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Original Article

Annual brown shrimp (*Crangon crangon*) biomass production in Northwestern Europe contrasted to annual landings

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The brown shrimp (*Crangon crangon*) fishery is economically one of the most important fisheries in the North Sea. Fishing is unregulated, apart from the number of licenses and technical measures. The fishery has long been considered sustainable in terms of the effect on the target species, even though annual stocks are not regularly assessed. Average landings constantly increased annually and since 2000 have been 40% higher than in the 1980s and 1990s. Because brown shrimp lack a clear age structure and reproduce almost year-round, an age-based stock assessment is not possible. In the absence of a formal estimate of stock size, it is difficult to judge whether current fishing practices can still be considered sustainable. Here, we use annual survey data collected during peak occurrence in late summer to obtain a depth- and area-stratified, swept-area estimate for the period 1970–2015. The resulting estimate of the total commercial-size shrimp biomass varied between 4000 and 21 000 tonnes over the years. Both parametric and non-parametric methods arrived at very similar results. In combination with length-based mortality estimates (as a proxy for production/biomass ratio), knowledge on the seasonal occurrence, catchability, gear efficiency, and their variation, total adult annual biomass production was estimated. Values ranged between 38 000 and 216 000 tonnes and overlapped at the lower end with total annual commercial landings, which varied between 8000 and 38 500 tonnes, indicating that in some years (1977, 1998, 2007), the larger part of the total brown shrimp production was harvested. Annual brown shrimp landings have gradually increased since the series started, whereas no trend in standing biomass and production was detected. Concurrent with the increase in landings, natural mortality of shrimp by predation has diminished. Considering the increase in fishing pressure and unknown consequence if natural predators recover or shrimp recruitment decreases, the lack of management for the brown shrimp fishery needs to be reconsidered.

Keywords: coastal area, crustaceans, mortality, shrimp fisheries, swept-area estimate, Wadden Sea.

Introduction

Brown shrimp (*Crangon crangon*) fisheries are economically important in northwestern Europe and especially in The Netherlands, Germany, and Denmark (ICES, 2014b). Between 2009 and 2013, the North Sea fishery for brown shrimp ranked 23rd in landings, but 6th in value, with an annual average of 109 million € [Food and Agriculture Organization of the United Nations database http://faostat3.fao.org]. Total annual commercial landings from the North Sea have increased consistently since the 1970s, with the highest recorded landings of 38 000 t in 2005 and 37 500 t in 2014 (ICES, 2014b). Over the last decade, total annual landings fluctuated around 35 000 t. Brown shrimp is a major food source for gadoids, an important predator of in- and epifauna in intertidal areas, and is assumed to control plaice and bivalve recruitment (Van der Veer *et al.*, 1990). These aspects underline the importance of the species with respect to the foodweb, coastal ecology, and economic value.

Apart from the number of licenses, the compulsory use of a sieve net—a net adaptation to reduce large sized bycatch—and a weekend closure in the Dutch shrimp fisheries, the current shrimp fishery is unregulated (ICES, 2013). The reason for a lack of management so far lies in the assumption that the fishery has been sustainable, a notion based on an earlier study by Welleman and Daan (2001) which concluded that natural mortality greatly exceeds fishing mortality.

Genetic studies have not indicated genetic differentiation within the North Sea brown shrimp population (Luttikhuizen *et al.*, 2008), and connectivity studies based on larval drift suggest substantial interconnections of regions (Hufnagl *et al.*, 2014). Due to its life history, characterized by a short lifespan (maximum 2 years), the lack of an age structure, a very long reproductive season, interannual variations in growth rate, and trends in natural mortality, a formal stock assessment using age-based methods is not possible (ICES, 2013). Attempts to estimate stock size using biomass models have not produced satisfactory results, due to high uncertainties in input data such as catch per unit of effort and thus wide confidence margins (van der Hammen and Poos, 2010). In order to estimate stock size and evaluate the sustainability question, remaining options include length-based methods and survey-based biomass and production estimates. The lack of a formal stock size estimate has so far been of concern relative to efforts to suggest management strategies for the shrimp fisheries and also to achieve Marine Stewardship Council certification. Obtaining reliable production estimates and contrasting them to commercial landings further allows for a data-based evaluation as to whether the brown shrimp fishery is still biologically sustainable.

In comparable cases, swept-area approaches have been used to determine fish or crustacean production (Kotwicki *et al.*, 2011; Landa *et al.*, 2014; Jansen *et al.*, 2015). We used German and Dutch annual coastal beam trawl surveys (ICES, 2014a) to estimate depth- and area-stratified densities of brown shrimp at the time of peak occurrence (September–October) (Tulp *et al.*, 2012). Generally, when applying a swept-area method, no data transformation is applied, even though the assumption of a normal distribution is not valid (Saville, 1977). The latter was also the case in the brown shrimp densities measured from our survey data. Therefore, we used two different methods to estimate and compare total biomass: (i) a simple parametric method in which total biomass was estimated using area- and depth-stratified density and with surface area of each stratum based on a linear regression, and (ii) a procedure in which biomass was estimated using non-parametric bootstrapping to validate the normal distribution of the mean assumption of the parametric method. Based on the results from the swept-area method, total annual brown shrimp production was calculated after corrections for catchability, gear efficiency, mortality [as a proxy for production to biomass (P/B) ratio (Allen, 1971)], and seasonality. The resulting estimate of the total annual brown shrimp biomass enables comparison with total annual landings in order to evaluate fishing pressure on the stock. Furthermore, by relating annual catches (C) to estimated biomass (B), a time-series of total annual fishing mortality (F) equivalent to C/B was determined and contrasted to existing values.

Methods

To obtain a biomass production estimate, a combination of methods was used. Survey data were used to estimate brown shrimp densities in different areas and depth strata. Densities at the time of the survey (late summer) were raised to the total surface area to calculate a swept-area estimate. Because densities are generally highest at the time of the survey, a factor to convert swept-area estimate in late summer to a mean annual value is needed. For this factor, we used the ratio of the landings per unit of effort (lpue) by the commercial fleet at the time of the survey to the mean annual lpue (ICES, 2015). Other corrections along with their uncertainties were made for catchability and net selectivity. Total annual production was then estimated from the product of the corrected total mean annual biomass and total mortality (Z). Total mortality was calculated using length-based methods (Hufnagl *et al.*, 2010). The different steps in the calculations are explained in more detail below.

