Witbaard, R, Duineveld, G.C.A, Bergman, M.J.N., Witte, H.IJ., Groot, L. & Rozemeijer, M.J.C, (2015). The growth and dynamics of *Ensis directus* in the near-shore Dutch coastal zone of the North Sea. Journal of Sea Research, 95, 95–105

Published version: dx.doi.org/10.1016/j.seares.2014.09.008

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The growth and dynamics of *Ensis directus* in the near-shore Dutch coastal zone of the North Sea.

Rob Witbaard[a], Gerard C.A. Duineveld[a], Magda J.N. Bergman[a], Hans IJ. Witte[a], Lennart Groot[a] & Marcel J.C. Rozemeijer[b].

a: Royal Netherlands Institute for Sea Research (NIOZ), Postbus 59, 1790 AB Den Burg, the Netherlands.
b: IMARES: Postbus 68, 1970 AB IJmuiden, the Netherlands.

Corresponding author. Tel: +31222369537.
E-mail addresses: Rob.Witbaard@nioz.nl
Gerard.Duineveld@nioz.nl
Magda.Bergman@nioz.nl
Hans.Witte@nioz.nl
Lennartgroot@gmail.com
Marcel.Rozemeijer@wur.nl

ABSTRACT

Here we present data on the wax and wane of a subtidal *Ensis directus* population which settled in 2009 off the coast of Egmond (North Holland Coast in the Netherlands). Initial densities decreased from a maximum of 700 m^{-2} in early 2010 to about 50 m^{-2} in June 2013. In this period the average length increased from ~ 4 cm to ~12 cm. In 2011-2012 the population was sampled at 3 to 6 week intervals and near bottom environmental conditions were monitored continuously. Samples of animals that were collected were used to follow the change in gonadal mass, tissue glycogen content, tissue weight and shell length. On basis of these data well defined seasonal cycles were observed. The data indicate that the maturation of gonadal tissue already starts early in the year, initially at the expense of somatic tissue. Main spawning takes place in May. After spawning net somatic tissue growth starts after compensation of losses due to spawning. Somatic growth precedes shell growth which starts at water temperatures exceeding 12-14 degrees. Mortality, growth and production are comparable to those found for populations in close-by intertidal areas. As such there is no indication that this offshore population significantly suffers from nearby beach nourishments along the Dutch Coast.

Key words;

North Sea
Ensis directus
Growth
Environment
Population dynamics
Beach nourishments

1. INTRODUCTION

The most abundant bivalve species occurring in dense aggregations along the Dutch coast is the invasive American razor shell, *Ensis directus.* The species was first observed in the German Bight in 1979 (Von Cosel *et al*., 1982). Since then it has spread rapidly in north- and southward direction (Armonies, 2001; Severijns, 2002) and has reached the Iberian coast around 2011 (Arias & Anadón, 2012). In Dutch coastal waters it dominates the biomass of the macrobentic invertebrate community (Goudswaard *et al*, 2013; Verduin *et al*, 2011; Verduin *et al*, 2012). Interestingly the presently known standing stock of *E. directus* is substantially higher than previously reported estimates of total bivalve biomass for that area. There is no evidence that this newcomer outcompeted native species (Dannheim & Rumohr, 2012). Most likely because its preferred (Dekker & Beukema, 2012) habitat of mobile sands with high currents speeds has never been occupied by native *Ensis* spp. nor by other local bivalves.

E. directus can live in these dynamic sedimentary conditions because it can rapidly retract itself deep in the sediment (Drew 1907; Trueman, 1967). Hence, accurate density estimates are often hampered by sampling difficulties. Moreover a significant part of *E. directus* population lives in areas like the very shallow shoreface at depths which are difficult to access with ships large enough to operate sampling gear which is suitable for collecting this species quantitatively. Population size in Dutch coastal waters is therefore, likely even higher than reported by for instance Goudswaard *et al* (2013). Nowadays, densities are that high that a commercial fisheries for this species has developed. As part of the regulation of this fisheries, annual stock estimates are being made which gives good insight in the long term population development (Goudswaard *et al*, 2013) along the Dutch coast. Where many researchers thought that the population of this invader would collapse after its first years of successful settlement, it managed to maintain high population levels.

Various studies illustrate that since *Ensis directus* invaded European waters it has become an ecologically important species in coastal waters (Tulp *et al*, 2010). Fish and birds have started feeding on *E. directus*. Armonies and Reise (1999) speculated that the presence of dense *E. directus* beds might indirectly lead to a higher diversity of associated fauna, especially since *E. directus* tends to occupy a habitat which formerly was underutilized by native fauna. The dense beds are also likely to facilitate ecological processes such as sedimentation and burial of the finest sediment fraction. In terms of processes the high population biomass also may act as means by which nutrients are retained which dampens the effects of eutrophication and seasonal river nutrient run off (Norrko *et al*, 2001; Vaughn & Hakenkamp 2001).

Large parts of the near-shore Dutch coastal zone especially those where highest densities of *Ensis directus* are found, are nowadays protected as habitat H1110 under the EU Habitat directive. At the same time this coastal area is prone to erosion and needs continuous maintenance by means of beach nourishments and shoreface replenishment of sand (Ellerbroek *et al*, 2008; Rozemeijer *et al*, 2013). The direct effects of such mass dumps of sand on the fauna will be evident but with the sand also a small percentage of silt is released. Tides transport this material and thereby potentially cause an effect over a larger area than the dumping plot (van Duin e.a., 2007). High concentrations of suspended fine sediments are known to interact negatively with bivalve filter feeding (Gremare *et al*, 1998, Roper & Kickey, 1995; Szostek *et al*, 2013). Concern about the possible impact of beach nourishments on the production of the local *Ensis directus* population led to a project initiated by Rijkswaterstaat (RWS-Ministry I&M) with the ultimate objective to develop a Dynamic Energy Budget (DEB) model (Kooijman, 2010) for *E. directus* allowing assessment of the effects of sand mining and beach nourishments on its secondary production. A first version of a DEB model for *E. directus* has been published (Wijsman, 2011), later adjusted and used by Schellekens & Witbaard (2012) and Schellekens (2012).

In the present study which was a part of the RWS project we focus on growth and development in a field population of *E. directus* living in a shallow coastal site where beach nourishments were taking place. The stock lives 1 km offshore of Egmond at ~10 m depth on the steep edge of the shoreface. In the summer of 2009 mass settlement of *E. directus* occurred in this area and this settlement was subsequently monitored from the end of 2009 till June 2013.

2. MATERIAL AND METHODS

2.1 Study site and research outline

The project started in September 2009 when a research partner (MEDUSA Explorations; http://www.medusa-online.com) commenced with measurements of the sediment silt composition. They sampled sediments along transects extending up to 6 km out of the coast off Egmond. Their methodology also included sampling of sediments with a boxcorer (Vries & Koomans, 2010). We continued their work in spring and autumn 2010 by sampling sediments and *Ensis directus* with a boxcorer along their southern transect and by deploying a measurement platform (lander) to collect semi continuous data on near-bottom environmental conditions. The platform (lander) carried various instruments (section 2.2) to monitor biotic and a-biotic conditions at heights between 30 cm and 200 cm above the bottom. The deployment site was located about one kilometre off the coast of Egmond at a depth of ~10 meter (Fig. 1). In February 2011 the platform was redeployed at this location and continuously kept in operation until the end of November 2012. At approximately monthly intervals the deployment site was visited for maintenance of the platform and for sampling of the *E. directus* population. In June 2013 the site was visited a final time to sample the *Ensis* population.

In June 2011 a supplementary sampling survey was carried out to determine the distribution and densities of *Ensis directus* at a wider scale covering a large part of the coast of the province of North Holland. During this survey boxcore samples were collected along 8 transects perpendicularly oriented to the coast. Each transect extended up to 6 km from the coast. The aim of this sampling survey was to determine if the distribution and densities of *Ensis directus* around the "lander" location represented distribution patterns over a wider area.

2.2 Long term environmental measurements

The measurement platform (lander) consists of an triangular aluminium frame (height×width: 2 x 2 m) with a series of ballast weights (total 500 kg) fixed onto the lower support that stands on the seafloor. The measurement platform was equipped with a series of sensors measuring current, temperature, salinity, turbidity and fluorescence. Current speed and direction (3D) were measured every 10 minutes at 140 cm above the bottom with a NORTEK Aquadopp Doppler current meter. This instrument also yielded a record of the acoustic backscatter. Temperature and salinity were measured every 10 minutes with a pumped version of the Seabird SM37 CTD system (http://www.seabird.com/). In addition to the NORTEK Aquadopp current meter a NORTEK Vektor current meter (http://www.nortek-as.com) was mounted at the lander at a height of 30 cm above the bottom. Every 10 minutes this instrument made burst measurements during 2 minutes with a frequency of 1 sec^{-1}.

