

Fluctuations of brown shrimp *Crangon crangon* abundance in the western Dutch Wadden Sea

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ABSTRACT: Long-term trends in brown shrimp *Crangon crangon* abundance were studied near the entrance of the Dutch Wadden Sea using a 34 yr time series of fyke net catches. A general trend of increasing abundance was observed. In autumn, brown shrimp abundance was 5 times greater than in spring, and interannual fluctuations were also more pronounced. Biotic and abiotic conditions showed effects with time lags of up to 1 yr, which is consistent with the species' life cycle. The population responded rapidly to changes in environmental conditions: abrupt declines after adverse conditions, as in spring 1999, were followed by steep recoveries in the following autumn. Two hypotheses were tested and discussed: (1) autumn recruitment is related to predator abundance and temperature during previous warmer seasons, and (2) overwintering adult abundance is determined by predation pressure and abiotic conditions in winter. In general, predator abundance was the main factor correlated to brown shrimp abundance, especially in autumn. Multiple linear regression modelling showed that predators altogether accounted for up to 55 % in spring and up to 85 % in autumn of the explained variance. Previous winter conditions such as sunshine duration, salinity and fresh water discharge, and the North Atlantic Oscillation Index (NAOI) were also correlated with autumn abundance. Yet, temperature conditions during the previous growing season did not determine the autumn stock size. Winter sunshine duration and the winter NAOI were correlated with spring stock size. Additionally, temperature and salinity were relevant factors affecting abundance during spring. A significant positive relationship between spring and autumn abundance and annual commercial landings was also found.

KEY WORDS: Long-term trends · *Crangon crangon* · Dutch Wadden Sea

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INTRODUCTION

The brown or common shrimp *Crangon crangon* is one of the most abundant benthic species in shallow soft bottom areas along the European coast (Tiews 1970, Campos & van der Veer 2008). Populations show a clear genetic structure, with distinct NE Atlantic and Mediterranean populations (Luttikhuisen et al. 2008). Due to its high abundance, *C. crangon* forms a key component of the trophic web: it is an important food source for several predators including fish, crustaceans and shorebirds (Pihl 1985, Henderson et al. 1992, del Norte-Campos & Temming 1994, Walter & Becker 1997) and, in turn, it preys heavily upon numerous

benthic species such as bivalve spat and juvenile flatfish (Pihl & Rosenberg 1984, van der Veer et al. 1991, 1998, Ansell & Gibson 1993, Oh et al. 2001, Amara & Paul 2003). In addition to its important ecological role, brown shrimp is a valuable fisheries resource, especially around the North Sea (Polet 2002, ICES 2008).

In the Dutch Wadden Sea, situated at intermediate latitude within the brown shrimp geographic distribution, egg-bearing females can be found all year round, although mainly in summer and winter (Boddeke & Becker 1979, Boddeke 1982, Kuipers & Dapper 1984). The summer generation might be subject to heavy predation pressure resulting in high mortality and low contribution to the fisheries standing stock (Kuipers &

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Dapper 1984). In contrast, the larvae originating from winter eggs migrate into shallow nursery grounds where they settle in spring/summer (Boddeke & Becker 1979, Boddeke et al. 1976, Feddersen 1993) and grow and increase in mass until autumn (Boddeke 1976, Kuipers & Dapper 1984, Beukema 1992, Cattrijsse et al. 1997). Most shrimps reach maturity in the first autumn of life, migrate to overwintering grounds and are recruited into the commercial fishery. Part of the winter generation survives their first winter, returning to the nurseries the following spring when they again become available to the fishery. At this time, the new winter generation also appears (Kuipers & Dapper 1984).

Despite these seasonal fluctuations, *Crangon crangon* is consistently highly abundant (Kuipers & Dapper 1984, Beukema 1992) and hence recruitment, measured as the number of juveniles joining the reproductive population, must be highly successful almost every year. However, the processes underlying recruitment of *C. crangon* juveniles to the adult stock are not clearly understood. Food availability (Broekema 1942, Lloyd & Yonge 1947, Beukema 1992), predation pressure (Cattrijsse et al. 1997) and environmental conditions such as water temperature (Ehrenbaum 1890, Havinga 1930, Boddeke 1975, Boddeke et al. 1976, Kuipers & Dapper 1984, del Norte-Campos & Temming 1998), salinity (Broekema 1942, Henderson & Holmes 1987, Spaargaren 2000), light intensity or day length (Spaargaren 2000) and dissolved oxygen (Attrill et al. 1999) have been found to correlate with species recruitment.

A number of studies on the abundance of brown shrimp at intermediate latitude within its geographical distribution, based on extensive time series of respectively 12 (Attrill et al. 1999), 30 (Boddeke 1968, Driver 1976, Welleman & Daan 2001) and 40 yr (Spaargaren 2000) suggested that predation pressure might be the most important source of mortality (Henderson & Holmes 1989), though top-down control alone seems insufficient to explain recruitment regulation. In German waters, a 30 yr study showed recently that the abundance of *Crangon crangon* in autumn was mainly influenced by river in-flow, winter water temperature and the Winter North Atlantic Oscillation Index (WNAOI) (Siegel et al. 2005). Nevertheless, none of these factors was found to influence brown shrimp abundance in spring (Siegel et al. 2005). In contrast, in the Bristol Channel, the number of recruits was found to be negatively correlated with the WNAOI in autumn and positively related to river run off and water temperature from January to August (Henderson et al. 2006). The severity of the winter and hence, winter temperature, has also been identified as a determinant for interannual oscillations in brown shrimp abun-

dance: after severe winters, *C. crangon* abundance is much lower than beforehand. This is probably due to emigration to deeper (Beukema 1979) offshore waters (Boddeke 1975, 1976), causing later arrival of the new generation (Beukema 1992).

Following juvenile abundance is difficult due to their presence over large areas and their continuous emigration to deeper waters as they grow. Only a few studies provide reliable information on juvenile abundance (del Norte-Campos & Temming 1998, Spaargaren 2000) and, therefore, to understand the key processes determining recruitment, we can presently only rely on available long-term data sets on adults. In the western Dutch Wadden Sea, near the island of Texel, a long-term fishing programme started in 1960. Fyke catches from this still ongoing project provide information on the abundance of adult brown shrimp and several of its predators. Seasonality in adult *Crangon crangon* abundance in this area is known to peak in spring and autumn (Spaargaren 2000), where autumn abundance represents emigration of mature shrimps towards overwintering grounds in the North Sea, and spring abundance corresponds to the immigration of adult shrimps returning to the shallow waters of the Wadden Sea after the winter (see Fig. 1). In the present study, we followed the approach of Spaargaren (2000), focussing on abundance of adult shrimps in spring and autumn. However, we expanded the analysis of Spaargaren until 2007, applying a thorough statistical analysis. For the first time, a 34 yr time series of this area is studied in relation to a number of abiotic and biotic variables to understand the fluctuations of brown shrimp stocks over the course of time. The study site is particularly important because it is a turning point of passage between 2 areas of different ecological significance for the species: seawards, towards the overwintering areas in the North Sea; and inwards, towards the shallow nursery grounds of the Wadden Sea. Therefore, the aim of the present paper was to analyse which physical and biotic factors influence *C. crangon*'s abundance and its seasonal and interannual fluctuations at the entrance of the Dutch Wadden Sea. The following hypotheses were defined:

(1) H_0 : The abundance of adults in autumn is determined by the abundance of predators and prevailing water temperature during the growing season.

(2) H_0 : The abundance of overwintering adults in spring is determined by predation pressure and environmental conditions during the winter.

The parameters used to test these hypotheses included predator abundance (as an indicator of predation pressure) and environmental variables which might reflect the seasonal conditions, such as water temperature, salinity, sunshine duration, daily precipitation, fresh water flow into the Wadden Sea and the North Atlantic Oscillation index (NAOI). Additionally,

the relationship between brown shrimp autumn and spring abundances and its commercial landings was analysed.

MATERIAL AND METHODS

Biological time series. Monitoring started in 1960 near the southern part of Texel, de Hors, in the Marsdiep, at the entrance to the Dutch Wadden Sea (Fig. 1) and has been continued ever since. Fishing takes place using a passive trap of the fyke net type (Nédélec 1982). This 'fyke-kom' or 'kom-fyke' is a combination of a pound net and a fyke supported by wooden poles. It has a leader of 200 m running from above the high water mark into the subtidal region where 2 terminal chambers collect and catch fish and crustaceans (see Fig. 1 in van der Veer et al. 1992). The mesh-size of the leader and the 2 chambers is 10×10 mm. The tide in the area is dominated by the semidiurnal lunar tide and the tidal range varies between 1 and 2 m depending on conditions (neap versus spring tide, day versus night, weather conditions). Normally, tidal current speed in the fishing area does not exceed 1 m s^{-1} , except for periods with strong wind stress.