Surveys

The Dutch Demersal Fish Survey (DFS) covers the coastal waters (down to 30 m depth) from the southern border of The Netherlands to Esbjerg, Denmark in the north, including the Dutch Wadden Sea, the outer part of the Ems-Dollard estuary, the Westerschelde, and the Oosterschelde (van Beek *et al.*, 1989). This survey has been carried out in September–October since 1970. Sampling along the German and Danish island coasts only began in 1978 and in the German Wadden Sea in 1997 (Table 1). The number of hauls per area was kept as constant as possible (Table 1); in the whole area, a total of 159–451 hauls were taken annually, depending mainly on weather conditions. All hauls were taken during daylight. In several years, some areas were not sampled [i.e. Dutch coastal area 1976 (401, 402, 403), Voordelta 1979 (401) and 2001, German and Danish coast 1998 (404–407)] due to adverse weather. For each haul, the position, date, time of day, and depth were recorded. The Westerschelde, Oosterschelde, and Wadden Sea were sampled with a 3-m beam trawl, while a 6-m beam trawl was used along the coast. The beam trawls were rigged with one tickler chain, a bobbin rope, and a fine-meshed codend (20 mm). Both gears were rigged similarly; only the size of the beam differed. The reason for the different sizes is that a 3-m trawl is more manoeuvrable in the estuaries, where sampling often took place in narrow gullies. This gear would be too light in less sheltered and deeper area; therefore, the 6-m trawl was used farther offshore. The assumption is made that densities derived from both these gears do not differ, although they have never been formally compared. For the calculations of recruitment indices as input for stock assessments, the data from both the 3- and 6-m trawls were treated in a similar combined way (ICES, 2011b). Fishing was restricted to the tidal channels and gullies deeper than 2 m because of the draught of the research vessel. The combination of low fishing speed (two to three knots) and fine mesh size resulted in the selection of brown shrimp >20 mm, smaller species, juvenile fish, and invertebrate epibenthos. Sample locations were stratified by depth.

The German Demersal Young Fish Survey (DYFS) has been carried out in September–October since 1974 in the Wadden Sea areas of the Elbe estuary, North and East Frisian Islands by commercially chartered fishing vessels. A 3-m beam trawl with a mesh opening of 20 mm (stretched mesh) was used as the standard

Table 1. Number of hauls per year and area for the combined surveys used in the analyses

Area	401	402	403	404	405	406	407	408	409	410	411	412	413	414	610	612	616	617	618	619	620	634	638	Total
Surface area (km^2)	986	499	466	1714	1322	1705	1712	306	589	400	624	495	1.398	393	600	135	824	268	223	258	794	88	389	16.186
Year																								
1970	6	11	11	22											23		24	16	10	12	20	31	26	212
1971	9	9	13	19											25		28	14	8	12	22	29	30	218
1972	8	15	11	20											18		25	11	10	10	20	29	28	205
1973	7	9	8	19											18	2	24	11	9	9	22	30	31	199
1974	8	16	11	19											19	7	24	12	10	11	21	31	32	221
1975	8	11	10	19											21	6	25	14	9	10	21	31	26	211
1976															21	7	25	13	10	10	21	26	26	159
1977	10	16	9	23											21	7	26	13	10	11	21	28	27	222
1978	1	15	10	23	8	16	18								21	7	26	13	10	10	21	30	28	257
1979		16	8	12	7	19	19								21		26	13	10	10	21	28	28	238
1980	9	7	10	23	7	16	21								21	7	26	13	10	10	21	27	29	257
1981	10	9	9	25	10	10									19	6	27	13	10	10	21	28	27	234
1982	18	8	9	28	14	22	6								21	7	26	13	10	10	21	28	27	268
1983	18	13	6	15	8	22	6								21	7	26	13	10	9	21	26	27	248
1984	23	13	8	31	15	22	4								22	7	25	12	10	10	21	27	27	277
1985	16	12	9	28	15	20	7								21	7	26	12	10	8	20	26	27	264
1986	17	13	9	28	15	21	5								21	7	26	13	10	9	21	26	27	268
1987	19	13	9	28	15	21	6								17	7	30	13	10	8	23	30	28	277
1988	18	14	8	28	15	22	5								22		26	13	9	8	22	25	27	262
1989	26	14	10	28	10	23	6								21		26	13	10	8	23	40	30	288
1990	25	13	9	28	15	21	6								21		25	13	11	8	23	39	29	286
1991	18	13	9	28	15	21	6								23	5	24	13	10	10	23	30	31	279
1992	26	16	13	28	15	21	6								23	6	26	12	6		28	36	28	290
1993	22	20	9	28	15	21	5								23		27	14	11	8	26	31	27	287
1994	21	16	13	28	15	19	6								24		26	12	10	7	25	36	33	291
1995	17	13	9	25	14	24	6								31		23	15	10	9	26	43	33	298
1996	17	12	10	29	14	21	6								28	6	28	15	10	9	27	43	33	308
1997	17	10	9	28	13				17	13	37	25		8	27		28	15	11	9	27	44	34	372
1998	9	10	8						18	9	33	23		29	28	6	29	15	9	10	27	43	34	340
1999	15	13	8	14	1				10	14	33	25		36	28		31	14	11	10	18	45	35	361
2000	15	7	2	17	10	19	6		16	14	30	23		28	41		26	15	11	10	25	45	41	401
2001		13	5	28	15	19	3		11	11	28	20		23	27		25	14	11	10	26	41	48	378
2002	21	13	8	26	14				13	11	27	23		19	27		25	13	11	8	25	44	41	369
2003	16	14	9	28	15	18	6		9	19	34	18		25	29		27	13	9	9	26	42	36	402
2004	17	13	4	19	15	17	6		11	14	24	23		19	28	6	27	14	10	8	25	40	31	371
2005	17	16	12	30	15	15	8	6	17	12	22		16	25	29	6	25	13	11	9	25	43	36	408
2006	15	14	10	28	15	17	6	5	14	11	23	28		23	28	7	28	16	8	9	29	41	36	411
2007	18	16	13	30	15	17	6		13	14	33		29	24	30	9	25	13	11	8	25	43	36	428
2008	16	11	5	19	11	4	6		15	14	19	19	24	22	30	7	24	12	9	9	30	31	37	374
2009	16	13	9	28	15	16	6		23	9	19	20	29	15	32	6	26	12	10	8	28	44	37	421
2010	17	13	9	26	15	16	6		23	9	29	8	20	21	31	6	24	13	10	6	28	41	36	407
2011	15	12	10	28	15	14	6		16	17	30	16	31	19	32	6	22	14	9	7	28	49	25	421
2012	17	28	9	28	14	16	3		20	11	29	17	41	17	26	7	27	15	8	10	28	43	37	451
2013	16	12	9	21	15	16	6		11	14	24	16	32	20	31	6	26	15	9	10	28	42	37	416
2014	19	14	10	28	15	16	6				31	21	34	21	28	6	29	15	9	11	27	42	39	421
2015	17	13	9	28	15	16	6		25	12	46		34	21	28	6	29	14	9	11	26	97	94	556
Total	664	589	407	1086	485	613	230	11	298	245	551	365	318	415	1144	192	1199	617	449	427	1148	1699	1522	14 674

fishing gear. In total, ca.160 stations were sampled each year, all during daylight. The 15-min tows were carried out with the prevailing tidal current at a towing speed of ca. three knots (Neudecker, 2001). Fishing depth usually ranged from 2 to 15 m. Between 1974 and 1996, shrimp were only measured in three size categories and are, therefore, not included in the analysis. From 1997 onwards, 200 animals (ca. 200 g) were measured from every haul.

Areas are delineated according to tidal basins or other geographic features and defined in the original survey design of the DFS survey (Boddeke *et al.*, 1972) (Figure 1). This division is in accordance with the Trilateral Monitoring and Assessment program (Bolle *et al.*, 2009; Jager *et al.*, 2009) and is similar to the one used by the ICES Working Group on Beam Trawl Surveys to calculate 0 group indices for the plaice stock assessment (ICES, 2014a).