Simultaneous measurements of optical backscatter (OBS) and fluorescence were made at four heights above the bottom, i.e. 30, 80, 140 and 200 cm, using ALEC Compact-CLW's (http://ocean.jfe-advantech.co.jp). In the following sections we refer to the material being measured by OBS as SPM (Suspended Particulate Matter). The fluorescent fraction is referred to as Chlorophyll or Chl-a. The ratio of Chlorophyll to total SPM is used to express the amount of chlorophyll per unit suspended matter and can be seen as an expression of food quality. All ALEC sensors were calibrated in the lab over a range of known Chlorophyll and SPM concentrations.

The data collected with this measurement platform were used as environmental characterisation of the research area. Detailed information on these long term time series of measurements on chlorophyll, suspended matter and hydrographical parameters has been reported by Witbaard et al, 2013.

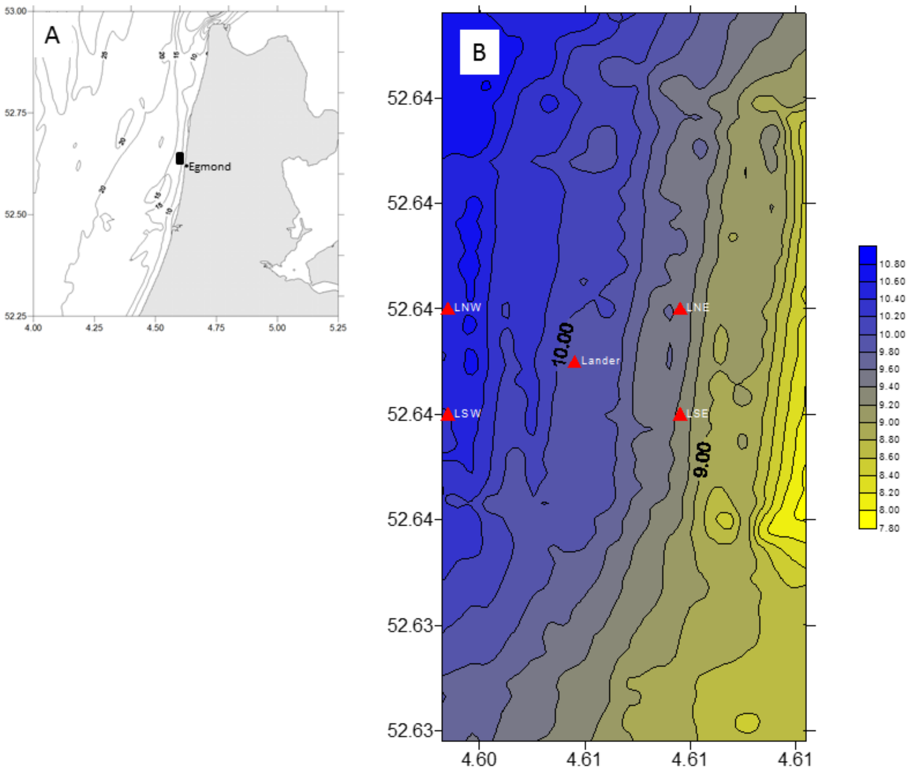

Figure 1. A) Study area offshore the coast of Egmond (the Netherlands; Province of North Holland) with (B) bathymetric map with locations of the measurement platform (lander) and the four surrounding sample stations (LNW, LNE, LSW, LSE). Colorscale indicates waterdepth in meter.

2.3 Measurements on the *Ensis directus* population near the lander

2.3.1 Sampling the stock

During the years 2011-2012 the site was visited every 3 to 6 weeks to service the platform (Fig. 1) and to collect *Ensis directus* from four locations (LNW,LNE,LSW,LSE) around the platform (Table 1 & Fig. 1). Hereto two boxcore samples were taken at each of the four corner locations around the measurement platform. If the boxcore sample was of sufficient quality, i.e. > 10 cm deep and with an undisturbed surface layer, a small subcore of the top 5 cm was preserved for sediment grain size analyses. The remainder of the boxcore was sieved over a 1 mm screen and the live *E. directus* were collected and stored for density estimates, size measurements and ash free dry weight (AFDW) determination. In this way a time series of the growth and population development of the local *E. directus* stock could be obtained on basis of population averages. For the analyses of shell and tissue growth also the boxcore samples taken in 2010 were used. In 2010 the site was visited 6 times. In 2011 and 2012 the site was visited 19 times. In 2013 the site was revisited once in June.

Table 1. Positions of the measurement platform ("Lander") and the four stations around it which were sampled 6 times in 2010 and 19 times in the period between 2011-2012.

Station	Lattitude (N)	Longitude (E)
LNE (Lander North East)	52° 38.280’	4° 36.356’
LSE (Lander South East)	52° 38.216’	4° 36.380’
LSW (Lander South West)	52° 38.220’	4° 36.220’
LNW (Lander North West)	52° 38.281’	4° 36.220’
Lander	52° 38.249’	4° 36.294’

In the 2011 and 2012 surveys the 8 boxcore samples around the measurement platform were supplemented with additional boxcores to collect about 70 *E. directus* specimens for the assessment of seasonal trends in condition related parameters and gonadal development. Samples for this purpose were not confined to any of the four stations, but were still taken in the vicinity of the measurement platform and its four surrounding stations. From all collected specimens a sub-sample of 50 *Ensis* was used for determination of their seasonal change in gonado-somatic index. Another 10 specimens were collected for analysis of the tissue glycogen content. On board all samples were stored refrigerated. In the lab the samples for glycogen content were stored at -80°C. Statistical analyses and description of the data was done in R (R-coreteam, 2012).

2.3.2 Size and weight measurements

For the determination of the seasonality of shell growth and tissue growth the living animals were measured with digital callipers to the nearest 0.1 mm. Three measurements were made: length, width and thickness. For incompletely sampled or broken animals the total length was estimated from shell width. In addition to these size measurements the ash free dry weight

(AFDW) was determined. For this, the soft tissue was removed from the shell, dried at 60°C until constant weight and then incinerated at 540°C during 4 hours. The weight difference of dry weight and ash-weight is the ash free dry weight (AFDW). These data were used to calculate the body mass index (BMI: Dame, 1996) or condition by dividing the AFDW by shell volume. Here we calculated shell volume as (length×height×width) .

2.3.3 Gonado somatic index.

For every survey date a selection of 50 individuals of different size classes was used to measure the gonadal development. Hereto the gonads were dissected from the somatic tissue under a stereomicroscope. Both tissue types were kept separate, dried and incinerated to obtain their AFDW (see above). These weights were used to calculate the contribution of the gonadal mass in the total AFDW of the animals. Based on these determinations and the collection of data over the two years, the seasonal change in gonadal mass over the years 2011 and 2012 could be determined.

2.3.4 Glycogen content.

The glycogen content of 114 specimens was determined according to the enzymatic-colourographic method of Keppler & Decker originally published in 1970 and adjusted in 1974 (Keppler & Decker, 1970; 1974). Average sample weight for each determination was approximately 40 mg. Glycogen present in the sample is first hydrolyzed to glucose. This glucose is enzymatically transformed (with glucose-6-P-dehydrogenase) into 6-fosfogluconolacton. In this reaction NADPH is formed which is spectrophotometrically determined at a wavelength of 340 nm. A calibration line was used to back calculate the observed extinction values into concentrations. The calibration line was determined on basis of pure mussel tissue glycogen (Sigma G1508-5G).

2.4 Sampling the *Ensis directus* population in the wider coastal zone

The aim of the sampling survey in June 2011 was to determine if the distribution and densities near the "lander" location represented distribution patterns over a wider coastal (along shore) area. During this survey the coastal zone between IJmuiden and Petten was covered. In total 8 transects perpendicularly to the coast with 12 boxcore stations each were sampled. Each transect extended up to 6 km from the coast. The three stations closest to the beach were approx. 100 m apart, the stations furthest away from the beach were 1000 m apart and the 4 stations in between were 300 meter apart. One boxcore was taken at each station. From each boxcore a small-sized 5 cm deep subsample was taken for the determination of sediment grainsize and mud content (% <63 µm). The remaining boxcore contents were sieved over a 1 mm screen. From the residue, living *Ensis directus* were collected, counted and shell sizes measured. Because of the draft of the ship, we could only sample in waters deeper than approximately 10 meter.