During part of the winter, the kom-fyke is removed to avoid possible damage by ice floes and in summer, large amounts of jellyfish or macroalgae occasionally clog the net. Therefore, we focus mostly on 2 periods for which there is data for all the years: spring (between April and June) and autumn (between September and November). During these periods, the kom-fyke was usually emptied every morning from Monday to Friday irrespective of the tidal phase, except during bad weather conditions. When catches were low, the net was emptied every other morning. Only samples representing fishing periods of less than 48 h were considered for the present analysis following van der Meer et al. (1995), since longer periods may have resulted in net clogging or in losses due to decay or consumption (predation and cannibalism). Apart from wind and tidal influence, catching effort (during spring and autumn) can be considered constant. Therefore, fyke catches were assumed to reflect the species abundance.

All fyke net catches were sorted immediately and identified to species level. Individuals were counted for each species. However, when numbers were large, total wet mass was determined by species. Prior to data analysis, masses were transformed into counts using a fixed ratio, i.e. a fixed mean individual mass based on actual measurements (minimum 100 individuals). All information was stored in a database for further analysis. Information on daily abundance (individuals, ind. d^{-1}) of brown shrimp (CRANG) and potential predators

grouped at Order level were then extracted from the database and mean daily abundances were determined for each season (see below). The potential predators included Clupeiforms (CLUP), Gadiforms (GAD), Perciforms (PERC), Scorpaeniforms (SCORP), Pleuronectiforms (FLAT) and Decapods (CRAB) (Tiews 1970, De Vlas 1979, Pihl 1985, Henderson & Holmes 1989, Henderson et al. 1992, Hamerlynck & Hostens 1993, Berghahn 1996, Cattrijssse et al. 1997).

The present study was based on the data collected between 1974 and 2007, a period with consistent brown shrimp observations. To test the 2 hypotheses stated above, the respective response variables were defined as the brown shrimp abundance in autumn (representing adults emigrating towards the North Sea) which was determined as the mean catches from September to November, and the abundance in spring (representing immigrating adults, returning to the Wadden Sea from April) which was determined as the mean catches of April to June. Summer (July and August) and winter

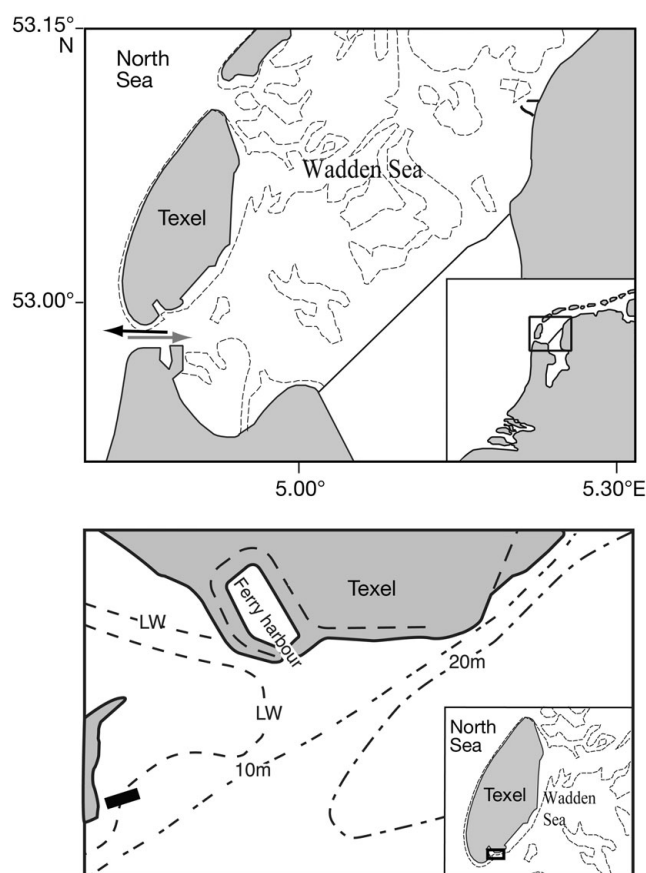


Fig. 1. *Crangon crangon*. Sampling location near the island of Texel (western Dutch Wadden Sea, The Netherlands). Upper panel: migration of adult shrimps. Inward (→) to the Wadden Sea in spring, outward (←) to the North Sea in autumn. Lower panel: fyke net position (black bar) at the entrance of Mok Bay. LW: low water mark

(from December to March; only available for some months in 18 of the 34 yr) data were used as parameters to evaluate possible effects of past shrimp abundances on the 2 response variables. Spring and summer were considered as the growing seasons.

Environmental variables and indices. The environmental variables chosen reflect to some extent the season's conditions and included water temperature, salinity, sunshine duration, daily precipitation and Lake IJssel fresh water discharge into the Wadden Sea. Time series of water temperature (°C) (van Aken 2008a) and salinity (van Aken 2008b) at the Marsdiep area, Texel, were available for the entire monitoring period. Seasonal temperature and salinity were determined by averaging respective monthly means, over the same seasons as for the biological data.

The NAOI, which reflects the large-scale pattern of climate variability in the North Atlantic Ocean, is determined by the difference between the normalised sea level air pressure between the Azores and Iceland (Jones et al. 1997) and was also used as a variable in the analysis. NAOI data was taken from the NOAA/National Weather Service (www.cpc.noaa.gov/index.php). The WNAOI and extended WNAOI were determined as the average NAOI from January to March and December to March, respectively. An average spring and autumn NAOI was also calculated with data from April to June and September to November, respectively. Meteorological information, which included sunshine duration (SUN, 0.1 h) and total daily precipitation (DAYPREC, 0.1 mm) was obtained from the Royal Netherlands Meteorological Institute. Data on the Lake IJssel fresh water out-flow (DEBIET, m³ s⁻¹) into the western Wadden Sea at the Afsluitdijk area was obtained from van der Hoeven (1982) for the period 1960 to 1975 and from Rijkswaterstaat for the period 1976 to 2007.

For the period 1973 to 1994, annual commercial brown shrimp landings (LANDINGS, t) from the North Sea were obtained from producer organisations (I. Tulp pers. comm.) and for the period 1995 to 2007, the information was taken from the logbooks of the Dutch fleet (VIRIS data base; Dutch Ministry of Agriculture, Nature and Food Quality), which until 2003 also included landings in foreign harbours.

Data analysis. Data were log-transformed, if necessary, to achieve approximate normal distributions. General trend, seasonal trend and serial correlation in the spring and autumn shrimp catch data were analysed by means of an autoregressive moving average (ARMA) (p , q) time-series model (Brockwell & Davis 1996). To fit the ARMA noise model, the sequence of observations has to constitute a weakly stationary process, i.e. a process with constant mean and variance. If necessary, data have to be transformed first in order to achieve stationarity. The noise model

was chosen by examining the sample and residual autocorrelation functions (ACF) and partial autocorrelation functions (PACF), and model parameters were estimated. The best of a series of alternative model complexities was selected based on the minimum biased-corrected Akaike's information criterion AIC_C (Hurvich & Tsai 1989). For a detailed description of the ARMA modelling steps see Chapter 5 of Brockwell & Davis (1996).

A possible effect of previous brown shrimp abundances on seasonal observations was studied for the spring and autumn data sets separately. Analysing series of data from the same season, only long-term temporal relationships (yearly lags) could be examined. To assess medium-term seasonal effects, correlations with variables from previous seasons were also computed. Therefore, spring and autumn shrimp abundances were also correlated to biotic and abiotic data from previous seasons, allowing assessment of the effects of past population (previous seasons' shrimp data) and predator or environmental conditions.

Cross-correlations between the seasonal shrimp abundances and abundances in the preceding spring and autumn seasons were computed. Cross-correlations were also computed for the seasonal shrimp abundances and other biological (predator abundances) and environmental variables. This analysis not only provided correlation values for time series but also showed possible temporal delay in correlation. Correlations were computed for all biological and environmental variables. A list of these variables and their main statistics can be found in Appendix 1.

The influence of one or more different biotic and abiotic variables on brown shrimp abundances in spring and autumn was studied through multiple linear regression modelling (McCullagh & Nelder 1983). The functions relate spring or autumn shrimp abundances as response variable with seasonal predator abundances and seasonal environmental conditions. To test the hypotheses mentioned above, including possible delayed responses of shrimp abundances to the predictor variables, the latter were taken from the response period and from previous seasons. Analysis for shrimp spring abundances considered: (1) shrimp data from the previous autumn and the previous spring; (2) predator and (3) environmental data from the same period as the response variable, from the previous winter (when available) and the previous autumn (see Appendix 1). Analysis for shrimp autumn abundances considered: (1) shrimp data from the previous spring and the previous autumn, as well as (2) predator and (3) environmental data from the same period as the response variable, from the previous winter (when available), the previous summer and previous spring. Since biological winter data were scarce (only avail-

able for 18 yr), 2 subsets were considered for each season: one considering only data available for the whole sampling period, and a second including shrimp and predator winter data but consequently with less observations. Interaction terms were not considered to keep the number of predictor terms manageable and model selection straightforward.

