF area was designated as fished using the raw pings method but this increased to 94.86% when ellipses were used (Figure 6.5, top row).

Although within the different case study areas, locations with highest fishing effort and catch were identified similarly by all methods as shown for catch in Figure 6.4, local differences between the methods were also found. In the smaller areas NTP-HH and WF especially, great differences arose in estimated proportions of catch and effort which were allocated to the different C-Squares (shown for catch weight in Figure 6.5, bottom row).

Greatest local differences in the estimated values of effort and catch were found in the large case study areas NTP-SH and NTP-LS, which were, however, also the areas with the highest effort and catch levels (Table 6.1). With increasing numbers of C-Squares per case study area (finer resolution), the absolute differences in effort and catch estimations per C-Square had the tendency to decrease as the allocated values were reduced due to the larger number of grid cells. Greatest differences between the estimated values of a certain C-Square however, were not found at a resolution of 1°x1°, but at 0.5°x0.5° (Table 6.1).

At a resolution of 0.5°x0.5° the greatest local difference between two methods in the allocated catch per C-Square was found between the amplification (112789.37 kg) and the spline method (133822.11 kg) in the NTP-LS and amounted to 21032.74 kg (Table 6.2). This was 2.45% of the total catch in September. At 0.005°x0.005°, the maximal local difference between two methods in the allocated catch per C-Square was the smallest of all resolutions tested. It was found in the NTP-SH between raw pings (0 kg) and the amplification method (3247.92 kg) and accounted for 3247.92 kg. Hence, the difference accounted for 0.38% of the total September catch.

Maximal local differences in the effort estimations per C-Square of 197.22 hours were found between the amplification method (304.05 h) and the ellipses (106.83 h) in the NTP-SH at a resolution of 0.1°x0.1° (0.0005% of the total September effort). Again, at the smaller resolution of 0.005°x0.005°, the maximal local difference that occurred in one of the C-Squares between the effort estimations of two methods was the smallest found of all tested resolutions. The maximal local difference at 0.005°x0.005° that occurred in one of the C-Squares amounted to 53.05 hours (0.0001% of the total September effort) and was found between the straight lines (53.33 h) and the ellipses (0.28 h) in the NTP-SH.

The pattern became clearer when the proportional effort per C-Square was used. Larger differences occurred with smaller grid cell size and in smaller case study areas. This is evident from maximal differences of about 98 percentage points in effort and catch in the WF-area at a resolution of 0.005°x0.005° (Table 6.2). At this resolution for example, raw pings identified a single C-Square within the WF as fished. Straight lines however, only distributed 1.02% of the catch in this considered C-Square and the other 98.98% in 25 C-Squares surrounding the WF.

One might have expected greatest differences between the different methods in such C-Squares which were only designated as fished due to interpolation or the incorporation of the spatial uncertainty of the pings. However, this was not the case. At all resolutions > 0.005°x0.005° the maximal differences in absolute catch were found in C-Squares in which also original pings were transmitted. For effort, this was the case at all resolutions ≥ 0.01x0.01°. Only at smaller resolutions could the greatest differences in effort also be found in grid cells which had not received an original ping.

Table 6.2 Maximal absolute and relative differences per C-Square measured in pairwise comparisons of the different methods. NTP-SH: National park "Wattenmeer Schleswig-Holstein" (ca. 4410 km²), NTP-LS: National park "Niedersächsisches Wattenmeer" (ca. 3460 km²), MPA: Marine protected area for porpoises (ca. 1240 km²), NTP-HH: National Park Hamburg (137.5 km²), WF: Windfarm Nordergründe (3.5 km²), A: Amplification, Spl: Splines, SL: Straight lines, R: Raw pings, E: Ellipses.

Resolution	Maximal difference per C-Square in absolute catch [kg] (CS-Area)	Maximal difference per C-Square in absolute effort [h] (CS-Area)	Maximal difference in catch per C-Square in percentage points (Per method: 100% catch was distributed in CS-area)	Maximal difference in effort per C-Square in percentage points (Per method: 100% effort was distributed in CS-area)
1°x1°	19436.26 (A-Spl, NTP-LS)	148.01 (A-Spl, NTP-LS)	6.27 (A-SL, MPA)	5.41 (A-SL, MPA)
0.5°x0.5°	21032.74 (A-Spl, NTP-LS)	159.31 (R-A, NTP-LS)	8.91 (A-E, NTP-HH)	8.44 (A-E, NTP-HH)
0.1°x0.1°	14741.54 (A-E, NTP-SH)	197.22 (A-E, NTP-SH)	39.18 (R-E, NTP-HH)	37.80 (R-E, NTP-HH)
0.05°x0.05°	11678.24 (Spl-E, NTP-LS)	110.74 (A-E, NTP-SH)	45.70 (R-E, NTP-HH)	41.90 (R-E, NTP-HH)
0.01°x0.01°	4618.57 (A-E, NTP-SH)	56.42 (A-E, NTP-SH)	92.44 (R-A, WF)	91.57 (R-A, WF)
0.005°x0.005°	3247.92 (R-A, NTP-SH)	53.05 (SL-E, NTP-SH)	98.82 (R-SL, WF)	97.65 (R-SL, WF)

6.4.3 Choosing a suitable resolution for German brown shrimp data

The examination of patchiness was carried out for the area described in the methods section, which contained no inaccessible areas. Considering this area and using a resolution of 0.005°x 0.005°, a C-value of 2.25 was found, indicating a patchy situation. Coarser resolutions lead to identical or higher C-values (0.01°x 0.01°: C= 2.25, 0.05°x 0.05°: C= 28.00, 0.1°x 0.1°: C= 79.94, 0.5°x 0.5°: C= 172.52). Therefore the use of a resolution coarser than 0.005°x 0.005° cannot be justified. On the other hand, using the complete raw ping data set, from one month at the beginning of the high season, generated by the comparably large fleet of German brown shrimp vessels leaves artificial gaps. With a resolution of 0.005°x 0.005°, 89.3% of the presumably fished grid cells were declared as unfished. Even with a non- permissible resolution of 0.5°x 0.5°, this rate amounts to 12.5% (Figure 6.6).

As track estimation methods cannot safely identify the true track of the vessel, it is desirable to choose a resolution that covers the same C-Squares irrespectively of whether straight lines or splines are used. In our data set the distribution of the distances between spline coordinates and straight lines was right tailed (min: 0 km, median: 0.14 km, mean: 0.27 km, max: 7.7 km). Hence, under the condition that grid cells should always cover all tracks of both splines and straight lines, a coarse C-Square resolution of 0.5°x0.5° was needed (Table 6.3). We can see that 90-99% of the tracks would be covered by a C-Square resolution of 0.05°x0.05° and 80-89% using a resolution of 0.01°x0.01°. This means that, for example, straight lines at a resolution of 0.01°x0.01° will allocate the fished area in 11-20% of the tracks in different C-Squares to those of splines. Using C-Squares with pre-defined resolutions and equal information on latitude and longitude (e.g. 1°x1° instead of 0.5°x1°), the suitable C-Square resolution covering tracks of both splines and straight lines, was mainly driven by the differences in longitude direction as in the German Bight 1° longitude is less than 1° latitude.

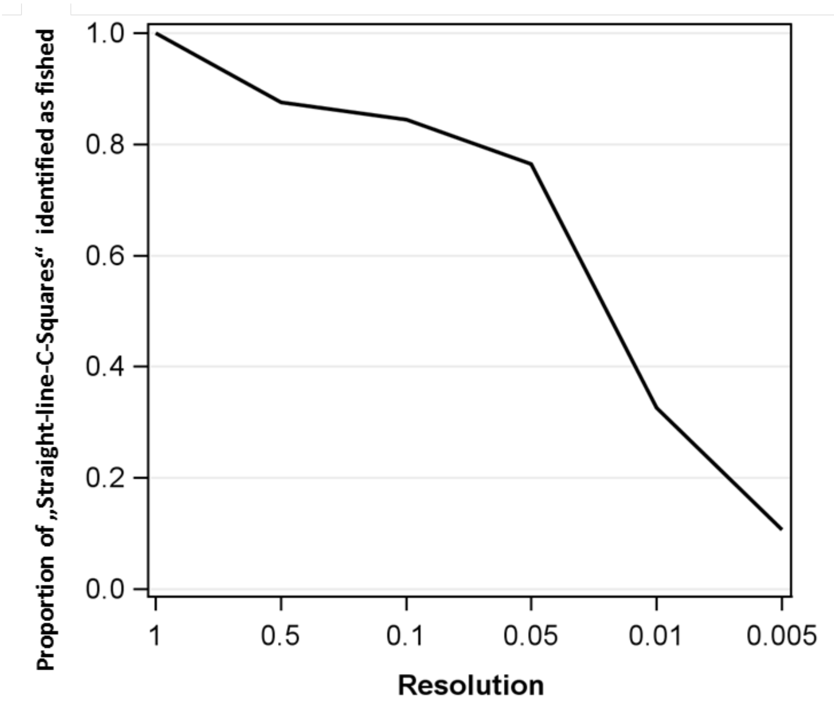

Figure 6.6 Proportion of C-Squares that is identified as fished when raw pings are used. It is assumed that straight lines symbolise the least complex way to cover all gaps in between consecutive pings. For example: 0.8 means that only 80% of the C-Squares are covered when using raw pings in comparison to straight lines.

Table 6.3 Possible C-Square resolutions covering different proportions of the deviations of splines to straight lines. Quantile: quantile of the distance between straight lines and splines; min. resolution: Minimal resolution covering splines and straight lines in a single C-Square; C-Square: next possible resolution based on C-Squares.

Quantile	Min. resolution [°lat x °lon]	C-Square [°lat x °lon]
Q_{50}	0.001° x 0.002°	0.005° x 0.005°
Q_{60}	0.002° x 0.003°	0.005° x 0.005°
Q_{70}	0.003° x 0.005°	0.005° x 0.005°
Q_{80}	0.004° x 0.007°	0.01° x 0.01°
Q_{85}	0.005° x 0.009°	0.01° x 0.01°
Q_{89}	0.006° x 0.010°	0.01° x 0.01°
Q_{90}	0.006° x 0.011°	0.05° x 0.05°
Q_{95}	0.009° x 0.016°	0.05° x 0.05°
Q_{99}	0.015° x 0.026°	0.05° x 0.05°
Q_{100}	0.069° x 0.118°	0.5° x 0.5°

6.5 DISCUSSION

Different methods can be applied to VMS data in order to estimate the spatial distribution of effort and catch by means of coupling logbook and VMS- data (Russo *et al.*, 2014; Gerritsen and Lordan, 2011; Bastardie *et al.*, 2010; Hintzen *et al.*, 2012).

6.5.1 Estimations on the fished area, effort and catch

If quantitative estimates of landings for smaller areas are needed, the choice of a particular method becomes relevant. For example if compensatory payments are paid in proportion to previous usage of a future no-take area. This study aimed to quantify the differences between the available methods taking into account the total amount of effort and catch the different methods allocated to case study areas of different sizes. Furthermore, differences in the estimated size and location of the fished area within the different case study areas were investigated. Based on five case study areas of different size, we were able to quantify the differences between the methods and quantify the uncertainty about fished area and the impact of fishery. We obtained three main findings when investigating the brown shrimp fishing impact:

(i) Expressed as proportion of the total September effort, the differences between the methods were < 5%. However, statements about the exact amount of total effort and catch made within the case study areas are difficult, as the estimations differed by 11- 160% compared to the mean effort and catch allocated to the different case study areas (mean over all methods). The differences were lower in large areas (NTP-SH NTP-LS and MPA) that included many pings and became larger and unstable in small areas which only received few pings (NTP-HH and WF).

(ii) The estimations of local effort and catch per C-Square became very unstable and differed strongly between methods (maximum: a difference of 98 percentage points) when the case studies were smaller and less information (lower ping rate) was available.

(iii) The methods neither indicated identical areas as fished (not even at a coarse resolution of 1°x1°), nor identical sized areas as fished. As an extreme example: At the smallest resolution of 0.005°x0.005° either 90% of the WF-area was identified as fished when using ellipses or declared as nearly unfished area (<5%) when raw pings were used. But even in the largest case study area NTP-SH at a relatively coarse resolution of 0.1°x0.1° the area within the NTP-SH identified as fished differed by > 15% (Figure 6.5, top row).

The differences in the estimations of effort, catch and the fished area were unexpected in so far as the usage of all methods is supported by plausible arguments. Straight lines, splines and ellipses were even tested against "reality" to quantify the uncertainty using high poll-rate data (Straight lines: Skaar *et al.* (2011), Lambert *et al.* (2012); splines: Hintzen *et al.* (2010), Lambert *et al.* (2012), ellipses: Mills *et al.* (2007)). None of the methods produced consistently highest or lowest estimations of effort or catch for all case study areas. Instead, the estimated amount of catch and effort seemed to depend on the size of the area, and possibly also on the actual number and distribution of the pings within the areas. This we surmised because the greatest deviance in the estimations was not found in the smallest case study area (WF), but in the NTP-HH, which being 137.5 km² is several times larger than the very small wind farm of 3.5 km² ,but only received half of the pings (18 instead of 37 in the WF). As we clipped the data along the exact borders of the case study areas and therefore always included identical sets of originally transmitted pings, the differences in the allocated total amount of effort and catch per case study area were surprising. However, they can be explained, as due to the clipping, parts of splines, ellipses, amplification points and straight lines which were located outside the case study areas. These parts included the additionally created way points. If located outside the considered case study area, these parts were removed and hence not considered in the allocation of catch or effort to the case study area.

The results of this study demonstrate that for the German brown shrimp fleet considerable differences in the estimations of effort, catch, and fished area occur, even between the validated methods, such as the ellipses and splines. For example, the identification of the fished area differed between ellipses and splines by about 30% at a relatively coarse resolution of 0.5°x0.5° in the National park of Schleswig-Holstein.

Hence, our study shows the limitations of the usage of VMS data. In impact assessment for areas in which relatively high proportions of the total catch (or effort) are made, the absolute difference between the estimations of the different methods will probably be irrelevant. An example for this situation is given in the NTP-LS where the proportion of the total catch in September 2010 was estimated to be within the range of 37.13% - 41.51%. In contrast, in areas of low effort or catch such as the NTP-HH, the proportional differences are low with, for example 0.28% - 1.41% of the total catch. The absolute differences between the estimations in the NTP-HH (2394 - 12074 kg), however, might be relevant.

For marine spatial planning, spatial effort and catch estimations for selected areas are needed. For example to evaluate the impact within Natura 2000 areas (Oostenbrugge *et al.*, 2010) or to assess the impact of the fishery according to the Marine Strategy framework directive (EC, 2008). Our study however demonstrates that impact assessment, especially in areas of low effort, is combined with a great uncertainty and strongly depends on the method chosen. It cannot even be determined which of the methods is likely to produce generally higher or lower estimations. The same uncertainty is given when sub-regions of case study areas are considered. In this instance the distribution of effort and catch within the case study areas was very different. Moreover, the results show that it could not be determined consistently whether a specific location within the case study area was fished. Therefore, we can only suggest treating effort and catch estimations for specific areas with caution as the differences due to methods may be great, especially in areas with few pings.

6.5.2 Suitable resolution for brown shrimp research in the German Bight

For German and Dutch offshore waters the bottom impact of the fishery on, for example, sandbanks and reefs has already been assessed by international projects (EMPAS, FIMPAS), and similar questions arise for coastal Natura 2000 sites. Typically sandbanks, areas of seaweed or reefs within Natura 2000 areas, are small structures requiring a high resolution to study the impact. The impact of bottom trawling in these areas could be assessed either by using raw pings or interpolated tracks (e.g. Deng *et al.*, 2005; Hiddink *et al.*, 2006; Lambert *et al.*, 2012). Raw pings often seem to be most attractive, especially for structured habitats such as the impact assessment on benthic communities (Dinmore *et al.*, 2003).

