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# Connectivity of local sub-stocks of *Crangon crangon* in the North Sea and the risk of local recruitment overfishing

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A R T I C L E I N F O

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A B S T R A C T

Monthly VMS and logbook data of the North Sea Brown shrimp (*Crangon crangon*) fleets of Denmark, Netherlands and Germany from 2009 to 2018 were analysed for trends and regional patterns in five subareas.

Effort increased by 12% while landings decreased by 9% from the first five to the second five years of the time series. All areas showed a significant decreasing trend of LPUE in the fishery of the first quarter of the year from 2009 to 2018. Fishing effort in Dutch and East Frisian waters during winter was negatively correlated with LPUE in the same and adjacent areas in March – April. Furthermore, highly significant negative correlations were found between fishing effort in January and February in Dutch waters and LPUE in July and August in areas further north, explaining up to 86% of the variance.

Together our results support the hypothesis that early recruitment in the Northern areas partially depends on a new cohort coming from the south and that reduced recruitment in Northern areas may be a consequence of previous local depletion of egg-bearing females further south. Egg bearing shrimp appear to concentrate in southern areas in January and February and migrate to adjacent northern areas for egg release in March and April.

To prevent economic and ecological consequences for the shrimp stock and the fishery, transboundary management measures need to be considered and implemented. Further investigations of migration and drift patterns of brown shrimp are recommended.

## 1. Introduction

The Brown Shrimp, *C. crangon* supports one of the most valuable European fisheries in the North Sea. The fishing fleets of Germany, the Netherlands and Denmark are responsible for over 90% of the yearly landings of Brown Shrimp from the North Sea (ICES, 2019b). The most recent years, however, were characterized by very large variations in the annual landings, especially in the northern regions. Both 2016 and 2017 were very poor years for northern Germany and Denmark, and while 2018 brought record landings, 2019 was again a very poor year in these northern regions.

Despite the large advances in the understanding of the life cycle, the assessment of the stock status of the brown shrimp (*C. crangon*) has been a challenge for decades. This is to a large part due to the lack of coherent effort data from the international fishery. In addition, biological traits such as the impossibility of age determination, the short life cycle and high predation mortality rates have impaired or complicated analytical assessments. Earlier studies concluded that overfishing of *C. crangon* is not occurring or even impossible given a predation mortality that exceeds by far the fishing mortality (Tiews, 1978; Redant, 1980; Wellemann and Daan, 2001). This view was supported by increasing landings over long time periods along with apparently constant or even decreasing effort (Neudecker et al., 2011).

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### 1.1. Difficulties to integrate fishing data from different countries

It was previously not possible to integrate the data of the three main fishing nations, the Netherlands, Germany and Denmark because the different measures of fishing effort. Even in the simplest form of fishing days data were incompatible and even changed within the national time series (e.g. ICES, 2005). In some cases fishing days were counted as full days regardless of the number of hours at sea, in other cases days were derived from the number of hours at sea divided by 24 and in other cases one day was subtracted to account for travel time. During decades, fishing effort of the German fleet was only recorded as the number of fishing trips, regardless of the duration of a trip. For some fleets the effort was also available in hp-days or hp-hours, but also here the definitions of the time component varied.

### 1.2. Fishing effort and efficiency have likely increased

In those fleets where hp-day were available, the data indicated increasing fishing effort over time, e.g. in the Dutch fleet the number of hp-days in the 200–300 hp. class approximately doubled between 1979 and 1989. Salz and de Wilde (1990) predicted that many large beam trawlers of the flatfish fisheries would switch to shrimp fishery due to lack of fish quotas. Their prediction became reality as there were 159 vessels in the hp-class 260–300 in 2019 compared to only 75 in 1988. Most of these vessels (140) are so called Euro cutters of >22 m length. In the German fleet the total engine power has increased by a factor of 1.57 between 1964 and 1989 despite a reduction in the number of vessels from 422 to 266 over the same period. In addition a Danish fleet started from scratch as late as in 1970, with landings increasing from 69 t to 2908 t between 1970 and 1999. Fishing effort in hp-days has increased between 1987 and 1999 by approx. 36% (mean of first half period compared to mean of second half) and remained on a high level since. Taken together these considerations already suggest a likely increase of the effective fishing effort of the total fleet.

However, fishing days or even hp-fishing days are only a poor approximation of the fishing mortality, as many other factors influence the catchability of Brown shrimp. Increasing mortality, however, could theoretically be detected in changing size distributions of the target species. Boddeke (1978) related decreasing shares of large shrimp in the Dutch commercial catches with increasing fishing effort. Temming et al. (1993) analysed the time series of size distributions from commercial bycatch and detected a doubling of total mortality between the periods 1974–78 and 1984–88, confirming Boddeke's observation. However, a relation between size distributions and increased fishing effort could only be hypothesized. Temming and Hufnagl (2015) extended the time series of total mortality using size compositions from survey data and combined these with estimates of total predation of shrimp in relation to commercial landings. This made possible a separation of natural mortality and fishing mortality which revealed a doubling of fishing mortality over the period 1971 to 2010, and suggested growth overfishing of brown shrimp at the current levels of fishing and natural mortality.

### 1.3. Effect of the winter fishery on recruitment

The demonstration of growth overfishing leads to the question if also fishing effort which targets adult, egg-bearing shrimp in winter and spring has a negative impact on recruiting shrimp in the subsequent summer and autumn. The work of Temming and Hufnagl (2015) showed that much of the increase in landings was likely a consequence of the decreasing predation on brown shrimp and hence not necessarily an indication of improved recruitment. Brown shrimp females carry their fertilized eggs attached to the body until the larvae hatch. Boddeke and Becker (1979) highlighted that this coupling of the fate of the eggs and the adults presents a risk of recruitment overfishing especially in winter, when due to very long development times of the eggs the risk is largest. The most visible winter fishery takes place off Sylt islands, where groups of large vessels fish in a relatively restricted area. The prediction of the intensification of this fishery due to the shift of even more large vessels from the Dutch flatfish fishery into the shrimp fishery since 1990 has provoked discussions about potential negative effects of the fishery in the Sylt area during winter, at least for the northern regions (Berghahn, 1991). However, since overall landings increased from an average of about 20,000 t before 1990 to about 30,000 t in the subsequent decade, this discussion faded subsequently. With the findings of Temming and Hufnagl (2015) of a steady increase in fishing mortality and the recent strong fluctuations in landings in the northern regions, the issue is worth a second look. Added relevance to this research question comes from new results on the life cycle, which highlight the importance of the winter egg production for the late spring peak in recruits on the tidal flats (Temming and Damm, 2002) and the first peak in late summer of adult shrimp (Temming et al., 2017).

Since 2007 a satellite-based vessel monitoring system (VMS) became mandatory also in the shrimp fishery, providing a fine spatial resolution of the fishing activity. These VMS data can be combined with effort and landings data from logbooks (e.g. Pedersen et al., 2009; Bastardie et al., 2010; Lee et al., 2010; Gerritsen and Lordan, 2011) allowing also the estimation of landings per unit effort (LPUE) on a finer spatial scale. Schulte et al. (2020) used these VMS data of the German fleet in combination with logbook data and data on size categories of landed shrimp from landing declarations to map the locations of high concentrations of large adult shrimp in winter. The analysis revealed relatively distinct distribution patterns of these mostly egg bearing females visible as two diagonal bands in NW directions: a southern one near Helgoland and a northern one starting off Sylt. Such stable structures pose risk of marked local depletion, if fishermen are able to aggregate on these structures.

However, since most of the winter fishery is carried out by Dutch and Danish vessels, a unique opportunity for an analysis of the North Sea wide situation arose at the annual meeting of the working group on Crangon fisheries and life history (WGCRAN) in 2019, when an integrated dataset on VMS derived effort and log book derived landings data of the main shrimp fishing fleets from Denmark, Germany and the Netherlands which are responsible for more than 90% of the annual landings in the North Sea became accessible for the first time. Based on this dataset we 1) investigate trends in effort (as proxy for fishing mortality) and of LPUE (as proxy for shrimp abundance) on a spatial scale with special focus on the winter fishery and 2) test for effects of varying winter effort in different areas on the resource availability in summer and autumn.

## 2. Material and methods

### 2.1. Aggregation of VMS/logbook data

VSM based effort and landings data of fishing fleets by métier and per month are requested yearly by ICES from the national authorities of the member states (ICES 2019a) in a spatial resolution of 0.05 °c-squares (Rees, 2003). In this study we use a subset of data of the Dutch, German and Danish fleets and is restricted to vessels with registered landings of *C. crangon* for the years 2009–2018.

According to the proposed workflow of the ICES data call, the VMS data were filtered by VMS pings recognized as “fishing” and the landings of a fishing trip were evenly distributed between the VMS pings using VMStools routines (Hintzen et al., 2012) and then aggregated per month and per c-square. For this study, the ICES data were further aggregated to ten larger fishing areas (Fig. 1). Five regions which follow the coastline are further split into an area close to the coast which contains the islands (inshore) and an offshore component, with the separating line roughly following the coastline. LPUE was calculated as landings in kg per hours fishing for each area.