To avoid the pitfalls of stepwise model selection, we performed an all-subsets regression (Miller 2002) calculating models with all possible combinations of a given size (i.e. including 1 predictor, 2 predictors, etc.). Considering sample sizes, we tested models with up to 10 predictors for the first dataset ($n = 34$) and with up to 7 predictors for the second ($n = 18$). The best 2 models of each size were submitted to leave-one-out cross-validation to aid model choice. Final models were chosen aiming at maximum parsimony and minimum cross-validation error, as well as inclusion of consistently chosen predictor variables. The relative importance of each predictor variable was determined by averaging sequential sums of squares over all orderings of regressors (Lindeman et al. 1980). Residuals were tested for normality and for autocorrelation.

Time-series analysis was undertaken in ITSM (Interactive Time Series Modelling, Hyndman 1994) and all other statistical analyses were performed using R (R Development Core Team 2005).

RESULTS

Seasonal and inter-annual variability in shrimp abundance

In autumn brown shrimp abundance in the Wadden Sea was approximately 5 times (mean abundance) or 3 times (median abundance) higher than in spring (Fig. 2, Appendix 1). Maximum abundance in spring occurred in 2000 (25 ind. d^{-1}), with peaks in 1986, 1987 (10 ind. d^{-1} in both years), 1998 (11 ind. d^{-1}), 2001 (22 ind. d^{-1}), 2002 (13 ind. d^{-1}) and 2006 (12 ind. d^{-1}). The highest catch in autumn was observed in 1999, reaching 220 ind. d^{-1} on average. Other peak abundances were observed in 1987 (52 ind. d^{-1}), 1991 (84 ind. d^{-1}), 1998 (94 ind. d^{-1}) and 2001 (72 ind. d^{-1}). Minimum spring abundance occurred in 1984 when no brown shrimps were captured. However, spring abundance was in general very low (6.1 ind. d^{-1} on average)

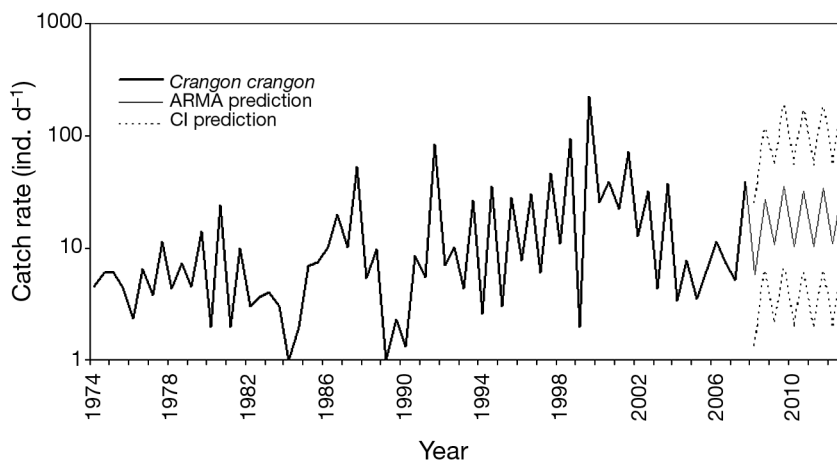


Fig. 2. *Crangon crangon*. Observed mean spring and autumn catch rate in the Dutch Wadden Sea and autoregressive moving average (ARMA) forecast (logarithmic y-axis) with 95 % confidence intervals (CI)

and average values of <4 ind. d^{-1} were detected in several years (1976, 1977, 1980 to 1983, 1989, 1990, 1994, 1995, 1999, 2004 and 2005). The lowest autumn abundance recorded was also in 1984 (0 ind. d^{-1}) with low values continuing for the following 2 yr.

The shrimp abundance data series showed an increasing trend, particularly until the early 2000s (Linear regression model 1975 to 2000: $p = 0.001$, adjusted R^2 0.17; 1975 to 2007: $p = 0.003$, adjusted R^2 0.12), and a seasonal component reflecting the differences between spring and autumn. The linear trend and seasonal component were fitted to the transformed data using ordinary least-squares. The resulting linear trend for the log-abundances $S(t) = 0.0196t + 1.4864$ (t , time in half yr periods), corresponds to an average increase of 1.02 ind. d^{-1} yr^{-1} for untransformed abundances. The seasonal components were -0.58277 and 0.58277 for spring and autumn, respectively. The residual ACF and PACF (Fig. 3) obtained after the linear trend and the seasonal signal were subtracted from the data and showed that an ARMA (2, 2) model fitted the data well. This means that only data from the previous year (1 spring and 1 autumn season) had a significant correlation with each observation. The obtained residual ARMA model was:

$$X(t) = 0.6176 X(t-1) - 0.3665 X(t-2) + Z(t) - 0.5617 Z(t-1) + 0.8028 Z(t-2) \quad (1)$$

with a white-noise variance of 0.5586 and an accuracy parameter of 0.0012. A forecast for the 5 yr following the sample period (Fig. 2) shows the increasing trend and the forecast uncertainty.

The positive correlation between shrimp abundances and those observed during the previous year, found in the time-series analysis was also found in the

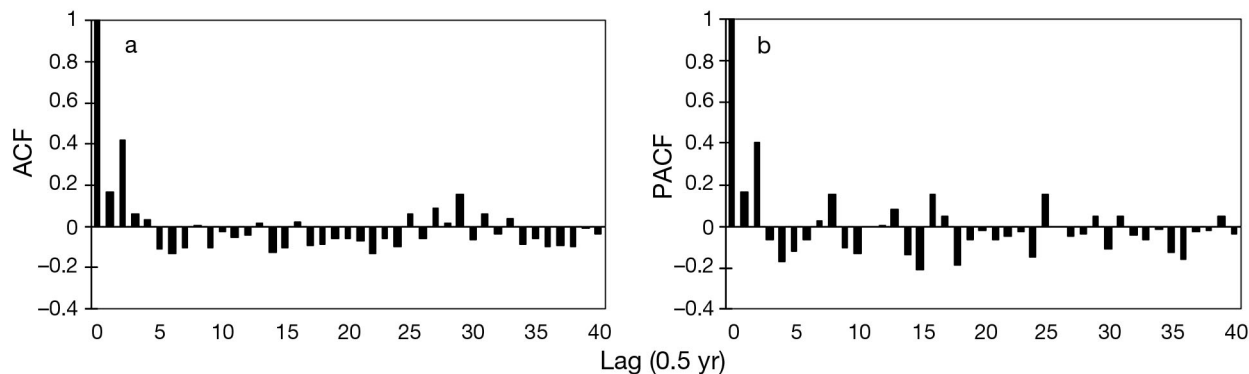


Fig. 3. *Crangon crangon*. (a) Auto-correlation function (ACF) and (b) partial autocorrelation function (PACF) with half-year lags, after subtracting the linear trend and the seasonal signal from *C. crangon* abundance in the Dutch Wadden Sea

correlation analyses (Table 1). Autumn abundance was significantly positively correlated to that of the previous autumn and to a lesser degree to that of the previous spring. Spring abundance was significantly positively correlated to that of the previous autumn. Note that all analyses were performed on log-transformed shrimp abundances.

Relationship between shrimp abundance, predators and environmental variables

The natural logarithm was taken for all biological data (shrimp and predators abundance), since this transformation normalised these data adequately. Environmental data did not need to be transformed. Cross-correlations relating (log-transformed) shrimp data to (log-transformed) predator data and (non-transformed) environmental variables are presented in Table 1, including significant correlations for non-zero lags. In terms of predators, spring shrimp abundances were significantly positively correlated with Clupeiforms and negatively correlated with Decapods. Autumn shrimp abundances were also significantly positively correlated with the season's Clupeiform and Perciform abundances, next to the Clupeiforms in the previous spring. Furthermore, there was a significant negative correlation with Scorpaeniform and Pleuronectiform abundances measured 2 yr before. Both spring and autumn shrimp data were positively correlated to landings and to sunshine duration of the previous winter. Spring data were furthermore positively correlated with autumn water temperature, whereas autumn data showed a negative correlation with the winter out-flow from Lake IJssel. Cross-correlation functions (CCF) could not be calculated for winter biotic data due to the incomplete time series. Time series of the spring, autumn and winter (when available) data of the most relevant variables are shown in Fig. 4.

Many of the considered independent variables were significantly ($\alpha = 0.05$) correlated. For both spring and autumn data sets, the highest correlations were found among abiotic variables. In the spring data, significant, positive correlations were found among: TEMP, NAOI, WNAOI and exWNAOI; and TEMP, SUN and LANDINGS. SAL was negatively correlated with DAYPREC, DEBIET and LANDINGS. For the autumn data set, there were positive correlations between: NAOI and exWNAOI; DEBIET and DAYPREC; and LANDINGS and SUN. Negative correlations were found between DEBIET and TEMP; SAL and SUN; and DAYPREC and SUN.

For the spring-data predators, positive correlations were found among: SCORP, GAD and PERC; PERC and FLAT; GAD, winter SCORP and FLAT; PERC, winter PERC and CRAB; SCORP, winter GAD and FLAT; and FLAT, winter FLAT and CRAB. There were also positive correlations with predators from the previous autumn, i.e. between SCORP and autumn GAD; SCORP and FLAT; and CRAB and autumn CRAB. Negative correlations were found between: SCORP and autumn CLUP; and among FLAT, autumn CLUP and PERC.