The gear used in the surveys conducted by The Netherlands and Germany differ slightly. A tickler chain is used only in the Dutch DFS. A 3-m trawl is used in the estuaries and a 6-m trawl outside the islands and along the coast in the Dutch DFS, whereas only a 3-m trawl is used in the German DYFS. A formal comparison between the three gears is thus far lacking; therefore, no correction was made to adjust for potential differences in gear efficiency between the two surveys and the 3- and 6-m beam trawls in the DFS. Two areas (405 and 406 in Figure 1) are sampled in both surveys. In these cases, densities from the Dutch DFS were used, because the coverage of hauls was spread more evenly over the different depth strata.

In both surveys, shrimp were separated from the fish and other epibenthos and measured to the mm below (total length). Density per haul was calculated based on the actual trawled distance. Mean abundance per area was calculated for all areas in the period 1970–2015 weighed by surface area for five depth strata (intervals of 5 m) within the subareas. Surface areas of depth strata used were taken from ICES (2011b).

Landings data

Landings data were taken from the annual reports of the ICES Working Group on Crangon Fisheries and Life History (ICES, 2012, 2014b). Landings were reported by country in cooked weight. The landed fraction is normally the result of three sieving processes: (i) on board the vessel to separate the commercial shrimp from other catch (small shrimp, fish, and benthos), (ii) on board after the commercial shrimp were cooked, and (iii) in the auction. Each country only reports the landed fraction of commercial-sized shrimp. Minimum sieve width is 6.5 mm (EG 2406/96) resulting in a minimum shrimp size of 45 mm, but depending on the market situation, wider sieves (e.g. 6.8 mm) are also used. Thus, reported landings of commercial size can be 45 mm or larger. For comparison with biomass production, cooked weight is converted to fresh weight by multiplying landings by a factor 1.18 (ICES, 2007).

Data analysis

Late summer biomass based on the swept-area estimate

Surface areas were calculated in ARCGIS in all ICES DFS areas per 5-m depth strata (0–5, 5–10, 10–15, 15–20, 20–25, and 25–30 m). In all areas, nearly all depth strata were represented (apart from the deepest depth class that does not occur in the Wadden Sea and Wester- and Oosterschelde). Densities of brown shrimp were calculated per year, area (Figure 1), and depth stratum taking into account the area covered per haul by the different gears. Not all depth strata in all areas were sampled every year. By including all strata in the analytical model, values for missing strata/year combinations were predicted based on the model.

The swept-area biomass estimate was calculated in two ways: (i) using a linear model with year, area, and depth strata as predictor variables for two different size classes (30–49 and ≥50 mm) representing small shrimp and the commercial-sized shrimp, respectively, with depth entered as a continuous variable and year and area entered as factors; (ii) using a non-parametric bootstrapping estimator to validate the normal distribution of the mean assumption of the parametric method (only for the ≥50-mm size class). The bootstrapping was conducted following the same sampling scheme as the survey, i.e. the same number of samples was randomly selected (with replacement) within each stratum. In the direct comparison between both methods, area was not used as a stratum (only depth class), because too few samples would then be available per stratum.

Total annual biomass production

The calculation of total annual biomass production was limited to shrimp of commercial size (≥50 mm). According to Polet (2000), all shrimp ≥50 mm are retained by the meshes used in both surveys. Therefore, the correction for selectivity was set at 1. A correction factor for catching efficiency was obtained from Reiss *et al.* (2006). They measured catching efficiency of a 2-m beam trawl at two sites in the German Bight at depths of 25 and 39 m and determined efficiencies for abundance of 31 and 43%, respectively. A value for catching efficiency of the 3- and 6-m beam trawls used in the surveys was never measured; therefore, we used the mean of the two values (37%) reported in Reiss *et al.* (2006) (in muddy sand: 43 ± 6% and coarse sand: 31 ± 7%).

To convert the estimated late summer biomass to the average annual biomass, the ratio of the landings per unit of effort (lpue) in the brown shrimp fisheries in late summer to the mean annual lpue was used (ICES, 2015) The lpue (used here as a proxy for biomass) measured at the time of the survey is assumed to be 1.6-fold ($SD = 22\%$) higher than the average annual biomass.

Annual biomass (B) was estimated with the following equation:

$$\bar{B} = c.f.\sum\nolimits_{n=1}^{\text{nareas}} \left[\sum\nolimits_{i=50}^{L_{\max}} (cpsm_i \cdot A_n \cdot a \cdot L_i^b \cdot S_i)\right]$$

where c is the catch efficiency correction (Reiss *et al.*, 2006), f is the factor converting the late summer biomass to an average annual biomass (Rückert, 2011), n is the area (e.g. 402, 403), i is the length of the shrimp, $L_{\max}$ is the maximum shrimp length, $cpsm$ is the shrimp catch per square meter, A_n is the surface of area$_n$, a and b are parameters to describe the length–weight relationship (ICES, 2007), L is the shrimp length, and s_i is the mesh selectivity for a shrimp of size i (Polet, 2000).

According to Allen (1971), biomass B can be converted to production P if total mortality (Z) is known, according to $Z = P/B$; therefore, $P = Z{\cdot}B$. Total mortality was calculated based on (Hufnagl *et al.*, 2012) and updated for the years after 2006 with updated values for the years 2007–2011 (Temming and Hufnagl, 2015).

Uncertainties in all individual estimates were taken into account, resulting in a minimum and maximum total production estimate. For the swept-area estimate, 95% confidence limits of the regression were used; for catch efficiency, we used an uncertainty of ±10% (27–47%); for Z, we used the lowest and highest of four methods (Beverton and Holt, 1956; Ssentongo and Larkin, 1973; Jones and van Zalinge, 1981; Pauly, 1983) to calculate mortality (Hufnagl *et al.*, 2012).

Fishing mortality (F) was then estimated as C/B, with $C =$ total annual catch and $B =$ total annual biomass production and contrasted with the estimate made by Temming and Hufnagl (2015).

Results

All tested factors (area, depth class, and year) were significant in the linear model predicting the total swept-area estimate (all $p < 0.001$; area: $F_{22,\,14086} = 40.5$; depth class: $F_{1,\,14086} = 316.3$; year: $F_{44,\,14086} = 20.3$), and the model explained 14.3% of the variation. The total swept-area estimate at the time of the survey for small shrimp (30–49 mm) was in the same order of magnitude as that of the commercial size (≥50 mm) and was 7000–38 000 tonnes (Figure 2). The swept-area estimate at the time of the survey for commercial size varied between 4000 and 22 000 tonnes, with a clear peak