For an initial descriptive analysis landings and effort of the two separate time periods 2009–2013 and 2014–2018 are compared for the first and the second half of the year separately. With each of the time

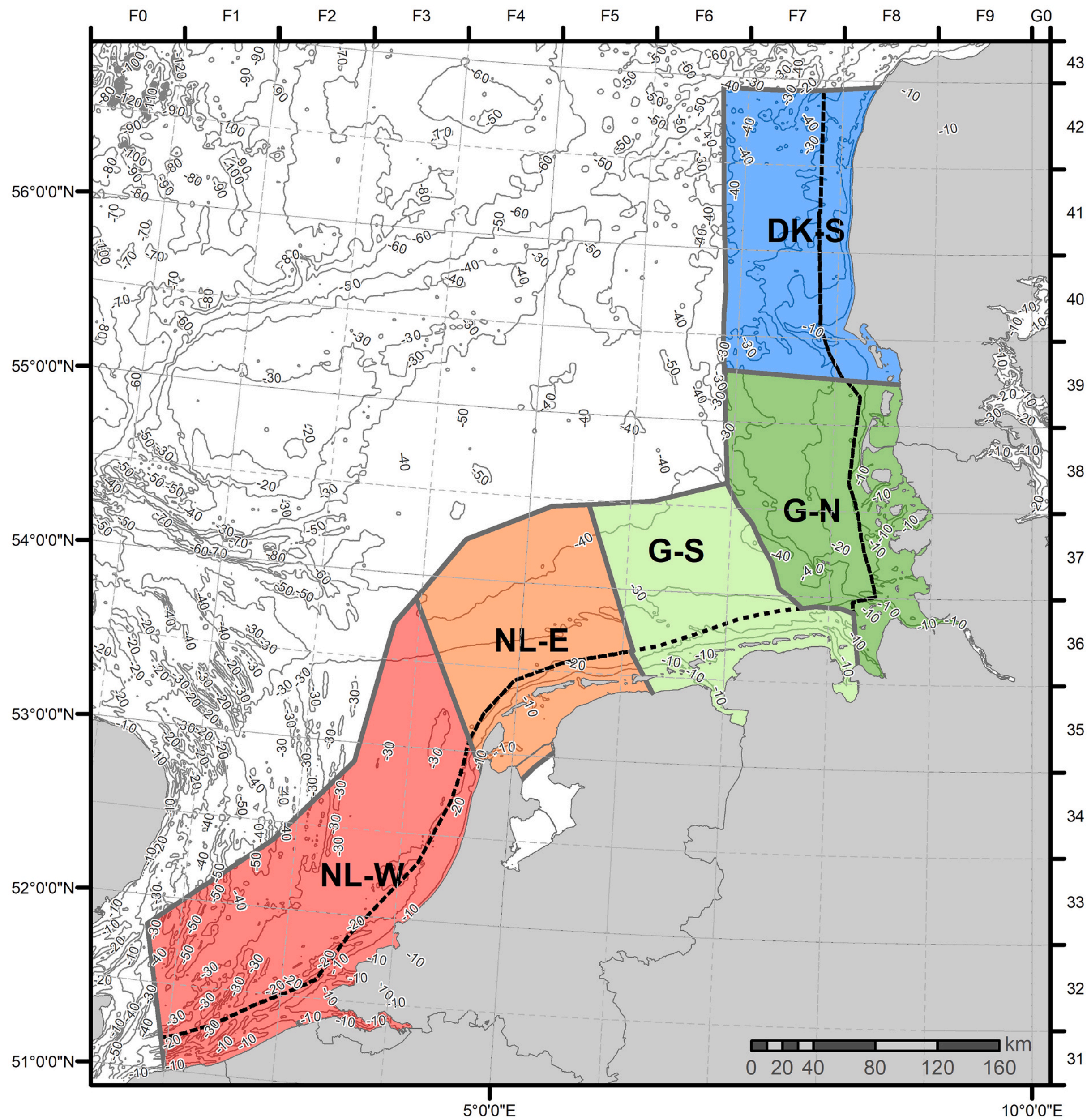


**Fig. 1.** Fishing areas used for data aggregation. NL-W Netherlands West; NL-E: Netherlands East; G-S: Germany South, G-N: Germany North; DK-S: Denmark South. Each area is separated in an offshore and inshore component as marked by the dashed line. X- and Y-axes show latitude and longitude. The combination of 31–42 on the right and F1 – F8 on the upper side stands for the ICES statistical rectangles 31F1 – 42F8. Thin black lines show the bathymetry in 10 m steps.

periods and half years having only five data points, no further statistical analysis was made. For this comparison, all 10 subareas are considered explicitly. Since in all but one off-shore area (G-N) less than 5% of the effort respective landings were located, the in- and offshore areas were combined for the subsequent correlation analysis. In addition, no significant effect on results of the following correlation analysis could be observed with data separated into in- and offshore areas. Thus, for each of fishing effort and landings, the data of each inshore area was combined with that for the associated offshore area before the subsequent analyses to reduce the number of area combinations substantially.

For the seasonal analyses the data of two adjacent month was aggregated: January and February, March and April etc. resulting in 6 effort and LPUE values per year and area.

To test for possible effects of fishing effort on shrimp abundance, we correlated bimonthly averaged effort and bimonthly averaged LPUE as in all area combinations. Based on our understanding of the life cycle (Temming et al., 2017), significant negative correlations of effort with the LPUE in adjacent months within the first half year are consistent with a depletion of the same cohort. Significant negative correlations of fishing effort in the first half year with the LPUE in months after July would be expected if the effects of fishing effort on spawning stock are reflected in subsequent recruitment. Linear regression equations using fishing effort as the explanatory variable and the LPUE as the response variable were fitted to the data for selected data sets with highly significant correlations.

If the size of the spawning stock in winter is expected to influence the subsequent recruitment in late summer and autumn, then winter LPUE – referring mostly to large egg bearing females – should reveal a positive correlation with LPUE in autumn – being dominated by small fast growing recruits of the new cohort. For this investigation also all area combinations were tested. Correlations were described with the Pearson correlation coefficient. For significant correlations we also performed a linear regression analysis.

All statistical analysis and the processing of the logbook and VMS data were conducted with the statistical language R, version 3.6.1 (2019-07-05).

### 2.2. Additional long-term effort and landings data

To put the winter fishery of VMS/logbook data starting in 2009 into perspective with earlier periods, we extracted additional data from different sources and plotted the resulting extended time series of annual landings and fishing effort in the first quarter of the year. Yearly landings and effort data for the fleets fishing for *C. crangon* in the North Sea were used (ICES, 2019b). For the German fleet, effort data start in 2000, while for the Dutch fleet the years 1995–2003 are available. For the Danish fleet, a full dataset is available since 1987. No spatial information is given for the German and Danish data. The Dutch data from 1995 to 2003 from the VIRIS logbook system was available in an aggregated anonymized format from a previous EU-project. In those records, spatial reference for catch and effort is given per ICES rectangle. For the comparison of historical and recent effort in the winter fishery, it was assumed that the German and the Danish fleet fish in waters off the Northern German and the Danish coast in the first quarter of the year. For the Dutch fleet, effort and landings from the ICES rectangles 37F-40F were assigned to the Northern areas, effort and landings from the ICES rectangles 29F-36F were assigned to the Southern areas. Effort from VIRIS logbooks was calculated in hours at sea as the difference between leaving and returning to port. Effort from the German and Danish fleet are available in days at sea and were back-calculated to hours at sea by multiplication with 24.

For the long term LPUE trend in the Danish fishery, also a homogeneous data set in kg landings per hp-hour-at-sea was used (ICES, 2019b). The number of new vessels per year was deducted from the building year of the vessels listed in the fleet inventory of the fishery.

## 3. Results

### 3.1. General effort and landings pattern

The mean annual effort between 2009 and 2013 was 612,155 h fishing in all areas combined. This value increased by 12% in the following time period from 2014 to 2018. The corresponding landings decreased by 9% from 33,074 to 29,952 t. The differences between both time periods were more pronounced in the first half of the year: the mean landings decreased by 34% (Table 1), while the effort increased by 10% (Table 2), simultaneously. In the second half of the year the landings increased slightly by 2% with a corresponding effort increase of 14%.

With the exception of G-N, offshore subareas account for less than 3% of the annual landings or effort (Table 1, 2, Fig. 2). However, G-N offshore is an important fishing area in the first half of the year accounting for 24% of the total effort. From the first to the second time period, landings and effort (Jan-Jun) in G-N offshore decreased by 53% and 17%, respectively (Table 1, 2, Fig. 2).

If in- and offshore areas are combined, the ranking according to effort increase from the first to the second period for the whole year is NL-W (28%), G-N (21%), G-S (16%), NL-E (11%), and DK-S (6%). The greatest increase in effort for separate seasons was observed in NL-E (70% in July-Dec.), DK-S (60% in Jan.-Jun.) and G-N (40% in Jan.-Jun.), while the strongest decrease occurred in DK-S (30% Jul.-Dec., inshore) (Table 1, 2, Fig. 2).

The ranking in landings is identical to the ranking in effort, if in- and offshore areas are combined. However, the pattern changes in the inshore areas between the two periods: some subareas show considerable declines (DK-S: −50% Jul.-Dec., G-S: −50% Jan.-Jun., NL-W: −30% Jan.-Jun.), while other areas exhibit increases (NL-W: + 90% Jul.-Dec., DK-S: +20% Jan.-Jun. and NL-E: +10% Jul.-Dec.) (Table 1, 2, Fig. 2).

In the first period, German regions (G-N and G-S) are most important with 55% of all effort and 57% of all landings compared to 37% of all effort and 36% of all landings in the Dutch regions NL-E and NL-W. However, in the second period, there is a clear shift towards the Dutch coast. The effort in G-N and G-S remains nearly stable (5% increase), while the effort off the Dutch coast (NL-E and NL-W) increased by 24%. At the same time the landings from the German regions decreased by 25%, now contributing 47% to the overall landings. The landings from the Dutch coast increased by 20% and contribute 47% to all landings in the second period.

A general pattern of half-year effort between both periods is an increase in inshore regions and a decrease in offshore regions. This effort increase is greater in the northern regions in the first half-year and greater in the southern regions in the second half-year. The increase in effort does not lead to similar increasing landings. Landings in most regions in the first half-year except DK-S declines. However, a 20% increase in landings in the first half year in inshore DK-S is accompanied by a 60% increase in effort. In the second half year, the gap between effort and landings is not that strong, but still the landings do not keep up with effort or decrease more than the effort. The only exemption is NL-W inshore, where a 70% increase in effort in the second half year leads to a 90% increase in landings.