For the autumn-data predators, there were significant positive correlations among: GAD, SCORP and FLAT; SCORP and PERC; CLUP and summer CLUP; GAD and spring and winter FLAT; summer GAD and PERC; SCORP and spring SCORP; summer GAD and PERC; winter CLUP, GAD, SCORP and FLAT; FLAT, spring GAD and SCORP; summer GAD and PERC; winter CLUP, GAD, SCORP and FLAT; and CRAB, spring CLUP and summer CRAB. Negative correlations were found between: CLUP and SCORP; summer and winter GAD, and summer FLAT; and SCORP and summer CLUP.

Spring GAD, PERC and SCORP were positively correlated with DEBIET; GAD was negatively correlated with WNAOI, and SCORP with TEMP and SUN. Autumn GAD, SCORP and FLAT were negatively correlated with LANDINGS. GAD and SCORP were posi-

tively correlated with DAYPREC and DEBIET, and negatively with SUN. GAD and FLAT were positively correlated with NAOI, yet negatively with WNAOI. CRAB was negatively correlated with SAL.

Table 1. *Crangon crangon*. Cross-correlation (CC) results (Pearson correlation) of spring and autumn abundances with environmental variables from the current season (no lower case letter), and with predators and environmental variables from previous autumn (a), spring (s), summer (sm) and winter (w) seasons; codes according to Appendix 1. Whenever correlation was highest and significant for a non-zero lag, this lag and its correlation is also mentioned (Maximum lag, CC). Significant correlations are printed in **bold**; variables selected in the final multiple linear regression models (LM) are given (1 = model considering variables available for the whole time series, 34 samples; 2 = model including winter variables, restricted to 18 samples)

Variable	Spring		Variable	Autumn		
	Zero-lag CC	LM		Zero-lag CC	Maximum lag CC	LM
CRANGa	0.400	1	CRANGs	0.439		
CRANGs	0.249		CRANGa	0.582		
CLUP	0.390		CLUP	0.368		
GAD	-0.181		GAD	-0.334		
PERC	0.222	1	PERC	0.512		1,2
SCORP	-0.218		SCORP	-0.230		
FLAT	-0.111		FLAT	-0.180	1 -0.326	
CRAB	-0.432		CRAB	0.080		
TEMP	0.048	1	TEMP	0.002		
SAL	-0.232		SAL	-0.251		
SUN	-0.011		SUN	0.222		
DAYPREC	0.038		DAYPREC	0.013		
DEBIET	0.221		DEBIET	0.065		
CLUPa	-0.555		CLUPs	0.499		1
GADa	-0.297	1	GADs	-0.214		
PERCa	0.229	2	PERCs	0.040		
SCORPa	-0.234	2	SCORPs	-0.334		
FLATa	-0.201		FLATs	-0.234		
CRABa	-0.086		CRABs	-0.241	2 -0.578	
TEMPa	0.419	1	TEMPs	0.276		
SALa	0.091	2	SALs	-0.061		
SUNa	0.129		SUNs	0.108		
DAYPRECa	0.025		DAYPRECs	0.142		
DEBIETa	-0.035		DEBIETs	0.055		
TEMPw	-0.039		TEMPw	0.002		
SALw	-0.073		SALw	0.105		1
SUNw	0.392		SUNw	0.418		
DAYPRECw	-0.045		DAYPRECw	-0.074		
DEBIETw	-0.130		DEBIETw	-0.373		1
			CLUPsm	0.205		1,2
			GADsm	-0.099		
			PERCsm	-0.070		
			SCORPsm	-0.103		
			FLATsm	-0.057		
			CRABsm	0.142	1 0.458	
			TEMPsm	0.223		
			SALsm	-0.184		
			SUNsm	0.084		
			DAYPRECsm	0.015		
			DEBIETsm	0.031		
LANDINGS	0.398		LANDINGS	0.465		
NAOI	-0.051		NAOI	-0.173		2
WNAOI	-0.039	2	WNAOI	0.218		
exWNAOI	-0.046		exWNAOI	0.017		

Regression models

The 2 best models for each subset of predictor variables for the *Crangon crangon* spring and autumn abundances are presented in Table 2a & b, respectively.

Based on the sample size and the cross-validation error and its evolution with increasing model complexity, the following 5-predictor model for the complete series of spring data was chosen:

$$\begin{aligned} \log(\text{CRANG}) = & 1.465 + 0.313 \log(\text{CRANGa}) \\ & + 0.878 \log(\text{PERC}) \\ & - 0.386 \text{TEMP} - 0.611 \log(\text{GADa}) \\ & + 0.312 \text{TEMPa} \end{aligned} \quad (2)$$

with CRANG and CRANGa representing *C. crangon* abundance in spring and in the previous autumn, respectively, PERC the abundance of Perciforms, TEMP spring water temperature, GADa the abundance of Gadiforms in the previous autumn and TEMPa water temperature in the previous autumn. All model terms were significant ($\alpha = 0.05$). The model explains 56.9% of the variance, with CRANGa accounting for 32%, TEMPa for 27%, GADa for 15%, PERC for 14% and TEMP for 12% of the explained variance.

For the autumn data the following model was selected:

$$\begin{aligned} \log(\text{CRANG}) = & 9.588 + 2.265 \log(\text{PERC}) \\ & + 0.321 \log(\text{CLUPs}) \\ & + 0.172 \log(\text{CLUPsm}) - 0.438 \text{SALw} \\ & - 0.003 \text{DEBIETw} \end{aligned} \quad (3)$$

with CRANG representing *Crangon crangon* abundance in the current autumn, PERC the abundance of Perciforms, CLUPs and CLUPsm the abundance of Clupeiforms in the previous spring and summer, respectively, and SALw and DEBIETw the salinity and discharge from Lake IJssel into the Wadden Sea in the previous winter. All model terms were significant ($\alpha = 0.05$). The model explains 79.0% of the variance, with PERC accounting for 39%, CLUPs and CLUPsm for 17% each, SALw for 16% and DEBIETw for 11% of the explained variance.

Model residuals were approximately normally distributed and did

not present significant temporal autocorrelation (Fig. 5), suggesting that model parameters account for the autocorrelation found in the seasonal brown shrimp abundance data. Regression model predictions correlate closely with the measured abundances (Fig. 6).

When also considering winter shrimp and fish data as candidate predictor variables, and therefore only 18 sample years, the selected spring model was:

$$\log(\text{CRANG}) = -6.766 + 2.253 \log(\text{PERCa}) - 1.068 \log(\text{SCORPa}) + 0.199 \text{SALa} - 0.913 \text{WNAOI} \quad (4)$$