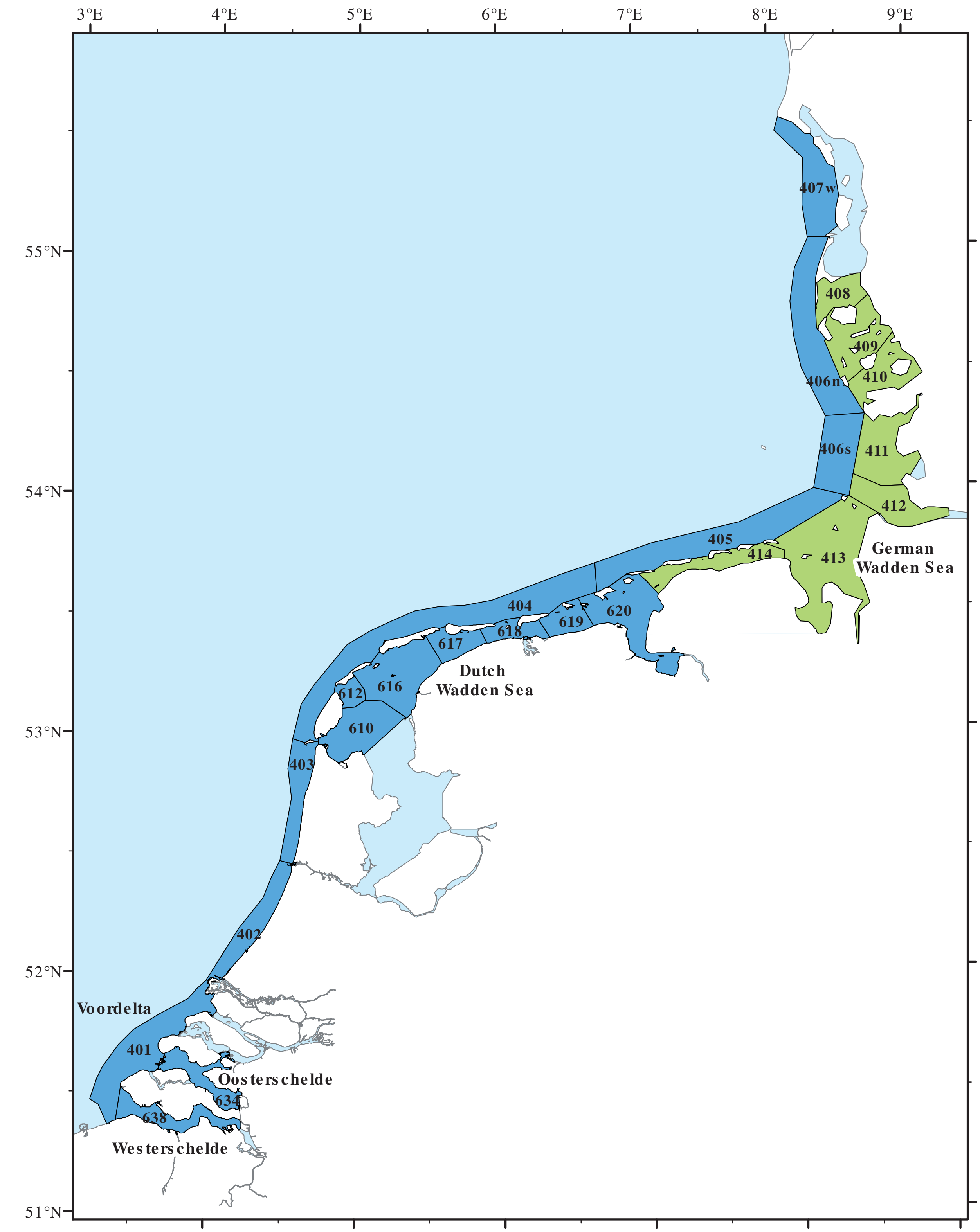

Figure 1. Study area with the survey areas for brown shrimp abundance along the North Sea coasts of The Netherlands, Germany, and Denmark, with areas covered by the Dutch DFS (dark grey) and German DYFS (light grey) indicated. Areas 405 and 406 are (partially) also covered by the DYFS, but only the DFS was used for this analysis.

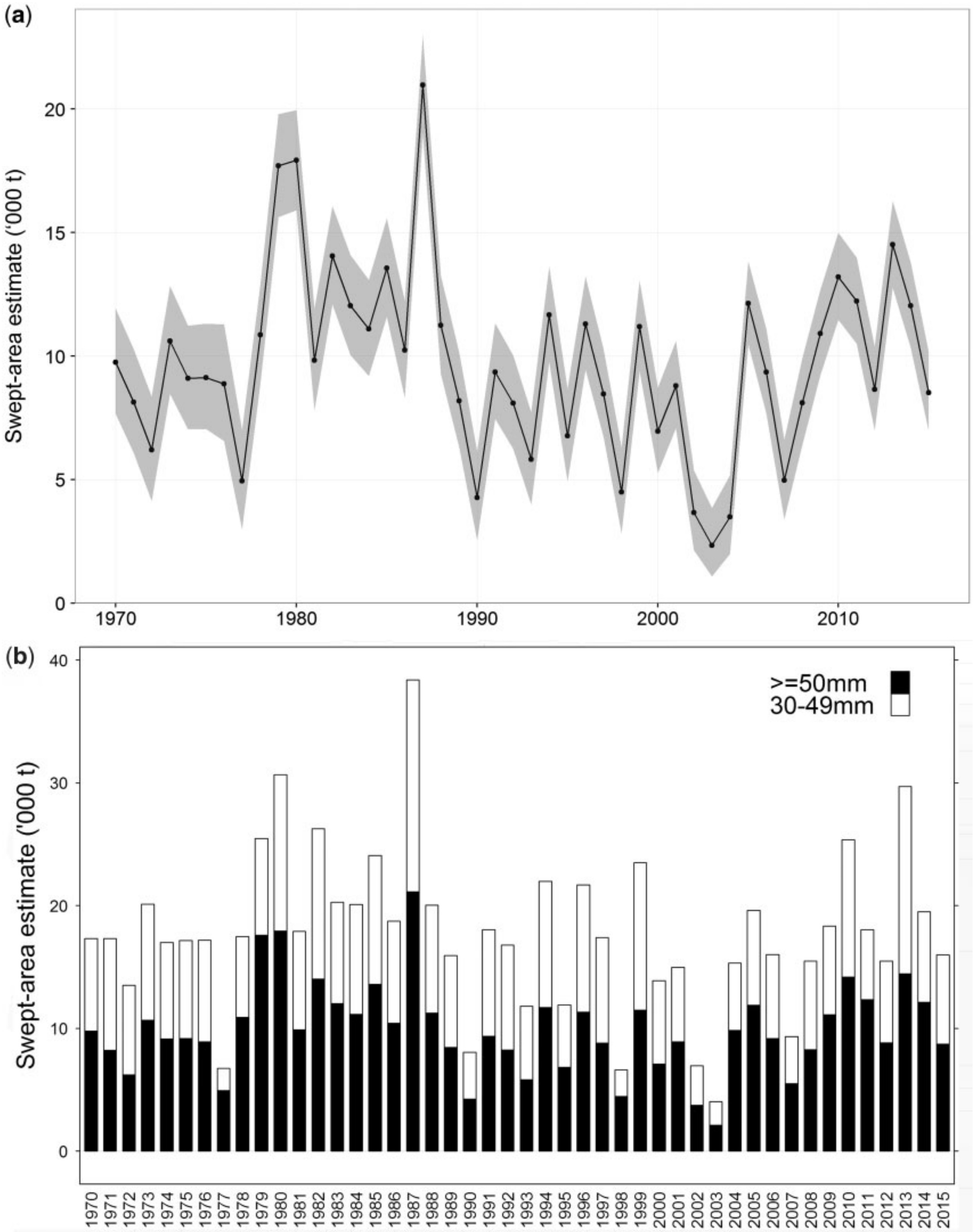

Figure 2. (a) Swept-area estimate and confidence limits of large-sized brown shrimp $\geq$50 mm and (b) swept-area estimate of brown shrimp for two different size classes (30–49 and $\geq$50 mm) (b). Both estimates are based on a linear model and represent results at the time of the survey.

period between 1979 and 1987. Biomass in the 1990s was relatively low, with a slight increase since the early 2000s. The subdivision of biomass estimates over depth zones clearly indicates the importance of the shallower areas for brown shrimp, with a declining proportion of the total estimate in the deeper areas (Figure 3). Despite higher densities, the Wadden Sea and the Wester- and Oosterschelde contribute ca. one-half of that of the coastal areas to the overall biomass due to the smaller surface area.