### 3.2. Trends in LPUE

The previously described increase in effort in combination with decreasing landings leads to significant negative trends in LPUE in the first quarter in all regions (Fig. 3) with steeper slopes in Danish and German subareas (DK-S: -2.47, G-N: −2.85 and G-S: −3.51) than in the Dutch regions (NL-E: −1.58 and NL-W: −1.73). While the LPUE in the traditional winter fishing areas in the North and also in G-S is nearly 10 kg/h higher than in the Dutch regions at the beginning of our time series,

**Table 1**
Mean annual landings per half-year (t) by subarea for two 5 year periods.

| Period | | 2009–2013 | | | | 2014–2018 | | | | Factor of change | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Region | in/off shore | Jan-Jun | | Jul-Dec | | Jan-Jun | | Jul-Dec | | (2014–18/2009–13) | |
| | | tons | % | tons | % | tons | % | tons | % | Jan-Jun | Jul-Dec |
| DK-S | in | 628 | 5.6 | 1149 | 5.3 | 785 | 10.3 | 618 | 2.8 | 1.2 | 0.5 |
| G-N | in | 2267 | 20.2 | 5295 | 24.2 | 1744 | 22.9 | 4558 | 20.4 | 0.8 | 0.9 |
| G-S | in | 1964 | 17.5 | 4043 | 18.5 | 1030 | 13.5 | 3840 | 17.2 | 0.5 | 0.9 |
| NL-E | in | 2171 | 19.3 | 6203 | 28.4 | 1882 | 24.7 | 7103 | 31.8 | 0.9 | 1.1 |
| NL-W | in | 616 | 5.5 | 2390 | 10.9 | 443 | 5.8 | 4438 | 19.9 | 0.7 | 1.9 |
| DK-S | off | 356 | 3.2 | 211 | 1.0 | 224 | 2.9 | 57 | 0.3 | 0.6 | 0.3 |
| G-N | off | 3005 | 26.8 | 2282 | 10.4 | 1420 | 18.6 | 1574 | 7.0 | 0.5 | 0.7 |
| G-S | off | 58 | 0.5 | 51 | 0.2 | 14 | 0.2 | 12 | 0.1 | 0.2 | 0.2 |
| NL-E | off | 94 | 0.8 | 169 | 0.8 | 52 | 0.7 | 112 | 0.5 | 0.6 | 0.7 |
| NL-W | off | 65 | 0.6 | 56 | 0.3 | 23 | 0.3 | 23 | 0.1 | 0.4 | 0.4 |
| Total | | 11,226 | 100 | 21,848 | 100 | 7617 | 100 | 22,336 | 100 | 0.7 | 1.0 |

**Table 2**
Mean effort per half-year (fishing hours) by subarea for two 5 year periods.

| Period | | 2009–2013 | | | | 2014–2018 | | | | Factor of change | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Region | in/off shore | Jan-Jun | | Jul-Dec | | Jan-Jun | | Jul-Dec | | (2014–18/2009–13) | |
| | | hours | % | hours | % | hours | % | hours | % | Jan-Jun | Jul-Dec |
| DK-S | in | 14,873 | 5.1 | 19,631 | 6.1 | 23,448 | 7.3 | 14,538 | 4.0 | 1.6 | 0.7 |
| G-N | in | 51,469 | 17.8 | 69,623 | 21.6 | 69,700 | 21.8 | 79,750 | 21.7 | 1.4 | 1.1 |
| G-S | in | 46,755 | 16.1 | 55,632 | 17.3 | 47,413 | 14.9 | 63,823 | 17.4 | 1.0 | 1.1 |
| NL-E | in | 63,915 | 22.0 | 100,026 | 31.0 | 80,232 | 25.1 | 115,550 | 31.4 | 1.3 | 1.2 |
| NL-W | in | 19,014 | 6.6 | 36,048 | 11.2 | 21,433 | 6.7 | 60,426 | 16.4 | 1.1 | 1.7 |
| DK-S | off | 7839 | 2.7 | 2676 | 0.8 | 7724 | 2.4 | 1174 | 0.3 | 1.0 | 0.4 |
| G-N | off | 78,602 | 27.1 | 34,263 | 10.6 | 65,238 | 20.4 | 30,499 | 8.3 | 0.8 | 0.9 |
| G-S | off | 1543 | 0.5 | 852 | 0.3 | 673 | 0.2 | 236 | 0.1 | 0.4 | 0.3 |
| NL-E | off | 3410 | 1.2 | 2605 | 0.8 | 2246 | 0.7 | 1591 | 0.4 | 0.7 | 0.6 |
| NL-W | off | 2478 | 0.9 | 902 | 0.3 | 1001 | 0.3 | 248 | 0.1 | 0.4 | 0.3 |
| Total | | 289,898 | 100.0 | 322,258 | 100 | 319,106 | 100 | 367,836 | 100 | 1.1 | 1.1 |

it reaches the same level at around 20 kg/h in the end of the time series.

In the second Quarter, only weak significant negative trends ($p < 0.1$) are observed in Southern areas (NL-E, NL-W and G-S), while the northern areas show less pronounced declines which are not significant. This is mainly caused by the high LPUEs in 2011. When the value for 2011 is left out, all trends except DK-S are significant in Q2 (not shown here).

In Q3 and Q4, declining although not significant trends can be seen in the North while the southern regions show neutral or positive trends. When the year 2018 with exceptional high LPUE is taken out, the negative trends in Q3 for G-N and G-S, and in Q4 for G-N all become significant on $p < 0.05$ level (not shown here). Furthermore, the stable or slightly positive trend in Q3 and Q4 for NL-E and NL-W turn negative although not significant.

### *3.3. Long-term trends in the winter fishery in the North*

A combination of the VMS-based data set (here G-N and DK-S) starting in 2009 with earlier data on landings and effort reveals a strong increase of the winter fishery with landings increasing from about 1000 t to about 3000 t in the years 2009–2012 (Fig. 4). Thereafter landings decrease again to about 1500 t. Fishing effort has almost doubled from about 50,000 h (2000−2003) to around 70–80,000 h (2009–2018) with peak values of 95,000 h (2018).

### *3.4. Long term LPUE trend in the Danish fishery*

For the Danish fleet a consistent data set of landings and fishing effort since 1987 shows a steady increase in LPUE between 1987 and 2005 and a likewise clear decline thereafter (Fig. 5). Over the same period (1987–2010) 25 of 28 vessels in the Danish fleet were replaced with modern new constructions.

### *3.5. Correlations of effort and LPUE*

#### *3.5.1. Intra-cohort correlations*

Correlations of winter (February–January) and spring (March–April and May–June) effort with LPUE in adjacent months within the first half year are consistent with a depletion of the same cohort. The significant negative correlation of winter effort (January–February) in the region G-S and LPUE of the regions located to the east and north (G-S, G-N, DK-S) is greatest in the same period (January–February), while the winter effort in the region NL-E correlates significantly negative with LPUE in the subsequent months of all regions (Fig. 6). In contrast, correlations with effort from other sub-areas are weak. No significant correlations were found between effort in March–April and the LPUE values in the first half year.

#### *3.5.2. Inter-cohort effects*

Out of all correlations performed, we found strong and significant effects of winter (January–February) and spring (March–April) effort on LPUE in the following summer season (July – August; Fig. 6). Note that these between season effects suggest recruitment effects on the subsequent cohort caused by reductions of the spawning stock (Temming et al., 2017). Specifically significant negative correlations were found for winter effort in NL-E and summer LPUE in all regions east and north of NL-E (Fig. 6). Likewise two significant negative correlations were found for winter effort in G-S and summer LPUE in G-S and G-N and an additional one with LPUE in September–October within the same area (G-S). Effort in early spring (March–April) in G-S is likewise negatively and significantly correlated with LPUE in July–August in NL-W, NL-E, G-N and DK-S (Fig. 6). The same effect can be seen with LPUE in September–October in NL-E and G-N (Fig. 6).

The highly significant negative correlations of winter effort and summer LPUE ($p < 0.01$) are illustrated in linear regressions (Fig. 8). The strongest linear model in terms of significance is the effect of effort in January–February in NL-E on the LPUE in July–August in the German regions G-S and G-N. Next to this South-North pattern, there is also a strong relationship of effort in G-S in January–February on LPUE more south in NL-E from July to August.

Effort in late spring (May–June) has mainly negative effects in the same season but there are some isolated negative correlations in later seasons. Quite surprisingly, four significant positive correlations were found for winter effort and LPUE in July–August (Fig. 6). These correlations can be better interpreted, when taking the correlation between winter effort in different regions into account (Fig. 7).

Effort in January and February correlated significantly negative between G-N and NL-W ($R2 = -0.88$, $p < 0.01$) and between G-N and NL-E ($R2 = -0.67$, $p < 0.05$). Effort in January and February correlated significantly positive between G- and NL-E ($R2 = 0.91$, $p < 0.01$). The linear regression plot for the most interesting combination of areas for our analysis, G-N and NL-E is shown in Fig. 7.

### *3.6. Effect of winter and spring LPUE on the LPUE of the following months*

#### *3.6.1. Intra cohort effects*

Most of the positive correlations are found between all regions in the period January – June, suggesting that the same good or bad year classes are dominating the catches in all regions. Interestingly in the regions NL-W the correlations disappear first, followed by NL-W and G-N.