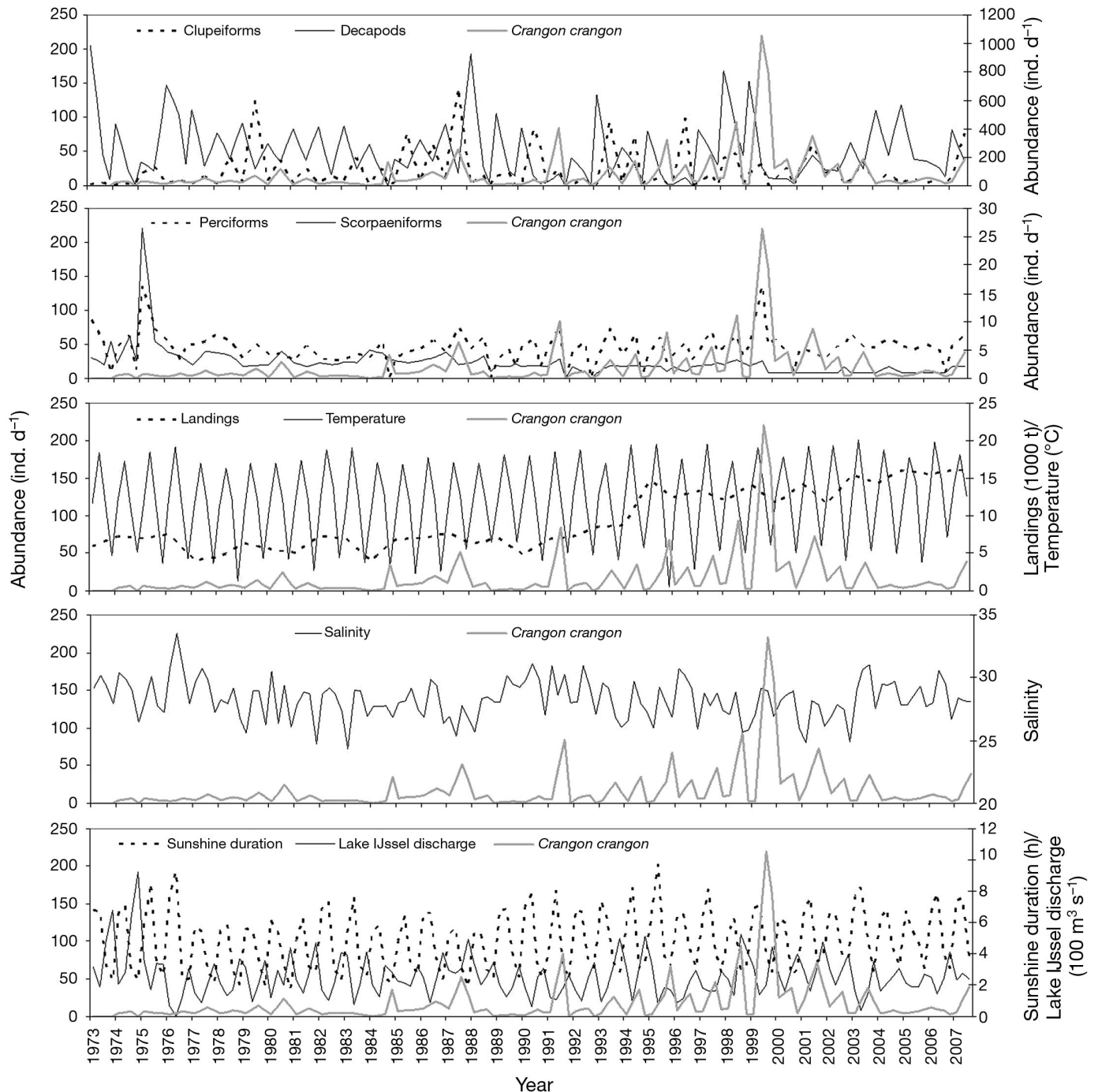


Fig. 4. Time series of the spring, autumn and winter (when available) abundance of *Crangon crangon* (left axis), Clupeiforms, Decapods, Perciforms and Scorpaeniforms in the Dutch Wadden Sea, and annual North Sea commercial landings of *C. crangon* (1000 t), water temperature (°C), salinity, sunshine duration (h) and freshwater discharge from Lake IJssel into the Wadden Sea (100 m³ s⁻¹)

with CRANG representing spring *Crangon crangon* abundance, PERCa and SCORPa the densities of Perciforms and Scorpaeniforms of the previous autumn, SALa the salinity of the previous autumn and WNAOI the NAOI of the previous winter. All model terms were significant ($\alpha = 0.05$). The model explains 79.5% of the variance, with PERCa accounting for 39%, WNAOI for 38%, SCORPa for 16% and SALa for 7% of the explained variance.

The autumn model was:

$$\log(\text{CRANG}) = -5.746 + 2.920 \log(\text{PERC}) + 0.542 \log(\text{CLUPsm}) + 0.433 \log(\text{PERCw}) - 1.060 \text{NAOI} \quad (5)$$

with CRANG representing autumn *Crangon crangon* abundances, PERC and PERCw autumn and previous winter Perciforms abundance, respectively, CLUPsm abundance of Clupeiforms in the previous summer and NAOI autumn NAOI. All model terms were significant ($\alpha = 0.01$). The model explains 90.9% of the variance, with CLUPsm accounting for 36%, PERC for 33%, PERCw for 16% and NAOI for 15% of the explained variance.

The regression model selection procedure prevented inclusion of strongly correlated variables into one model. Given the data sets used and the selected models, only the spring model excluding winter biotic vari-

Table 2. The 2 best regression models each with 1 to 10 parameters (df), for the (a) spring and (b) autumn data excluding biotic winter variables ($n = 34$), their model terms, multiple R^2 , leave-one-out cross-validation error (CV) and p-value; model terms are superscripted according to their significance (0.001***, 0.01**, 0.05*, 0.1* and >0.1); the selected model is printed in **bold**; codes according to Appendix 1 and Table 1

df	Model terms	R^2	CV	p-value
a) Spring				
1	TEMPa*	0.175	0.407	0.0137
	CRAB*	0.186	0.415	0.0108
2	CRAB**+SAL*	0.299	0.361	0.0040
	CRANGa*+TEMPa**	0.323	0.359	0.0023
3	CRANGa**+TEMPa*+WNAOI*	0.407	0.335	0.0012
	CRANGa**+TEMPa*+TEMPa**	0.408	0.335	0.0012
4	CRANGa***+TEMPa*+CLUPa*+TEMPa**	0.479	0.305	0.0006
	CLUP*+PERCa**+TEMPa**+exWNAOI*	0.479	0.327	0.0006
5	CRANGa***+PERC**+TEMP**+GADa*+TEMPa**	0.569	0.270	0.0002
	CLUP*+GAD*+PERCa**+TEMPa**+exWNAOI**	0.570	0.279	0.0001
7	CRAB**+SAL**+GADa**+PERCa**+SALa*+exWNAOI**	0.618	0.281	0.0001
	CRAB*+DEBIET**+GADa**+PERCa**+SALa*+exWNAOI**	0.620	0.283	0.0000
6	CRAB*+DEBIET***+SUNw**+GADa**+PERCa**+SALa**+exWNAOI***	0.674	0.261	0.0000
	CRANGs*+CRAB**+DEBIET**+GADa**+PERCa**+SALa*+exWNAOI**	0.683	0.258	0.0000
8	FLAT*+CRAB**+DEBIET***+SUNw**+GADa**+PERCa**+SALa**+exWNAOI**	0.714	0.239	0.0000
	CLUP*+CRAB*+SAL**+DAYPREC*+GADa**+PERCa***+SALa**+exWNAOI**	0.715	0.247	0.0000
9	CLUP*+CRAB*+SAL***+DAYPREC*+SUNw**+GADa**+PERCa**+SALa**+exWNAOI**	0.742	0.241	0.0000
	FLAT*+CRAB**+DEBIET***+SUNw**+GADa**+PERCa**+SALa**+LANDINGS*+exWNAOI***	0.743	0.230	0.0000
10	CRANGa*+CLUP*+DAYPREC*+DEBIET**+DAYPRECw**+GADa*+PERCa**+TEMPa*+SALa**+exWNAOI**	0.767	0.225	0.0000
	FLAT*+CRAB**+DEBIET***+SUNw**+DEBIETw*+GADa**+PERCa***+SALa***+LANDINGS*+exWNAOI***	0.768	0.219	0.0000
b) Autumn				
1	PERC**	0.262	0.902	0.0020
	CRANGa***	0.339	0.806	0.0003
2	PERC***+CLUPsm**	0.495	0.707	0.0000
	CRANGa***+PERC**	0.513	0.613	0.0000
3	PERC***+SALw***+DEBIETw**	0.538	0.618	0.0000
	PERC***+CLUPs***+SCORPs***	0.643	0.507	0.0000
4	PERC***+CLUPsm**+SALw***+DEBIETw**	0.735	0.405	0.0000
	PERC***+CLUPs***+SALw***+DEBIETw***	0.686	0.501	0.0000
5	CRANGs**+PERC***+CLUPs**+SALw***+DEBIETw***	0.770	0.425	0.0000
	PERC***+CLUPs*+CLUPsm*+SALw***+DEBIETw***	0.790	0.370	0.0000
6	CRANGs***+PERC***+SUNsm**+SALw***+DAYPRECw**+DEBIETw***	0.819	0.320	0.0000
	PERC***+CLUPs**+FLATs**+CLUPsm**+SALw***+DEBIETw***	0.831	0.302	0.0000
7	CRANGs***+PERC***+DEBIETs**+SUNsm**+SALw***+DAYPRECw***+DEBIETw***	0.859	0.265	0.0000
	CRANGs***+PERC***+SUN**+CLUPs***+SCORPs***+DEBIETs**+SALw***	0.863	0.283	0.0000
8	CRANGa**+PERC***+FLATs***+DAYPRECs***+DEBIETs***+CLUPsm***+SUNsm**+TEMPw***	0.897	0.206	0.0000
	CRANGs***+PERC***+SUN***+DEBIET**+CLUPs***+SCORPs***+DEBIETs***+SALw***	0.902	0.202	0.0000
9	CRANGs***+PERC***+SUN***+DEBIET**+CLUPs***+SCORPs***+DEBIETs***+SALw***+NAOI*	0.914	0.185	0.0000
	CRANGa**+PERC***+CLUPs**+FLATs***+DAYPRECs***+DEBIETs***+CLUPsm***+SUNsm**+TEMPw***	0.918	0.187	0.0000
10	CRANGs***+PERC***+CLUPs**+GADs*+DEBIETs***+GADsm**+SUNsm**+SALw***+DAYPRECw***+DEBIETw***	0.930	0.165	0.0000
	CRANGa**+PERC***+CLUPs**+FLATs***+DAYPRECs***+DEBIETs***+CLUPsm***+SUNsm**+TEMPw***+NAOI*	0.934	0.163	0.0000