The non-parametric estimate of the total biomass and its variance are comparable with those of the parametric method (Figure 4). This confirms the central limit theorem assumption of the parametric method that the mean biomass density per stratum follows a normal distribution.

The total annual biomass production (swept-area estimate corrected for catch efficiency, mesh selectivity, seasonality in densities, and mortality based on the parametric method) varied between 38 000 t in 1998 and nearly 216 000 t in 1987, nearly a sixfold range (Figure 5, Table 2). The minimum and maximum estimates indicated that uncertainties are large. Total annual landings have gradually increased since the start of the series and

Table 2. Overview of total landings, mean annual biomass swept-area estimate (corrected for seasonality), *Z* values (mean and according to the four methods; see Hufnagl et al., 2010), and total annual production with uncertainties

		Biomass swept-area estimate (tonnes)			Z							Total annual production (tonnes)		
Year	Annual landings	Mean	Min	Max	Mean	Min	Max	Beverton and Holt (1956)	Jones and van Zalinge (1981)	Ssentongo and Larkin (1973)	LCCC (Pauly 1983)	Mean	Min	Max
1970	10 910	6045	4593	7497	4.7	3.8	6.0	4.5	4.7	4.6	5.5	76 768	50 522	117 056
1971	8324	5053	3614	6493	5.4	3.9	6.3	5.8	5.1	6.0	4.7	74 158	40 943	106 522
1972	9037	3835	2366	5304	5.5	4.4	6.2	5.7	5.6	5.9	5.0	57 294	30 361	85 677
1973	15 556	6636	5152	8120	5.8	5.2	7.0	6.0	5.7	6.2	5.3	103 671	77 946	147 679
1974	19 488	5678	444	7112	5.0	3.8	5.6	5.1	4.7	5.3	4.5	76 178	47 195	103 408
1975	19 098	5696	4241	7152	6.0	5.0	7.3	6.2	5.8	6.6	5.4	92 178	61 432	135 790
1976	24 632	5508	3897	7120	5.3	3.9	7.1	5.4	4.9	5.6	5.3	78 819	44 445	131 442
1977	14 475	3039	1607	4471	5.5	4.4	6.9	5.1	6.2	5.4	5.6	45 514	20 223	79 539
1978	16 995	6785	5427	8143	5.2	4.3	6.7	5.4	5.2	5.1	5.1	95 537	67 907	142 674
1979	22 481	11 051	9655	12 447	4.7	4.2	5.4	4.8	4.6	4.9	4.3	140 808	117 447	174 080
1980	21 990	11 158	9804	12 513	5.5	4.4	6.4	5.6	5.3	5.7	5.7	167 070	123 864	208 810
1981	21 041	6126	4724	7528	6.2	5.3	7.5	6.7	5.8	6.8	5.5	102 239	72 618	147 123
1982	27 540	8746	7406	10 085	5.8	5.1	6.7	5.8	5.7	6.1	5.4	136 948	108 767	174 879
1983	19 868	7471	6097	8845	5.0	3.9	6.2	5.5	4.9	5.1	4.5	100 914	67 984	141 278
1984	14 531	6906	5581	8231	5.7	4.9	6.7	5.7	5.9	5.9	5.2	105 787	79 170	142 405
1985	21 479	8429	7086	9773	5.7	4.4	6.8	6.1	5.5	6.2	5.1	130 104	89 826	171 744
1986	20 581	6362	5024	7700	5.9	4.9	7.2	6.1	5.8	6.1	5.4	101 200	71 489	144 082
1987	23 386	13 076	11 751	14 401	6.1	4.8	7.5	6.6	5.9	6.6	5.4	215 933	161 503	278 967
1988	19 655	6 993	5 643	8344	6.1	4.8	7.3	6.2	6.0	6.5	5.6	114 658	77 915	158 590
1989	19 163	5 106	3 793	6418	6.5	5.2	8.0	6.9	6.5	6.5	6.1	89 770	57 270	132 848
1990	11 188	2 607	1 293	3920	6.6	5.3	8.2	6.2	6.8	6.6	6.8	46 507	19 700	82 936
1991	17 680	5 810	4 485	7135	6.4	5.2	8.2	6.2	6.6	6.6	6.3	100 909	67 380	151 444
1992	18 518	5 087	3 780	6394	7.3	6.4	8.8	7.0	7.0	7.8	7.1	100 050	69 605	145 896
1993	20 785	3 595	2 283	4906	7.6	6.6	9.0	7.3	8.0	7.6	7.4	73 608	43 339	115 024
1994	23 854	7 300	5 992	8608	5.6	5.0	6.2	5.9	5.6	5.6	5.3	110 814	86 595	137 426
1995	26 815	4 189	2 887	5491	6.4	5.4	8.4	6.7	6.3	6.9	5.9	72 993	44 698	120 327
1996	27 055	7 053	5 769	8337	6.5	5.8	7.0	6.5	6.8	6.2	6.4	123 003	96 057	151 739
1997	31 919	5 498	4 272	6723	6.0	5.5	6.4	5.9	6.2	5.9	5.8	88 515	68 037	112 243
1998	26 392	3 023	1 761	4286	4.7	4.0	5.5	4.5	5.2	4.5	4.4	38 028	20 422	61 109
1999	31 852	7260	6018	8501	6.3	5.8	7.0	6.3	6.6	6.2	6.2	123 932	100 385	154 641
2000	28 459	4545	3347	5742	6.5	5.7	7.2	6.6	6.7	6.5	6.2	79 782	55 498	107 000
2001	28 507	5698	4485	6912	4.7	3.7	6.2	4.7	5.3	4.6	4.2	72 519	47 884	110 764
2002	28 712	4069	2843	5294	5.6	5.3	6.0	5.5	5.9	5.4	5.4	61 038	43 371	82 617
2003	32 795	4368	3173	5562	6.7	5.6	7.6	6.6	6.9	6.6	6.5	78 591	51 549	110 132
2004	32 844	5343	4123	6564	5.5	4.7	6.1	5.5	5.8	5.4	5.4	79 516	56 009	103 620
2005	38 454	9675	8548	10 801	5.2	4.6	5.9	5.2	5.6	5.2	4.9	136 587	114 815	165 598
2006	35 609	6066	4893	7240	5.5	4.7	6.4	5.5	5.8	5.6	5.1	90 676	67 114	120 164