#### *3.6.2. Inter cohort effects*

The logic for these tests is complementary to the tests of negative effects of winter effort on the subsequent LPUE of the new cohort. If such a relation exists, one would also expect high LPUE in winter and early spring as a proxy of the spawning stock to correlate positively with the

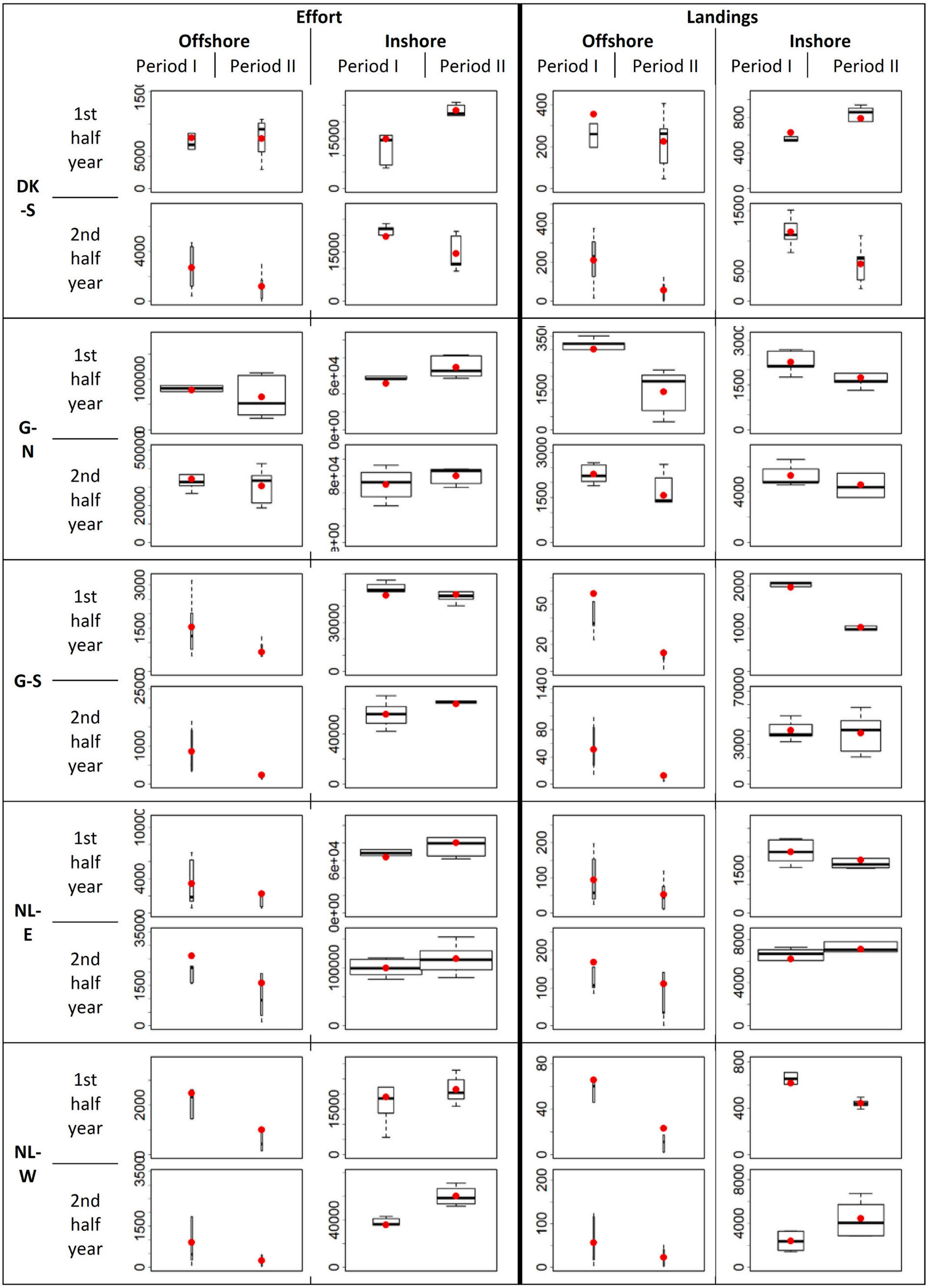


**Fig. 2.** Boxplots for each area, half-year and time period (for values see Table 1 -2). The width of the boxes is proportional to the contribution of the respective area to the overall effort per time period and season. The black lines of the boxplots show the median, the red dot show the mean value. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

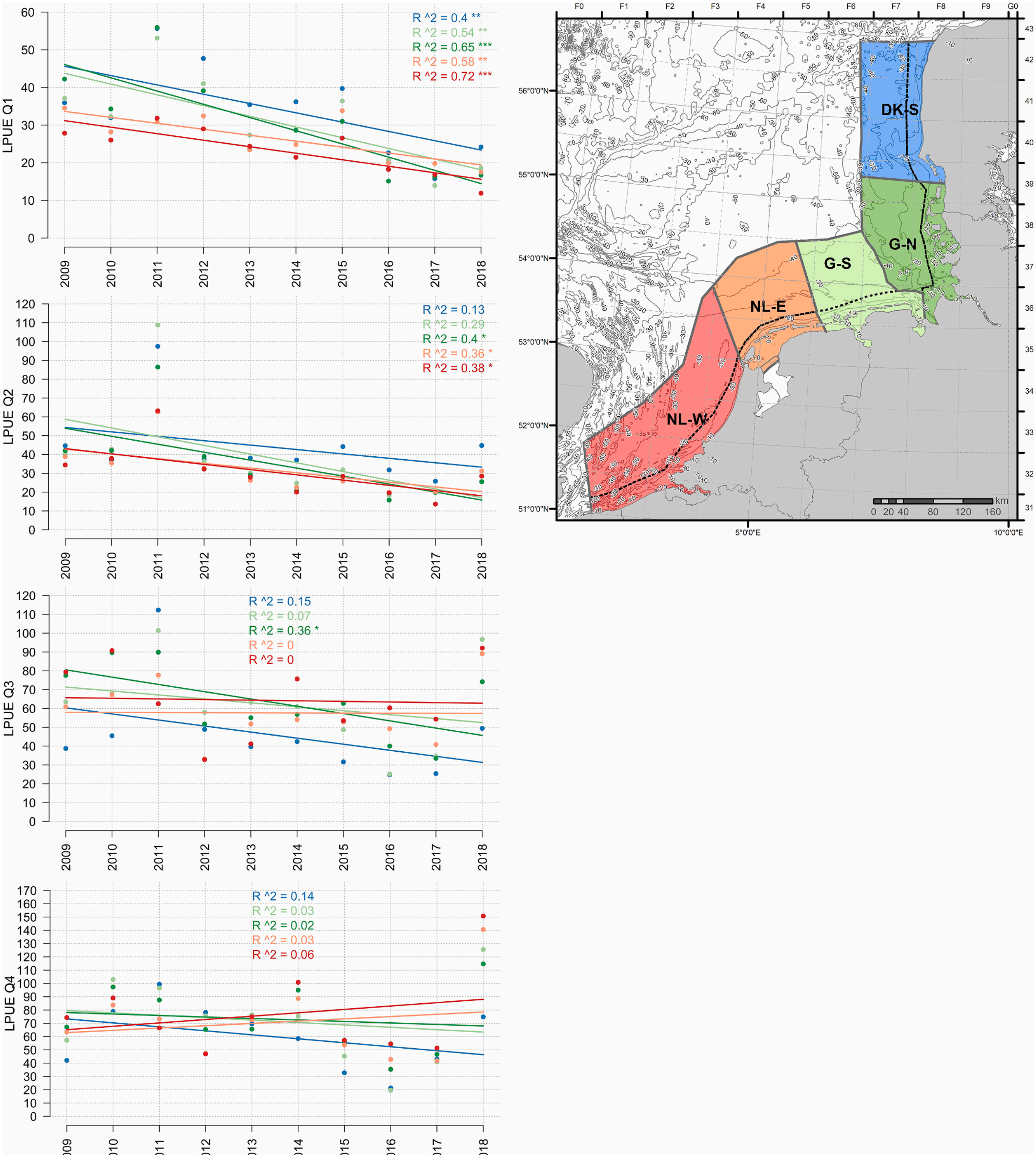


**Fig. 3.** Landings per unit effort (LPUE in kg/h) per quarter of the year. Colour code for subareas corresponds to the colors Fig. 1, with red colors for Dutch areas, green for German areas and blue for Danish area. The stars mark the significance level with $p < 0.01$ ***, $p < 0.05$ **, $p < 0.1$ *. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

subsequent recruitment which manifests in summer/autumn LPUE. However, the LPUE in January and February was not significantly correlated with the LPUE in July and August or September and October in any region except for the combination DK-S (Jan-Feb) – DK-S (Sep-Oct) (Fig. 9).

In contrast, LPUE in March–April correlated positively and significantly with the LPUE in July–August for all combinations of G-S, G-N and DK-S (Fig. 9). For LPUE in September–October only the region DK-S correlates significantly with LPUE in March–April of southern regions (NL-W, G-S, G-N (Fig. 9).

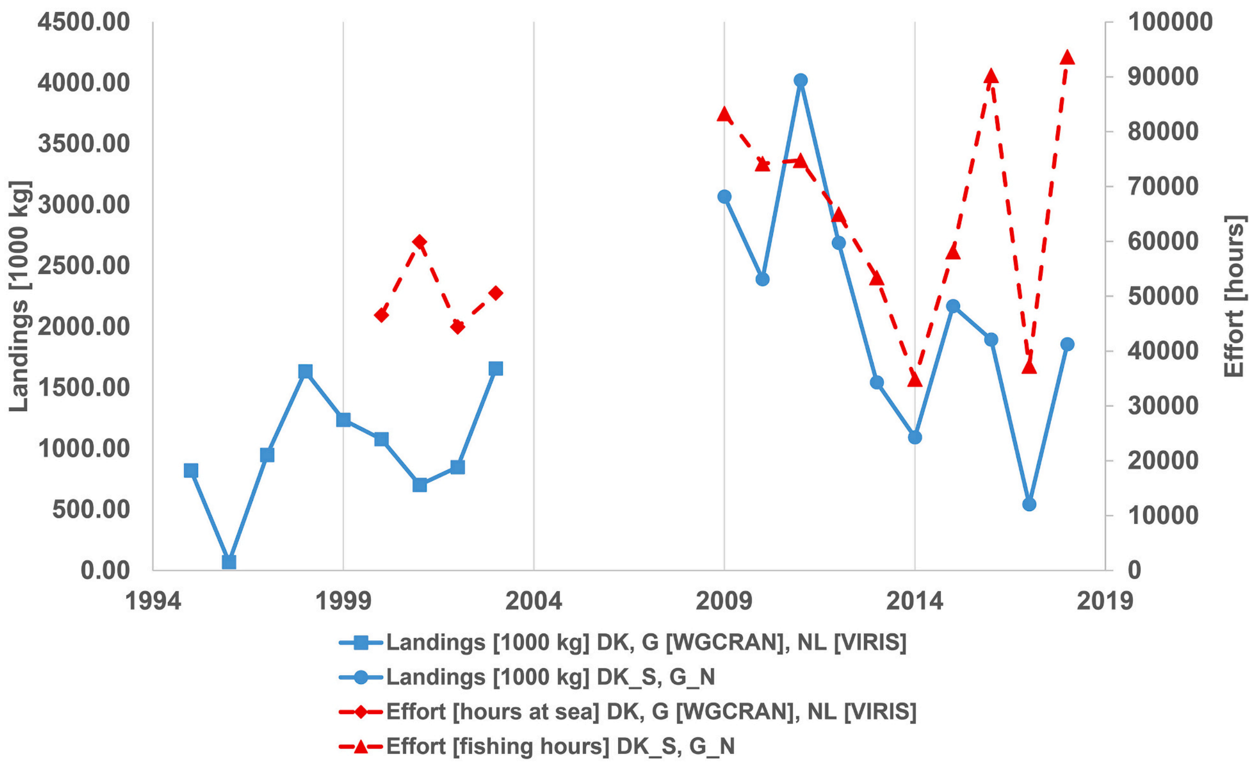


**Fig. 4.** Effort and landings for the first quarter of the year off the Northern German and Danish coast, reconstructed from WGCRAN data (1995–2003) and from the combined VMS-Logbook data (2009–2018). Effort data from WGCRAN data (1995–2003) are in hours at sea for the full German and Danish fleet and those Dutch vessels fishing in ICES rectangles 37F—40F.