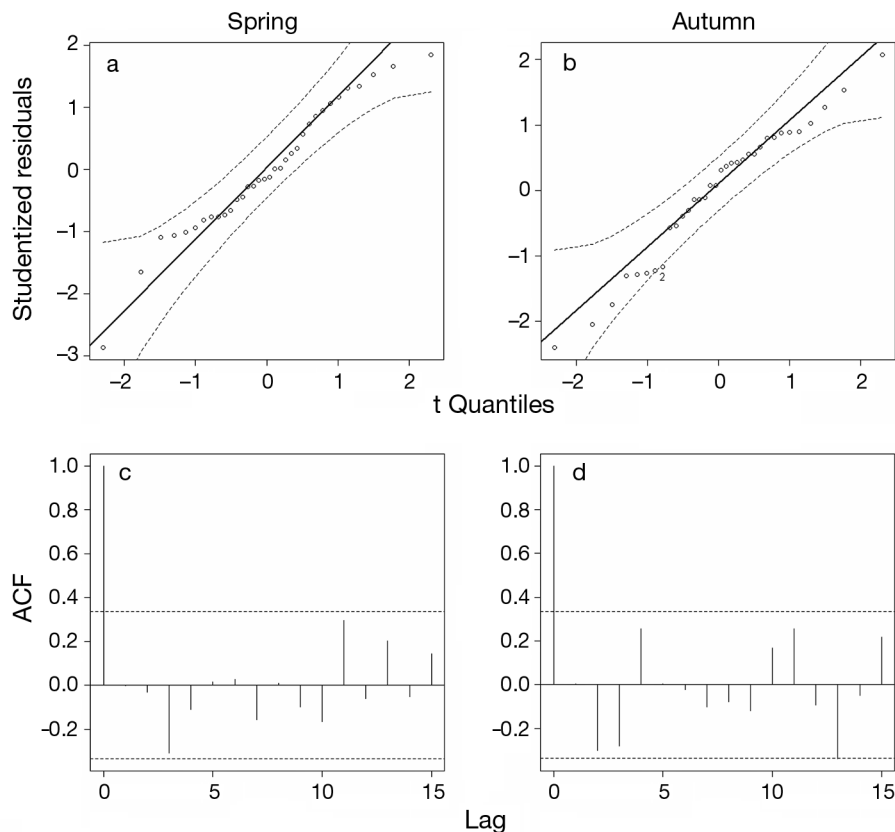


Fig. 5. QQ-plot of regression model residuals (a,b) and residual autocorrelation functions (ACF; c,d) for the selected spring (left; $\log(\text{CRANG}) = 1.465 + 0.313 \log(\text{CRANGa}) + 0.878 \log(\text{PERC}) - 0.386 \text{ TEMP} - 0.611 \log(\text{GADa}) + 0.312 \text{ TEMPa}$) and autumn (right; $\log(\text{CRANG}) = 9.588 + 2.265 \log(\text{PERC}) + 0.321 \log(\text{CLUPs}) + 0.172 \log(\text{CLUPsm}) - 0.438 \text{ SALw} - 0.003 \text{ DEBIETw}$) regression models. (O): residual; dashed line: 95% confidence limit; continuous line: 45° reference line

ables included a pair of significantly, negatively correlated predictor variables, TEMP and GADa (−0.405).

DISCUSSION

Long-term trends in annual abundance

For the last 34 yr, despite large fluctuations, the abundance of adult *Crangon crangon* in the Dutch Wadden Sea shows an overall increasing trend. The ARMA prediction therefore showed a positive seasonal trend for the next 5 yr. However, there seems to be a decreasing trend in the stock size after 2000, which was not analysed separately as the available time series is presently too short for a sound time-series analysis of the divided data. Future monitoring will reveal whether brown shrimp abundance will recover from the recent downward trend. In the Bristol Channel, a general increasing trend was also found until 2005 (Henderson et al. 2006), while in the German Wadden Sea, no trend was found in brown shrimp den-

sities between 1974 and 2002 (Siegel et al. 2005). Brown shrimp landings in the North Sea have also been increasing since the 1970s, despite a considerable decline from the mid to late 1980s of about one third of previous landings, and reached a maximum of 16 000 t in 2006 (ICES 2008). However, it should be kept in mind that this increase in landings is also partly due to an increase in fishing effort (ICES 2008).

The increasing *Crangon crangon* abundance observed in the Dutch Wadden Sea, as well as in the Bristol Channel and in the North Sea landings, might reflect global warming effects as observed in fish species (Roessig et al. 2004, Rose 2005, Harley et al. 2006, Portner & Knust 2007). For the past 25 yr the mean annual water temperature at the entrance of the Dutch Wadden Sea has increased by about 1.5°C (van Aken 2008a). Such variation has complex effects at several levels, from organism physiology to ecosystem function, through trophic relationships (Freitas et al. 2007). A decline in total fish biomass in the area, from 1985 until early 2000, has already been reported (Tulp et al. 2008), suggesting a possible reduction in the overall

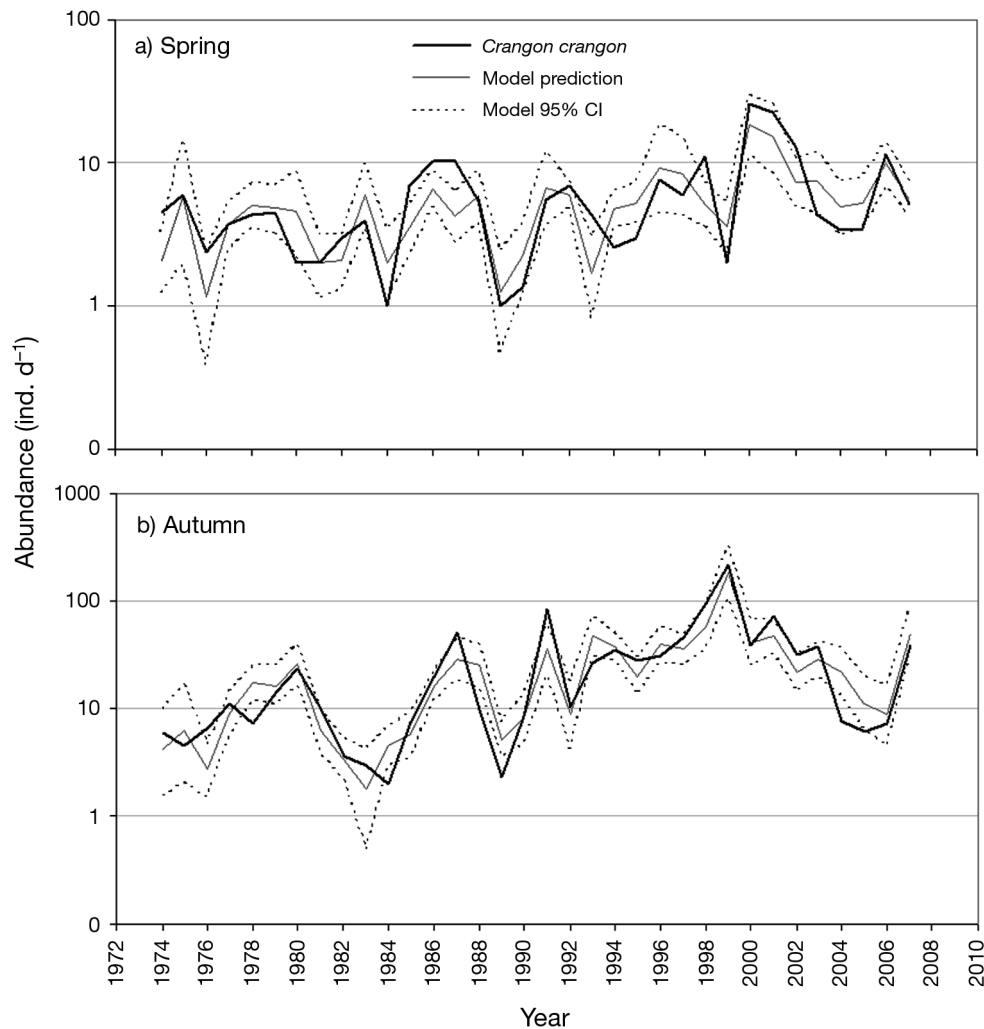


Fig. 6. *Crangon crangon*. (a) Spring and (b) autumn abundances in the Dutch Wadden Sea, regression model predictions and their 95 % confidence intervals (CI); spring model: $\log(\text{CRANG}) = 1.465 + 0.313 \log(\text{CRANGa}) + 0.878 \log(\text{PERC}) - 0.386 \text{TEMP} - 0.611 \log(\text{GADa}) + 0.312 \text{TEMPa}$, and autumn model: $\log(\text{CRANG}) = 9.588 + 2.265 \log(\text{PERC}) + 0.321 \log(\text{CLUPs}) + 0.172 \log(\text{CLUPsm}) - 0.438 \text{SALw} - 0.003 \text{DEBIETw}$

predation pressure on the *C. crangon* population, which favours its increased abundance. In the same way, the population might have benefited from the increased food availability due to rising water temperature. *C. crangon* is an opportunistic feeder with a very varied diet, mainly composed of demersal, in- and epifaunal organisms during its juvenile and adult life; during larval stages its diet probably consists of plankton (Campos & van der Veer 2008). *C. crangon* is not particularly sensitive to pollution levels but the reduced nutrient loads reported from the 1970s onwards (van Raaphorst & De Jonge 2004), might also contribute to changes in shrimp abundance. However, whether or not the nutrient reduction has caused a decrease in the productivity of the coastal waters is still under discussion (Cadee & Hegeman 2002, Philippart et al. 2007).