2.5 Data analyses

Generalized additive modelling (GAM) (Wood, 2006) was used to describe the average seasonal trends in shell growth, tissue growth and condition parameters. GAMs were also used to describe the average seasonal trends in environmental parameters. In this method the determination of the seasonal trends is based on the calculation of a smoothed regression spline which is penalized by the number of variables used. This modelling was done with the package “mgcv” (Wood, 2006) within R (R Core Team, 2012).

3 RESULTS

3.1 Environmental setting lander site

In 2011-2012 the lander study site has a marked seasonal cycle in bottom water temperature, with highest temperatures of about 18°C at the end of summer (Fig. 2). Salinity varies between 26 PSU in winter-spring and 32 PSU in summer. At 140 cm above the seafloor the alongshore semi-diurnal tidal current has maximum speeds which vary over the neap-spring cycle between 70 and 120 cm s^{-1}. The average pressure difference measured over 10 minute long intervals during the deployment corresponds to an average wave height of 1.3 m. The maximum measured pressure amplitude was equal to a water column height difference of 6 m (in December 2011), which is about half of the local water depth. Hence the area can be characterized as an energetic environment.

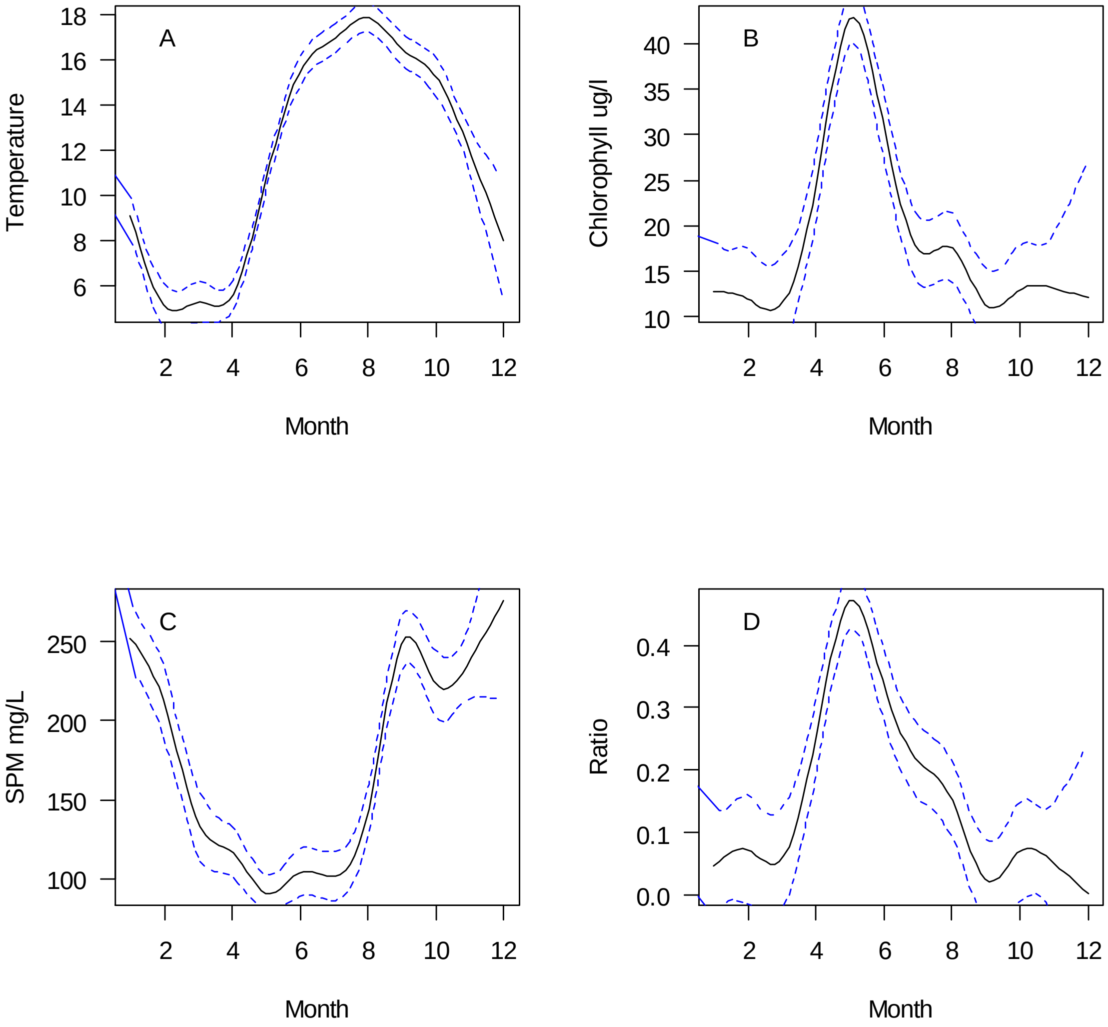

Figure 2. GAM fits describing the averaged (2011-2012) seasonal cycles in (A) temperature, (B) Chlorophyll, (C) SPM and (D) Ratio of Chl-a/SPM as measured over the period February 2011-November 2012. Curves are GAM fits with 95% confidence limits around it. GAMs were constructed with the R package "mgcv" (Wood, 2006).

Chlorophyll concentrations peaked in May with an average near-bottom concentration of 50 µg l^{-1}. Total SPM concentrations 30 cm above the bottom are at minimum (~100 mg l^{-1}) between April and August. In autumn and winter the average SPM concentration is here approximately 250 mg l^{-1}. During storms, SPM peak concentrations surpassing 3000 mg l^{-1} have been measured.

3.2 Measurements on the *Ensis directus* population.

3.2.1 Population density

In 2009 a new cohort of *Ensis directus* had settled in the near coastal area off Egmond and in early March 2010 we found initial densities of ~2300 ind m^{-2} close to but not at the permanent sampling stations (Lander, LNW, LNE, LSW, LSE). At that time a maximum density of ~700 ind m^{-2} was found at these four stations (Fig. 3). Initially the average densities at the southern two stations (LSW and LSE in Fig. 1) were higher than at the northern stations (LNW and LNE). Later this difference disappeared. At all stations, densities gradually decreased over time. At the end of November 2012 the average density was 80 ind.m^{-2} and half a year later on June 6th 2013 the average density had decreased to 46 ind m^{-2}. On basis of this observed decrease and over an annual time base, the finite survival rate was estimated to be 49% (Fig. 3) which is very similar to rates reported by Armonies & Reise (1999) and for the Wadden Sea by Dekker & Beukema (2012).

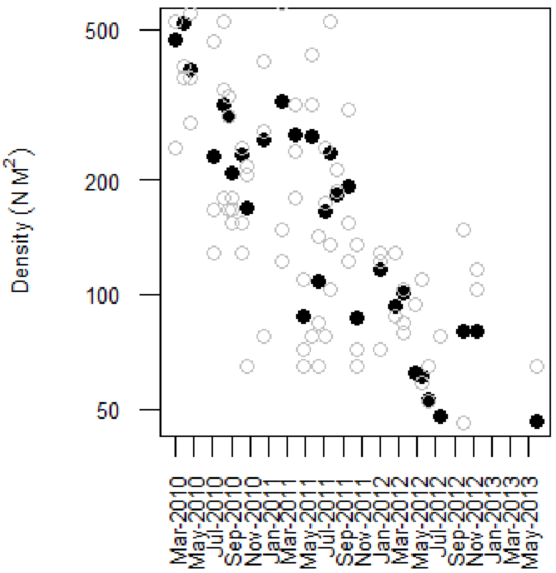

Figure 3. Densities of *Ensis directus* over time sampled at the locations around the measurement platform (LSE, LSW, LNW, LNE) between spring 2010 and June 2013. Grey open circles the density estimates for each of the four stations. Filled dots give the average densitities. Note the logarithmic y-axis.

Morisita's index of dispersion (Young & Young, 1998) was calculated on basis of numbers caught in all separate boxcore samples during each sampling occasion. This yielded values which were smaller than those expected in case *Ensis directus* had a clumped distribution suggesting that at this location and spatial scale of sampling *Ensis directus* is randomly to evenly distributed.