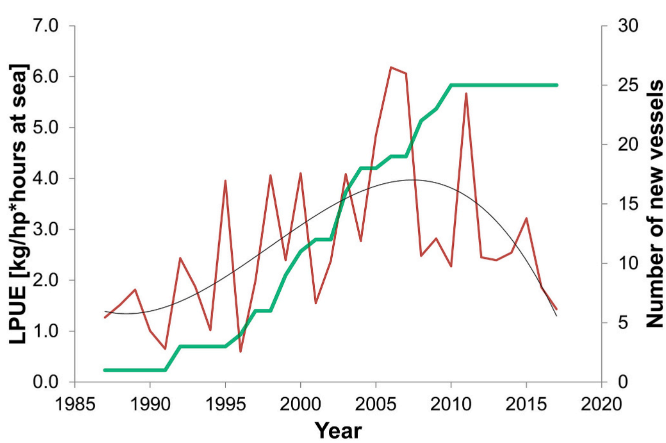


**Fig. 5.** Danish LPUE in kg/hp-h and number of new vessels. Red line: mean LPUE of the months January – June. Thin black line: polynom 3rd degree fitted to the mean LPUE of the months January–June. Fat green line: number of Danish vessels replaced with a new construction of a total fleet of 28 vessels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

## 4. Discussion

### 4.1. Trends in effort, landings and LPUE

#### 4.1.1. Effort increase of 12% over the 10 year period

Mean effort in fishing hours showed an increase of about 12% from 2009 to 2013 to 2014–2018 while mean landings decreased by 9% (Table 1 and 2). However, due to the limited time series and strong annual variations, no significant trend over the full period and all areas could be detected in effort.

The estimated effort increase confirms indications from previous analysis (ICES, 2005), which however suffered from non-comparable effort measures. Estimations of the swept area (Neudecker et al., 1999) demonstrated a likely small effort increase in the German fleet in spite of a reduction of the number of vessels by a factor of 2.5 between the 1956 and 1996. This was mainly due to larger vessels operating larger gear with increasing numbers of fishing hours per day. The entrance of large beam trawlers which previously fished for flatfish (Dutch) and of newly build shrimpers likewise accelerated this trend even after the mid-1990s.

The estimation of fishing hours from VMS data may still lead to under- or overestimation of the actual time spend fishing due to the ping frequency of only 2 h (Schulte, 2015) and the since activity is estimated from the observed speed (Hintzen et al., 2012; ICES 2019a) and not a recorded status. A haul in the Brown shrimp fishery may be anything from 15 min to four hours depending on the catch and fishers preference. Thus, the VMS ping does only give a snapshot of the activity at a single moment and does not contain information on the activity between two pings. Nevertheless, throughout the time series considered here it is unlikely that this bias has changed and hence the observed trends are considered accurate.

However, even if accurate, fishing hours will underestimate the effective fishing effort – being proportional to fishing mortality –, because the corresponding information on vessel dimensions, technical installations and skipper skills is missing. New vessels with new technical designs of gear, hull and propulsion system catch more per fishing hour with the same engine power than traditional ones. New automatic boilers and sorting devices reduce the processing time and hence increases the haul frequency. Effective fishing effort is also strongly influenced by the degree of overlap between fishing tracks and shrimp concentrations. Here information is the crucial point, which is not entering any measure of nominal effort. The necessary information is gathered from experience, digitally stored successful tracks of the own vessel or "copied" tracks of other successful vessels. Also automatic

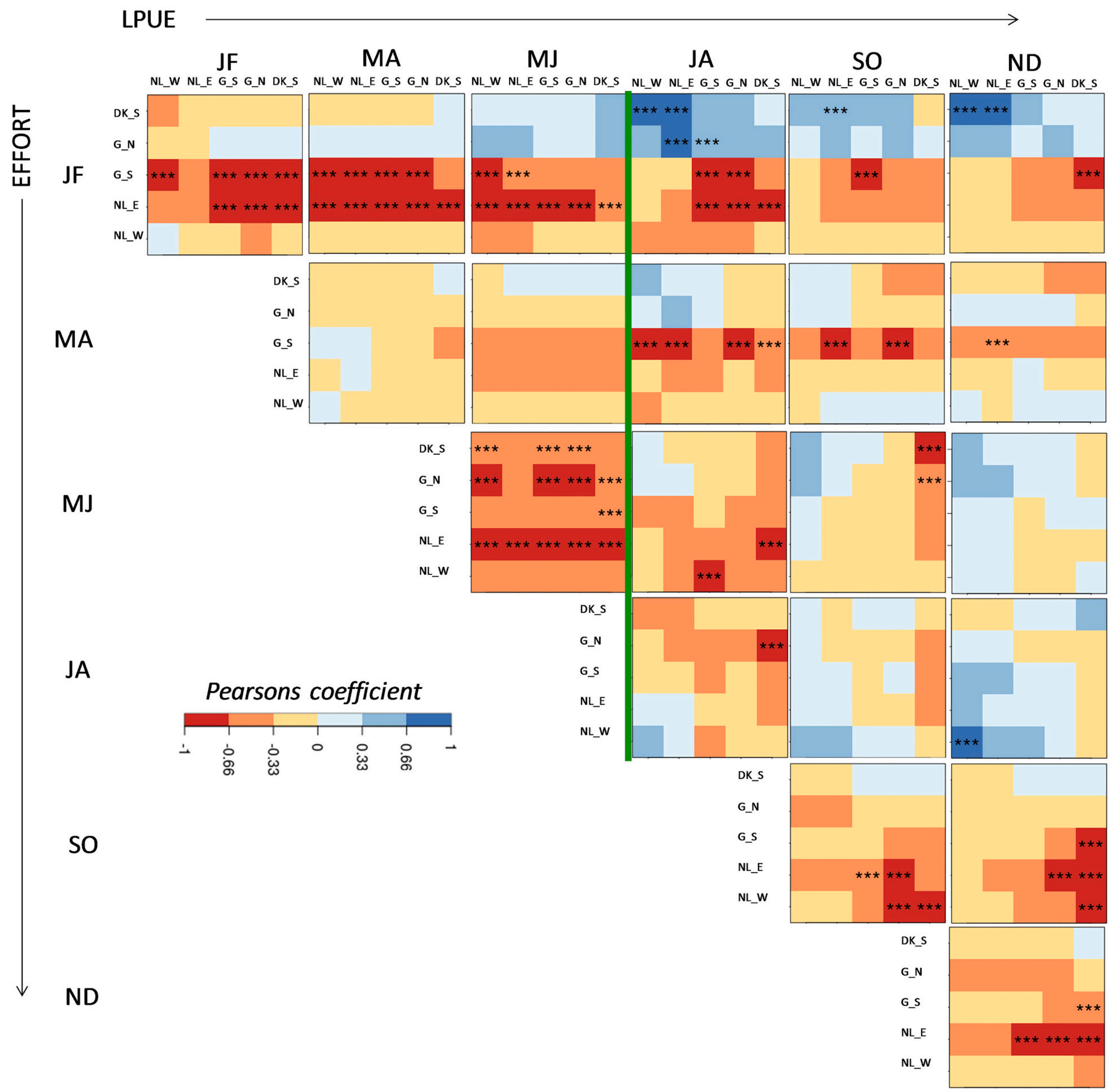


**Fig. 6.** Colored contour plot for Pearson's correlation coefficients of fishing effort versus LPUE for bimonthly intervals (JF = January–February, MA = March–April, MJ = May–June, JA = July–August, SO = September–October, ND = November–December). Each rectangle stands for a correlation between two areas (DK-S, G-N, G-S, NL-E, NL-W). Three stars indicate a 5% probability of error. The thick green line displays the change from the "old" to the "new" cohort as indicated by modelling work. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

steering equipment and radio communication contribute to fishing effort becoming more effective. Schulte et al. (2020) estimated a factor of four in LPUE under comparable conditions between the most and the least effective German vessel of similar size, age and engine power.

Hence it is likely that the fishing pressure on the Crangon stock increased even stronger than the estimated 12% from VMS/logbook data during the last decade.

This so far undocumented increase in fishing pressure has been deduced before from indirect methods. By comparing increased landings with stable total biomass estimates Tulp et al. (2016) assumed increasing fishing mortality as main factor behind increasing landings. The same conclusion was reached by Temming and Hufnagl (2015) from the analysis of a time series of total mortality and total predation in relation to total landings.

#### 4.1.2. North – South shift

Both Northern offshore areas show a 20% decline in effort over the 10 year period. These areas are well known as "traditional" winter fishing areas. The retraction of the fishery from these areas is likely explained by strongly decreased landings with reductions between 40% (G-N) and 50% (DK-S) between the first and the second half of the 10-year period (Table 1 and 2, Fig. 2). While the northern off-shore regions have seen a decline in effort and landings the westernmost inshore region (NL-W) has seen a strong increase in effort with 50% plus between periods, now representing 12% of all effort. The increase in effort corresponds to an even stronger increase in landings (+ 60%).