Our study shows clearly, that the usage of raw pings for the brown shrimp fishery would produce artificial gaps, if used at any resolution finer than 1°x1°. Even the use of the very fine grid cell size of 0.005°x0.005° would not ensure that within a single grid cell the same conditions exist, as the data at that resolution were still found to be highly patchy. Hence, the smallest resolution possible, as suggested for example by Rijnsdorp *et al.* (1998), Dinmore *et al.* (2003) and Piet *et al.* (2007), would need to be even finer than 0.005°x0.005°. This, at the same time, would strongly underestimate the probably fished area, as more than 90% of the fished area would be designated as unfished. An alternative to the raw ping usage to estimate impact on small scale structures is the usage of methods that try to reconstruct the track of the vessel using interpolation methods. However, splines and straight lines may deviate from the true vessel track (Deng *et al.*, 2005; Skaar *et al.*, 2011; Lambert *et al.*, 2012). For Norwegian demersal stern trawlers it was shown that original tracks deviated mostly > 3 km from the straight lines with a maximum of > 8 km (Skaar *et al.*, 2011), for Isle of Man Scallop dredgers and trawlers the deviation between splines and straight lines was about 2 km (Lambert *et al.*, 2012). In this study, for German brown shrimp fishing vessels, the maximal distance between straight lines and splines was 7.7 km but as German brown shrimp vessels operate in waters with complex topography, a different behaviour in tidal creeks than in that of open water is likely. Fishing areas considered in this study contain tidal creeks and flats but neither the splines, the ellipses, the straight lines nor the amplification method account for permanently or temporarily impassable areas. Therefore, they are likely to assign effort to regions in which fishing is impossible.

To avoid artificial gaps between subsequent pings and to be able to answer questions on small areas, for example the effort exerted within planned wind farm areas or within planned no-take areas, we see two different possibilities: 1) A method has to be developed to assign splines or straight lines according to the present topography, i.e. away from land positions, including those land positions which exist only during the time of the ebb stream. Then analyses must be based on updated maps, as the location of the tidal flats and creeks varies in short time. 2) The ping rate should be increased to facilitate the reconstruction of the vessels' track at a small resolution without gaps, as suggested by Deng *et al.* (2005), Skaar *et al.*(2011) and Lambert *et al.* (2012). This is in line with the recommendations of other authors who already suggested higher ping rates for other fisheries such as the Australian prawn fishery (Deng *et al.*, 2005), Scallop dredgers and Otter Trawls (Lambert *et al.*, 2012) of the Isle of Man. This refinement is already a reality in Denmark where pings are transmitted on an hourly basis (Miethe *et al.*, 2014).

However, under the given conditions of 2-hourly pings, our study showed that for the German brown shrimp fleet a resolution of 0.01°x0.01° would ensure that the straight lines and the spline method would designate the same C-Squares as fished. This resolution is fine enough to represent quite small-scaled structures and still incorporates the majority of possible vessel tracks (89%). All possible tracks would only be covered when a C-Square resolution of 0.5°x0.5° was used. However, in Northern Germany where 1° longitude is, in absolute values, shorter than 1° latitude, C-Squares might not be ideal as smaller resolutions would have been possible if other forms of gridding were used (Table 6.3).

6.6 CONCLUSION

The present analysis shows that the estimations of location, size and utilization of the fished area differ between the methods compared (raw pings, straight lines, splines, ellipses and amplification) without any predictable pattern. To estimate location, size and impact of the fished area it is shown that both method of track reconstruction and the grid size used for display are important. This holds particularly if quantities on a small spatial scale are estimated. All methods exhibit methodological weaknesses that need to be removed to generate more realistic results. Track reconstruction should account for areas that are permanently or temporarily inaccessible. The spline method, using all transmitted information, seems most appropriate for suitable modification such as the linkage to topography. Point methods seem less appropriate because of their expressed dependence on cell size. If grid cells are small, they underestimate the fished area and create gaps. If grid cells are large, they are not able to describe areas with fine internal structure. Increasing the number of pings per time would reduce the amount of necessary track reconstruction and therefore reduce the amount of errors introduced by using reconstructed instead of observed tracks.

A modified method should be validated by recording a certain number of vessel tracks with dense pings, applying the reconstruction method and then comparing observations with reconstructions. This would provide a sound assessment of the reconstruction method and the choice of grid cell size.

Given that currently new developments are lacking, for the coastal German brown shrimp fishery, a C-Square resolution of ≥ 0.01°x0.01° with straight line or spline based track estimation seems most appropriate. Considering the present data, this approach combines a high coverage of likely tracks and provides an acceptable spatial accuracy.

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7 MANUSCRIPT 3

SPATIAL AND TEMPORAL DISTRIBUTION PATTERNS OF BROWN SHRIMP (*CRANGON CRANGON* L.) DERIVED FROM COMMERCIAL LOGBOOK, LANDING AND VESSEL MONITORING DATA

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7.1 ABSTRACT

Brown shrimp (*Crangon crangon* L.) support a large, but so far unmanaged fishery with in total > 500 vessels, 200 of which are German. In this study, logbook-, landing and VMS data of these vessels are combined to analyse spatiotemporal patterns in the brown shrimp distribution. The spatial and temporal distribution of different sized brown shrimp from 2007 – 2013 is determined based on kg landings per hour of effort (LPUE), which are standardised to the efficiency level of a mean German brown shrimp vessel. The standardisation alters the spatiotemporal patterns of the landings per hour, as the vessels differ by > 20% in their efficiency. Efficient vessels are generally fishing further offshore.

The spatiotemporal distribution differs clearly between small brown shrimp (50 – 73 mm) and large brown shrimp (> 73 mm). We show that the earlier increase of brown shrimp catches in summer in the westernmost areas was entirely due to local landings of undersized brown shrimps and not linked to warmer water temperatures in those regions. In winter, strongest migration signals of large brown shrimp are found in the core distribution area, namely in Dutch and East Frisian waters, while the migration signal diminishes towards the North.

Hence, our results show that commercial data can be used for biological research and provide comprehensive information on the spatial and temporal distribution of brown shrimp which has not been available so far. The results give indications that help clarifying different aspects of the life cycle of brown shrimp.

Keywords: Crangon crangon, commercial data, LPUE, spatial distribution, spawning grounds, selective tidal stream transport, migration

7.2 INTRODUCTION

Brown shrimp occur in high densities in the southern North Sea and support a large multi-national fishery with over 500 active vessels and landings of > 30 000 t annually (ICES, 2014a). This fishery however, is so far unmanaged. Recently, management of the brown shrimp population has been discussed both within ICES and in the context of an MSC-Certification (Temming *et al.*, 2013; ICES, 2013b; ICES, 2014b). In these reports, main data gaps have been identified. Those include a largely unknown spatial distribution and unidentified seasonal distribution shifts of adult and juvenile brown shrimp and the locations of spawning grounds.

Comparing fishing hours of commercial vessels to fishing hours of survey vessels reveals that the fishing time of survey vessels is about 0.009% of the fishing time of commercial vessels. Hence, commercial vessels data form a large and so far unused data source which can help to address these unknown distributions, locations and seasonal shifts.

Brown shrimp are supposed to hatch either between October and March (winter-eggs) or between April and September (summer-eggs, Havinga, 1930). Though the summer- egg production is higher than the winter production (Siegel *et al.*, 2008), the population is dominated by shrimp originating from winter eggs (Hufnagl and Temming, 2011b). These winter- spawned shrimp invade the shallow Wadden Sea areas in May/June (Temming and Damm, 2002) and retreat into sub-tidal areas with increasing maturity and length (Kuipers and Dapper, 1981). It is assumed that German waters are in part receiving offspring drifting from winter spawning grounds off the Dutch coast, where development of larvae is completed earlier due to slightly higher temperatures (Temming and Damm, 2002; Daewel *et al.*, 2011). Commercial catches, recorded in the logbooks , are shown to have already increased in July in Greetsiel, one of the most westerly German harbours, but not until September in Cuxhaven (a port, located further in the east, Respondek *et al.*, 2014). Respondek *et al.* (2014) suggested that the earlier start of the fishing season in Greetsiel was linked to the differential warming in Dutch waters in contrast to that of north-eastern waters. This would imply warmer conditions off the coast of the Netherlands (Daewel *et al.*, 2011) and hence faster larval and juvenile growth in the westernmost areas (Temming and Damm, 2002; Hufnagl and Temming, 2011a).

The annual peak in commercial catches was usually observed in autumn (September – November) (ICES, 2012) and the catches decreased thereafter. Such a decrease was also found in research samples by Havinga (1930) and Boddeke (1976) who concluded that from October to March mature shrimp migrate towards the "open sea" to reach their spawning grounds in order to release their larvae in deeper waters. The offspring from those brown shrimp located at the spawning grounds in winter will make the main contribution to next year's peak of landings in autumn (Hufnagl and Temming, 2011b). Studies on brown shrimp are typically conducted in shallow areas, in depths of ≤ 20 m (Havinga, 1930; e.g. Boddeke, 1976; Siegel *et al.*, 2005). Hence, statements about the depth of spawning grounds were mostly based on indirect conclusions from higher catch rates in samples of deeper areas (Boddeke, 1976) in winter, or by not catching any large females at all in depths ≤ 10 m (Havinga, 1930). However, in Germany a winter survey was conducted in January or February from 1990-2010 which aimed at estimating the effects of the expanding commercial winter fishery on the shrimp stock (Siegel *et al.*, 2008). A further goal was to resolve the winter distribution of adult, especially egg-bearing shrimp, in the German Bight outside the Wadden Sea. The latter survey covered a depth range from 12 - 54 m. Its analysis revealed that females carrying eggs (berried females) were distributed more evenly over all measured depths strata than brown shrimp without eggs (unberried shrimp), which were concentrated rather in shallower water (Schulte *et al.*, manuscript 1).

Spring migration towards the coastal nursery grounds, and offshore autumn migration towards spawning grounds, could be explained by the selective usage of tidal streams (Selective tidal stream transport, STST, Cattrijsse *et al.*, 1997).This was evident in laboratory trials where brown shrimp were indeed found to be more active during times of low tide (Hufnagl *et al.*, 2014) or high tide (Al-Adhub and Naylor, 1975). Flood stream usage in spring would allow the juveniles to reach their coastal nursery areas (Daewel *et al.*, 2011) and usage of the ebb stream in autumn would allow the adults to reach their offshore spawning grounds in January (Hufnagl *et al.*, 2014).

In German waters, information on the spatial and temporal distribution of the brown shrimp stock is mainly acquired from the annual ''Demersal Young Fish Survey, DYFS'' in autumn (Siegel *et al.*, 2005). This survey was originally designed to monitor the densities of 0-group plaice. However, this survey also provides useful information on the brown shrimp in terms of catch per hour, proportions of berried females and length-frequency distributions. Nevertheless, it only covers a short period of the year and does not consider seasonal changes in distribution patterns including possible migration to deeper waters.

In contrast, commercial German brown shrimp fishers command more than 200 vessels (ICES, 2014a), fishing on average 200 days/year and thereby generating about 40000 log book entries covering a large area. Commercial brown shrimp catches for human consumption consist of brown shrimp of at least 6.5 mm (carapace width, CW), which corresponds to a total length of > 50 mm (Sharawy, 2012). Therefore, commercial brown shrimp catches predominantly include mature females (Hartnoll and Oh, 2004).

The fishers are obliged to keep a logbook, recording their trip dates, fishing times and estimated catch. These data can be combined with landings data, where catch and the size of the different sieving fractions of brown shrimp for human consumption along with amount of undersized brown shrimp is recorded. Subsequently, these data can be integrated with vessel monitoring system (VMS) data, including the vessel's position, speed and heading transmitted roughly every two hours. This combined data set is of course spatially less precise than survey data.

However, it has the advantage of a high temporal and spatial coverage, especially due to the high number of active brown shrimp vessels.

Hence this data set is highly attractive as an alternative source of information. However, using these data for biological purposes is associated with some problems which need to be considered:

(i) It is assumed that brown shrimp vessels cover the total area in which brown shrimps occur in considerable densities. Due to the high number of vessels, the coverage of the area can be assumed to be reasonably good. However, it cannot be excluded that certain areas, in which considerable densities of brown shrimps may exist, are not detected and have therefore not been fished, for example due to obstacles that might damage bottom trawls or too shallow water depths.

(ii) At times and in places, where only few vessels are fishing, only limited information exist, thus creating great uncertainty. This uncertainty should be recognisable in any of the produced maps.

(iii) Vessels of high efficiency will probably have higher mean landings per unit effort (LPUE) than less efficient vessels. Hence, high/low LPUE at certain times or in certain regions may not reflect high/low densities but could just be caused by these differing levels of vessel efficiency. Hence, the LPUE needs to be standardised.

As described earlier, the brown shrimp fishery is unmanaged to date, but management is considered to be required as the stock is currently growth overfished (ICES, 2014a; ICES, 2014b; Temming and Hufnagl, in press.). At present, the discussed management plan is based on the monitoring of the commercial LPUE. An effort reduction is demanded as soon as a decrease in the mean LPUE of the total fleet under a predefined threshold occurs. An effective management is thus only possible if the threshold is of a relevant, science- based value. Furthermore, an effective management can only be obtained if the variability in the commercial LPUE and the distribution of the brown shrimp is well understood. Thus, for the effective management of the brown shrimp stock it is essential to know about seasonal patterns in the spatial distribution of brown shrimp, and to identify spawning grounds and spatial patterns of the incoming new cohort.

As scientific surveys are mainly conducted in autumn (since 1974, Siegel *et al.*, 2005) and winter (1991 to 2010, Siegel *et al.*, 2008), the spatial distribution of brown shrimp has not, until now, been studied comprehensively. Scientific knowledge about the exact locations of spawning grounds does not, to our knowledge, exist. Nevertheless, the localisation of areas of high densities of berried females is a prerequisite for making concrete assumptions about effort reduction in areas affected by reduced stock sizes.

With this study we aim to fill the above described gaps which are necessary for the management of brown shrimp stock. We used German logbook-, landing and VMS data from 2007 - 2013. We applied a form of direct standardisation, typically known from epidemiology (Fleiss *et al.*, 2004) but so far unused for commercial fisheries data. We standardised the catches to the catches of a hypothetical "mean German vessel" to reappraise current ideas on the spatial distribution and its temporal dynamics of brown shrimp stock in the German Bight.

By using this standardisation we evaluated whether the mean LPUE in their originally recorded forms, are comparable with different regions and seasons and independent of the composition of the active vessels. As a result of this standardisation the present study describes the spatiotemporal distribution of the brown shrimp population in the German Bight. Three different hypotheses were tested relating to the brown shrimp distribution:

(iv) The earlier increase of landings in western harbours as opposed to north-eastern harbours in early summer is evident only when commercial brown shrimp for human consumption (> 50 mm total length) are included in the analysis. If this was the case it would strengthen the hypothesis that the differential warming in Dutch and north-eastern waters could lead to faster larval and juvenile growth in the westernmost areas (Temming and Damm, 2002; Hufnagl and Temming, 2011a).

(v) Spawning grounds in winter (December – March) are generally localised seawards or in the "open sea" as described by Havinga (1930) and Boddeke (1975).

(vi) The observed spatiotemporal patterns from commercial data in the brown shrimp densities match the results of the simulation model. The simulation model results suggest a seasonal migration of adult females to deeper waters in winter and an onshore migration of juveniles in spring, based on selective tidal stream transport (Daewel *et al.*, 2011; Hufnagl *et al.*, 2014).

7.3 MATERIAL & METHODS

7.3.1 Data

We included all German brown shrimp vessels operating from January 1, 2007 to December 31, 2013 for which logbook-, VMS- and landing data were available.

Log book data: In Germany, fishers record fishing start and end times. Only these recorded fishing periods were used for analysis, whereas the steaming times were excluded.