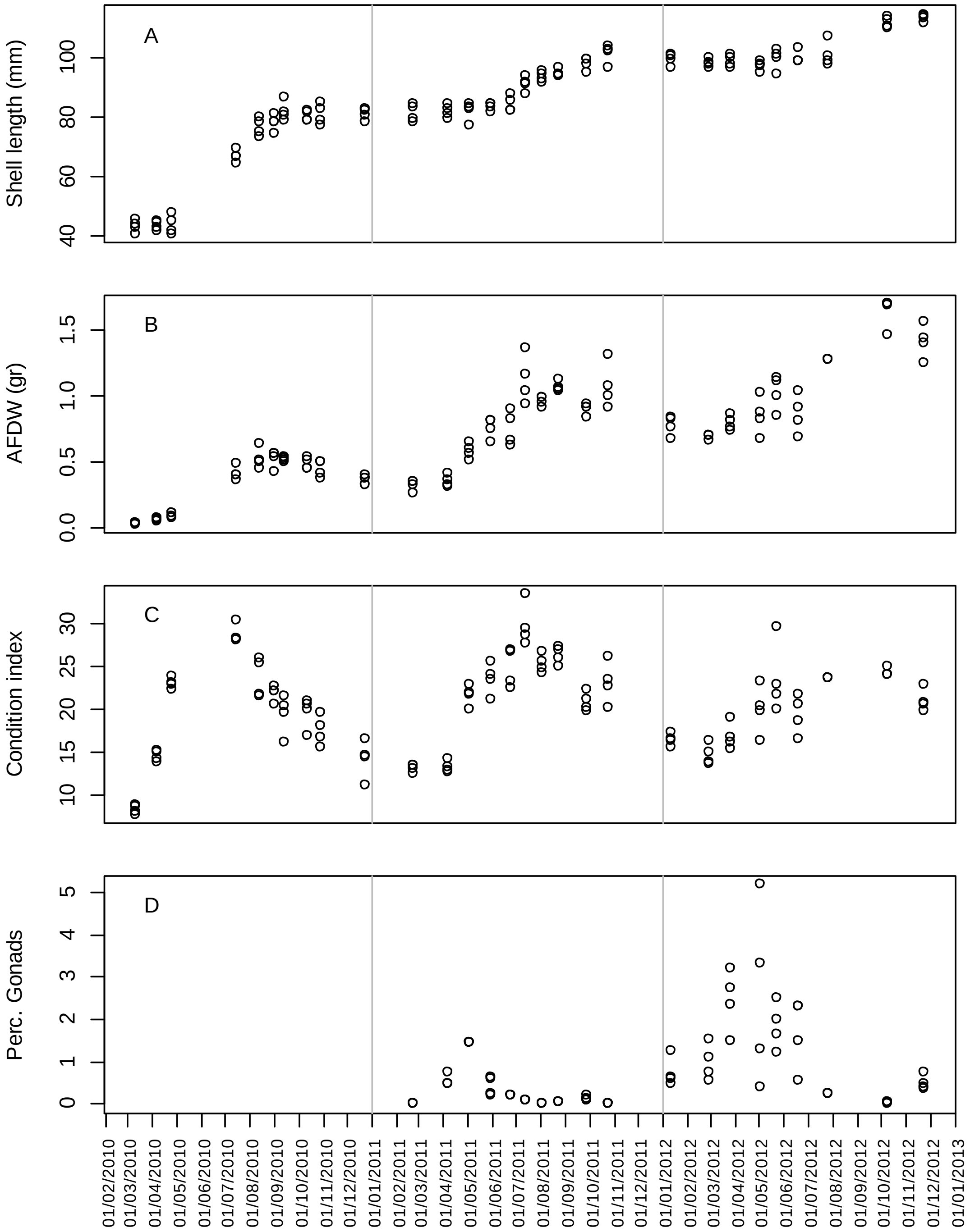

Figure 4. Temporal development of (A) shell length, (B) AFDW, (C) condition index (AFDW shellvolume^{-1}) and (D) the amount of gonad tissue as percentage of total bodymass between February 2010 and November 2012 measured for the 2009 cohort of *E. directus*.

3.2.1 Shell length, AFDW, condition, gonads

The temporal variation of shell length, AFDW and condition index of individuals which had settled in 2009 and were collected at the four locations around the measurement platform (LNW, LNE, LSW, LSE) during the study period are shown in Fig. 4. Determination of age (cohort 2009) was made on basis of externally visible growth lines (Cardoso *et al.*, 2013). The patterns in Fig. 4A, B illustrate that tissue growth (AFDW) starts before length growth. The total AFDW increases in spring and early summer. In autumn and winter AFDW decreases again.

Because AFDW is linked to shell size the seasonal change in condition index being AFDW divided by shell volume (Fig. 4C) might give a better estimate of the temporal evolution of tissue weights as it is independent of shell size. This shows that the increase in condition is largest between April and June and parallels the development of the spring bloom (Fig.2B). After the bloom period, the condition of *Ensis directus* almost immediately starts to decrease and reaches minimum values in winter and early spring of the following year. This leads to a cyclic seasonal evolution of the condition index.

The proportion of gonad tissue is largest in the beginning of May. (Fig. 4D). The gonadal mass increases from about 0.5% to a maximum of 3.5 % of the AFDW. Around the time of spawning 90 % of the dissected specimens had developed gonads and could be sexed. The difference in the average percentage of gonadal mass between subsequent sampling dates was used to detect the main spawning season (Fig. 5). This illustrates that in 2011 the largest loss of gonadal mass was at the end of May. In 2012 the loss of gonadal tissue was spread over a longer period and lasted from the end of May until the end of July. This evidences inter-annual variability in the length of the spawning period. In 2012 the one year older and thus larger animals have a larger proportion of gonadal mass which might imply that a population with larger and older animals may spawn over a prolonged period.

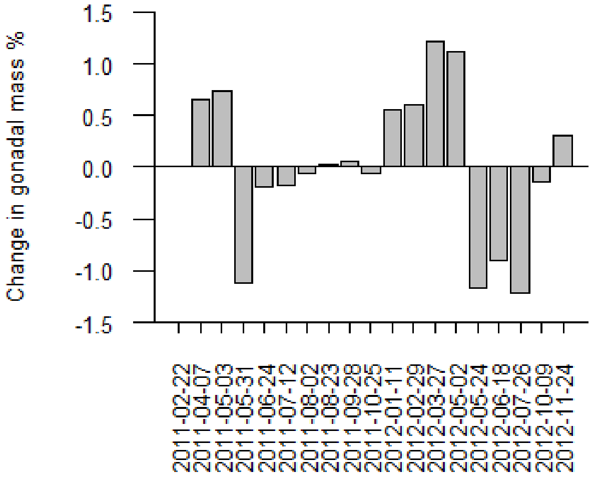

Figure 5. Change in the percentage of gonad tissue between February 2011 and November 2012

On basis of the average shell sizes per sample, location and date, shell growth rates could be estimated from the change in average length divided by the time (days) passed since the previous measurement. For this calculation only shells which belonged to the 2009 cohort were used. Figure 6 shows that maximum growth rates decrease with time and illustrates that the older and larger animals have lower absolute shell growth rates. Maximum shell growth rates decreased from about 0.25 mm day^{-1} in the first year to approximately 0.05 mm day^{-1} in their third year (Fig 6). The maximum rates were achieved in the summer months only.

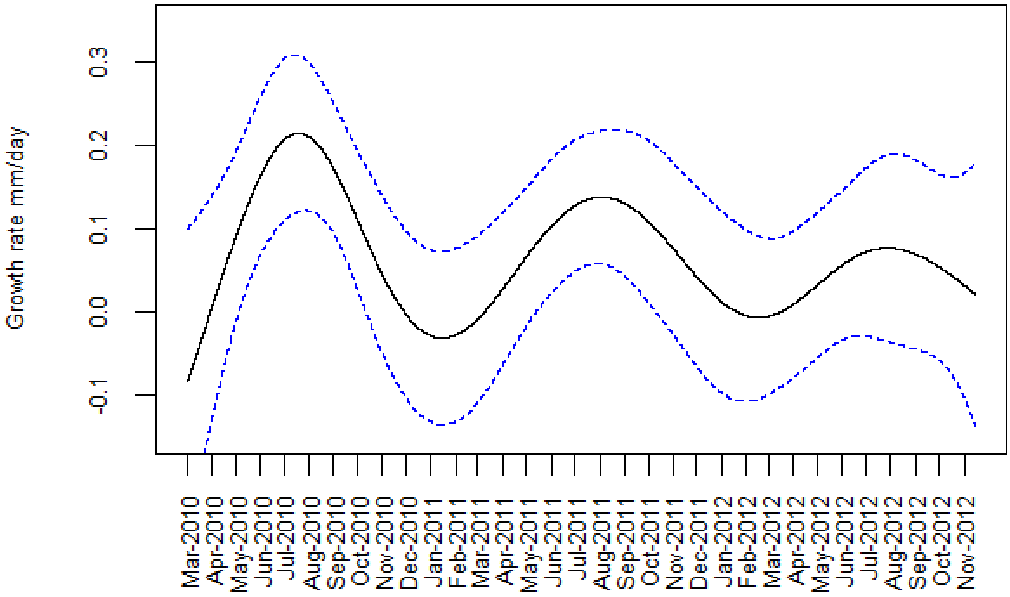

Figure 6. Variation in estimated shell growth rate over time for the 2009 cohort. the black line is a fitted GAM model (Wood 2006) illustrating the change in absolute growth rates over time with its 2.5 % confidence limits around it (dotted lines). The fitted function is highly significant p<0.01.