This shift in importance to south-western waters contradicts the apparent shift of the Crangon population to the north as discussed earlier (ICES, 2005). The earlier statement was based on high Crangon densities found along the Danish coast, increasing commercial LPUE values from the Danish fishery on the one side and steadily decreasing LPUE values

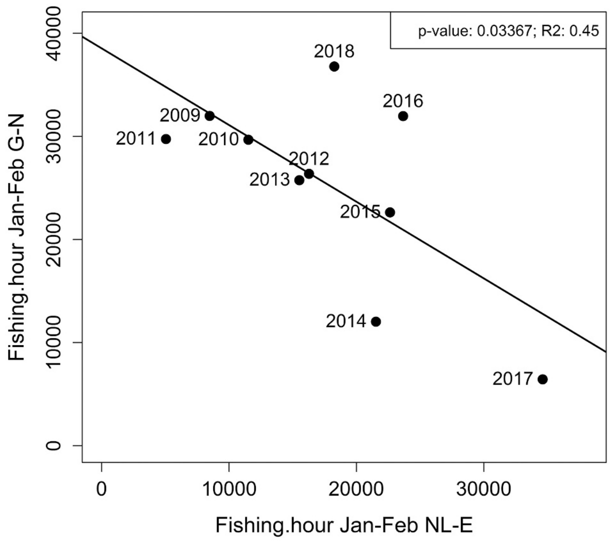


**Fig. 7.** Linear Regression of Effort in NL-E (x-Axis) and Effort in G-N (Y-Axis) in January and February. The significance – levels are p- $< 0.01$ and $p < 0.05$. R2 values display the variance explained by the linear model.

of the Belgian fleet. However, the negative trend in the northern regions has even continued after 2018: In 2019 the landings from Schleswig Holstein were well below average with 3560.379 t compared to the mean of the previous decade 2009–2018 (5495.988 t) (LLUR, 2019).

*4.1.3. Hydrography and predation as explaining factors?*

It was speculated that the Crangon population was shifted towards colder waters driven by increasing North Sea water temperatures (ICES, 2005). This interpretation is, however, not compatible with the recent trend demonstrated here. Furthermore the multi-decadal downward trend in Belgian LPUE has been reversed since late 1998 with again increasing landings (ICES, 2019b). Extensive studies on temperature preference of adult and juvenile *C. Crangon* did also not provide evidence for a narrow range of preferred temperatures (Reiser et al., 2014, 2016) while growth studies indicate that juvenile C.crangon exhibit the highest growth rates at the highest temperatures tested (25 °C, Hufnagl and Temming, 2011). At temperatures above 27 °C juveniles leave the tidal flats towards deeper waters (Berghahn, 1983, 1984), but on the other hand adult shrimp are found in locations with up to 30 °C (Havinga, 1930; Tiews, 1970). These results make a temperature related shift in the distribution pattern unlikely.

Based on survey data from 1974 to 2002, Siegel et al. (2005) did not detect any significant trend in Crangon abundance in spring or autumn and failed to detect any influence of biotic or abiotic factors on spring Crangon abundance. Also investigation on temperature trends in the North Sea only revealed a long-term increase from 1982 to 2012, but no specific trend which corresponds to our time series starting in 2009 (Høyer and Karagali, 2016). Furthermore investigations in the Dutch Wadden Sea from 1970 to 2010 did find neither salinity nor temperature to be critical in structuring brown shrimp population densities in autumn (Tulp et al., 2012). Studies of adult Crangon temperature preference also found no evidence of such preferences as mentioned above (Reiser et al., 2014, 2016). Since we did pool the data over three months, also possible artefacts like delayed migratory patterns are unlikely as cause for the trend.

In the last decades, a de-eutrophication process, detectable in the reduction of nutrient river loads to the sea, caused a decrease of nutrient concentrations in coastal waters under riverine influence in the Wadden Sea (Desmit et al., 2020). This process is linked to decreasing chlorophyll *a* concentrations in those waters (Desmit et al., 2020; van Beusekom et al., 2019) and is discussed to have caused a decline in copepod densities at Helgoland stations (Boersma et al., 2015). The decline in nutrient loads but also in copepod densities is most pronounced until the beginning of the 2000s, then levelling off on a low level. During this period, we rather observe strongly increasing landings in the Crangon fishery which are most likely related to decreased predation (Temming and Hufnagl, 2015). However, no decline in macrozoobenthos linked to this de-eutrophication could be detected. In contrast, macrozoobethos densities are increasing in recent years in the Wadden Sea, particularly in the north-eastern parts (Drent et al., 2017). Given that our data indicate the strongest negative trend in Crangon abundance in the northern parts, a bottom-up effect of decreasing nutrient loads on the egg-bearing shrimp in winter or on the subsequent life stages is unlikely.

In his long-term analysis in 2005, Siegel already assumed an unknown predatory effect as mechanism behind the variation in spring Crangon abundance. Known predators of large adult shrimp are mainly gadoids. However, although the impact of 0-group gadoids on shrimp stock in autumn is widely assumed (Tulp et al., 2016; Siegel et al., 2005), a significant negative effect in spring has not yet been detected. In contrary, the stocks of the main gadoid predators, namely cod and whiting, are still at very levels. The mortality of Brown shrimp from predation is reported to have decreased in the last decades, leading to the fishery taking over the role as main source of mortality (Temming and Hufnagl, 2015; ICES, 2019b; Tulp et al., 2012).

*4.1.4. The role of increased fishing effort on Q1 LPUE*

The negative trend in LPUE is most pronounced in the first quarter and for all regions, with the northern regions showing the steepest decrease (Fig 3). The positive or stable trend in the southern regions in Q3 and Q4 is only held up by the exceptional high LPUE in 2018. A general increase in effort levels, specifically in summer and autumn on the incoming cohort increases the landings and simultaneously reduces the number of shrimp surviving into the winter period. The landings in the beginning of the year are composed of individuals from the same cohort that is fished as smaller adults in autumn. Only later in spring the contributions from the late summer recruitment of the previous year are growing into the fishery (Temming et al., 2017; Schulte et al., 2020). Such a shift with increasing fishing mortality to more autumn landings and less winter and spring landings has also been demonstrated with an earlier version of the life cycle simulation model by Rückert (2011).

*4.1.5. The impact of the winter fishery in northern areas*

A comparison of the VMS-based data set from 2009 to 2018 with earlier data on landings and fishing hours for the period 1995–2003 (Fig. 4) reveals a strong increase of the winter fishery with landings tripling from about 1000 t (1995–2003) to about 3000 t in the years 2009–2012. Thereafter landings decrease again to about 1500 t. Fishing effort has approximately doubled from about 5000 h (2000–2003) to above 8500 h (2009–2018) with peak values of 12,000 h (2018) and since stayed at a high level. The mortality effect on the overwintering shrimp stock is probably stronger than these effort data suggest, as vessel size and effectiveness are not taken into account. Especially in the Danish fleet a complete modernization has taken place over the same period with 25 out of 28 vessels being newly built between 1987 and 2010. This modernization together with learning effects of new captains could theoretically also explain the initial increase in the LPUE. Likewise the Dutch winter fishery in northern areas is carried out by the largest boat class, often switching from flatfish to shrimp fishing. These captains have also local information on fishable grounds further off-shore, where egg bearing shrimp were previously undisturbed in winter.

While this is the first time that a significant decreasing trend in LPUE has been detected, concerns about the potentially negative effect of the winter fishery on the shrimp stock arose before (Boddeke and Becker, 1979; Berghahn, 1991) based on the fact that the catch consists mostly of large egg bearing females. Generally, landings of *C. crangon* used for human consumption as recorded in logbooks refer to shrimp with a carapax width (CW) of at least 6.5 mm (minimal sieve width for commercially used shrimps). This corresponds to a total length of 50 mm (Sharawy, 2012). The proportion of females at this size is already between 60 and 80%, and further increases to 100% at around 60 mm total length (Siegel et al., 2008). While the onset of sexual maturity in males can only be estimated since they have no external feature revealing this status, it is clear that they become mature at a smaller size than females. The minimum size of maturity for males is reported as 22 mm (Boddeke, 1966), while Tiews (1954) observed a range of 38–42 mm total length as size of maturity. It is thus clear that male Crangon mature before they recruit into the fishery. Due the size and the habit of carrying the eggs under the abdomen until hatching, the fishing pressure on females is the most likely link to possible recruitment effects of fishing.

The northern winter fishery has been shown to concentrate actively on spatially restricted aggregations of these large shrimp (Schulte et al., 2020) which are mostly egg bearing females (Hünerlage et al., 2019; Siegel et al., 2008). These winter eggs in turn, are responsible for the first massive wave of recruits and the first increase in late summer and autumn catches at least in the German Bight (Kuipers and Dapper, 1984; Temming and Damm, 2002; Temming et al., 2017)). Furthermore a study linking larval drift from spawning grounds and adult migration patterns suggested that sub-populations could be regionally self-sustained (Hufnagl et al., 2014). Hence, theoretically a local northern spawning stock component could have been decimated by too high fishing effort in winter, leading over time to reduced recruitment and a subsequent gradual decline in abundance these areas.

### 4.2. Connectivity between regions: remote effects of fishing effort

#### 4.2.1. Winter effort in southern regions explains 86% of LPUE in late summer in the northern regions

In our results, a single variable, winter effort, explained up to 86% of the variability of the following summer landings in various regions (Fig. 6). The linear model does still explain more than 70% of the variance for the combinations with the highest correlation coefficient (Fig. 8). This is clearly more than previous attempts trying to explain variability in survey abundance of shrimp in German waters with the NAO index of the previous year, winter temperature, river run-off and a predator index leading to 57% explained variance (Siegel et al., 2005).

Based on previous work (Temming et al., 2017; Siegel et al., 2005) we can assume that LPUE in July–August is dominated by the new incoming cohort and not by survivors of the previous year. This is also supported by the lack of significant LPUE – LPUE correlations (Fig. 9) between January–February and July–August. This excludes a hypothetical explanation of the correlation resulting from fisher's behavior. If fishers would investigate the areas for high abundance early in the year, they may in years with poor abundance in the North decide to put all effort in the South. This would then lead to the same negative correlation if the abundance in summer would be related with that in winter.