VMS data: Vessel monitoring system (VMS) data are legally required to be recorded since 2005 on all vessels longer than 15 m fishing in European waters (EC, 2003). The VMS information provides data on vessel activity which includes position, heading and speed with a temporal resolution of one signal (ping) every two hours. Brown shrimp fishers usually trawl at speeds of about 3.5 knots. Thus 2-hourly pings imply that during gear operation a ping is transmitted approximately every 6.4 km. As VMS data give no information about the track between two consecutive ping positions, we used the straight line interpolation (Eastwood *et al.*, 2007; Stelzenmueller *et al.*, 2008). 100 additional way-points in between two consecutive pings were created. A C-Square resolution of 0.05°latitude x 0.05°longitude (Rees, 2003) was used. The straight line interpolation is a simple approach to acknowledge that the vessel has to cover at least the shortest distance between two consecutive pings. It does not take the information about heading and speed of the vessel into account. However, for brown shrimp vessels at a resolution of 0.05° x 0.05° the area covered using straight lines is, in more than 90% of the cases, identical to the area identified as fished when using the more time consuming cubic Hermite splines as suggested by Hintzen *et al.* (2010), see Schulte *et al.* (manuscript 2).

Landings data: These data represent the landed weight of the catch for which the fishers received revenue. These are usually brown shrimps with a CW > 6.5 mm which corresponds to a TL of about 50 mm (Sharawy, 2012). These brown shrimps are used for human consumption.

Brown shrimp although sieved on board are again sieved when landed in sieving stations of the different buyers or producer organisations. In these stations the catch is sieved with different bar widths to split the catch into several fractions which are of different value and determine the price the fisher receives. In the landing data, brown shrimp for human consumption are coded as "1" or "2". The fraction coded as "1", represents the largest shrimps. Smaller shrimp still having a CW > 6.5 mm are less valuable and carry the code "2". In the vast majority of sieving stations the code 1 represents a CW > 9.5 mm. This includes sieving stations of the largest buyers (Heiploog and Klaas Puhl, and also, since 2013, the sieving stations of the greatest producer organisation Erzeugergemeinschaft der Deutschen Krabbenfischer GmbH; Oberdoerffer, de Beer, Kock, Höller, Michelsen, pers. comm.). As the CW corresponds to 13-15% of the TL (Sharawy, 2012), the largest sieving fraction corresponds to TL > 73 mm ("large shrimps") and the smaller ``code 2" shrimp have a TL between 50 - 73 mm ("small shrimps").

Due to sexual size dimorphism, males do not grow as large as females (Ehrenbaum, 1890; Tiews, 1954; Tiews, 1970) and hardly ever reach a size > 70 mm. Females on the other hand may exceed a size of 80 mm (Hufnagl *et al.*, 2010). Females mature at about a size of 33- 55 mm (Campos and van der Veer, 2008). In the smaller sized fraction (CW: > 6.5 - ≤9.5 mm ≙ TL ca. 50 - 73 mm) the proportion of males can therefore be considered low and they are probably not present in the larger fraction since for shrimps > 60 mm (TL), the proportion of females in the catches equals 100% (Siegel *et al.*, 2008). Hence, the majority of the commercial catches will be comprised of mature females (Hufnagl and Temming, 2011b).

Whether females carry eggs depends on their size and the season. The lowest proportions of berried females occur between mid-August and early December and highest proportions between March and June (Siegel *et al.*, 2008). During the entire year less than 40% of the shrimps < 50 mm (TL) carry eggs. The proportion of berried females between 50 – 73 mm (TL) ranges between 2% (for brown shrimp of 50 mm in

September) and 95% (for brown shrimp of 73 mm in April). The proportion of brown shrimp > 73 mm (TL) varies between 15% (for brown shrimp of 73 mm in September) and 98% (for brown shrimp of 73 mm in May, Siegel *et al.*, 2008). In this study we used the estimated catch locations of large shrimps as a proxy for the spatial distribution of berried females.

German landing data also contain records of the weight share of undersized brown shrimps (CW < 6.5 mm). Those shrimp are landed in some harbours for industrial use only and are processed as animal food. We used these undersized brown shrimp to test whether they caused the earlier increase in the landings in westernmost harbours found by Respondek *et al.* (2014). We based our analysis on the same harbours as those used by Respondek *et al.* (2014). These are from West to East: Greetsiel (53.5°N ,7.1°E), Norddeich (53.63°N ,7.16°E), Cuxhaven (53.87°N, 8.7°E), Büsum (54.13°N,8.85°E) and Husum (54.48°N,9.04°E).

Combination of data: In order to obtain spatial estimations of fishing effort and catch, all three data sets (VMS, landing data and logbook data) can be combined (e.g. Pedersen *et al.*, 2009; Bastardie *et al.*, 2010; Lee *et al.*, 2010; Gerritsen and Lordan, 2011).

Landing data are available per trip but in the logbooks the fishers record the estimated catch per haul. When both data sets were combined, the landed kilograms were distributed to the different pings according to the proportions of the catch recorded in the logbooks, as suggested by Schulte *et al.* (manuscript 2). This works to our advantage as usually not all hauls are equally successful. Hence, in this way all available information is used for distributing the catch (and, hence, the LPUE) in the best possible way. Furthermore, this probably enhances the precision of the spatial allocation of the catches.

Trips that included pings with speed greater than 6.4 knots during the stated fishing periods or with a difference of > 3 hours between two consecutive pings were excluded from the analysis. This resulting dataset included 226 different vessels and 81319 trips which had transmitted a total of 1333821 pings (Table 7.1).

Table 7.1 Active vessels with VMS, logbook and landing data of the different years, number (N) of trips and pings transmitted per year from 2007 – 2013. Note that in the dataset 226 vessels were active, some of them being only active in some of the years.

YEAR	Active vessels	N trips	N pings
2007	200	13155	243529
2008	199	12738	238878
2009	184	12864	223329
2010	176	12136	200746
2011	173	8499	121629
2012	175	12031	202939
2013	180	9896	102771
Sum		81319	1333821

Furthermore, the VMS positions were linked to the fishing depths and added to the data set. This was achieved by using the bottom layer of the three dimensional, baroclinic shallow-water circulation model HAMSOM (Backhaus, 1985), modified by Pohlmann (2006). The bathymetry is based on a 3 km grid. Though this grid is relatively fine, it should be noted that these depths might not represent the actual absolute depth at a certain location in the highly variable environment of the Wadden Sea. It does nevertheless allow for identification of general tendencies without any great difficulty.

In order to localise preferred brown shrimp spawning grounds and to examine whether the migration of large and in particular berried females into deeper water in winter can be verified by our data, we defined five different regions based on the use of ICES rectangles (Figure 7.1 a, Table 7.2). We also classified the depth into five strata (≤ 5 m, > 5 - 10 m, > 10 - 20 m, > 20 - 30 m, > 30 m). The defined regions covered the majority of all transmitted VMS pings. However, 1613 pings (0.12% of the total number of 1333821 transmitted pings) were not located in any of these five regions.

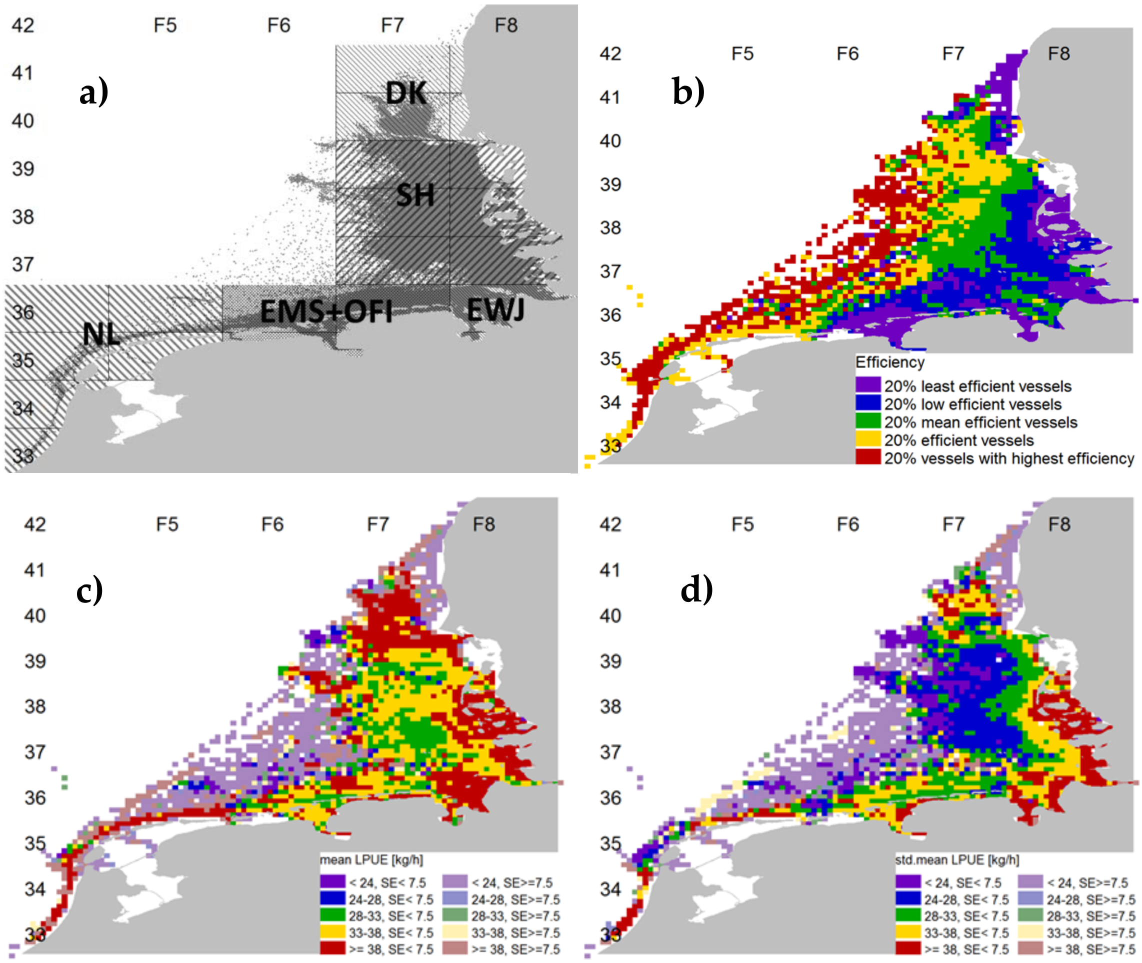

Figure 7.1 a): transmitted VMS-pings from 2007 – 2013 and regions defined based on ICES statistical rectangles. b): Mean distribution of the vessels of different efficiency from 2007 – 2013; bottom: Comparison of non-standardised (c) and standardised (d) LPUEs for brown shrimps used for human consumption (total length ca. > 50 mm) caught from 2007 - 2013.

Table 7.2 Definition of the different regions according to ICES statistical rectangles and number and proportion of transmitted VMS pings within those regions.

Region (N to SW)	*Name of region* and ICES - statistical rectangles	Pings transmitted from 2007 - 2013	% of total number of pings transmitted
DK	*Denmark* 40F7,40F8,41F7,41F8	16100	1.21
SH	*Schleswig-Holstein* 37F7,37F8,38F7,38F8,39F7,39F8	744163	55.79
EWJ	***E**lbe-**W**eser-**J**ade-Estuary* 35F8,36F8,36F9,35F9	201693	15.12
EMS+OFI	***Ems** Estuary and East Frisia* 35F6,35F7,36F6,36F7	366163	27.45
NL	*The Netherlands* 33F4,34F4,35F4,36F4,35F4,35F5,36F5	4089	0.31

7.3.2 Standardisation

The density of brown shrimp at a certain location can be estimated as mean landings per unit effort (LPUEs) in kilogram per hour fishing. However, for data from commercial fishing vessels neither a fixed trawling speed nor reliable information about gear width or mesh size, etc. is available. Hence, the estimated mean LPUEs are also influenced by the vessels efficiency, the expert knowledge of the captain and other unknown factors. To minimise these effects a standardisation is needed, which requires a quantification of the different vessel-dependent effects.

Total vessel length (length over all: *loa*), power (*kw*), tonnage (*ton*) and the year of construction (*yc*) of the vessel are known parameters. Since not all factors influencing the efficiency of the vessel are recorded (Temming *et al.*, 2013) a random intercept (*ri*) was introduced for each of the different vessels. As it is possible that certain vessels only operate in certain years, months, depth ranges (in meters) or regions, these factors also have to be included in the model. The interaction between year and month was included to allow for seasonal effects, which may differ from year to year. The inclusion of further interactions into the model led to convergence-problems. Note that region, year and month of activity have only been included into the model to ensure a good model fit and to find the best possible estimates for the vessel dependent factors, such as length or power. For the calculation of the correction factor (see below), region, year, depth and month of activity have therefore not been used. In order to obtain normally distributed residuals, we fitted a log-linear model. The full model was formulated as:

$$\ln(LPUE) = \beta_0 + \beta_{ri.ves} + \beta_y \cdot year + \beta_m \cdot month + \beta_{loa} \cdot length + \beta_{ton} \cdot tonnage + \beta_{yc} \cdot year\ of\ construction + \beta_{kw} \cdot kw + \beta_{depth} \cdot depth + \beta_{region} \cdot region + \beta_{ym} \cdot year * month. \quad \textbf{(eq. 7.1)}$$

Significance was determined with type III tests of fixed effects which are robust against their order of inclusion. Furthermore, type III tests aim to reduce the bias caused by an unbalanced design (Pendleton *et al.*, 1986). Starting with the full model, backward selection was used to obtain a parsimonious "final" model (explaining much variance with few parameters) for the data set. During the backward selection process non-significant model terms were excluded from the model, but insignificant main terms that were also part of significant interactions were kept. It was checked, whether the random intercept was needed, by testing the model against a null model of complete independence.

By using all vessels recorded in the data base a "mean vessel" was defined, and all LPUEs were standardised to the LPUEs this "mean vessel" would have reached. In a next step the expected ln(LPUE) for the mean vessel were calculated. This expected ln(LPUE) is attained by a mean vessel under mean conditions of year, month, depth and other vessel- independent factors. The expected ln(LPUE) was calculated as:

$$\text{expected } ln(LPUE_{mean\ vessel}) = \widehat{\beta_0} + \widehat{\beta_{ri.mean\ vessel}} + \widehat{\beta_{loa}} \cdot \text{length}_{mean\ vessel} + \widehat{\beta_{ton}} \cdot \text{tonnage}_{mean\ vessel} + \widehat{\beta_{kw}} \cdot \text{kw}_{mean\ vessel} + \widehat{\beta_{yc}} \cdot \text{year}_{mean\ vessel} \quad \textbf{(eq. 7.2)}$$

The conversion to linear scale was carried out by:

$$\text{expected } LPUE_{mean\ vessel} = e^{\text{expected } \ln(LPUE_{mean\ vessel}) + 0.5 \cdot \sigma_{log}} \quad \textbf{(eq. 7.3)}$$

using the standard deviation of the residuals of the final model (Aitchison and Brown, 1969).

The calculation of the expected LPUE was done for all 226 vessels present in the data set. Subsequently, a correction factor for each of the vessels was calculated. This correction factor (F) converts the LPUEs of the "real vessels" to the efficiency level of the "mean vessel":

$$F = \frac{\text{expected } LPUE_{real\ vessel}}{\text{expected } LPUE_{mean\ vessel}}. \quad \textbf{(eq. 7.4)}$$

In order to attain vessel-standardised LPUEs, which only depend on vessel independent variables, such as depth, temperature, salinity, year, month etc., the last step of standardisation was to divide the recorded LPUEs by F:

$$LPUE_{standardized} = \frac{LPUE_{recorded}}{F}. \quad \textbf{(eq. 7.5)}$$

39 of the 226 vessels changed one or several of the recorded vessel characteristics. Out of these 39, four vessels changed the combination of power, tonnage or length

twice within the period from 2007 – 2013. In these cases, the efficiency factor for the vessel was altered in the month the change took place. Therefore, 269 different factors were applied to standardise the LPUEs. These standardised LPUEs were used as proxy for brown shrimp densities.