3.2.2 Glycogen values

Likewise as the condition index, the energy content of the soft tissue mass also reflects a change in condition as relative amounts of fat, proteins and carbohydrates vary.

One of the carbohydrates which is stored as reserve is glycogen. The analyses of the glycogen content showed that the maximum glycogen tissue percentage (by weight) is about 10% (Fig. 7). In autumn the percentage glycogen rapidly decreases and between November and March a minimum of less than 1% was found. The observed seasonal cycle in glycogen content matches the observed seasonal cycle in overall condition index (Fig. 4C). The condition index (bodymass shellvolume^{-1}) appeared to be a good predictor of the period averaged glycogen content. The regression between both is highly significant and the condition explains 72% of the variance in glycogen content ($p<0.05$). This strong relationship shows that the classical determination of the condition index based on AFDW and shell size is a good predictor of the energy reserves stored within the animal. Sample size per collection date was too small to examine a potential relationship between glycogen content and body (shell) size.

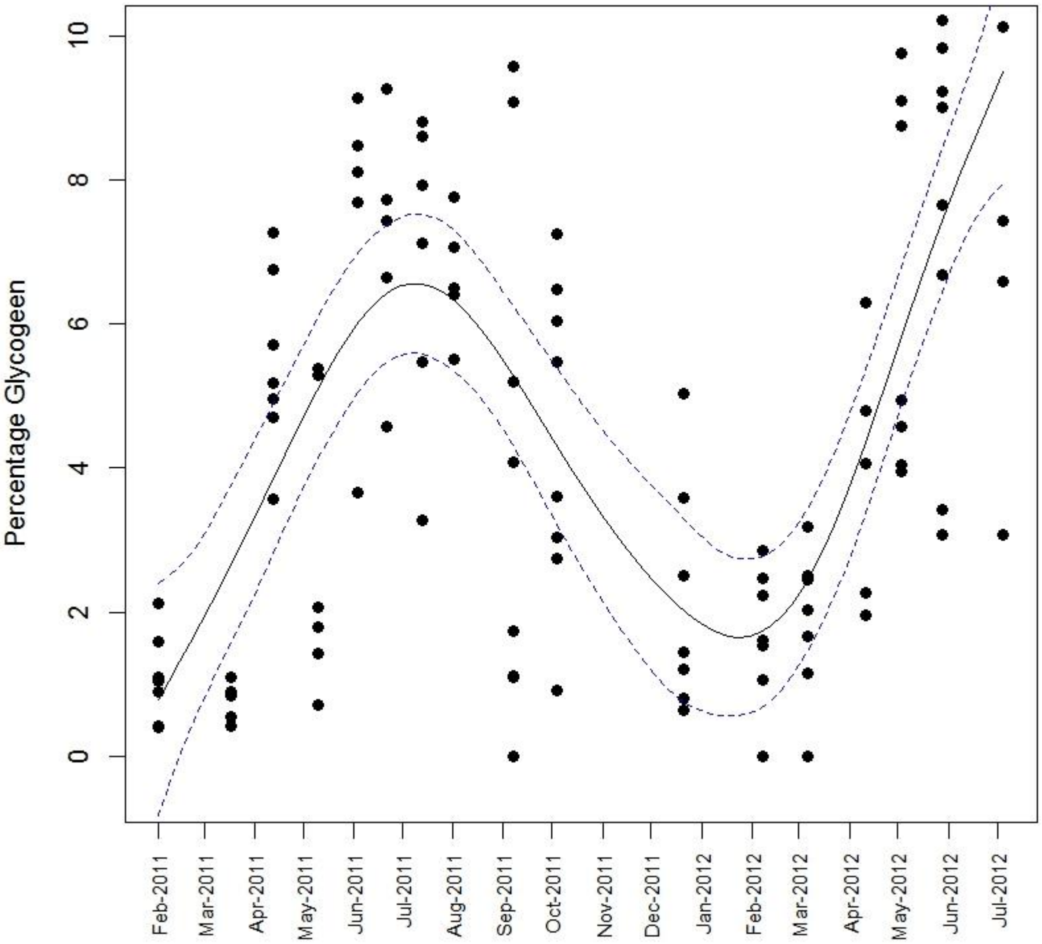

Figure 7. Gam fit (Wood, 2006) of the percentage glycogen in homogenized freeze dried *Ensis directus* tissue in the period 2011-2012. Fitted line is significant at $p<0.001$.

3.3 - Distribution *Ensis directus* in the wider coastal zone

The distribution of *Ensis directus* in the deeper parts of the (>10m) coastal zone is plotted in Fig. 8 which shows that the highest densities are found in a rather narrow band closest to the coast. The maximum observed density during this inventory in 2011 was 397 individuals m^{-2} with a mean density of 90 individuals m^{-2}. At the stations nearest to the shore, the average size of the animals was considerably smaller (88 mm) than at the stations lying further offshore (120 mm). This was mainly due to the difference in age of the specimens collected from near shore and off shore locations. Over the entire area the average size was ~99 mm.

The analyses of the sediment samples taken along the transects showed that median grain size increased with distance from the coast. The stations furthest away from the coast had slightly lower mud concentrations when compared to the near coastal stations. Over the sampled area the median grain size decreases from north to south, but only the most northerly transect had a significantly different median grain size (Tukey HSD, $p<0.05$). The mud content did not differ between transects.

The map in Fig. 8 furthermore illustrates that densities of *Ensis directus* at the sampling sites near the platform (lander) and hence the data on growth and production of the *E. directus* population, are representative for a larger part of the near-shore coastal zone of North Holland.

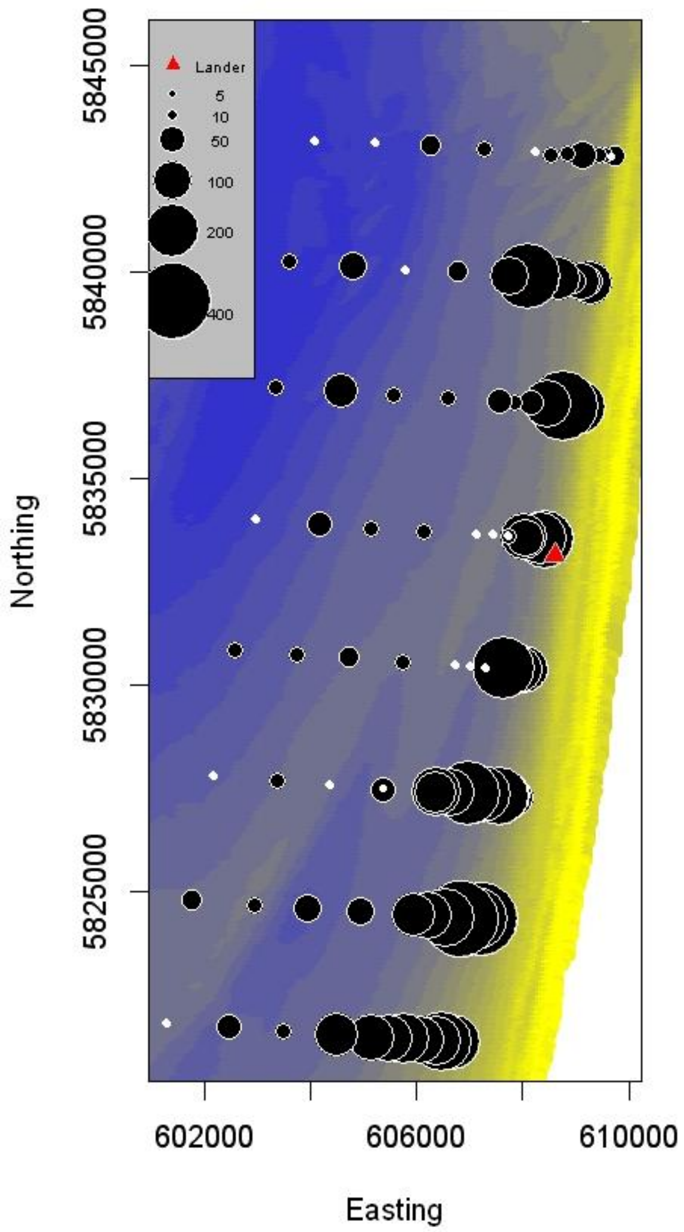

Figure 8. Distribution and density of *Ensis directus* (all year classes) along the coast of North Holland in June 2011. The shallow area (<10m) could not be sampled. Hence, no information on densities in this area are available. Black filled circles of different size indicate density. White circles indicate absence from sample. The triangle indicates the deployment location of the measurement platform (lander).