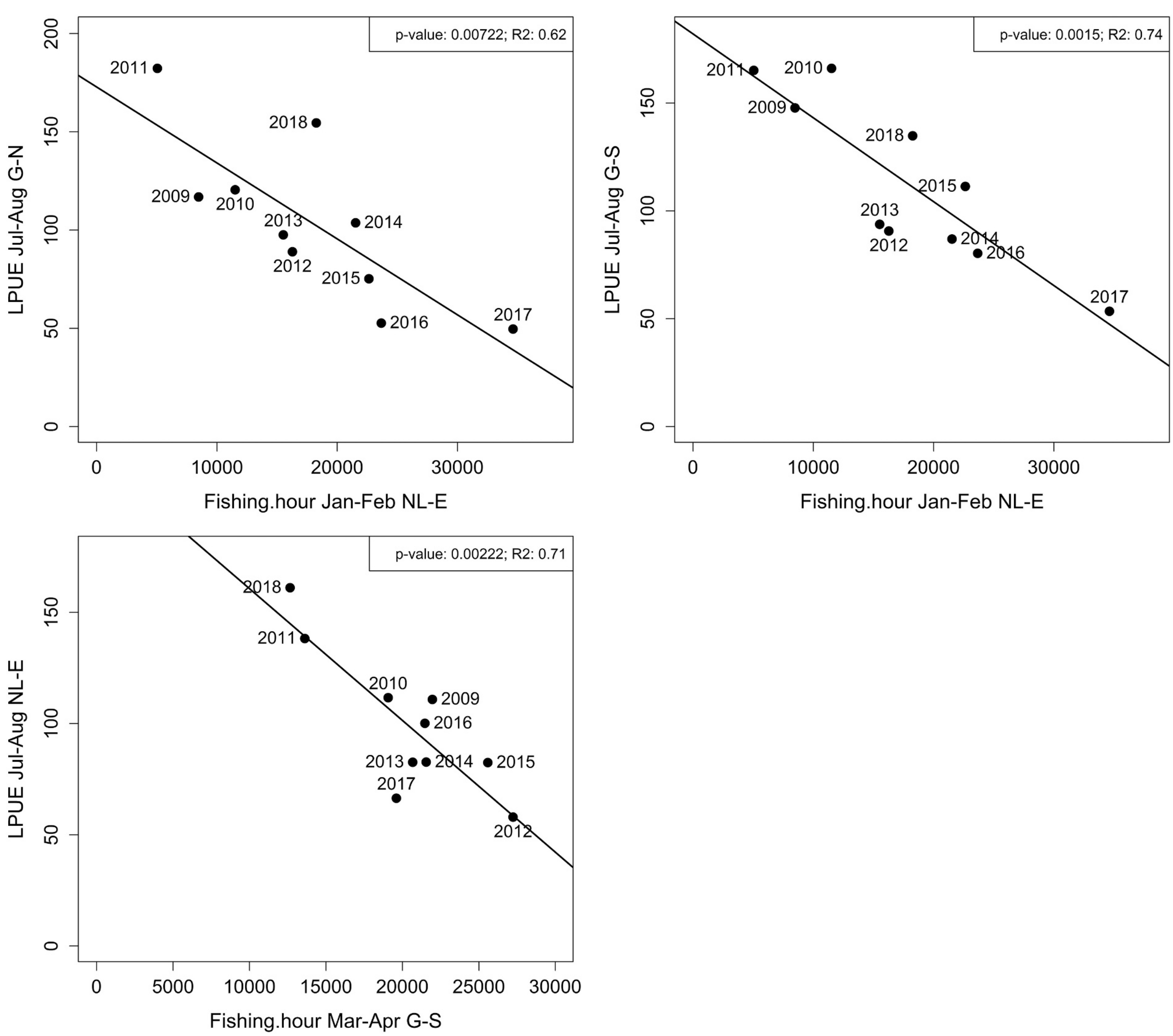


**Fig. 8.** Linear Regression of effort (x-axis) in winter/spring and LPUE in the following season (y-axis). The significance – levels are $p < 0.01$ and $p < 0.05$.

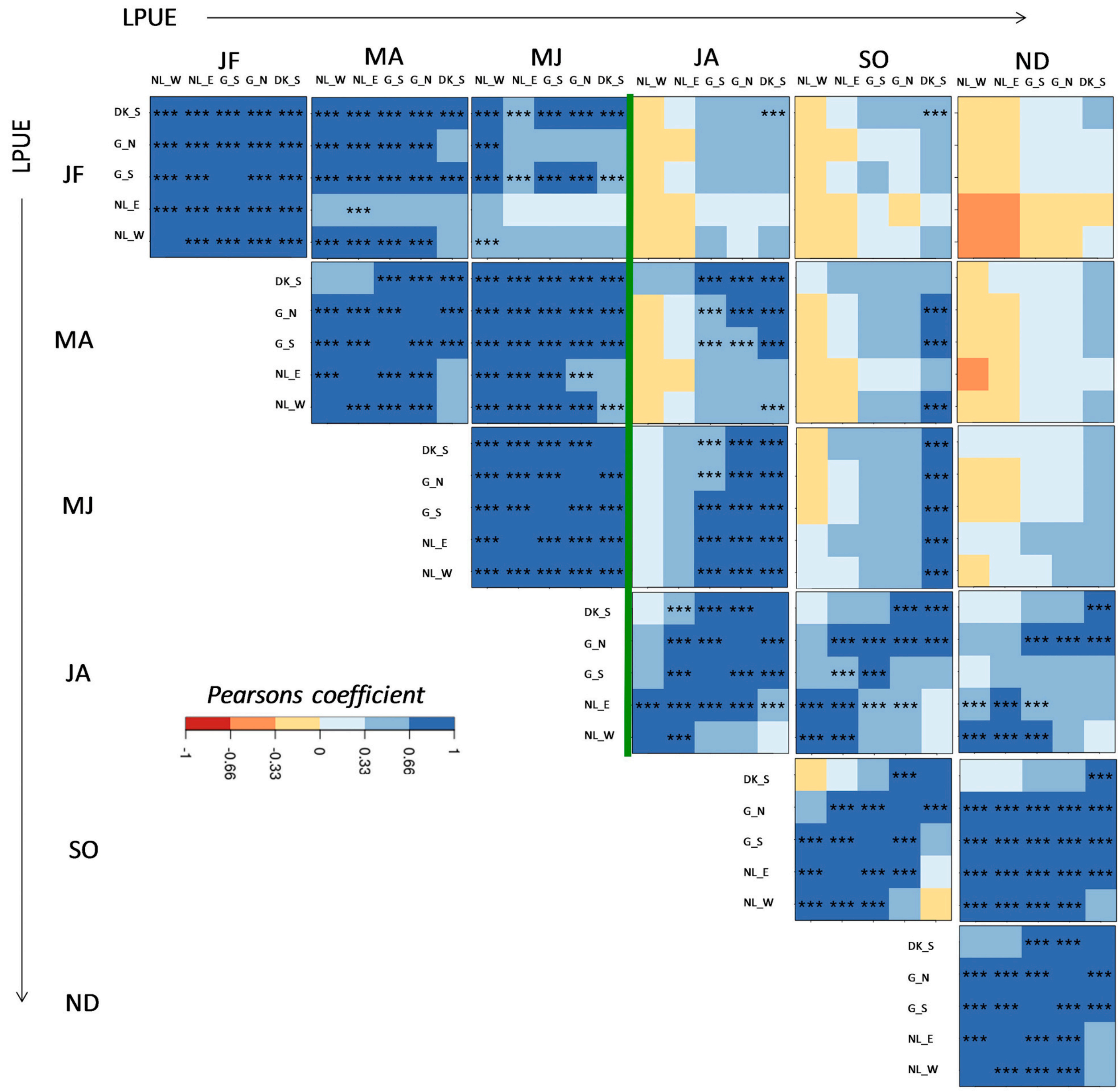


**Fig. 9.** Colored contour plot for Pearson's correlation coefficients of LPUE versus LPUE for bimonthly intervals (JF = January–February, MA = March–April, MJ = May–June, JA = July–August, SO = September–October, ND = November–December). Each rectangle stands for a correlation between two areas (DK-S, G-N, G-S, NL-E, NL-W). Three stars indicate a 5% probability of error. The thick green line displays the change from the "old" to the "new" cohort as indicated by modelling work. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

However, the abundance of Crangon in July–August is simply independent of the abundance in January–February, as described before by Siegel et al. (2005).

#### 4.2.2. Predation pressure

For 2016, high predation pressure by whiting has been suggested as an explanation of low abundance of Crangon in autumn in the German Bight and in Danish waters. Effects of extreme gadoid predator abundance and autumn Crangon abundance have been documented by Siegel et al. (2005), but they did not consider fishing effort as a variable at all. It may be speculated, that the correlation between high whiting abundance and low landings in autumn may actually result from an indirect effect: In years with average or good recruitment, juvenile Crangon settle over a large area were they are accessible to predators. In years with weak recruitment, whiting are forced to search for shrimp closer to the coast, thus appearing in larger numbers in those surveys which sample juvenile fish and Crangon in the Wadden areas. This interpretation is consistent with the observation that high whiting abundance in the Wadden area does not correspond well with strong year classes of whiting. The most extreme occurrence of whiting in the Wadden Sea in 1990 came from a below average year class while the year classes 2001 and 2016 – both with high densities in the Wadden Sea - were not stronger than those of adjacent years with no whiting invasions, namely 1998–2000 and 2014–2015.

#### 4.2.3. Possible recruitment overfishing?

The strongest correlations and regressions involve the effort in January and February (Fig. 6); hence the months before the eggs of the winter period are released. Schulte et al. (2020) showed that standardized LPUEs for large shrimp (TL ca. > 69 mm) are considerably higher than for the smaller size class (TL ca. 48–69 mm) in January and February. It can thus be assumed that the fishery in these months targets mostly large, egg-carrying females. These large females are concentrated in characteristic areas in those month (Schulte et al., 2020), showing a certain depth preference of 10–20 m of the females. Along the Dutch and East Frisian coasts the relevant depth range is compressed into a narrow area, making potential aggregations quite vulnerable.