continued

Table 2. Continued

Year	Annual landings	Biomass swept-area estimate (tonnes)			Z			Beverton and Holt (1956)	Jones and van Zalinge (1981)	Ssentongo and Larkin (1973)	LCCC (Pauly 1983)	Total annual production (tonnes)		
		Mean	Min	Max	Mean	Min	Max					Mean	Min	Max
2007	34 225	3294	2141	4448	4.6	4.1	5.1	4.4	4.8	4.3	5.0	41 194	25 546	58 740
2008	32 106	5273	4062	6484	4.7	4.2	5.6	4.4	4.9	4.4	5.0	66 769	48 769	94 884
2009	33 875	7015	5836	8195	4.8	4.5	5.2	4.5	5.1	4.5	4.9	90 110	75 297	111 074
2010	35 909	8469	7278	9660	5.6	5.0	6.1	5.6	5.8	5.6	5.6	128 729	105 331	153 803
2011	33 408	7857	6676	9038	4.6	4.4	4.9	4.5	4.8	4.5	4.5	97 383	84 788	113 995
2012	33 605	5432	4277	6587	5.7	5.1	6.4	5.5	6.0	5.5	6.0	84 131	63 074	108 708
2013	34 547	9263	8079	10 448	6.3	6.0	7.0	6.1	6.4	6.1	6.6	157 729	139 382	190 048
2014	37 513	7716	6542	8890	5.3	4.7	6.2	5.6	5.0	5.6	5.1	110 526	89 164	142 130
2015	31 376	5324	4353	6350	5.8	5.3	6.4	5.9	5.7	5.9	5.7	83 390	66 634	105 778

approached the estimated total annual production levels in some years (1977, 1998, 2007).

Values for *F*, as derived from $F = C/B$ values, ranged between 2 and 10 (Figure 6), with a clearly increasing trend from the early 1990s towards 2007 and a stabilization thereafter.

Discussion

The estimate

The swept-area estimate and subsequently the total biomass production estimate are characterized by large uncertainties. Most of the uncertainties originate from the different factors that have been accounted for: catch efficiency, mesh selectivity, and mortality. Another uncertainty not accounted for involves the behaviour of brown shrimp. Using the results from a bottom gear for our estimate, we assume that most shrimp are close to the seabed. However, a vertically resolving stow net sampling scheme carried out in the Jade Bay inlet in the German Wadden Sea (Daenhardt and Becker, 2011) showed that an average of 73% of the total number of brown shrimp present were located above the beam trawl height (0.5 m) (ICES, 2012; Schulte, 2016). The possibility that ascending higher into the water column might be beneficial behaviour in order to make effective use of currents was demonstrated in a modelling study (Daewel *et al.*, 2011; Hufnagl *et al.*, 2014) and was also observed in field (Hartsuyker, 1966) and laboratory (Al-Adhub and Naylor, 1975) investigations. However, we did not correct for the effect that such behaviour might have on catchability, as this behaviour was observed under a specific local tidal situation, and it is unknown whether such behaviour is common throughout the distribution area and when and where brown shrimp make use of it. Under the assumption that 73% of the brown shrimp are not caught in the survey bottom trawl, the biomass estimate and subsequently the production estimate would be at least threefold higher.

Gear efficiency is usually determined by the behaviour of the target species, habitat, and gear characteristics (Hoffman *et al.*, 2009). We used a catch efficiency of 37% (Reiss *et al.*, 2006) in the swept-area estimate. This estimate was derived from a series of three towed 2-m beam trawls. Estimates of the absolute catch efficiency of the gear used in the survey were never carried out, but are crucial in swept-area biomass estimates. An alternative approach would be to use the difference between catches by a traditional trawl and an electrical beam trawl, assuming that an electrical beam trawl would catch 100% of the brown shrimp present in front of the gear (Verschueren *et al.*, 2012). Brown shrimp catches by the electric shrimp trawl can be up to 50% higher than those by a traditional shrimp trawl (Verschueren *et al.*, 2012), translating into a catch efficiency of 66% of the traditional gear. Using this estimate instead of 37% would produce a nearly 50% lower swept-area estimate. Apart from the translation from the relative densities to absolute densities, another uncertainty factor is the comparability of the different gears used: the 3- and 6-m beam trawl used in the DFS and the 6-m beam trawl in the DYFS. The different gears used could potentially cause structural differences in densities caught, which stresses the need for formal tests to be carried out in the near future.

In comparing biomass production to total landings, we assume that landed brown shrimp are always in the size range $\geq$50 mm. However, the sieving process at the auctions adapts to availability, and wider sieves are applied in years with a good supply of large-sized shrimp and smaller minimum sizes when shrimp are small.

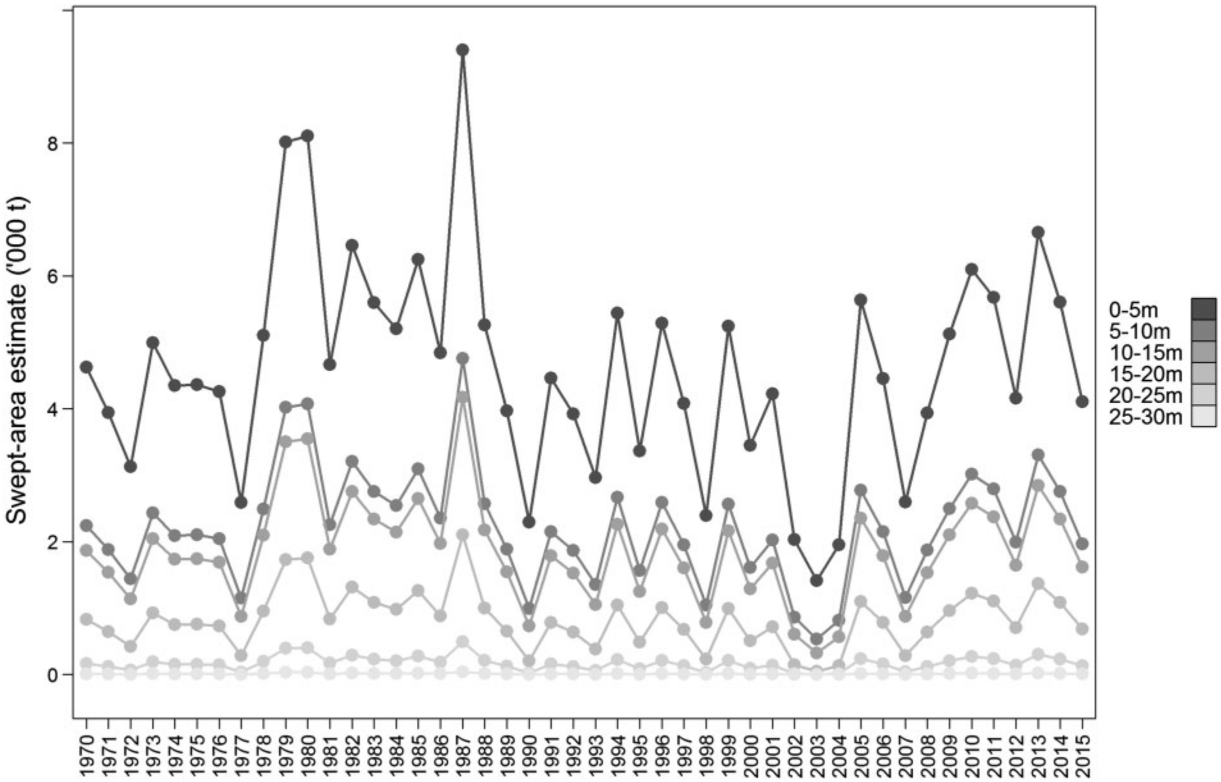

Figure 3. Swept-area estimate of brown shrimp $\geq$50 mm based on a linear model by depth class.