7.4 RESULTS

7.4.1 Effects of standardisation

Since all covariables apart from tonnage were significant (p = 0.998), tonnage was eliminated from the full model and the final model was formulated as

$$\begin{aligned} ln(LPUE) = {} & \beta_0 + \beta_{ri.ves} + \beta_y \cdot year + \beta_m \cdot month + \beta_{loa} \cdot length \\ & + \beta_{yc} \cdot year\, of\, construction + \beta_{kw} \cdot kw + \beta_{depth} \cdot depth \\ & + \beta_{region} \cdot region + \beta_{ym} \cdot year * month. \end{aligned} \qquad \textbf{(eq. 7.6)}$$

Type-III-tests of the final model showed that all covariables were able to explain a significant part of the variance in the data (Table 7.3). The random intercept was significant (p< 0.0001), confirming our assumption that not all vessel dependent variables affecting the vessels efficiency are known. The final model explained 56.20% of the variance in the data. As the model was only able to explain 39.94%, when the vessel dependent factors were excluded (length, power, year of construction and the random intercept per vessel), this implies that the latter factors explain 16.26% of the variance in the LPUEs. From the final model we obtained estimated parameters for each of the vessel dependent factors and for the general intercept (Table 7.4).

Table 7.3 Type-III-Tests for fixed effects of the final model (for more details see text).

Effect	F-Value	Pr > F
Year	3487.31	< .0001
Month	7530.85	< .0001
Length [m]	55.32	< .0001
Year of construction	36.07	< .0001
Power [kw]	34.56	< .0001
Region	130.31	< .0001
Depth [m]	14.22	< .0001
Year*month	1113.51	< .0001

Table 7.4 Parameters for the vessel dependent factors estimated using the final log-linear model.

Parameter	Estimate (ln scale)
Intercept	-15.32179
Length [m]	0.026454
Year of construction	0.008984
Power [kw]	0.000702

The mean vessel was constructed in 1977, had a length of 18 m, 194 kw power and a random intercept of 0. Using the estimated parameters shown in Table 7.4 the expected ln(LPUE) was calculated as:

$$\text{expected } \ln(LPUE_{mean\ vessel}) = -15.3218 + 0 + 0.02645 \cdot 18 \text{ m} + 0.000702 \cdot 194 \text{ kw} + 0.008984 \cdot 1977 \qquad \textbf{(eq. 7.7)}$$

For the conversion to linear scale, the standard deviation of the residuals of σ_{log}= 0.3999 was used.

Correction factors (F) for the different vessels, rendering them as efficient as a "mean vessel", were estimated in the range between F_{min} = 0.42 and F_{max} = 1.98. Hence, the least efficient vessel was only 21.21% as efficient as the most efficient one. This indicated that the efficiency of the vessels differed considerably, depending on their length, power and age. Efficient fishing vessels were more often operating in offshore regions, while less efficient (usually smaller) vessels fished in coastal regions (Figure 7.1 b). Hence, non-standardised LPUEs would overestimate the densities especially in offshore regions, while densities in coastal areas would be underestimated, as illustrated in Figure 7.1 c and d (bottom row).

The commercial vessels usually covered almost the total area in which brown shrimps occur in high densities (Figure 7.2). This became apparent as areas with low densities usually had large standard errors (SE ≥ 7.5). This indicates that data from commercial brown shrimp vessels can be used successfully to identify regions and seasons of high brown shrimp densities.

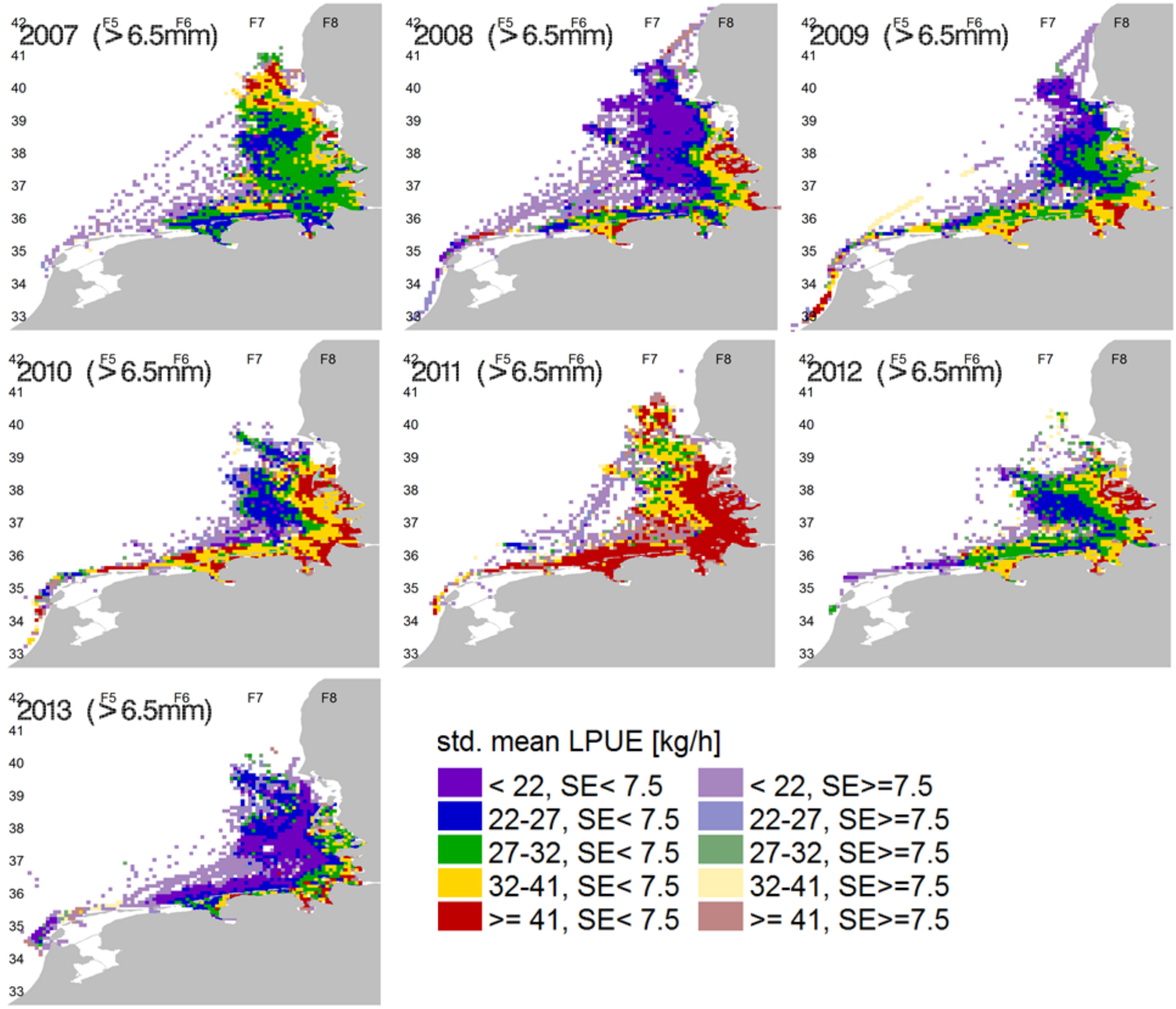

Figure 7.2 Spatial distribution of standardised mean LPUEs of commercial brown shrimps for human consumption (carapace width > 6.5 mm ≙ total length of ca. >50 mm) in different years.

7.4.2 Variation in the spatiotemporal distribution of brown shrimps and the fishery

German shrimpers showed a tendency during the most recent years to decrease their fishing effort in areas north of Blåvand (55.56°N; 8.13°E, Figure 7.2). Based on 38 German vessels a mean annual standardised density of > 41 kg/h was determined in 2007. In 2008 and 2009 on the other hand, only standardised LPUEs of < 27 kg/h based on 20 vessels were observed. In 2010, 2012 and 2013 this area was hardly fished (less than eight active vessels). Despite this general trend of less fishing effort and lower catches in Danish waters, ten German shrimpers fished in these areas in 2011 with good success and a standardised LPUE of > 41 kg/ h.

Highest brown shrimp densities of 37.48-51.47 kg/h (CW: >6.5 mm) were found in autumn between August and November while lowest densities were observed in February and March (22.18 – 25.94 kg/h with CW: >6.5 mm). This pattern was different in 2007 and 2011. In these years spring densities were higher than autumn densities with 36.35 kg/h in April 2007 compared to a maximum of 34.34 kg/h in September 2007 and 80.86 kg/h in May 2011 compared to a maximum of 69.19 kg/h in October 2011 (Figure 7.3, top row).

The first increase in brown shrimp densities in spring does not show any regional differences when only commercial brown shrimps for human consumption (CW: > 6.5 mm) were considered (right panel, Figure 7.4). Not so the case when undersized industrial brown shrimps were also included in the analysis. These were mainly landed in East Frisia (Greetsiel, left panel in Figure 7.4). If the brown shrimps for industrial use are included, peak landings from 2007 – 2010 were recorded in Greetsiel, one of the most south-westerly German harbours. This effect was already observed in July, while in more north-easterly harbours the landings peaked later around September (Figure 7.4).

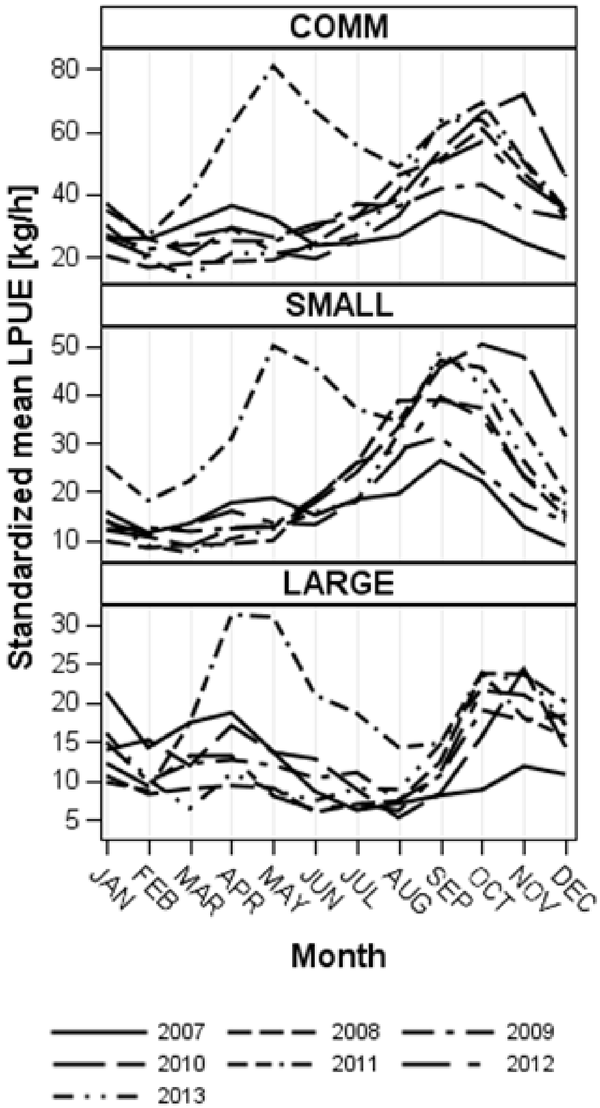

Figure 7.3 Course of the different years of the standardised mean LPUEs of commercially used brown shrimps for human consumption (COMM: all brown shrimps used for human consumption, ca. > 50 mm total length; SMALL: small fraction of brown shrimps for human consumption total length: ca. 50 mm – 73 mm; LARGE: large fraction used for human consumption. Total length: ca. > 73mm). Note, that the y-axis is differently scaled.

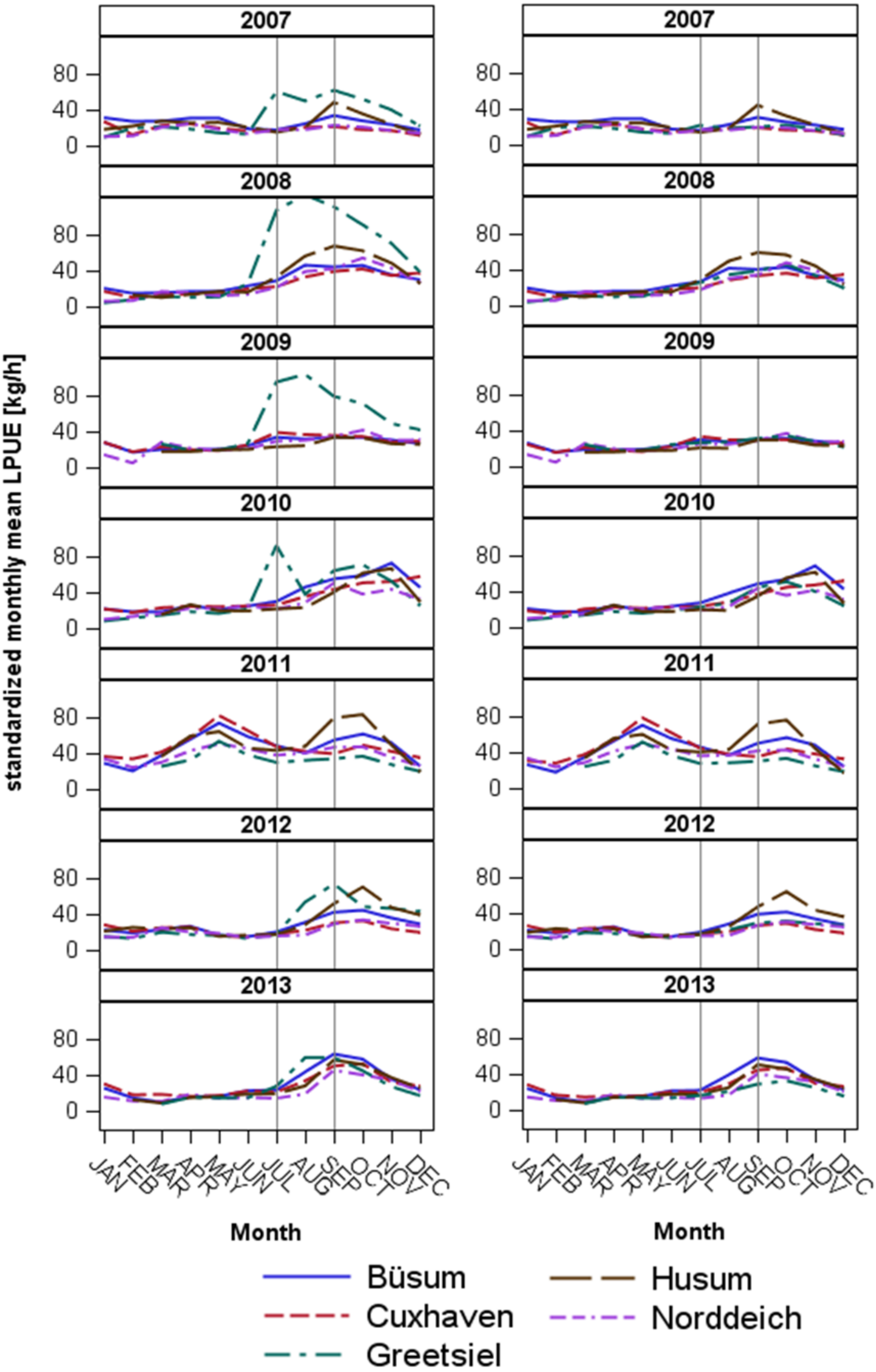

Figure 7.4 left panel: all sizes landed (including undersized shrimps used for industrial use); right panel: brown shrimps for human consumption (total length ca. > 50 mm).Reference lines are positioned in July and September.

The standardised LPUEs of the smaller sieving fraction (CW: >6.5 - ≤9.5 mm ≙ TL: 50 – 73 mm) are with an overall average of 21.87 kg/h higher than the 12.76 kg/h for the large sieving fraction (CW: > 9.5 mm ≙ TL: 73 mm). Usually the density peak of small brown shrimp can already be observed at the end of September (ca. week 40, Figure 7.5) with LPUE > 39 kg/h while highest densities of large brown shrimp are found from week 42 (mid-October) until week 46 (mid-November) with densities > 21 kg/h.