3.4. Growth and condition of *Ensis directus* in relation to environmental conditions

We used a redundancy analyses (RDA, R-package: vegan, Oksanen *et al*, 2013) to obtain insight in the relation between shell and tissue growth of *Ensis directus* and seasonal variations in environmental factors. For this we used the data collected with and around the permanent measurement platform (Fig. 1). During the deployment of the platform we continuously measured several variables, i.e. temperature, salinity, pressure (waves), SPM and fluorescence, all of which can potentially influence the growth of *E. directus.* For this RDA analyses we used the station averaged data, i.e. the means of growth and condition of the four stations (LSE, LSW, LNE, LNW) during each of the measurement periods, together with the period averaged environmental conditions simultaneously recorded by the lander at the central location (Fig. 1). Selection of explanatory variables and covariates used in this analyses was made on basis of their contribution to variance inflation (VIF<3). Therefore condition and glycogen were omitted from the analyses. The result of the RDA analysis is given in Fig. 9.

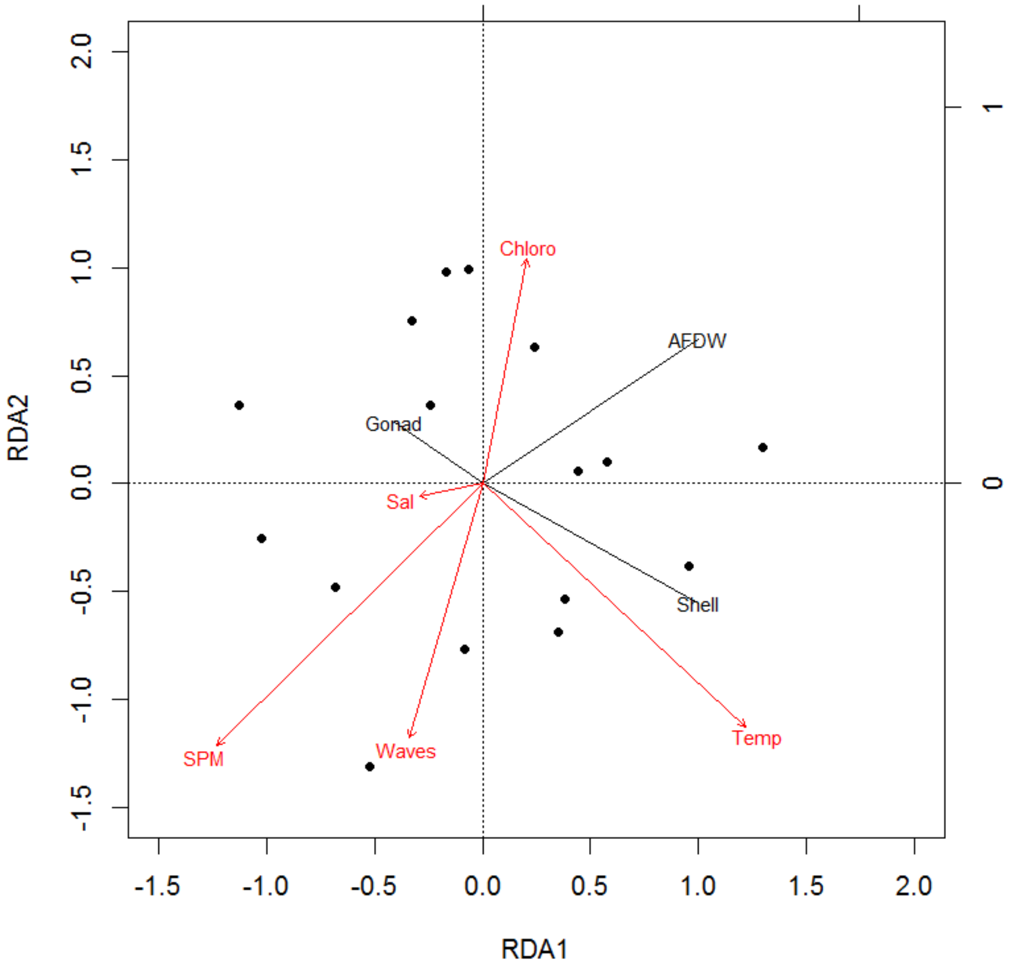

Figure 9. RDA correlation triplot showing the relationships between abiotic variables (averaged over periods) and the *E. directus* growth parameters determined at the end of each of these periods. Measurements cover the years 2011-2012. Shell= shell growth, AFDW= Ash free dry weight growth, Gonad,=change in relative gonadal mass., Chloro=average chlorophyll concentration at 30cm above the seafloor, Sal=average Salinity, SPM = average Suspended matter concentration, Waves = average waveheight and Temp= average temperature.

The explanatory variables explain about 49% of the observed variance in growth and condition parameters of *Ensis directus*. The (correlation) triplot made on basis of the first two RDA axis shows that wave height and SPM are strongly linked and are inversely related to tissue growth. Tissue growth (AFDW in Fig. 9) is positively related to chlorophyll (Chloro). Strikingly, shell growth (Shell) appears to be unrelated to tissue growth (AFDW). Instead shell growth is positively correlated to water temperature. The change in gonadal mass (Gonad) is unrelated to SPM or chlorophyll. The plot in Fig. 9 suggests an inverse relationship between gonadal mass and temperature and independency from tissue growth or condition.

A permutation test was used to determine the order of importance of separate environmental factors in explaining the observed growth responses. This showed that both temperature and SPM contribute significantly in explaining the observed shell and tissue growth rates and condition changes (Table 2).

Table 2. Overview of the test statistics of the permutation test to determine the order of importance of the various environmental factors in explaining growth and condition parameters (Shell growth, AFDW growth, change in Gonadal mass and average caloric content as measured in *E. directus* in 2011 and 2012.

	Df	AIC	F	N.Perm	Pr(>F)
SPM	1	16.549	3.9725	9998	0.007301 **
Temp	1	13.891	4.3925	9998	0.007401 **
Chloro	1	14.115	1.4090	9998	0.253925
Sal	1	15.721	0.2743	9998	0.852485
Waves	1	17.633	0.0549	9998	0.981798

The calculated variance inflation factors suggest that SPM and Chlorophyll could be used simultaneously in the RDA (correlation <0.7). Nevertheless there is an inverse relationship between both as they have strong opposite seasonal trends (r=-0.61). This not necessarily indicates a causal relationship but complicates the interpretation of Fig. 9. Therefore the RDA analyses was repeated with the ratio (Chloro:SPM) instead of the separate factors (Chloro and SPM). The ratio expresses qualitative aspects (µg Chlorophyll per mg SPM) and circumvents the potential dependency of Chlorophyll and SPM in the RDA. It describes the seasonal effect in the relative amounts of SPM and Chlorophyll as one quantity. Incorporating the ratio in the RDA analysis showed that the total variance explained by the explanatory variables becomes 38%. This analysis suggests that tissue growth is positively correlated to the quality of suspended matter (Chloro:SPM =Ratio). Shell growth remains indifferent to the suspended matter quality. A permutation test showed that both temperature and the Ratio (Chloro:SPM) are highly significant (p<0.05). The RDA analyses suggests relationships between growth and environmental controls with SPM concentration being most important. It is however not entirely clear whether the absolute amounts of SPM or the quality of the SPM (ratio Chloro:SPM) is the key factor.

4 DISCUSSION

4.1 Growth of the *E. directus* population

Concern about the possible impact of beach nourishments on the production of the local *Ensis directus* population initiated the present project. There are various studies which review the potential effects of beach nourishments (Essink, 1999; Greene, 2002; Speybroeck et al, 2006). Increased turbidity is one of the potentially important factors identified by above studies. However, actual measurements on turbidity close to the bottom where bivalves live, its natural seasonal variations and how they relate to maintenance activities are lacking.

Therefore we focussed on growth and energy allocation in *E. directus* in relation to variation in environmental conditions. These data were anticipated to give insight into factors that are important for shell and tissue growth and their seasonal timing.