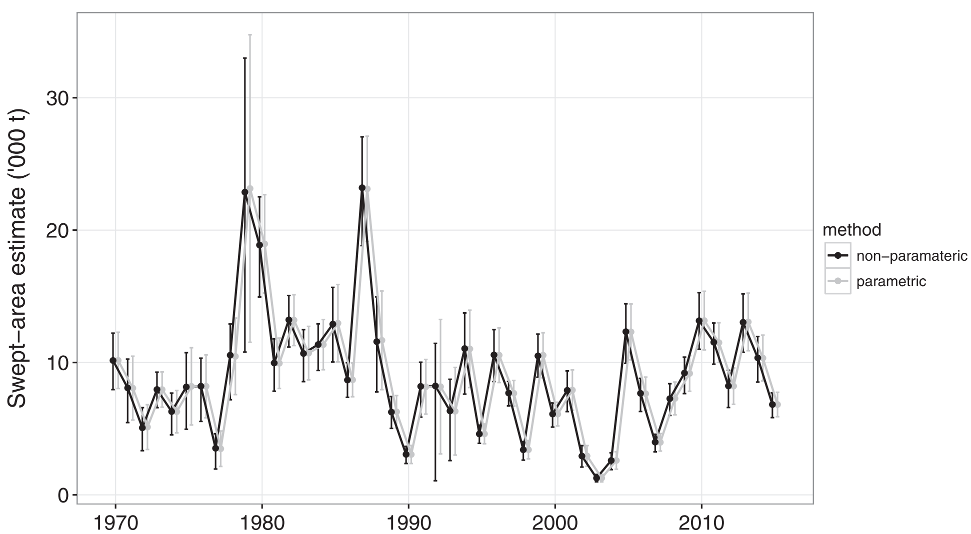

Figure 4. Comparison of biomass estimated from the linear model (parametric) and the bootstrap approach (non-parametric).

Based on the 2014 survey data, 38% (in numbers) and 26% (in biomass) of the brown shrimp caught in the DFS were between 45 and 50 mm and 62% (74%) were $\geq$50 mm. Between 45 and 60 mm, the biomass decreases an average of 5% with each mm. A shift from a sieving width from 6.5 mm (corresponding to about 45 mm total length) to 6.8 mm (49 mm total length) would, therefore, lead to a change in landed biomass of 15%. This means that uncertainties are also included in the landings data and that in years when biomass production was estimated close to the landed biomass, the sieving width at the sieving stations in the auctions may have been reduced. If a similarly shifted minimum size would have been applied to the biomass estimate, the resulting total biomass production would have been higher in such years.

A swept-area estimate based partially on the same data for the period 1970–1999 was calculated earlier by Welleman and Daan (2001). They obtained much higher biomass estimates (9000–60 000 t vs. 4000–22 000 t) mainly for two reasons: (i) they included all shrimp, not only the commercial sizes ($\geq$50 mm), and (ii) the distribution area used for the shrimp biomass calculations was

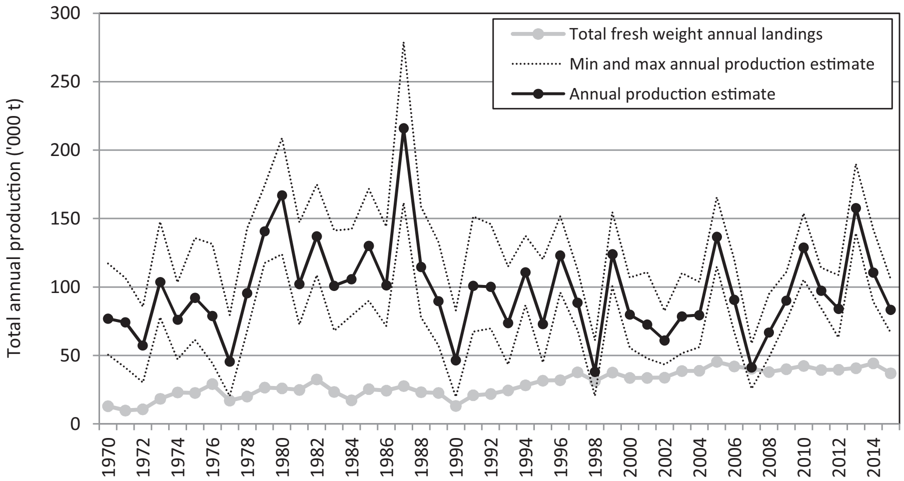

Figure 5. Total annual production in the period 1970–2015 and total landings (corrected from cooked to fresh weight by a factor 1.18; ICES, 2007) by the Northwestern European brown shrimp fishing fleet as estimated based on the swept-area estimate calculated using the linear model. Indicated are the mean, minimum, and maximum estimates based on uncertainties as described in the text.

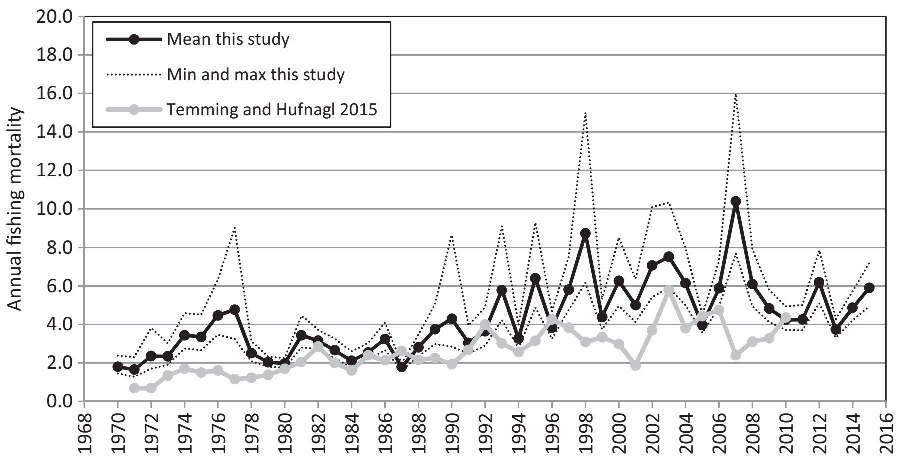

Figure 6. Annual mean fishing mortality (*F*) with minimum and maximum as estimated by C/B and independently estimated F from Temming and Hufnagl (2015).

much larger and included areas (ICES roundfish area VI) well outside the depth limit of 30 m applied in our study. We considered only brown shrimp of commercial size ($\geq$50 mm), because the fishery targets large brown shrimp and total mortality estimates were available only for this size class (Hufnagl *et al.*, 2010).