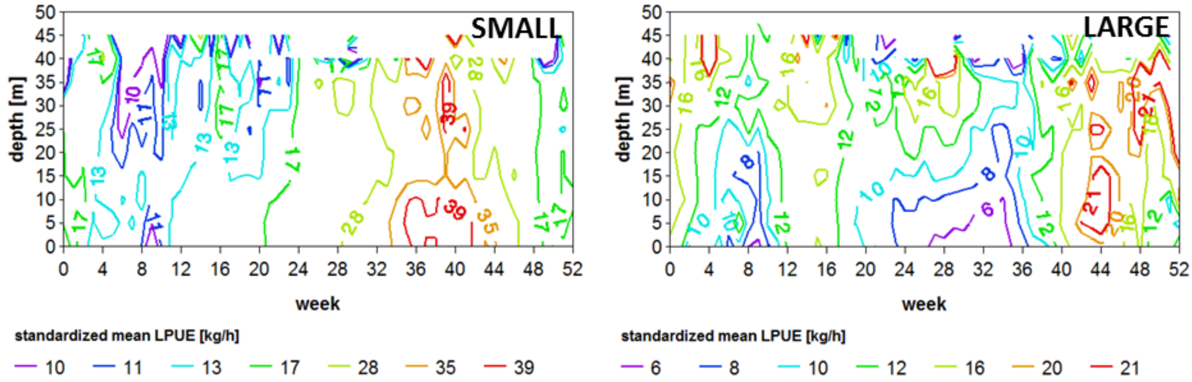

Figure 7.5 Contourplot for the densities of small (total length ca. 50 – 73 mm, left) and large (total length ca. >73 mm, right) brown shrimps for human consumption over depth in the different weeks of the year, based on the standardised LPUE from 2007 – 2013.

We found spatiotemporal patterns in the distribution of brown shrimps differed between large and small brown shrimp in the following manner: Densities of small shrimp start to increase from > 13 kg/h in estuaries in March around week 10 (Figure 7.5 and Figure 7.6) to their annual peak densities of > 39 kg/h in week 40 (ca. end of September). This is the time when such high densities are found in almost all fishing grounds.

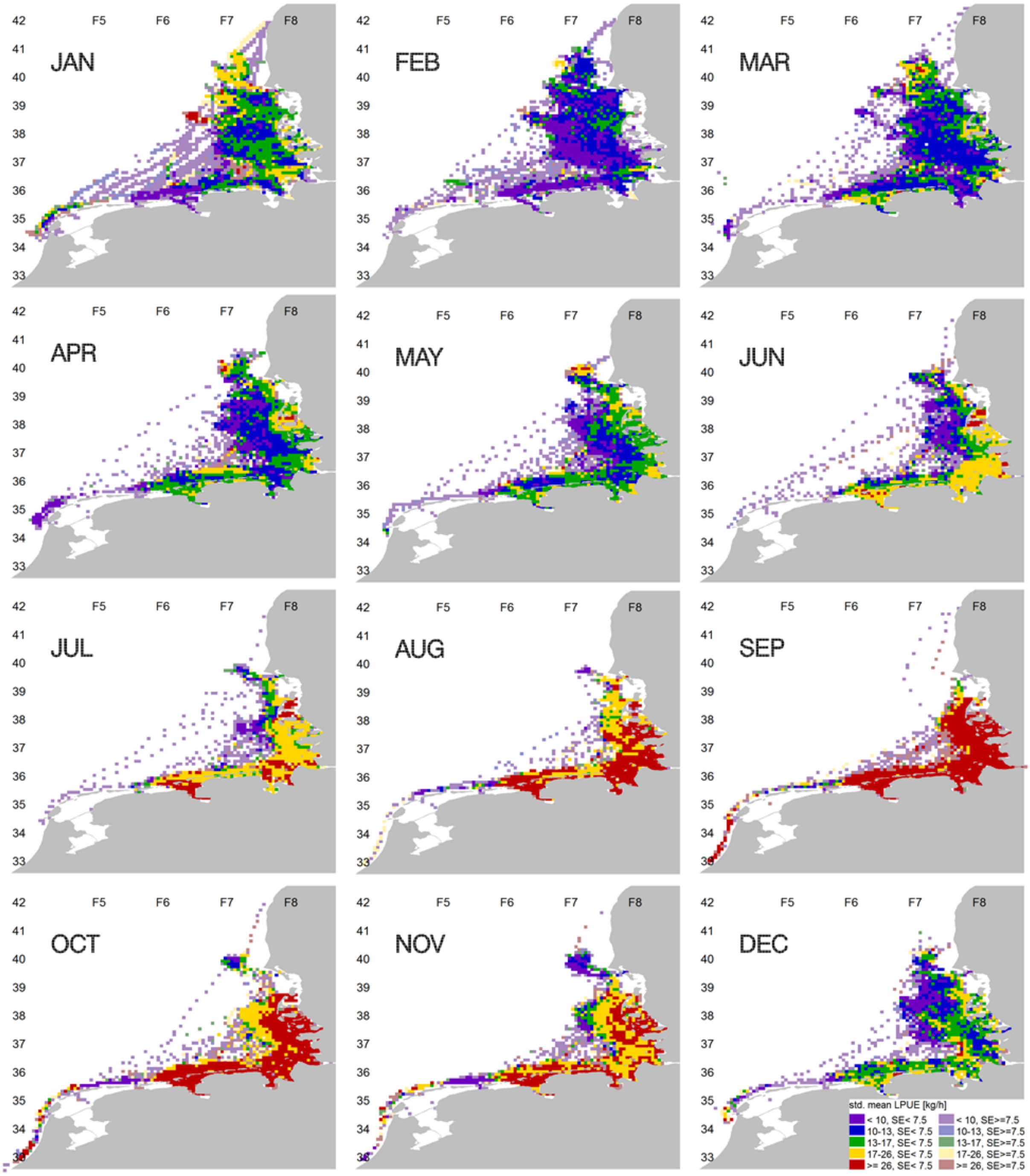

Figure 7.6 Mean monthly distribution from 2007 – 2013 of the standardised mean LPUEs of the fraction of small shrimps for human consumption (total length ca. 50 – 73 mm). Resolution: 0.05°x0.05° latitude/longitude.

In contrast, a clear density increase over all depths was not observed for large brown shrimps > 73 mm total length (Figure 7.5) until autumn. Instead, very low densities of < 8 kg/h were obtained in depths < 20 m from week 7 to 9 (February) and from week 24 (mid-June) to week 36 (begin of September). High densities of > 21 kg/h were measured in depths > 35 m (Figure 7.5) in January, April and July. The autumn peak in the large brown shrimp densities occurred later (around week 44, end of October - beginning of November) and the peak occurred over a shorter period than was observed for the small brown shrimps. During these weeks the high densities of large brown shrimps occurred almost equally across all depth strata and regions (Figure 7.5 and Figure 7.7).

7.4.2.1 Large brown shrimps in winter

We found that the described general tendency of increasing densities of large shrimps with depth (Havinga, 1930; Boddeke, 1976) mainly holds true for the westernmost areas used by the German fleet (Dutch and East Frisian waters), but diminishes when further north- and eastward areas are considered (Elbe-Weser-Jade-estuary, waters off the coast of Schleswig-Holstein and Danish waters, Figure 7.8). The pattern of increasing densities of the large brown shrimp with depth was also found to differ regionally over time, starting in the South-West and continuing towards North-East. In Dutch waters (NL) a steep increase of 22.14 kg/h from 0 to 30 m depth is already observable in October. In comparison the increase in densities over depth in the neighbouring eastern areas East Frisia and the Elbe-Weser-Jade estuary is considerably smaller and occurs later. An increase of 14.35 kg/h in East Frisia and 8.36 kg/h in the Elbe-Weser-Jade estuary occurred in December (Figure 7.8). In waters off the coast of Schleswig-Holstein an increase of 8.00 kg/h from 0 to >30 m was observed in January, but in October and November a reverse trend of decreasing densities with depth was found (-15.17 kg/h in October and -9.78 kg/h in November). In the most northern area (off the coast of Denmark) the densities were relatively stable over all fished depths until January. It was only in February that the densities decreased by -10.92 kg/h with depth.

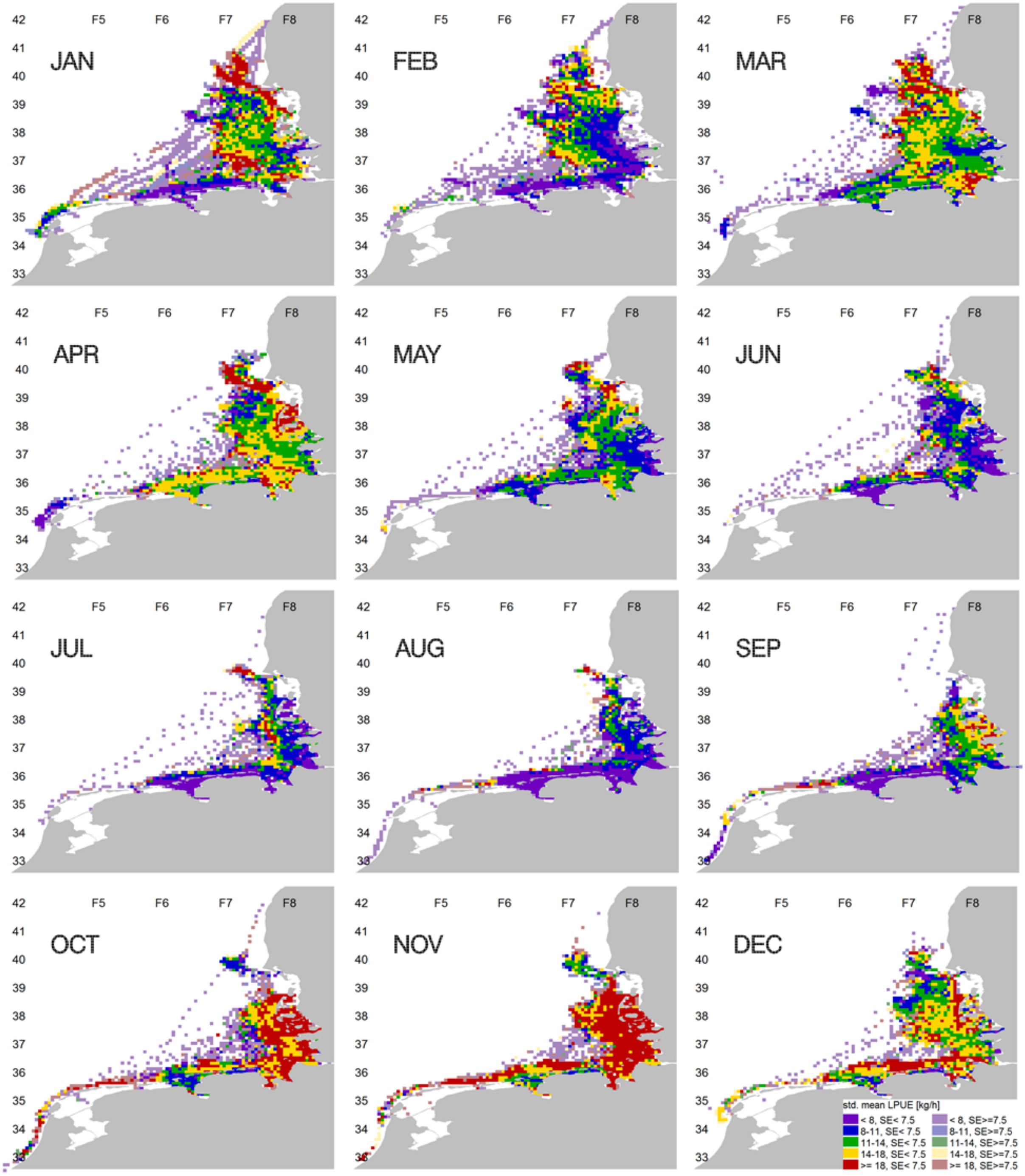

Figure 7.7 Mean monthly distribution from 2007 – 2013 of the standardised mean LPUEs of the fraction of large shrimps for human consumption (total length ca. > 73 mm). Resolution: 0.05°x0.05° latitude/longitude.

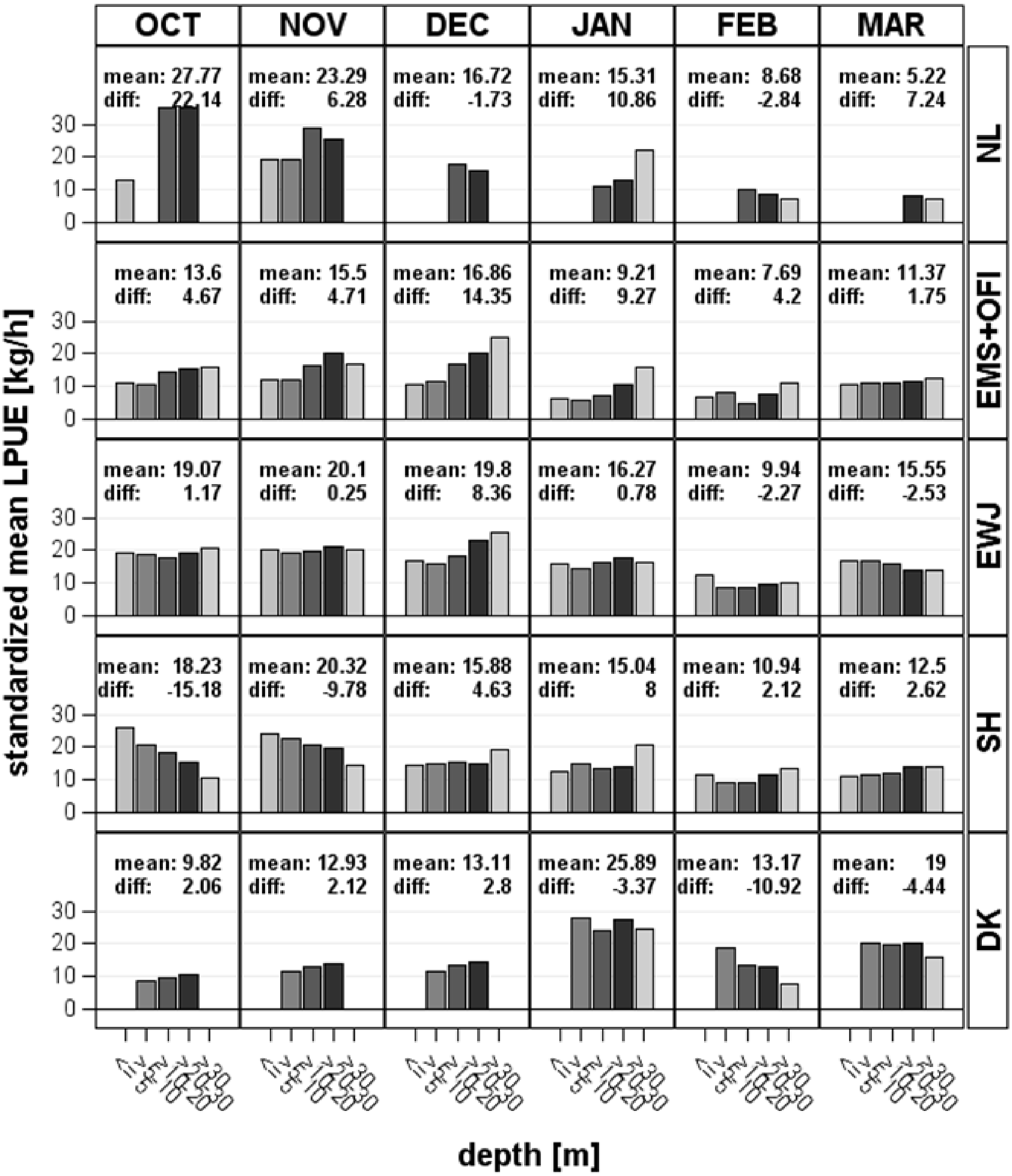

Figure 7.8 Mean standardised LPUE (used as proxy for densities) of the large fraction of brown shrimps for human consumption (total length ca. > 73 mm) from 2007 – 2013 per depth stratum and region. This fraction consists of females only. In each of the panels the mean density [kg/h] and the increase or decrease in LPUE from the shallowest to the deepest depth stratum is given as the positive or negative difference (in kg/h)

From October to March a shift from the South-West to the North-East and from deeper to shallower waters was found in the densities of large brown shrimps > 73 mm TL: In October and November the highest mean densities of > 23.29 kg/h of large brown shrimps were observed in Dutch waters with greatest densities in depths between 10 -30 m (Figure 7.8). In December highest mean densities were found in the Elbe-Weser Jade-estuary (19.8 kg/h), with greatest standardised LPUEs in depths > 20 m. From January to March highest densities were found in Danish waters with values of 25.89 kg/h in January, 13.17 kg/h in February and 19.00 kg/h in March. Highest densities were always recorded in depth strata between 5 – 30 m.