Hence the mechanism behind our correlation is most likely a reduced spawning stock impacting negatively the subsequent recruitment, as landings in July–August stem from eggs of the previous winter which were released as larvae in March–April (Temming et al., 2017). The correlations are still negative, but no longer significant if the months September and October are considered. In these months increasing contributions from the summer egg production are arriving, which are to a lesser degree depending on mere biomass as egg numbers increase exponentially with female size and spawning frequency increases with temperature. With increasing temperature in spring and summer development times become short and larval drift occurs only over short distances (Daewel et al., 2011; Temming et al., 2017). This leads to a closer spatial connection between egg production and recruitment (Daewel et al., 2011). The fact that no correlations with similar explanatory power are found here suggests a stronger impact of environmental factors on the autumn landings and a smaller role of fishing effort.

Most surprisingly, the correlations and linear regression of effort in NL-E in winter and LPUE in the following season in Northern Regions are highly significant even though three years with extreme LPUE values are included: 2011, 2016 and 2018. The plots of the linear regression do clearly show those years well within the range of the linear trend (Fig. 8).

#### 4.2.4. *The winter fishery affects local recruitment only in remote regions*

Contrary to our expectations, the detected strong effect of effort on subsequent recruitment works across regions rather than within regions. The sole exception is G-S, where the effort in Jan/Feb also impacts the LPUE in the same region in July to October (Fig. 6). The correlations between remote areas suggest that at least the early recruitment in July–August of the Northern regions originates from the South, with no or very little local northern recruitment.

Larval drift or juvenile migration involving selective tidal stream transport (STST) from southern areas towards the North has been suggested before based on a temporal mis-match of simulated and observed patterns of young recruits entering the tidal flats in Germany, when German water temperatures were used in the simulations (Temming and Damm, 2002). This mis-match could only be resolved with Dutch water temperatures. Subsequent studies with 3 D ocean models confirmed the long drift routes of winter larvae and the import into German waters (Daewel et al., 2011; Hufnagl et al., 2014). Due to higher temperatures in the Southern areas, egg and larval development is accelerated and could lead to an early wave of recruits in the North originating from southern-hatched larvae. The larvae from local northern recruitment would then be expected to reach the juvenile stage later in the year and contribute to the landings beginning in September.

#### 4.2.5. *Spring LPUE as a proxy for spawning stock size*

Given the strong negative effects of winter effort in NL-E and G-S on the subsequent summer LPUE of the new cohort in eastern and northern areas, one would also expect high LPUE in winter to correlate positively with respective summer/autumn LPUEs. Contrary to expectations, the LPUE in that region and period, where the winter fishery impacts the recruitment most, namely NL-E in January–February, did not correlate significantly with summer/autumn LPUE. However, there are several significant positive relationships of the LPUE in March–April in G-S and the summer/autumn LPUE in the northern regions (Fig. 9). The region G-S is somewhat special with negative effects of effort in both periods (January–February and March–April). From the current state of knowledge regarding the lifecycle of brown shrimp in the North Sea, it is clear that correlations between LPUE in March–April and July–August can only be caused via recruitment rather than reflecting an intra-cohort correlation. A complex simulation model of the *C. crangon* life cycle (Temming et al., 2017) reveals that commercial landings in July and August originate mostly from winter eggs fertilized in the months November and December, which will hatch in March–April as larvae.

Interestingly corresponding positive correlations exist also for the regions G-N and DK-S. Since the March–April LPUE in all regions is strongly negatively influenced by the winter effort in regions NL-E and G-S (Fig. 6) it must be concluded, that those shrimp that release larvae in March–April in all regions must have concentrated during winter - as egg bearing females - in the two regions NL-E and G-S. In this area they are under the influence of the local winter fishery which determines the size of the surviving fraction of this spawning stock component that subsequently spreads out to adjacent regions where the larvae are released (see schematic drawing in Fig. 10).

Such a migration pattern of the adults has been proposed in a more general form by Boddeke (1976), however, he did not refer to regions but rather postulated that the adult shrimp would target warmer regions, which means in winter also deeper regions. Since the southern North Sea is on average warmer this may also explain a possible migration of shrimp from the North German and Danish coast into the regions off East Frisia and the Netherlands. This migratory behavior of *C. crangon* seems likely unrelated to size or sexual category (Boddeke, 1976). This finding has been supported by the work of Siegel et al. (2008), who observed the same pattern of sex ratio of migrating shrimp in each year as well as in the different seasons (Winter, Spring and autumn) (Fig. 1, Siegel et al., 2008), but with high fluctuations between years.

#### 4.2.6. *Why does the winter effort in Northern regions not have any negative effects?*

For these regions we could only demonstrate a positive effect of winter fishery on subsequent LPUE in summer/autumn, which appears rather paradoxical at first glance. However, the likely explanation is that the same fleet components fish during winter either in Northern or in Southern regions. This is indicated by a significant negative correlation of effort in the North (G-N) and effort in the South (NL-E) (Fig. 7). Hence high effort in the North indicates low effort in the South, which is then causing the benefits indirectly.

Nevertheless the winter fishery in the North targets large concentrations of mostly egg bearing shrimp and lands often at least the same amounts as is caught in southern regions during winter. Unless one assumes that the fishery is so effective, that most of the spawning stock is wiped out, there must be a recruitment contribution from these regions. The question is, why we do not see any related signal. In our data there are indications of decreasing LPUEs in the first quarter especially in the northern regions (Fig. 3). This may indicate that the winter fishery in northern areas has increased over longer periods substantially and may have reached a point where local recruitment overfishing leads to a steady decline of this stock component. This may at least partly be a factor, but the picture is more complex. In the northern regions the seasonal temperature development is somewhat delayed compared to the Dutch coast waters as Temming and Damm (2002) demonstrated in a comparison between temperatures from Büsum harbor and Texel lightship. The resulting longer egg development has also the negative side effect of a longer exposure of egg bearing shrimp to the winter and spring fishery. At the same time the longer development leads to recruits occurring later in the fishery and hence correlations between winter effort and LPUE in July–August do not show a signal, but are rather influenced by the southern recruitment component. In the subsequent months, however, the recruitment components from the northern spawning grounds might get mixed with migrating recruits from both the winter- and summer-egg production of southern regions.

Any recruitment contribution of larvae from the northern areas to the same region requires specific behavioral patterns of either larvae, juveniles or both to remain in the same region. In simulations conducted

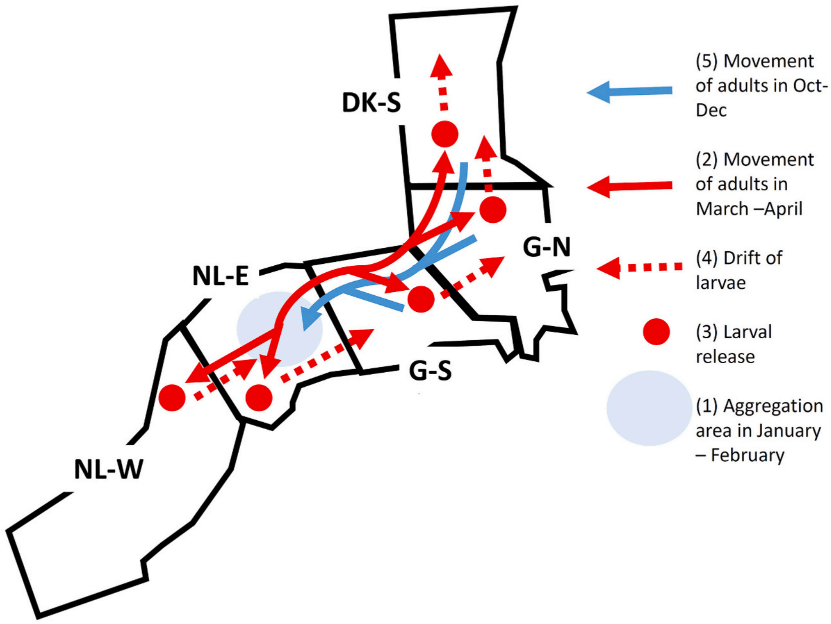


**Fig. 10.** Schematic drawing of the assumed underlying mechanism regarding the impact of the winter fishery on recruitment. The fishery targets large female shrimp in January and February (1), part of the surviving shrimp migrates to adjacent areas (2), the larvae hatch from winter eggs in March–April (3) and are distributed by currents and drift along the coast (4). It is likely that adult shrimp move back along the coast with decreasing temperatures again in October–December (5). The recruitment mechanism on the east and south Netherlands coast is still unknown.

by Hufnagl et al. (2014) larvae from the zoea stage 3 on were assumed to perform selective flood stream transport, which brings larvae rapidly to shallow coastal waters. If this assumption is not accurate, larvae without this behavior will drift much further north into areas with an even more delayed temperature pattern. These areas are not fished normally. However experimental fishing with RV Solea in 2008 and 2009 revealed considerable densities of *C. crangon* along the Danish coast up to the Limfjord (Neudecker, internal cruise reports). While growing shrimp may then gradually return south to the spawning stocks and hence not contribute to the increasing LPUE in summer but rather later in the season.

## 5. Conclusion and outlook

The analysis of the first integrated dataset covering the main fishing areas and –fleets for Brown shrimp *C. crangon* did reveal.

a) An overall increase in effort of 12% in terms of fishing hours over a decade.
b) a general depletion of local spawning stock components in the first quarter.
c) a stronger decline in landings in northern off shore areas and an increase in landings in southern inshore areas.
d) a strong negative impact of the winter fishery in southern areas on summer LPUE in northern areas.
e) indications for a concentration of egg bearing shrimp in southern areas in January and February and a subsequent migration to adjacent northern areas.
f) increasing effort in the northern winter fishery in the past as a possible explanation for decreasing LPUEs in northern areas.

Our results suggest that intensive fishing in one area might influence LPUE in other areas by means of indirect effects, i.e. decreased recruitment. Hence the precautionary inclusion of limitations on the winter fishing effort into the current management plan operated for the MSC certification might be a strategy counter these negative effects. To better understand the across-region effects demonstrated here more research is needed with regard to migratory behavior of adults and drift of larvae. Furthermore, information on shrimp fishery from regions even further south could help understanding the effects on the stock in the southern regions in the present study.

## Declaration of Competing Interest

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

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