There is no generally accepted method for ageing brown shrimp, and all methods for estimating productivity rely on size- or growth-related methods. Independent estimates of biomass (and productivity) are, therefore, of high importance in assessing stock status in relation to fishing effort. To improve these estimates, more reliable measures of the afore-mentioned parameters are required. This includes a better understanding of the available and catchable fraction of shrimp and the seasonal variability in biomass. In relation to productivity, the factor with the highest impact is total mortality (*Z*) as it scales between 2.8 and 9.0 among years and between methods. Several modelling exercises and validation analyses have been performed to reduce and enumerate uncertainties (Hufnagl *et al.*, 2010, 2012). The estimated total fishing mortality as derived in this study from *C/B* ranges between 2 and 10 year^{-1} and provides an estimate of *F* independent of the one published by Temming and Hufnagl (2015). They estimated *Z* from size-composition data from the DFS and DYFS (Hufnagl *et al.*, 2010) and used predation estimates by cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) together with commercial landings to partition independent estimates of total mortality into fishing and predation mortality. The estimates of *F* by Temming and Hufnagl (2015) varied from 0.68 year^{-1} in 1968 to 5.8 year^{-1} in 2003.

In this study, *F* was determined as *C/B* and in the earlier approach by Temming and Hufnagl (2015) as $F = C/(C + Pred) \times Z$, where *Pred* is the amount of shrimp eaten by predators. As *C* is the same in both estimates, this will not cause the difference, but it needs to be kept in mind that *C* does not include the cooked and discarded fractions in either estimate. This means that either (i) *B* is underestimated here or (ii) *M* was overestimated, and/or (iii) *Z* was underestimated by Temming and Hufnagl (2015). Underestimating *Z* could occur if the surveys did not sample the smaller shrimp in a representative way, which would bias the length-based Z estimates towards a lower value compared with the real one. However, no spatial Z differences were observed (Hufnagl *et al.*, 2010). M being overestimated is less likely as no other predators than cod and whiting were considered when determining the F estimate. A final possibility for the difference between the two estimates being caused by an overestimate of M is that the swept-area estimate is too low, caused by the earlier mentioned uncertainties in the estimate. Assuming, e.g. that 50% of the population is located in the water column would already halve the F estimate. So, giving exact F levels is difficult with both methods as they are all indirect and include various uncertainties. More interesting is the increasing trend in both estimates, indicating an increase in fishing mortality despite a stable (or in some countries even decreasing) fleet size and a stable fishing effort (ICES, 2015). This suggests that an unmonitored increase in fleet efficiency must have occurred, as also discussed by Temming and Hufnagl (2015). Understanding the pressures acting on the brown shrimp population thus requires a better understanding of the increasing catch efficiency. Furthermore, the earlier mentioned uncertainties in Z, F, M, and B need further investigation, mainly the seasonal and spatial distribution of the shrimp, the efficiency of the used gears, and the number of shrimp in very shallow areas or areas deeper than 40 m.

Implications for management

In relation to annual brown shrimp catches, which have above 30 000 t in recent years, the standing stock biomass of 10 000–15 000 t is relatively low. On the other hand, productivity of the stock is relatively high due to the short lifespan of the species. The maximum age of brown shrimp is <2 years, and the catch is mainly comprised of age 0 and 1 shrimp, which partly explains the variability in catches between years and areas. Fish and larger crustaceans normally have much lower production rates than brown shrimp. According to Allen (1971), P/B equals Z; therefore, production in shrimp is ca. fivefold higher than biomass (Hufnagl *et al.*, 2010). For larger or pelagic fish like cod, haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), or sandeel (Ammodytidae), Z is about 0.3 [stochastic multispecies model (ICES, 2011a)]; therefore, biomass is ca. threefold higher than production. In the latter case, the fisheries are based on biomass and how many fish are available. For brown shrimp, the fisheries are based on recruitment and the productivity of the whole population.

Our analyses showed that, at least in some years, the major part of the total biomass production of commercially sized brown shrimp equals the amount exploited by the fishing fleets. In years when natural predators were still highly abundant, the biomass consumed by these predators amounted to 2- to 20-fold the amount taken by fisheries (Welleman and Daan, 2001). With the disappearance of the major predators—the larger gadoids—the situation has changed markedly. Concurrent with the diminishing gadoid stocks, fishing pressure for brown shrimp has increased; since 1992, fishing mortality is three- to fivefold higher than natural mortality (Temming and Hufnagl, 2015). However, a major difference between the estimates by Welleman and Daan (2001) and Temming and Hufnagl (2015) is that the former included the total number of shrimp in all size classes, while the latter and also this study used only shrimp larger than (Temming and Hufnagl, 2015) or equal to (this study) 50 mm.

Based on the same data from the period until 1999, Welleman and Daan (2001) concluded that there was no indication that the brown shrimp stock is fished at unsustainable levels. Temming and Hufnagl (2015) updated their analysis and found that the ratio of natural vs. fishing mortality has reversed, compared with the period analyzed by Welleman and Daan (2001). Our independent estimate of fishing mortality based on catch/biomass is similar to that of Temming and Hufnagl (2015), confirming their conclusion. In addition, a yield-per-recruit model (Beverton and Holt, 1956) indicated that the current fishing intensity potentially results in growth overfishing (Temming and Hufnagl, 2015).

Brown shrimp are characterized by a high biomass production rate and clearly fulfill an important ecosystem function. The one factor that is very different from the beginning of the time-series is the vast decline in the main predator stocks (cod and whiting) to very low levels since the 1990s. Both species suffered from high fishing levels, and reduced recruitment was related to a reduction in their main prey: large copepods (Beaugrand and Kirby, 2010; Kristiansen *et al.*, 2014). Temming and Hufnagl (2015) suggested that, in addition to the lower levels of gadoid predators, the overlap with the brown shrimp distribution area and that of their predators may also have decreased as a result of the lower tolerance for the increasing temperatures by cod and perhaps also whiting. Although recovery of gadoid stocks to pre-2000 levels is not likely (Kirby *et al.*, 2009), a return or spatial shift of these predators or an increase in other potential predators that fill the niche may change the situation drastically. Although gadoids are traditionally the most important predators in terms of biomass consumed, there are more fish species for which brown shrimp are an important prey. Generally, such predators take the smaller-sized shrimp (<30 mm), mainly due to the fact that these predators are small sized, even at the adult stage, e.g. sand goby (*Pomatochistus minutus*), hooknose (*Agonus cataphractus*), viviparous eelpout (*Zoarces viviparous*), common seasnail (*Liparis liparis*), and rock gunnel (*Pholis gunellus*) (Kühl and Kuipers, 1978). Species large enough to also take larger brown shrimp (≥50 mm) besides cod and whiting are grey gurnard (*Eutrigla gurnardus*), dab (*Limanda limanda*), bib (*Trispoterus luscus*), bullrout (*Myxocephalus scorpius*), and five-bearded rockling (*Ciliate mustela*). But even these species take predominantly the smaller shrimp (<50 mm) (Hislop *et al.*, 1991). Given the timing of the life cycle of shrimp and the growing season for fish, most predation is on small-sized individuals in the growing season in summer before commercial fishing begins targeting the larger-sized shrimp in autumn. An increase in predation pressure caused by increasing brown shrimp predator populations will likely affect the stock size of brown shrimp in autumn (Siegel *et al.*, 2005). Whether fishing pressure can also reduce brown shrimp available to predators in the next growing season is, however, unclear.

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