7.5 DISCUSSION

7.5.1 Standardisation

One of the main goals of this study was to evaluate whether the mean LPUE calculated from commercial data could be used as a meaningful indicator for brown shrimp stock monitoring. Using the LPUE as indicator implied that the obtained LPUE are assumed to be comparable between different regions and seasons and, furthermore, independent of the properties of the active vessels. In accordance with direct standardisation as known from epidemiology (Fleiss *et al.*, 2004) we standardised the obtained LPUE to the level of the LPUE obtained by a "standard" mean vessel. This approach revealed that the usage of non-standardised LPUE would have led to a biased picture of the spatiotemporal pattern of brown shrimps, mainly caused by considerable differences in the efficiency of the different vessels. The most efficient German vessel was, for example, 4.71 times as efficient as the least efficient vessel.

The ICES advice for a brown shrimp management (ICES, 2014b) suggests a fleet inventory, the monitoring of the whole fleet and a management based on monthly mean LPUE from commercial logbook data. This study gives an additional dimension to the suggestion of the ICES advice: It is clearly shown that a standardisation of the LPUE to the level of a "standard vessel" is needed. Omitting the standardisation, the obtained monthly mean LPUE will be biased due to the different efficiency of the vessels, not at least, because not all vessels of the fleet are active during all times of the year. Further, non-standardised LPUE will, in general, predict unrealistically high densities in offshore areas as more efficient vessels in general fish further offshore. Moreover, the results imply that a fleet inventory is not only important to identify an effort creep as suggested in the ICES advice (ICES, 2014b). The inventory should also be used to identify the most realistic "standard vessel" to obtain the best possible estimations of the monthly mean LPUE.

Furthermore, a reliable description of spatiotemporal patterns in the brown shrimp stock can only be obtained, if the sampled data cover the area in which brown shrimps occur in considerable densities. Our data suggest that the number of 226 German vessels is sufficiently large to cover almost the entire German coast, especially in the near coast zones, and hence the core distribution area of brown shrimp in the German Exclusive Economic Zone. Typically, standardised scientific surveys are used to obtain data on abundance and density of shrimp (for example see Ehrenbaum, 1890; Havinga, 1930; van der Baan, 1975; Boddeke, 1976; Siegel *et al.*, 2005). The present study, in contrast, took an alternative approach and used data from commercial fishery. To our knowledge, this is the first study, which uses commercial data to investigate stock densities and does not focus on fleet behaviour or distribution of effort and catch (for example see: Bastardie *et al.*, 2010; Gerritsen *et al.*, 2013; Miethe *et al.*, 2014).

7.5.2 Variation in the spatiotemporal distribution of brown shrimp and the fishery

The standardised data set enabled us to provide a comprehensive depiction of the spatiotemporal distribution of the densities of brown shrimp off the German coast, which would not have been possible using survey data collected only once a year. Based on the mean standardised LPUE from 2007 – 2013 we found a general seasonal pattern of density peaks of large and small shrimps which corresponded to the described life cycle of brown shrimps. The population is thought to be dominated by the shrimps originating from winter eggs (Hufnagl and Temming, 2011b), hatched between October and March (Havinga, 1930). These recruits invade the German Wadden Sea in May/June (Temming and Damm, 2002) as the Wadden Sea serves well as a nursery area (Kuipers and Dapper, 1984). With increasing length and maturity, brown shrimp shift into deeper waters (Kuipers and Dapper, 1981) and so in September these recruits reach commercial size of 50 mm total length (TL) (Hufnagl and Temming, 2011b).

Hence, we did not expect an increase in the small adult brown shrimp (TL: 50 – 73 mm) densities until early autumn. Our results however show that their densities begin to increase in estuaries and coastal regions from March onwards. From this we can surmise that the spring increase was related to brown shrimps originating from summer eggs of the previous year. Larvae hatched between April and September could reach commercial size in following spring (Hufnagl and Temming, 2011b). Increasing densities of this cohort would then be overlaid by the signal of the incoming new cohort originating from the winter eggs, the latter reaching commercial size in autumn. This could explain the continuous increase in the densities of small brown shrimp from March to September, observed in this study. Furthermore, we found a spring density peak in March and April for large shrimp (> 73 mm total length). This phenomenon might be explained by the existence of individuals originating from winter eggs. As described, these animals have reached 50 mm TL in September. In the subsequent spring they have reached a TL of > 73 mm and have therefore grown into the large size group. This, more than likely explains the spring peak for large brown shrimp in our results.

Our data also show that during summer large shrimp are not present in areas shallower than 15 m depth. This corresponds to observations of Meredith (1952) who also reported an absence of brown shrimps > 65 mm (TL) in shallow waters in July and August. The absence of the large shrimps > 73 mm TL could be caused by a size-dependent migration into deeper waters. A migration of this form might be necessary, as energy loss of shrimp increases exponentially with increasing temperature (Taylor and Peck, 2004). Additionally, the food supply might not be sufficient in coastal areas to compensate for this increased metabolic cost. A migration towards deeper areas with lower temperatures during the summer might therefore be an effective strategy for large shrimp.

The described seasonal pattern is valid for the mean standardised LPUE from 2007 - 2013. However, annual variances in the distribution of the brown shrimp and the fished area exist. Annual maps show that German fishers, except in the extremely "good" year 2011, increasingly avoided fishing in Danish waters even though densities off the Danish coast were on average high during spring of 2007 - 2013. This phenomenon might be caused by the modernisation of the Danish fleet (ICES WGCRAN, pers. comm.). The increased efficiency of the fleet has led to a different seasonal pattern of landings. While the average landings since 1987 were characterised by annual peak landings in spring, nowadays the annual peak of landings of the Danish fleet is observed in autumn. This is in contrast to the general pattern observed in the German, Dutch and British fleet (ICES, 2012; ICES, 2013a). In German data, from 1954 – 1988, Temming *et al.* (1993) observed a decrease in the relative importance of the spring catches compared to the autumn catches. It can be suggested that an increased fishing mortality in autumn removes those shrimps from the population which could have been caught in spring. This hypothesis was verified in a simulation model (Rückert, 2011). Reduced densities and, hence, lower catch rates would explain reduced fishing effort off the Danish coast since 2008.

7.5.3 Immigration of the new cohort from Dutch and East Frisian waters

Using German logbook data, Respondek *et al.* (2014) found an increase in the catches in Greetsiel, one of the westernmost harbours of Germany already in July, while in more eastern harbours (e.g. Cuxhaven) this increase in the catches was not found until September. The authors linked their finding to the suggestion that German waters are partly receiving recruits drifting from winter spawning grounds off the Dutch coast, where development of larvae is completed earlier due to slightly higher temperatures (Temming and Damm, 2002; Daewel *et al.*, 2011). Our results indicate that the earlier increase in the catches landed in Greetsiel is caused entirely by the increase of locally landed industrial catches of undersized shrimp, which are only landed in this area. If only brown shrimp landings for human consumption (CW > 6.5 mm) are considered, the seasonal increase in landings is comparable to the other harbours, independent of the location of the harbour. Hence, this study shows that the fishing season of commercial brown shrimp starts concurrently along the German coast. At least two different scenarios may lead to the results found in this study. Firstly, faster larval and juvenile growth in Dutch and East Frisian waters might be present (Temming and Damm, 2002; Hufnagl and Temming, 2011a) but due to their usage of residual currents and STST (Daewel *et al.*, 2011) the juveniles are able to reach all locations along the German coast until they have grown to commercial size of > 50 mm TL. Secondly, spawning activity takes place to a similar extent in all regions and depths. Hence, juveniles and later on, landings of brown shrimps > 50 mm can be observed at all locations at almost the same time. The latter assumption would also be in accordance with findings of Schulte *et al.* (manuscript 1) who found an almost even distribution of berried females over all depths in winter.

7.5.4 Locations of overwintering areas

According to Boddeke (1975) and Havinga (1930) mature females migrate to offshore waters between October and March. A temperature dependence of the seasonal migration of adult brown shrimp was suggested by van der Baan (1975) and Boddeke (1976). Boddeke (1976) further stated that berried females in particular show temperature dependent migration and suggested they are more sensitive to temperature fluctuations than unberried females. He concluded this since he could not find any berried females in a tidal creek surrounded by tidal flats in winter, whereas they were present in another part of the tidal creek which was not surrounded by tidal flats. Boddeke (1975), van der Baan (1975) and Havinga (1930) made their observations in Dutch and East Frisian waters. In the most western areas analysed in the present study, the patterns match their observations, as here in winter we found decreasing densities of large brown shrimp with depth. However, in more northern areas the increase in densities with depth occurred later and was less pronounced. The trend even reversed in February. A possible explanation for the strong increase in densities with depth in the westernmost areas and the opposite trend in more northern areas could be related to regional differences in temperature. The observed density pattern corresponded to the pattern of daily temperature variation along the Dutch, German and Danish coast obtained from the ocean circulation model outputs (Hufnagl *et al.*, 2014). The daily temperature variation in Dutch waters was greater, maybe because of a higher tidal mixing, and decreases towards the North. This would confirm the suggestions of Boddeke (1976) but is still conjectural.

The results of this study differ from the findings of Schulte *et al.* (manuscript 1) who found that berried females in January and February distribute almost evenly over all measured depths between 12 and 54 m. In the present study however, indications for migration patterns were found as the densities of large brown shrimps with depth differed temporally and regionally. A possible explanation for the differences could be that in the commercial data brown shrimp could only be distinguished by size, while in the survey data brown shrimp are also classified according to their reproductive state (with or without eggs). Schulte *et al.* (manuscript 1) found that densities of unberried brown shrimp in winter slightly increased with depth, while berried females distributed almost evenly over all measured depths (12 – 54 m). Hence, the trend found in this study could be driven by the proportion of unberried large females which were also included in the largest brown shrimp sieving fraction (TL > 73 mm) reported from the commercial data. This would imply that large brown shrimp might usually migrate into deeper waters in winter, but as soon as they carry eggs they start to distribute as evenly as possible by avoiding density peaks of other berried females. In this case the proportion of berried females in the catches might have been large in Danish waters, where the trend of increasing densities over depth was not observed. This assumption can unfortunately not be tested easily, as it would require a classification of the commercial catches considering also the reproductive state of the brown shrimp. Another possible explanation is that the differences in the results are related to the relatively lower sampling time i.e. less than 178 hours of the survey data in comparison to nearly 71451 hours of the commercial fishing data. Hence, the non-identification of regional differences in the distribution over depth was potentially caused by the comparably low sample size in the survey data, but this needs further evaluation.

7.5.5 Match of observed data to simulated STST usage

To clarify whether it is possible that STST is used for this density-shift over depth simulation studies were conducted by Daewel *et al.* (2011) and Hufnagl *et al.* (2014). In those simulations it was already shown that a migration of adult females to deeper waters in winter and an onshore migration of the juveniles would be possible, if the tidal streams were used selectively for transportation. Though van der Baan (1975) observed peaks of brown shrimp in the catches that depended on season and tidal currents during winter, the theory of the STST usage was never validated with field data covering larger areas. Our data show with a reasonable spatial resolution that highest densities of small brown shrimps are located mostly in estuaries in July while density-peaks of large brown shrimps are found further offshore in January. This corresponded to the modelled distribution pattern including STST (Hufnagl *et al.*, 2014). The results of this study correspond well, especially in Dutch and East Frisian waters and off the coast of Schleswig- Holstein, with the results of their drift simulation. In these areas also highest densities were found in depths > 30 m in January. In these depths daily fluctuations in temperature, salinity and tidal range (suggested trigger values for the STST) varied by less than 10%, and might hence, be too low to be detected by brown shrimp. However, in the present study the densities of large brown shrimp in Danish waters in January were found to be on average almost equal in all depth strata between 5 and > 30 m. It is possible that migration towards deeper waters might be easier and more pronounced in the westernmost parts because the 30 m depth line is closer to the coast than in northern regions. Another possibility is that regionally different migration behaviour is observed because of different temperature variations. This could be tested in the simulation model by attributing more importance to temperature variation than to the other selected trigger values (salinity and surface elevation). If this leads to a better alignment between the simulation model and the observed data this would be a further indication that temperature fluctuations impact the behaviour of brown shrimp as suggested by Boddeke (1976).

Between 2007 and 2013 we found a consistent pattern with a northward shift of large brown shrimp starting with high densities of > 23 kg/h in Dutch and East Frisian waters in October and November and ending with highest densities of 13-26 kg /h in Danish waters from January to March. In our study, the high average densities in Danish waters from 2007 – 2013 were mainly influenced by the years 2007 and 2011.

Hence, a general shift of the brown shrimp population towards Danish waters can probably be excluded confirming Siegel *et al.* (2005). From regionally uncorrelated brown shrimp densities in spring they concluded, that migrations of the adult East Frisian stock along the coast towards Denmark are unlikely. A possible explanation might be a regionally different fishing pressure. Along the Dutch and East Frisian coast not only German but also Dutch vessels fish extensively. For example in 2010 the Dutch fishing effort was equally high in Dutch and East Frisian waters but lower in the Elbe-Weser-Jade estuary and off the coast of Schleswig-Holstein (Schulze *et al.*, 2012). The Dutch fleet comprises about 180 active vessels, which are mostly longer and more powerful than German vessels (ICES, 2012). Hence, it can be suggested that the fishing pressure and consequently mortality of mature brown shrimp in Dutch and East Frisian waters is higher than in more northern areas. Due to slow growth rates in winter (at 5°- 10 °C: <0.1 $mm \cdot d^{-1}$, Hufnagl and Temming, 2011a) and high fishing mortality off the coast of the Netherlands and East Frisia, the densities of large brown shrimps in these areas are probably lower at the end of winter (February and March) than in other regions (e.g. the Elbe-Weser-Jade estuary or off the coast of Schleswig-Holstein). This situation will probably not change before the cohort hatched from summer eggs of the previous year reach commercial size as discussed before.

7.5.6 Spatial Management considerations

The maps presented here allow a first rough estimation of potential effects of spatial closures in German parts of the Wadden Sea on the brown shrimp population, whose core distribution area is located in exactly these areas (Tiews, 1970; Campos and van der Veer, 2008). The Wadden Sea has been designated as a Natura 2000 site (EC, 2011) and the Wadden Sea has also become a UNESCO World Heritage Site in 2009 (WHC, 2009). Meanwhile, areal closures within the Natura 2000 sites for the brown shrimp fishery are discussed repeatedly (Ministry of Economic Affairs, 2011; Ziebarth *et al.*, 2014). Spatial closures usually lead to effort shifts to alternative locations (Dinmore *et al.*, 2003; Poos and Rijnsdorp, 2007). Hence, it can reasonably be suggested that this would also be the case for the German brown shrimp fleet if parts of the Natura 2000 areas were to be closed to this fishery. The German Natura 2000 sites cover a depth range from 0 to about 25 m. An effort displacement to areas outside the Wadden Sea of especially the more efficient vessels will lead to more fishing effort in more offshore areas. According to the results presented here, an effort shift would potentially be an additional risk for the berried female brown shrimp. This would particularly the case in the westernmost areas (Dutch and East Frisian waters) in winter, where a clear increase of the brown shrimp densities with depth was observed.