All our measurements on tissue composition and growth of *E. directus* demonstrated strong seasonal cycles most of which closely followed the spring bloom peak in chlorophyll concentrations except for gonadal development which started before the spring bloom. In our study the earliest signs of a seasonal increase of the gonadal mass were visible in December 2012 (Fig. 4D). But also in the previous winter of 2011-2012 the gonadal mass had already started to increase in February-March. This early start of gonadal development implies that most of the energy uptake in winter is allocated to gonad growth as by that time no shell or significant tissue growth was observed. In fact our data suggests that this early in the year, total AFDW still decreases thus gonad weights apparently increase at the expense of the somatic tissue. In early May, the gonadal mass is maximal and is followed by spawning. Gonad development peaks during the phytoplankton spring bloom and as a consequence of this timing the planktonic larvae appear in a period in which they optimally profit from rich food conditions in the water column. For *Ensis arcuatus* Darriba et al. (2005) observed similar timing with an early gonadal development before the phtyoplankton blooms in their study area had started. This shows that the gonads in *E. arcuatus* also developed at the expense of stored energy but that the larvae of *E. arcuatus* are released in a period of maximal food availability.

In *Ensis directus* we observed that shortly after the observed peak in gonadal mass and spawning, the somatic tissue starts to increase but at this time shell growth is still not yet evident. We observed that significant shell growth did not take place before the water temperature was about 12-14 °C. Latter observation is confirmed by the carbonate stable oxygen isotope data as reported by Cardoso *et al.* (2013) and similar uncoupling between tissue growth and shell growth has also been observed for other species (Hilbish, 1986; Lewis & Cerrato, 1997).

The sequence of changes in the growth of gonads, somatic tissue, and shell as described here was seen in both 2011 and 2012. In 2010 this sequence of tissue and shell growth could not be determined. Various other studies have reported on the timing of reproduction of *Ensis directus*. Mühlenhardt-Siegel et al (1983) estimated that a population living in the German

Bight spawns in March and April. This seems earlier in the year than what we found. But the data collected by Pulfrich (1997) in the German Wadden Sea as well as the observations by Cardoso *et al* (2009) are in line with our observations for the Egmond population in 2011 and 2012. While most studies report the main spawning in the spring, Cardoso *et al.* (2009) found a second (small) peak in gonadal mass in July and August. Pulfrich (1997) and Philippart et al (2014) found a similar second peak in larval abundance in the German and Dutch Wadden sea respectively. It is thus likely that a second spawning event might exist in late summer. This also has been suggested by the findings of Armonies & Reise (1999) and Strasser & Günther (2001) and multiple spawning peaks have been observed for closely related species as well (Darriba et al, 2004, Barón et al, 2004).

In our Egmond population we could identify a small peak in the number of animals which could be sexed in September 2011 but it is questionable whether the percentage of gonadal mass (0.1%) is high enough to represent a secondary spawning peak. The data however show that in 2012 the period over which ripe animals were present was much longer than in 2011. This suggests that spawning may take place over an extended period or in several pulses. Partial release of gametes may be possible in large animals whose energy reserve is sufficiently large to maintain or build such a large gonadal mass. We observed that in the primary spawning period (Feb-June) indeed a relation exists between the maximum percentage of gonadal tissue and animal size. The data also show that the percentage of gonadal mass in 2012 in comparison to 2011 was significantly larger (ANOVA, $P<0.01$). These observations thus suggest that larger and older animals in a population not only have a relatively larger contribution to the total spawning mass but also might be able to generate multiple spawning peaks.

Unpublished NIOZ-data collected in 2007 and derived from monthly water samples along a east-west transect across the same coastal area, shows that pelagic larvae of *Ensis directus* are present almost year round. This can only be explained by spawning which takes place over prolonged periods possibly in combination with lateral transport of larvae, originating from other source populations. Despite the above observations of an almost continuous presence of larvae and the likely existence of multiple spawning peaks, we never observed significant recruitment of new spat between 2010 and 2012. Only by the end of 2012 when the density of adult *E. directus* had dropped to 40-60 m^{-2}, low numbers of recruits were found. This suggests that density dependent processes might regulate settling. Other observations that point to density dependent recruitment processes come from a pilot settlement experiment performed prior to the present study in 2010. In this experiment we observed settling of high numbers of juveniles in tubes which were filled with clean defaunated sand while in tubes filled with living or dead *Ensis* no spat was found.

4.2 Relating density and growth to environmental conditions

The distribution of *Ensis directus* along the Noord-Holland coast (Fig. 8) shows that within the extent of our survey, the highest densities are found in the transitional zone where the seafloor abruptly descends to a depth of 10 meter and where waves have a strong effect on the seabed due to the shallow depth and topography. This is also the type of habitat where this species is typically found along the east coast of the US and Canada (Kenchington, *et al.*, 1998). Also in the Wadden Sea, maximal densities are found in a transitional zone between intertidal and sub-tidal area (Armonies & Reise, 1999; Dekker & Beukema, 2012; Freudendahl *et al*, 2010). These areas are characterized by strong tidal currents and mobile sands with low silt contents (Dekker & Beukema, 2012). The lander observations in this study corroborate the view that *Ensis directus* prefers a dynamic environment. However, our data do not support the idea that high *E. directus* densities are necessarily found in the sediments with lowest mud contents. At the outermost stations (Φ 222 µm, Mud=2.9%) of the survey grid only low densities of large animals were found. High densities of *E. directus* were found close to the coast at water depths of approximately 10 meter and in sediments with an average percentage of mud of approximately 5% and a median grain size of 185 µm. Dannheim & Rumohr (2012) also found the highest densities in fine silty sands at water depths between 10 and 13 meter. We cannot exclude that *E directus* densities at our location may attain even higher levels in shallower water i.e. between low water mark and 10 m depth where we could not sample due to the draft of our vessel. Therefore the survey does not give a complete view of the distribution of this species over the entire depth range in the near coastal zone.

In this study, we have correlated growth of *Ensis directus* with in-situ measured environmental parameters. A different approach to determine effects of silt and algae on growth was adopted by Kamermans *et al* (2013) who tested the effects of increased levels of kaolin and algae on clearance rate and growth of of *Ensis directus* at ~18°C. They observed that the clearance rate was reduced at suspended silt concentrations of 300 mg l^{-1}, but found that this condition stimulated growth for medium sized animals. Their study showed that at the same silt concentrations, a higher algal concentration led to increased tissue growth. The final AFDW appeared dependent on the Chl-a concentration, but not on silt concentration. This corresponds with our field observations showing a positive relationship between tissue growth and Chlorophyll and between tissue growth and the Chl-a:SPM ratio.

The average SPM background concentration at 30 cm above the seafloor and over the entire measurement period was 161 mg l^{-1}. During sand nourishments in June 2011 close to our Egmond location, SPM showed elevated levels to approximately 250 mg l^{-1}. This value approaches the critical concentration of 300 mg l^{-1} where the clearance rate of *E. directus* is affected (Kamermans et al., 2013). In comparison to SPM concentrations measured during wind events the SPM increase due to the local maintenance works were relatively small. We observed that waves during storms generate peaks in SPM to over 3000 mg l^{-1}. At our location the observed variability and short lasting increase in SPM due to maintenance works evidently fell within the natural variability range of SPM close to the bottom. Our time series furthermore showed that during the main growing season for *Ensis directus* (March-Aug) the SPM concentrations surpassed the 300 mg l^{-1} threshold during only 6 % of the time. On basis of this limited amount of time, it seems unlikely that a significant effect of elevated SPM levels on growth, mortality and production of the local *Ensis directus* population can be demonstrated. Especially since Kamermans et al (2013) also observed a positive effect of elevated SPM on growth of medium sized animals.

To coroborate this assumption we have put our data on density, mortality and production of *E. directus* off Egmond in wider perspective by comparing them with data from studies on populations living elsewhere. Although the various studies refer to different years, cohorts and locations the results enable a comparison with our data of the Egmond population.

The densities of early juveniles (end 2009 early 2010) at the lander site near Egmond (700-2300 ind m^2) appeared to have the same order of magnitude as found for spat and juveniles in the subtidal and transition zone of the Balgzand area in the Wadden Sea (Dekker & Beukema, 2012). The spat densities at various locations in the German Bight (Dannheim & Rumohr, 2012) are based on sampling in July. These estimates are therefore much higher when compared to our first density estimates which are based on sampling in December 2009 after mortality during autumn has already reduced the number of settlers.

Densities of older animals around the measurement platform are comparable to densities reported in subtidal areas in the Wadden Sea (Armonies & Reise, 1999; Dekker & Beukema, 2012) or for the German Bight (Dannheim & Rumohr, 2012).