In addition to the long-term increasing trend, seasonality in brown shrimp abundance was observed, with considerably lower (5 times) abundances in spring compared to autumn. This corroborates previous observations (Siegel et al. 2005, Henderson et al. 2006) reflecting shrimp production in the coastal zone (Kuipers & Dapper 1984). Also, commercial landings are highest in autumn and lowest in spring (ICES 2008). Since the fyke mesh size (10×10 mm) was too large to capture the small juveniles entering the Wadden Sea, the observed low spring abundance represents the adult shrimps which have overwintered offshore (Temming & Damm 2002) and survived winter mortality. The large autumn abundance represents mature shrimps leaving the nurseries for the overwintering areas in the coastal zone. The variability of

spring abundance was also lower than that of autumn abundance, as revealed by the deviation in relation to the mean (see Appendix). This is the opposite of what was found in the German area, where, although spring abundance is also lower than in autumn, autumn densities are relatively more stable in comparison to spring densities (Siegel et al. 2005).

Some peaks and lows in *Crangon crangon* abundance in the Dutch Wadden Sea coincided with or occurred close to those observed in time series from other sites: the 1987 autumn peak of the present study preceded the 1988 maximum observed in the Bristol Channel and followed the 1986 peak in the German Bight; the 2003 peak in the Dutch Wadden Sea followed the 2002 autumn maximum in the Bristol Channel; and the 1998 spring peak coincided in the Dutch and the German Wadden Sea. From 1976 to 1978, spring minima were registered both in the German and in the Dutch Wadden Sea; the 1983 and 1989/90 spring minima of the present study preceded respectively the 1984 and the 1991 minima in the German area. Other fluctuations did not correspond with the dynamics observed at the other 2 locations and might be related to local conditions. Regional variability has been detected in 3 areas of the German Bight with occasional opposing trends in abundance for the same year (Siegel et al. 2005).

Seasonal trends in abundance

The brown shrimp life cycle follows a seasonal pattern. At intermediate latitudes of distribution (within the 45 to 55°N latitudinal range) reproduction occurs in more saline waters throughout the entire year with spawning peaks in spring-summer and winter (Boddeke 1982, Kuipers & Dapper 1984, Henderson & Holmes 1987, Oh & Hartnoll 2004). Pelagic larvae are found over almost the entire year (Lebour 1947, Kuhl & Mann 1963, van der Baan 1975) though mostly from May to September (Plett 1965, Feddersen 1993), migrating into shallow nurseries often situated in estuaries. Hence, the bulk of larval settlement takes place in the warmer seasons (Kuipers & Dapper 1981) and might contribute to the high autumn recruitment to fisheries (Kuipers & Dapper 1984). Remarkably, over the period of scientific observation, *Crangon crangon* recruitment has been very successful. In the same way, in most years and across its geographic distribution, *C. crangon* is continuously highly abundant in shallow coastal areas (Campos & van der Veer 2008).

Time-series and cross-correlation analyses revealed population effects with lags of up to 1 yr (i.e. 1 spring and 1 autumn season), which is consistent with *Crangon crangon* life history and lifespan of 1 to 3 yr (Cam-

pos & van der Veer 2008). Given the short life span of the species, rapid seasonal changes in abundance could be expected with abrupt drops due to adverse environmental conditions and steep recoveries under favourable circumstances. Such rapid changes of abundance were observed in the present study in 1999: a spring minimum was followed by an autumn maximum in the same year. This was the maximum abundance and the greatest change observed in the entire time series.

Factors affecting autumn abundance

Apart from previous shrimp abundances (representing temporal autocorrelation), other variables were related with the size of the autumn recruit stock. As hypothesised, predator abundance was observed to consistently influence brown shrimp autumn abundance, explaining up to 85 % of the variance in autumn models when considered altogether, reflecting their high importance. Predation and even cannibalism, which represents about 20 % of the species annual food consumption (Pihl & Rosenberg 1982), are known to be important causes of brown shrimp natural mortality (Henderson & Holmes 1989), though fluctuations in predator abundance might be difficult to relate to *Crangon crangon* stock fluctuations (Henderson et al. 2006). Nevertheless, brown shrimp densities have been identified as one of the explanatory variables for the long-term trends in abundance of several fish species observed in Dutch waters (Tulp et al. 2008).

Concerning the predator groups, Clupeiforms, Perciforms, Scorpaeniforms, Pleuronectiforms and Decapods were the groups with the greatest influence in autumn, though the last 2 had 1 and 2 yr lag, respectively. Autumn *Crangon crangon* abundance was positively cross-correlated with the Clupeiforms, which comprised mostly herring *Clupea harengus* but also included twaite shad *Alosa fallax*, and was further related to the abundance of this group in the previous spring. Clupeiforms are planktivorous (Dalpadado et al. 2000) and do not feed on adult shrimps. The positive correlation between *C. crangon* and Clupeiform abundances suggests that they share environmental resources but do not compete. However, Clupeiforms might feed on *C. crangon* planktonic larvae, which would explain the time lag between autumn abundance and spring fish abundance. Perciforms were also positively cross-correlated with autumn abundance and a selected term in the models. In contrast, shrimp abundance was negatively related to Scorpaeniforms and Decapods, probably due to mortality losses by predation. The Decapod group only included the crab *Carcinus maenas* and was the second most

abundant group in the entire time series, following the Clupeiforms, while the Scorpaeniform group was the least abundant predator group on average.

The environmental variables which were related to autumn brown shrimp abundances were (1) sunshine duration, (2) salinity, (3) out-flow from Lake IJssel into the Wadden Sea, and (4) the NAOI, the first 3 during winter. However, temperature conditions during the growing season (spring and summer) were not related to the autumn stock, contradicting Hypothesis 1. Autumn abundances were more closely related to previous winter conditions. Winter sunshine duration was positively correlated with autumn abundance, while salinity and out-flow from Lake IJssel, both from the previous winter, were negatively related to autumn stock. Winters with more saline conditions, probably associated with lower precipitation and out-flow from Lake IJssel, seem thus to favour autumn recruitment. Salinity directly affects brown shrimp ecophysiology and influences their migrations; it also indirectly influences the stock through changes in productivity and therefore food availability. Primary and secondary productivity effects were not tested, though their influence might also be related to sunshine duration and river run off. River discharge also affected the autumn recruitment in the Bristol Channel (Henderson et al. 2006) and in the German Bight (Siegel et al. 2005). Finally, the NAOI was only a relevant factor in the model when winter variables were included.

Factors affecting spring abundance

Crangon crangon adult stock in spring (recruits) was positively related to the previous autumn recruitment, but not to the adult stock in spring 1 yr earlier. This was expected since the spring population represents overwintering adults and thus belongs to the same generation as the previous autumn population. In addition, the abundance of predators was also very relevant in determining shrimp stock, though with less importance than in autumn, explaining up to 55% of the spring models' variance. This supports the hypothesis that shrimp abundance depends mainly on predator abundance, especially in autumn. Although the research hypothesis considered predation impact during winter, the fyke catch in this season might not correspond to the predators affecting shrimps in the overwintering areas since they migrate offshore.

Apart from Pleuronectiforms, the same groups which were related to autumn abundance also affected the stock in spring, but Clupeiforms were more important in spring and Perciforms in autumn. As in autumn, Clupeiforms were positively, whereas Scorpaeniforms and Decapods were negatively, related to shrimp

abundance during spring. Finally, Gadiform abundance in autumn was included in the spring model and negatively related to *Crangon crangon* abundance. Despite including whiting *Merlangius merlangus*, a very abundant and important predator of brown shrimp (Henderson & Holmes 1989, Henderson et al. 1992, Hamerlynck & Hostens 1993, Singh-Renton & Bromley 1999), Gadiforms did not show a significant cross-correlation with the Dutch Wadden Sea shrimp abundances, contradicting the observations in the German area (Siegel et al. 2005) and in the Bristol Channel (Henderson et al. 2006). However, the abundance of Gadiforms was correlated with the abundance of other predators especially Scorpaeniforms. The effect of Gadiforms is therefore possibly related to a confounding variable, such as other predators. Also, the strong correlation with temperature might interfere with its detection.

Environmental conditions correlated to brown shrimp spring abundances included (1) winter sunshine duration, (2) temperature, (3) autumn salinity and (4) the WNAOI (Table 1). While winter sunshine duration, temperature and salinity, both in autumn, were positively related to spring abundance, spring temperature and the WNAOI were negatively related. However, as in autumn, the WNAOI, which was previously considered important in the Bristol Channel (Henderson et al. 2006), only appeared to be relevant when the winter variables were included, accounting for 38% of the explained variance in the spring model.