7.6 CONCLUSION

In this study we have described how commercial data from the brown shrimp fishery can be used for the advancement of biological knowledge. Standardisation of the

LPUE allowed drawing a comprehensive picture of the spatiotemporal patterns of the brown shrimp stock in the German Bight. As the German vessels differ considerably by > 20% in their efficiency and also in their area of activity, this study advises against the usage of non-standardised LPUE as recorded in the landing or logbook data for a brown shrimp management as suggested in the ICES advice for a brown shrimp management (ICES, 2014b). Preferably, the monitoring should be based on standardised LPUE including region, season and vessel dependent factors. This requires a fleet inventory to evaluate the extent of all factors potentially impacting the efficiency of the vessels.

The earlier increase of commercial landings in summer in the westernmost German harbours reported by Respondek *et al.* (2014) was shown to be due to local landings of undersized shrimps and not necessarily linked to the warmer and hence, better juvenile growth conditions in Dutch and East Frisian waters (Temming and Damm, 2002; Daewel *et al.*, 2011). Strongest migration signals were found in the westernmost areas in autumn, with highest densities of large brown shrimps in depths > 30 m. Diminishing depth dependent migration signals occurred towards the North. Together these findings indicate that spawning grounds are not generally localised in the "open sea" as suggested by Boddeke (1975).

Future analysis should combine standardised commercial data with environmental data including temperatures, salinity, sediment type, etc. to localise and predict brown shrimp spawning grounds even more precisely. Furthermore, a cross validation with spatial trends obtained from survey data is required. The adaptation of the simulation model of Hufnagl *et al.* (2014) is also suggested. Adapted, the model should place more emphasis on daily temperature fluctuations as trigger values for seasonal migration in order to align the model output to the observed data. Overall, this study provides previously unavailable maps of potential brown shrimp spawning grounds and implies that a closure of the Natura 2000 areas would potentially be an additional risk for the berried female brown shrimp stock component, especially in Dutch and East Frisian waters due to effort allocation of especially the more efficient vessels.

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8 GENERAL DISCUSSION

The motivation for this study was to fill knowledge gaps concerning the brown shrimp biology with relevance to the management of the brown shrimp stock. A management for brown shrimp in the North Sea was advised by ICES in autumn 2014 (ICES, 2014c). Typically, and also for other crustacean species, such as *Pandalus borealis* (ICES, 2014a) or *Homarus americanus* (ASMFC, 1997; ASMFC, 2013), a management is based on annual data. For brown shrimp this is not suitable. The brown shrimp age cannot be determined and they have a short life span, usually not exceeding one year (Hufnagl and Temming, 2011). Therefore, the management advised by ICES is based on monthly stock monitoring using commercial LPUE and supplemental, independent survey sampling on at least annual basis.

Stock size monitoring from commercial data is not trivial, because commercial landing data are non-standardised and hence vary according to the fishers experience and according to vessel and gear characteristics. But also in survey data, which are standardised regarding trawling speed, haul duration and gear used (Siegel *et al.*, 2005; Tulp *et al.*, 2008), the 'catchability' of the gear is assumed to be constant, i.e. it is presumed that always the same amount and composition of abundant brown shrimp is caught. This might not be the case as the catch rates and the composition might depend on the brown shrimp biology, including their preferred locations and their migration patterns. Further, information about the proportion of brown shrimps caught with the bottom gear was so far lacking. Only if the factors influencing the catchability are known and used for standardisation, a reliable monitoring of the stock is possible.

Furthermore, a precautionary management is only possible, if a clear picture on the spatial and temporal distribution of the stock is available. To describe the spatiotemporal distribution of the stock, vessel monitoring system (VMS) data can be used. Several methods and resolutions are available to produce spatial estimations. However, until now it is unknown to what extent these methods differ in their estimations and which method and resolution is optimal for the assessment of the coastal brown shrimp fishery. This needs to be evaluated in order to describe the spatial- temporal distribution of the brown shrimp stock in the most reliable form. With this knowledge, the assumptions of seasonal migration can be assessed and the still unknown localisation of the spawning stock in winter can be described. In winter, growth rates of brown shrimp are low, high proportions of adult shrimp carry eggs and high fishing impact in these areas potentially has large effects on the stock. In the present thesis these described knowledge gaps were closed and hence this study contributes to a sound basis for a brown shrimp management.

8.1 BROWN SHRIMP STOCK ASSESSMENT AND ACCOMPANYING UNCERTAINTIES

8.1.1 New insights into brown shrimp catchability demonstrate need for further standardisation of research data

All research survey data used in this thesis have the advantage of being sampled and processed in a predefined way. They furthermore provide a data source independent of fisheries data. Nevertheless, this thesis showed that the assessment of estimates such as the biomass estimate or the large shrimp indicator, which describes the fraction of large brown shrimp in the catches and is thus, together with the estimated mortality an indicator for the present fishing pressure (ICES, 2014c), need some additional attention before being uncritically considered as comparable between different surveys.

Presuming a benthic way of life, field research on brown shrimps is mostly made with push-nets or beam trawls (e.g. Amara and Paul, 2003; Berghahn, 1983; Al-Adhub and Naylor, 1975; Beaumont and Croucher, 2006; Campos *et al.*, 2009; del Norte-Campos and Temming, 1998; Boddeke *et al.*, 1986; Hufnagl *et al.*, 2010a), which do not sample the entire water column. Though stow nets were described to be in use for brown shrimp fishing, this net type is disappearing (Tiews, 1970). The vertically resolved stow net used for the analysis in **manuscript 1** covered almost the entire water column. The results suggest that current biomass estimates, based on beam trawl hauls and thus missing the pelagic fraction, need to be at least doubled, as at a water depth of 9.3 m on average 73% of the brown shrimps are predicted to be inaccessible for beam trawls. This result already led to a reconsideration of the current biomass estimate within the scientific advisory body (ICES, 2012).

The beam trawl survey data allowed investigating the horizontal distribution of the brown shrimp (**manuscript 1**). On the one hand the analysis of the beam trawl survey data confirmed known seasonal differences in the composition and size of the catches with generally larger catch rates and concomitant low proportions of berried females in autumn as described by several authors (e.g. Maes *et al.*, 1998; Henderson *et al.*, 2006; Siegel *et al.*, 2008; Hufnagl and Temming, 2011). On the other hand, this thesis showed that the brown shrimp catches from autumn and winter differ significantly in their size and sex composition depending on sampling depth and on tidal state (in winter). The proportions of small and unberried females decreased with increasing depth. In contrast, with increasing size, brown shrimps tended to distribute evenly over the water column, which was especially visible in winter, where a large depth range of 42 m was sampled. Further, daylight had a significant role in the beam trawl survey data and also had a strong effect on the catch rates in the vertically resolving stow net data. In the vertically resolving stow net data the estimated catch rates were more than twice as high during darkness than during the day. The latter result of higher catch rates during darkness was in line with the findings of beam trawl samples of Addison *et al.* (2003). Generally higher catch rates during darkness, as found by Addison *et al.* (2003) and in this study can be presumed to be related to feeding behaviour as other studies showed that brown shrimp feed at night (Pihl and Rosenberg, 1984) and for this purpose leave their shelter of being buried in the sediment (Norkko, 1998).

This thesis therefore revealed brown shrimp biology influences the catch rates and the size and sex composition of the catches. Hence, the results of **manuscript 1** clearly show the need for standardisation of the survey data in a more detailed way than currently done. Future standardisation of the catches should not only include trawling speed, gear and haul duration but also season, depth, daylight and tidal state. Furthermore, the need for a vessel and date dependent random intercept in the statistical model in **manuscript 1** suggested a significant impact of environmental conditions and also of vessel characteristics.

This implies that environmental variables, possibly influencing the catch rates, for example salinity (Broekema, 1942), water temperature (Broekema, 1942; van der Baan, 1975), visibility depth and sediment (Addison *et al.*, 2003) should be recorded on the surveys during each of the hauls. The results of this study have already led to a corresponding adjustment of the data collection during the surveys. However, sediment type is still not recorded frequently and the catch rates might not only depend on present conditions but also on an accumulation of stimuli (Boddeke, 1975) or on temperature gradients over depth (van der Baan, 1975). Due to the high variability of the Wadden Sea, comprehensive environmental data including up-to-date sediment and depth maps of coastal regions are not easily available for scientific research but they could help to disentangle the impact of different environmental effects on the brown shrimp catch rates and the composition in the catches.

The significant impact of vessel characteristics found in **manuscript 1** implies that the standardisation should also account for the different vessel characteristics used during the survey. As results of **manuscript 3** further revealed regional differences in the standardised commercial catches, standardisation according to the location of the haul in the survey data is also recommended.

8.1.2 Vessel effects bias brown shrimp stock assessment based on commercial data

Despite of the advantages of using commercial catches (LPUE) for the monitoring of the brown shrimp stock, such as the large spatiotemporal coverage and their short-term availability, these data cannot be used directly. The ICES advice (ICES, 2014c) suggested the calculation of monthly mean LPUE based on logbook data of the total fleet. Using data of the total fleet is necessary, as random sub-samples of the fleet do not meet the monthly mean LPUE (Temming *et al.*, 2013). However, even if the total fleet is included into the monitoring program, the LPUE calculation from logbooks data as proxy for present stock densities will be hampered by the fact that not all vessels of the fleet are active during all times of the year. Instead, the mean number of active vessels ranges from about 50 in January and February to 170 in autumn. As the vessels differ in their efficiency, this situation would bias the mean LPUE which is compared to the reference values. Further, the spatial coverage of the fished area differs seasonally, as visualised in **manuscript 3.** The raw LPUE calculated from logbooks will therefore only give a rough indication about the brown shrimp stock, although strong signals will probably be still evident in the catches. However, a certain monthly variability of active vessels, a particular spatial displacement of the main fishing areas or an increase in the fleet efficiency might also, even in times of a decreased stock size, temporarily mimic stable or even increasing LPUEs.

The findings of **manuscript 3** show that the calculated LPUEs considerably depend on vessel characteristics, region, season and depth. Having included the sieving fractions from the landing data into the combined commercial data set in **manuscript 3**, we were able to show different spatiotemporal distributions for large brown shrimp (ca. > 73 mm) and small brown shrimp (ca. 50 – 73 mm). Hence, not only the composition of the catches in the survey data but also the catches from commercial data and hence the LPUE are influenced by the size composition of the catches. Therefore it would be advantageous to include the sieving fractions recorded in the landing data into the monthly monitoring. This would allow the calculation of more accurate stock indicators from the commercial data.

In this thesis, many separate vessel dependent factors were included as one random effect per vessel. However, a separation of these factors would be advantageous, especially, if new vessels enter the German fleet. To find appropriate correction factors, a fleet inventory, for recording currently undocumented vessel and gear characteristics, such as the type of kort nozzles, hull design, mesh type, etc. is a prerequisite. Also, the deployment of electric gear should be recorded in the logbooks by default as an electric beam trawl potentially increases efficiency (Stepputtis *et al.*, 2014). Recording these additional parameters by default would allow the estimation of correction factors for each of the vessel dependent factors (see **manuscript 3**), and would prevent a bias in the LPUE estimates due to vessel composition.

8.1.3 Searching for an appropriate methodology to obtain spatial catch and effort estimations from commercial brown shrimp data

Spatiotemporal LPUEs are calculated from spatial estimations of effort [h] and catch [kg] from combined logbook, landing and vessel monitoring system (VMS) data. In **manuscript 2** we showed that the effort and catch estimations for the brown shrimp data strongly depended on both method and resolution.

All of the methods tested (raw pings (Dinmore *et al.*, 2003; Murawski *et al.*, 2005), straight lines (Skaar *et al.*, 2011; Lambert *et al.*, 2012), splines (Hintzen *et al.*, 2010; Lambert *et al.*, 2012), ellipses (Mills *et al.*, 2007), amplification (Fock, 2008)) differed in their results concerning their estimations of the fished area, effort or catch. These differences were observed even at a very coarse resolution of 1° x 1°: For example comparing ellipse and spline interpolation with each other revealed that the identification of a fished area differed by about 30% at a relatively coarse resolution of 0.5° x 0.5° in the National park of Schleswig- Holstein. In areas that received only few pings, such as the National park “Hamburgisches Wattenmeer” or the windfarm

"Riffgat," effort or catch estimations varied by more than 100% in contrast to areas which received more pings (in this study these were case study areas > 1240 km² that received > 152 pings). The estimations of effort and catch in these larger areas differed by less than 11% between the methods, compared to the mean estimation of all 5 methods for the considered area. Findings of **manuscript 2** allow for the first time, to estimate the variation in effort and catch calculated by different methods from commercial data. This is relevant for future natural conservation management measures for specific sites and habitats, as it clearly shows the uncertainty in the estimations based on combined logbook, landing and VMS data. This study was based on German brown shrimp data and the results therefore depend on the characteristics of the brown shrimp fishery (trawling speed of about 3 knots, a relatively high number of 226 active vessels in the German data, fishing in a limited coastal area). However, the results show clearly, that the certainty of effort and catch estimations depended on the density and distribution of pings. Hence, for other fleets, any situation resulting in lower ping density, such as higher fishing speed or a lower number of active vessels per area will increase the uncertainty in the estimations.

To be able to describe spatiotemporal patterns in the distribution of brown shrimp, the usage of small grid cells (i.e. a fine resolution) is desirable as the spatial distribution of this species is considered patchy (Siegel *et al.*, 2005). It cannot be assumed that the same estimated brown shrimp density value applies to the whole area of a large grid cell. However, the findings of **manuscript 2** show that the resolution cannot be reduced arbitrarily, because this gives a false impression of the accuracy of the data and would also, if non-interpolating methods are used, strongly underestimate the fished area. Testing resolutions from 0.005° x 0.005° to 0.5° x 0.5° it was found that for the German brown shrimp fleet a resolution of ≥ 0.01° x 0.01° is appropriate, but only if a straight line or a spline interpolation method is used to estimate tracks. This approach ensures that > 80% of the possible vessel tracks between two consecutive pings cover the same grid cells, i.e. are identically identified as "fished". This procedure is therefore a good compromise to minimise the underestimation of the fished area and to remove a maximum of the uncertainty about the vessels' track. Provided that fishing positions are continued to be transmitted every two hours, this approach leads at present to most adequate spatial estimates for the German brown shrimp fleet. Based on the results of **manuscript 2** it is thus recommended to use the straight line or spline interpolation at a resolution of ≥ 0.01° x 0.01° for future requests considering effort and catch estimations of German brown shrimp vessels in specific sites and habitats.

8.2 NEW KNOWLEDGE ON THE SPATIOTEMPORAL DISTRIBUTION OF BROWN SHRIMP

Brown shrimp management suggestions may, for example, include seasonal closures during periods of high plaice bycatch (ICES, 2014c) or other species. To assess or to model the effects of such seasonal closures on the brown shrimp population, reliable scientific knowledge on the seasonal variation in the spatiotemporal patterns of the brown shrimp catches is relevant. This also includes knowledge about depths and locations of brown shrimp spawning grounds in the German Bight. For precautionary management the risk of an increased fishing pressure on brown shrimp stock component of berried females in winter should be avoided, assuming some form of stock recruitment relationship, even though so far it could not be established for this species (Siegel *et al.*, 2005).

8.2.1 Locations of the spawning stock in winter

Adult females carry their eggs until the larvae hatch (Havinga, 1930; Lloyd and Yonge, 1947). Due to low temperatures in winter the incubation time of the eggs is longer than in summer and may, at a water temperature of 6°C, exceed three months (reviewed in Campos and van der Veer, 2008). Hence in winter the adult females make the brown shrimp spawning stock and carry eggs with an increasing proportion of ca. 50% in December and > 80% in February (Siegel *et al.*, 2008). As spawning of the winter eggs takes place from October – March (Havinga, 1930) the locations of berried females in winter also identify the spawning grounds. So far a distinct description of the spawning grounds was lacking. **Manuscript 3** provides previously unknown information about probable depths and locations of brown shrimp spawning grounds in the German Bight.