Survival and mortality rates are strongly dependent on the age and the cohort which has been studied. For the Egmond location the 2009 cohort had an average survival rate of 49% over the entire study period. This value compares well with the rate (51-45%) which is found for *E. directus* living in the subtidal and transitional zone of the western Wadden Sea (Dekker & Beukema, 2012) and the value of 55% given by Armonies & Reise (1999) for the German Bight. Survival of the 0-age class appears to be very variable and is often only a few percent of the initial densities. For our study area we could not estimate this quantity as we have no data on densities shortly after settlement in summer and autumn 2009.

Longevity seems to be area dependent. For the Wadden Sea maximum ages of 5 years have been mentioned (Dekker and Beukema, 2012). Palmer (2004) as well as Armonies & Reise (1999) report a maximum age of 7 years for the Wash and the German Bight, respectively. Based on external ring counts (see Cardoso et al, 2013) we estimate a maximum age of 8 to 9 years for individuals from the Egmond population. The maximum shell length found at Egmond was 18.2 cm which compares well to the maximum shell lengths reported by Armonies & Reise (1999) for the population around the isle of Sylt (German Bight).

Indicative for the conditions of growth is the average size at age. At the end of the first growing season after settlement, the Egmond specimens have obtained a shell length of ~ 4-7 cm. This fits the range as reported in the summary table made for various populations by Dannheim & Rumohr (2012). The population and cohort we studied however seems to have retarded shell growth in their 3rd and 4th year. Maximum sizes found in these years were respectively 10.6 and 11.4 cm. Beukema & Dekker (1995) reported shell lengths of 12.6 cm and 14.4 cm for the same yearclasses. Also Mühlenhardt et al (1983) and Armonies & Reise (1999) report larger sizes for the third and fourth year of growth. Thus while densities, mortality, maximum age of the Egmond population vary within the ranges reported in literature, shell size at later age appears to be relatively small. This can point to an effect of the coastal maintenance works in 2011. Therefore we checked whether body condition parameters showed a potential effect of coastal maintenance works.

Because we used a slightly different way to calculate the BMI a recalculation was done which showed that the BMI (sensu Dekker & Beukema, 2012) for the Egmond population ranged between 0.3 and 1.6 mg AFDW cm^{-3} which compares well to the range given in Cardoso et al (2009). The minimum value we found (0.3) is slightly lower than the absolute minimum (0.37) mentioned by Dekker & Beukema (2012).

Another measure for the condition of bivalves is the percentage of glycogen stored in their tissue (Fernadez-Reiriz et al, 2007, Hummel et al, 1988). The seasonal trend in this percentage shows that high values in *E. directus* follow periods of high food availability (Fig. 7, Fig 2B). It shows that glycogen is stored as energy reserve during such periods. In other species a similar seasonal trend has been found (Hummel et al., 1988). The maximum percentage glycogen in *E. directus* from Egmond was about 10% during the summer months. This value is lower than the ranges of total carbohydrates (Glucose + Glycogen) in bivalves as given by Beukema (1997) but is twice the maximum amount of glycogen which was found in adductor muscles of the closely related *E. arcuatus* (Darriba et al, 2005). This suggests that *E. directus* near the lander site had a good condition. A good condition is furthermore supported by the strong correlation between the percentage glycogen and the condition index ($r=0.88$, $p<0.001$, this study) especially since the condition indices compared well (see above) with data published by Cardoso (2009) or Dekker and Beukema (2012). Also the maximum amount of reproductive tissue which we found in *E. directus* from Egmond is very similar to that found in specimens from the Wadden Sea (Cardoso et al, 2012). Thus the values of various parameters indicative for the condition do not provide clear evidence that *E. directus* from Egmond are performing poorly in the area of study.

From an ecosystem point of view, production by the *E. directus* population might be a good measure of performance of the local population. Over the research period the biomass off Egmond, varied between 50 and 322 gr AFDW m^{-2}. Total production of the *Ensis* population was estimated to range between 200 gr and 50 gr AFDW m^{-2} yr^{-1} in 2011 and 2012, respectively. These values are substantially higher than the average estimates (8.6±3.4, max 100gr AFDW m^{-2} yr^{-1}) for the subtidal Wadden Sea population as given by Dekker & Beukema (2012). Thus although length growth of individuals at Egmond in their 3rd and 4th year seems to be less compared to other populations, annual production equals or even exceeds that of the subtidal population in the western Wadden Sea.

In summary, there seems no evidence that population development and production of the Egmond *Ensis* population deviates markedly from what could be expected on the basis of data from other populations. Hence, we cannot prove that there is a negative effect of elevated SPM levels on performance of *Ensis directus* in this area.

4.3 Potential explanations for the dense near coastal distribution of *E. directus*

Within our suvey the highest densities were found in a distinct zone at approximately 10 meter depth. This pattern was observed along all transects perpendicular to the coastline and below we present some hypothetical explanations for this pattern.

A first hypothesis involves the temporal mismatch between temperatures high enough for shell growth in *E. directus* and the presence of food with a sufficient high quality. Our data as well as those by Cardoso *et al.* (2013) show that there is no or minimal shell growth at temperatures below 14 °C during times that food quality peaks. The zone where we found highest *E. directus* densities (Fig. 8) coincides with persistingly high near-bottom concentrations of SPM (van der Hout, 2014 submitted) but at the same time is so close to the upper shoreface that the seasonal rise in water temperatures will closely follow the seasonal rise in air temperature and thus minimize the mismatch between food availability and occurrence of temperatures high enough for shell growth.

A second hypothesis explaining the peak in densities of *E*. *directus* so close to the coast is that high numbers of larvae passively accumulate in this zone similarly as high concentrations of SPM. The hydrography in this area (van Rijn, 1995; de Boer, 2009) triggers cross shore currents with down and upwelling in case of salinity stratification due to fresh water discharge by the river Rhine. The persistent presence of high SPM loads close to the bottom in this area (van der Hout, 2014) lends support to the “larval accumulation” hypotheses. A comparable mechanism has been proposed by Shanks & Brink (2005) to work on much larger spatial scales. Such a mechanism would imply that the high *E. directus* densities in this nearshore zone are merely caused passively and not based on larval selection.

An alternative hypothesis is that summer growth of microphytobenthos in the shallow foreshore might be important for the nearby *E. directus* population. Our continuous measurements of chlorophyll and SPM showed that chlorophyll concentrations peaked after strong winds, even in periods outside the main bloom season. Microscopic analyses of macro aggregates which were collected in June 2011 indeed showed the presence of large numbers of benthic diatoms in this material. We speculate that the chlorophyll peaks, observed during strong wind events, originate from the shallow part of the shoreface where enough light reaches the bottom to generate primary production by benthic diatoms. During strong winds these algae are detached from the substratum and become resuspended and concentrate just below the steep slope of the shore face where SPM accumulates and high densities of *Ensis* are found as well. Tidal mixing in this zone keeps these algae in resuspension and available to the dense *Ensis* beds. This source is likely to provide them with fresh algal material outside the (pelagic) phytoplankton bloom season. Due to depth limitations of the research vessel we could not test this hypotheses but preliminary measurements of light intensity at our 10 meter deep study site suggest that at that depth and during calm weather sunlight reaches the sea floor. So for the more shallow shore face it is even more likely that enough light reaches the seafloor to support primary production by an epi-benthic diatom community.

5. CONCLUSIONS

Following a local *Ensis directus* population at a shallow subtidal coastal North Sea site revealed marked seasonal cycles in gonadal development, soft tissue growth and shell growth. Somatic tissue growth does not take place until spawning in May. Thereafter shell growth begins when temperatures reaches 14°C or higher. The population characteristics such as mortality, growth and production are comparable to population variables measured in the Wadden Sea or German Bight. On basis of this observation in combination with the observed range of variation in measured SPM concentrations we assume that the supposed negative effects of elevated SPM concentration due to coastal maintenance works are minimal.

An inventory of *Ensis directus* along the North Holland Coast shows that within the extent of our survey the highest densities of *Ensis directus* are found closest to the coast at depths of approximately 10 meter. To explain this distribution alternative hypothesis have been put forward.

ACKNOWLEDGEMENTS.

This work has been made possible by financial support of the La Mer foundation (ref nr;LM-006588), a grant of Ecoshape (projectnr NTW3.1 – NTW2.5) within the framework of BWN and NIOZ itself. The practical work could not have been done without the enormous input of the crews of RV "Terschelling", "Pelagia" and the "Navicula". We would like to thank Joost van der Hoek, Evaline van Weerlee, Charlotte Saul, Job ten Horn and Carola van der Hout for their help on board.

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