The hypothesis established for the spring season considered only winter conditions. Yet only sunshine duration in winter was a significant determinant. Its positive relationship with brown shrimp stock size in spring and also in autumn suggests that mild winters with more clear days favour increases in the stock later in the year, which might be related to an overall increase in the productivity of the area. In contrast, after severe winters with lower mean sunshine duration, brown shrimp abundance declines and they might even be practically absent, as has been observed previously on the Wadden Sea tidal flats (Beukema 1992). This confirms the hypothesis that spring abundance (related to overwintering survival) is determined by the severity of winter conditions, probably due to direct consequences of temperature and, indirectly, to variations in food availability and predation pressure. Nevertheless, in the present study, winter sunshine duration was not correlated with any other winter environmental variable, such as temperature.

In conclusion, over the last 34 yr, a general increasing trend in the abundance of *Crangon crangon* in the western Dutch Wadden Sea was observed, which is consistent with trends observed in other areas and reported by fisheries. Autumn abundance was 5 times

higher than spring abundance and presented more pronounced variability, which conforms to the brown shrimp life cycle. The abundance of adults in autumn was positively related to predator abundance, while the abundance of overwintering adults in spring was related to the severity of winter conditions in addition to predation pressure. The chosen multiple regression models for the spring and autumn time series fitted the data very well, especially the autumn models which explained up to 90.9% of the variance. Less or more complex models could have been chosen, and also different models of the same complexity, as some of the biotic and abiotic variables available for regression modelling are correlated and may produce similar levels of fit in a multiple regression model. Variables may also interact, and inclusion of interaction terms might have improved our models. It will be interesting to validate the selected and alternative models on future brown shrimp data which continue to be sampled. More data will allow a better insight into the effects of climate variables and predation pressure on brown shrimp abundances and confirm or refute the recent downward trend in the shrimp population.

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Appendix 1. List of variable codes, description and minimum, maximum, median, mean and standard deviation (SD) of all variables for spring and autumn datasets. Outflow: Lake IJssel outflow into the Wadden Sea ($\text{m}^3 \text{s}^{-1}$)

Code	Description	Spring					Autumn				
		Max	Min	Median	Mean	SD	Max	Min	Median	Mean	SD
Daily abundance											
Crangon crangon											
CRANG	Current season	25.38	0.00	4.43	6.14	5.49	220.14	2.00	12.71	29.61	41.06
CRANGs	Previous spring	25.38	0.00	4.34	5.99	5.59	25.38	0.00	4.43	6.14	5.49
CRANGa	Previous autumn	220.14	0.10	10.78	28.48	41.33	220.14	0.00	10.78	28.48	41.33
Clupeiforms											
CLUP	Current season	188.78	3.24	20.88	35.48	39.25	686.39	12.52	127.11	200.50	170.06
CLUPs	Previous spring			188.78	3.24	20.88	35.48	39.25			
CLUPsm	Previous summer			2623.98	3.25	72.66	189.03	472.56			
CLUPa	Previous autumn	686.39	12.52	124.66	190.39	170.15					
CLUPw	Previous winter	294.23	0.00	2.47	20.24	68.69	294.23	0.00	2.47	20.24	68.69
Gadiforms											
GAD	Current season	19.64	4.49	8.01	9.09	4.06	34.10	3.34	8.29	10.26	6.25
GADs	Previous spring			19.64	4.49	8.01	9.09	4.06			
GADsm	Previous summer			31.92	1.00	6.44	8.86	7.72			
GADa	Previous autumn	34.10	3.34	8.29	10.23	6.28					
GADw	Previous winter	13.77	0.00	3.49	4.54	4.03	13.77	0.00	3.49	4.54	4.03
Perciforms											
PERC	Current season	16.31	3.00	5.05	5.23	2.34	16.31	3.22	6.46	6.60	2.32
PERCs	Previous spring			16.31	2.20	4.01	4.48	2.34			
PERCsm	Previous summer			13.07	1.00	4.47	4.93	2.44			
PERCa	Previous autumn	16.31	3.22	6.37	6.56	2.32					
PERCw	Previous winter	6.00	0.00	1.79	2.30	2.18	6.00	0.00	1.79	2.30	2.18
Scorpaeniforms											
SCORP	Current season	26.52	1.00	2.17	3.07	4.29	7.42	1.00	2.33	2.76	1.56
SCORPs	Previous spring			26.52	1.00	2.17	3.07	4.29			
SCORPsm	Previous summer			7.03	0.00	1.00	1.19	1.59			
SCORPa	Previous autumn	7.42	1.00	2.38	2.77	1.55					
SCORPw	Previous winter	6.50	0.00	2.11	2.11	1.50	6.50	0.00	2.11	2.11	1.50
Pleuronectiforms											
FLAT	Current season	39.02	7.62	11.70	14.84	7.74	20.70	5.17	9.01	10.01	3.53
FLATs	Previous spring			39.02	7.62	11.70	14.84	7.74			
FLATsm	Previous summer			29.71	3.78	12.27	12.97	5.88			
FLATa	Previous autumn	20.70	5.17	9.15	10.07	3.51					
FLATw	Previous winter	101.50	0.00	5.06	12.84	23.52	101.50	0.00	5.06	12.84	23.52
Decapods											
CRAB	Current season	926.96	8.29	391.62	379.12	222.15	495.14	49.92	118.76	144.31	90.54
CRABs	Previous spring			926.96	8.29	391.62	379.12	222.15			
CRABsm	Previous summer			1999.41	16.62	202.91	353.51	432.93			
CRABw	Previous winter	211.33	0.00	20.25	55.17	68.62	211.33	0.00	20.25	55.17	68.62
Water temperature (°C)											
TEMP	Current season	14.24	10.60	11.91	11.96	0.95	14.77	10.70	12.17	12.45	0.91
TEMPs	Previous spring			14.24	10.60	11.91	11.96	0.95			
TEMPsm	Previous summer			20.07	16.30	18.05	18.14	1.04			
TEMPa	Previous autumn	14.77	10.70	12.17	12.44	0.91					
TEMPw	Previous winter	6.48	0.51	4.35	4.30	1.37	6.48	0.51	4.35	4.30	1.37

Appendix 1 (continued)

Code	Description	Spring					Autumn				
		Max	Min	Median	Mean	SD	Max	Min	Median	Mean	SD
Salinity											
SAL	Current season	30.93	24.33	28.04	28.08	1.69	31.04	25.68	28.95	28.82	1.09
SALs	Previous spring			30.93	24.33	28.04	28.08	1.69			
SALsm	Previous summer			33.50	25.40	29.10	29.14	1.47			
SALa	Previous autumn	31.04	25.68	29.00	28.86	1.08					
SALw	Previous winter	29.25	24.74	26.99	26.95	0.94	29.25	24.74	26.99	26.95	0.94
Sun duration (h)											
SUN	Current season	7.69	4.79	6.41	6.25	0.81	5.07	2.41	3.36	3.47	0.61
SUNs	Previous spring			7.69	4.79	6.41	6.25	0.81			
SUNsm	Previous summer			9.78	5.35	6.77	6.94	1.15			
SUNa	Previous autumn	5.07	2.41	3.35	3.46	0.61					
SUNw	Previous winter	3.74	1.73	2.59	2.66	0.50	3.74	1.73	2.59	2.66	0.50
Total daily precipitation (0.1 mm)											
DAYPREC	Current season	2.42	0.49	1.63	1.53	0.42	5.33	1.67	2.86	2.92	0.83
DAYPRECs	Previous spring			2.42	0.49	1.63	1.53	0.42			
DAYPRECsm	Previous summer			4.50	0.37	1.85	2.10	1.07			
DAYPRECa	Previous autumn	5.33	1.67	2.92	2.94	0.81					
DAYPRECw	Previous winter	3.01	0.94	1.93	1.91	0.55	3.01	0.94	1.93	1.91	0.55
Outflow (m³ s⁻¹)											
DEBIET	Current season	390.74	65.78	220.23	224.57	81.52	630.00	119.38	237.20	255.46	100.74
DEBIETs	Previous spring			390.74	65.78	220.23	224.57	81.52			
DEBIETsm	Previous summer			292.45	0.00	134.10	144.78	70.07			
DEBIETa	Previous autumn	630.00	119.38	239.00	262.43	107.64					
DEBIETw	Previous winter	926.75	168.19	364.12	394.35	134.04	926.75	168.19	364.12	394.35	134.04
Annual landings											
LANDINGS	Previous year	16141.65	3998.90	7252.44	9036.12	3809.45					
LANDINGS	Current year			16141.65	3998.90	7394.07	9335.57	3955.15			
North Atlantic Oscillation Index											
NAOI	Current season	1.39	−0.96	0.02	0.08	0.52	1.81	−1.14	−0.09	−0.05	0.64
WNAOI	Winter NAOI	1.67	−0.78	0.41	0.34	0.58	1.67	−0.78	0.41	0.34	0.58
exWNAOI	Extended Winter NAOI	1.41	−0.99	0.35	0.29	0.56	1.41	−0.99	0.35	0.29	0.56

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