The preferred depth of large, potentially berried females in winter was addressed in **manuscript 1** and **manuscript 3**. Results of **manuscript 1** suggested that berried brown shrimps with a total length of > 60 mm are generally distributed evenly over all depths between 12 and 54 m. However, according to **manuscript 3**, regional differences in the distribution of large brown shrimps > 73 mm (total length) over depth exist. Especially in Dutch and East Frisian waters highest densities of large brown shrimps > 73 mm total length can be found in depths > 30 m. At least regionally these results seem to contradict each other, but this is not necessarily the case as the data sets were very different: While the reproductive state is regularly recorded in the survey data, in the commercial data the reproductive state can only be derived indirectly by the brown shrimp size. It is therefore possible that brown shrimp, as soon as they carry eggs, seek to distribute evenly over all depths and, hence, either stay where they are or migrate to another preferred depth where the density of berried females is lower than in their present location. The proportion of brown shrimp > 73 mm in the survey catches amounts to 39% in December and 13% in March (Siegel *et al.*, 2008). These large, but according to Siegel *et al.* (2008) not (yet) berried females could in the commercial data used in **manuscript 3** not be separated from the berried individuals. Hence, this fraction of not (yet) berried brown shrimp might have therefore altered the results presented, even though the brown shrimp of this size group were the best possible proxy for berried females available.

Regional differences in the survey data were initially also considered in the statistical model, but as this does not lead to a significantly better model fit, region was omitted from the model. Several explanations for the lack of significance are possible. One possibility is that regional differences were not found in the survey data because they were not present, when most of the winter survey data were sampled (2003 – 2010), but since then became relevant which is reflected in the commercial data from 2007 – 2013. However, though this possibility cannot easily be ruled out it is more likely that the lack of significance might be explained by the comparatively short cumulative sampling time (178 hours) in the survey data with a minimum of 3.75 hours per region (Table 8.1). In contrast, the commercial data included 71451 hours of fishing time in January and February and the shortest amount was spent in East Frisia with 636 hours. Hence, even though the winter survey data was able to cover the total area fished by the commercial vessels if the total time period from 2003-2010 is considered, it is impossible for a survey to cover the total commercially fished area within a single trip. Due to the low number of samples per region the probably existing regional differences might therefore have been undetectable in the survey data.

Table 8.1 Hours of fishing time per region in January and February calculated from survey (2002-2010) and commercial data (2007 – 2013)

Region	ICES rectangle	Winter Survey Fishing time [h]	Commercial data Fishing time [h]
East Frisia (EMS + OFI)	35F6,35F7,36F6, 36F7	61.25	636.00
Elbe-Weser-Jade estuary (EWJ)	35F8,36F8,36F9, 35F9	3.75	4487.25
Schleswig-Holstein (SH)	37F7,37F8,38F7, 38F8,39F7,39F8	82.00	5135.75
Danish waters (DK)	40F7,40F8,41F7, 41F8	14.00	56986.95
Other fished areas	other Rectangles	16.75	576.50
	SUM	177.75	71450.95

The regional depth dependent differences in brown shrimp densities found in **manuscript 3** suggest a modification of the simulation model described by Hufnagl *et al.* (2014). In this model a seasonal migration of the adult females to deeper waters in winter and an onshore migration of the juveniles in spring based on the employment of selective tidal stream transport is suggested. According to the findings of **manuscript 3** in the simulation model more importance should be attributed to temperature variation than to the other trigger values (salinity and tide level) used. This would potentially lead to a better alignment between the simulation model and the observed data, which becomes relevant for management purposes as soon as the effects of potential area closures need to be estimated.

8.2.2 Seasonal variation in the catch rates

In **manuscript 1** and **manuscript 3** catch rates were found to be higher in autumn than in winter, corresponding to research data from Henderson *et al.* (2006) and Maes *et al.* (1998) and also to the autumn peak in commercial catches (ICES, 2012). However, with **manuscript 3** we were able to provide spatial information on the brown shrimp densities, which has not been available before this study. This information showed, for example, that the high densities in autumn can be observed almost everywhere in the total area fished, while in the other seasons the densities may differ considerably between the regions. Furthermore, the results of **manuscript 3** confirm the growth rates modelled by Hufnagl and Temming (2011). The growth rates suggested in their model are in line with a time difference of 2-3 months between the peak of densities of the smaller sieving fraction (50 – 73 mm TL) from August to October and highest densities of large brown shrimps (>73 mm TL) in October-November from this study. A suggested explanation for the seasonal and regional differences in the spatial patterns of brown shrimp densities is the usage of selective-tidal stream transport by the juveniles in spring and by adult brown shrimp in autumn and winter (STST, Cattrijsse *et al.*, 1997; Daewel *et al.*, 2011; Hufnagl *et al.*, 2014).

8.2.3 Evidence from empirical data in support of the selective tidal stream transport hypothesis

The results of **manuscript 1** and **manuscript 3** both supported the suggestion of STST being used for transportation in winter. In **manuscript 1** tidal state was shown to influence the catch rates significantly, suggesting that brown shrimp, independently of their size or reproductive state, in winter either seek to stay "nearshore" or "offshore".

In **manuscript 3** the support of the STST was indirect as the densities of large brown shrimp > 73 mm increased with depth in winter in the majority of the regions. No difference in the large brown shrimp densities over depth was observed in Danish waters. This phenomenon was potentially caused by different physical conditions such as daily temperature variation (Hufnagl *et al.*, 2014), compared to more south-westerly regions. STST is the most likely explanation for observed density differences. This is supported also by STST-simulation results (Hufnagl *et al.*, 2014). The usage of tidal streams for either on- or offshore transportation, depending on the present location on the one hand and regional differences in the observed densities of large brown shrimp (> 73 mm) on the other hand may both be present. If the proportions of "onshore" and "offshore" brown shrimps would be of similar size, STST could be used without causing different densities over depth. If the proportions of "onshore" and "offshore" brown shrimp would differ regionally, this might not be identifiable in the model for the survey data which did not allow for regional effects (see above). A method to provide direct evidence for the STST usage is not yet established and hence, the support of the STST usage in this thesis was indirect. Nevertheless, accounting for STST usage in empirical data is relevant as migration behaviour at certain times or in certain regions probably causes brown shrimp movements into the pelagic zone of the water column. In the pelagic zone the brown shrimp are unreachable for the beam trawl. This would alter the catchability (in terms of larger/smaller beam trawl catch rates or a biased composition of the catches) seasonally and/or regionally and again strengthens the need for standardisation of the catch rates according to season and region.

8.2.4 Potential impact of spatial closures (Natura 2000)

The results of this thesis help to improve biomass estimation for the brown shrimp stock and clearly demonstrate the need for standardisation of the catch rates. This is important, if the brown shrimp stock is to be managed on the basis of a Harvest control rule, as it was suggested by ICES and supported by the stakeholders (ICES, 2014c). But even if the brown shrimp stock was managed in a sustainable way, the main brown shrimp fishing grounds are located in the sensible and protected Wadden Sea, almost entirely designated as Natura 2000 site. For these Natura 2000 sites a management plan has to be provided soon (92/43/EEC 4(4), EEC) and nature conservation issues are demanded to be considered (Ziebarth *et al.*, 2014). One promising tool for marine resource management are spatial closures (Abbott and Haynie, 2012) and considering the Natura 2000 sites in the south-eastern part of the North Sea, areal closures are discussed repeatedly (Ministry of Economic Affairs, 2011; Ziebarth *et al.*, 2014). However, it can be expected that the complexity of the biological and socioeconomic effects of area closures increases with the size of the closed area (Olsen *et al.*, 2011) but the extent of impact of potential areal closures on the brown shrimp population are still unknown.

Manuscript 3 provides comprehensive maps of the spatiotemporal patterns of brown shrimp, whose core distribution area is located in exactly these protected coastal Wadden Sea areas (Tiews, 1970; Hufnagl *et al.*, 2010b). The maps presented allow a first impression of potential biological and socioeconomic effects of spatial closures in German parts of the Wadden Sea. In autumn (September – November), when usually highest annual LPUE (ICES, 2012) and also highest brown shrimp densities are observed (**manuscript 3**), an overwhelming proportion of the brown shrimp fishing grounds are located within with Natura 2000 sites (Figure 8.1).

Hence, spatial closures within the Natura 2000 sites especially in autumn will probably have a large socioeconomic impact on the brown shrimp fishery. In **manuscript 2** proportions of effort and catch of the total fishing effort and catch were estimated for September 2010. In that month about 40% of the monthly catch (and 31% of the monthly effort) was made in the National Park "Niedersächsisches Wattenmeer" and 25% of the catch (28% of the effort) in the National Park "Wattenmeer Schleswig-Holstein".

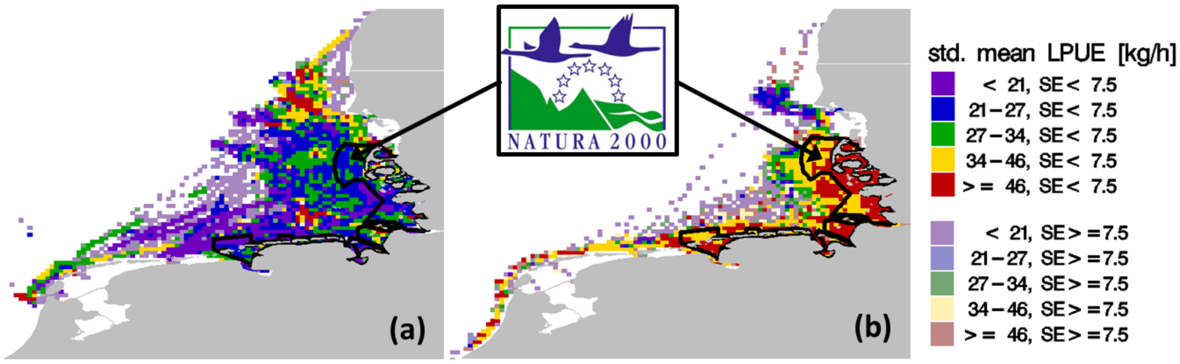

Figure 8.1 Overlap of Natura 2000 sites in the Wadden Sea (surrounded by black lines) and the fishing areas (a) in winter (January – March) and (b) in autumn (September – November). Colours are based on the quantiles of the distribution of the LPUE standardised to the level of a mean vessel from 2007 – 2013. High saturation: mean could be determined with high certainty (SE< 7.5); low saturation: calculated mean LPUE deviated by ≥ 7.5 or was based on single values.

But also in other seasons than in autumn, area closures within the Natura 2000 sites for this coastal fishery have clearly the potential to cause socioeconomic impacts. This is mainly due to the fact that spatial closures result in displaced fishing effort to alternative locations (Dinmore *et al.*, 2003; Poos and Rijnsdorp, 2007). In consequence, and very likely for the coastal brown shrimp fishery with comparably short trip durations of on average about 25 h (Temming *et al.*, 2013), fishers are expected to have higher costs in combination with lower revenue. To estimate the socio-economic impact of spatial closures for the brown shrimp fishery, future studies should consider to apply a socio-economic model on the German brown shrimp fishery as done for the North Sea saithe fishery (Simons, 2014). Further, other management options than spatial closures should be considered for the Natura 2000 areas in the Wadden Sea, e.g. gear adaptations as currently investigated in a project ("CRANNET").

An effort shift of the German brown shrimp fleet, due to area closures, probably leads to higher fishing effort in areas further offshore, where the most efficient vessels are fishing already (**manuscript 3**). Spatial closures covering a depth range from 0 to about 25 m would potentially generate higher mortality for brown shrimp stock component of berried females in winter. This spawning component is according to Hufnagl and Temming (2011) responsible for the increase of LPUE in the main fishing season in autumn. According to the findings of **manuscript 3** this effect can be assumed to be particularly strong in the westernmost regions (off the coast of the Netherlands, East Frisia), where in winter a clear increase of the brown shrimp densities with depth was observed. It can also be expected that area closures, from a certain size onwards, will potentially also alter the spatiotemporal pattern of the brown shrimp distribution. This could be either due to an increased fishing pressure on the spawning stock outside the closed areas or due to habitat limitations because of too high stock densities within the protected areas. Area closures will probably also induce other effects, as documented by Abbott and Haynie (2012).

These effects could include a different bycatch composition or a change to a different target species, if possible, due to diminished fishing opportunities for their usual brown shrimp fishing.

8.3 CONCLUSION

The standardisation of the brown shrimp catch rates should include correction factors for season, region, daylight, tidal state, depth and also for vessel characteristics. To obtain correction factors for the different vessel characteristics, a fleet inventory is recommended. Without standardisation according to the named factors the population cannot be assessed, as, for example, an increase in the efficiency of the fleet, or a shift of fishing activity to other depths or regions could mimic stable catch rates despite of a decreasing stock size.

The spatial analysis of commercial German brown shrimp data using several methods and resolutions lead to the recommendation of using straight lines or splines for connecting subsequent VMS-signals on a relatively fine resolution of $\geq 0.01° \times 0.01°$ to achieve best possible spatial effort and catch estimations.

A proxy for stock densities was derived by developing a method that has never been applied to commercial data before. Thereby, we were able to visualise spatiotemporal patterns of brown shrimp densities in the German Bight at a high resolution. In consequence, we were able to show clear short-term changes in densities, strengthening the recommendation of a monthly monitoring for the brown shrimp stock as advised by ICES (2014c). Further, areas of high densities of large, potentially berried females (spawning grounds) were located off the coast of the Netherlands and East Frisia in depths > 30 m, while towards the North the overall densities increased and the density increase with increasing depth diminished. Due to the uneven distribution and stock structure shown in this thesis, it must be concluded that potential closures for the fishery in the Natura 2000 areas of the Wadden Sea may affect the brown shrimp stock and have regionally very different socioeconomic effects for the brown shrimp fleet.

For frequent monitoring of the brown shrimp stock, commercial data are found to be more suitable than survey data. This is mainly because of their broad spatiotemporal coverage. We were able to show clear short-term changes in densities, strengthening the recommendation of a monthly monitoring for the brown shrimp stock as recommended in the ICES advice (2014c). Ideally, the monthly monitoring should not only include the (vessel - corrected) monthly mean LPUE, but also the different sieving fractions. This information would provide evidence for changes in the composition of the brown shrimp stock. The sieving fractions are recorded in the landing data but their coding is different from the coding on the landing bills. Here, an alignment between the recorded sieving fractions on the landing bills with the coding of the sieving fractions documented in the landing data by the Federal Office for Agriculture and Food (Bundesanstalt für Landwirtschaft und Ernährung, BLE) should be envisaged.

Nevertheless, spatial and temporal differences in the fished area, the market situation and differences in fleet behaviour will alter the mean LPUE. Hence, some standardised reference survey for LPUE and stock structure should be established in the mid-term. As described by Temming *et al.* (2013) this could either be a survey conducted by commercial vessels under standardised conditions (gear dimension, weight, rollers, shoes, net dimension, mesh size speed) and the vessels should further be allocated to specific regions. However, in this case further analysis was needed to determine the details of such surveys in terms of number of boats, detail of catch information and number of seasons to be covered. But also the annual research surveys are essential to provide fleet independent stock estimates, including for example the proportion of large shrimps, biomass and mortality estimates (ICES, 2012; ICES, 2014b). The findings derived from survey data in this thesis revealed that brown shrimps have complex behavioural patterns altering the composition of the catches, according to their reproductive state, their size, daylight, tidal state, depth and season. Further survey data provided new insights into the brown shrimp life and revealed that more than 70% of the brown shrimps are located in the pelagic zone unreachable for a beam trawl. The latter finding already led to a modification of the biomass estimate for the brown shrimp stock.

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LIST OF FIGURES

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10 DECLARATION ON OATH

I hereby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, 6th November 2015

Katharina Schulte

Signature