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Investigations into growth and nutritional condition of *Crangon crangon* (L).

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SUMMARY

The following overview outlines the four manuscripts included in this thesis focusing on the most productive area in the world the Wadden Sea. The thesis aims to contribute to the general biology and the understanding of the life cycle of brown shrimp *C. crangon.*

Previous studies on brown shrimps are mainly limited to only those areas which are easily accessible with push nets or small boats, e.g. Kuipers and Dapper, (1981 and 1984), Hufnagl and Temming, (2011b). Another set of studies (Hufnagl et al., 2010) estimated mortality based on the DYFS and DFS surveys, which are only conducted in Autumn, when brown shrimp do not carry eggs. On the other hand, some studies such Kuipers and Dapper 1984 and specially Temming and Damm, 2002 highlighted that the winter egg production in deeper off shore waters may be of crucial importance to the stock dynamics. Therefore, the spatial population structure of *C. crangon* during winter 2009/2010, especially with regard to sex differences is not well known so far, and was hence studied in **Manuscript 1**. Samples were provided by Johann Heinrich von Thünen Institute from a winter survey, to: (a) describe the species population structure during winter, (b) analyze sex ratio in dependence of total length, water depth and region, (c) investigate maturity and egg development stages and (d) indicate maturity using "setae" as a new maturity indicators. For the analysis the survey area was partitioned into three zones Eastern (Dutch), Central (German) and Northern (Danish) Wadden Sea. Based upon shrimp numbers, mean total length, abundance and condition, for each male, female without eggs and ovigerous female (12 variables), two groups of stations were identified using hierarchical cluster analysis. Group 1 consisted of samples situated in sub-tidal areas (> 20 m) water depth while the second mainly included the samples from shallow waters (≤ 20 m). Factors determining the spatial distribution were depth (less abundance in deeper areas), size (smaller animals in shallow areas) and sex (males in more shallow areas) with regard to the main areas for egg carrying females based on densities (50.7 % in shallow areas). The Size of females at maturity was determined from the proportion of ovigerous females (apparent mature) and females with setae at the endopodite (mature). The size at which 50% (TL_{50}) of females were mature (based on our new indicator "setae") was lower (between 9 to 18 mm) than the TL_{50} values calculated based upon only ovigerous females. This indicates that setae are developed prior to egg development. Sex ratio (males/females) decreased with size in all cases examined.

The growth trajectory under natural environment towards recruitment to fisheries has received some attention in the past, especially in the Wadden Sea. Here reproduction occurs throughout the year with more intense settlement in late spring and summer/autumn (Boddeke and Becker, 1979), while maximum catches in the commercial fishery are consistently observed in autumn (ICES, 1996). Hence a major discussion is still under debate: are late spring settlers recruiting to fisheries in autumn? What is the contribution of the summer generation? This discussion was initiated by Boddeke (1976) who considered summer reproduction to yield the recruits to autumn commercial caches of the same year. In contrast, Kuipers and Dapper (1984) suggested that winter reproduction sustains the subsequent autumn fisheries through heavy spring settlement. The different perspectives mainly rely on growth rates under field conditions. However, until now great uncertainties exist about *in situ* growth rates, mainly because growth was mostly studied under laboratory conditions and observed growth rates are highly variable both within and between different studies. Therefore in **Manuscript 2** for the first time, *in situ* growth rates of brown shrimp *C. crangon* in the German Wadden Sea off Büsum were measured during 2010. Growth rate was measured using the instantaneous growth rate (IGR) method which involved measuring the changes in individual total length (*L*) before and after moult. This approach has so far not been applied to brown shrimp *C. crangon*. We used the IGR technique to determine the effects of sex (male and females), size class (small, medium and large shrimps) and temperature (from 7.0 to 22.0 °C) on *in situ* growth of brown shrimp. In the first two days following catch, we observed shortest mean intermoult period, 6 and 5 days for males and females respectively at 20 mm length, and large mean moult increments with average of 3.34 mm (20 mm length with 14.7 °C) and 6.28 mm (30 mm length with 22.3 °C) for males and females respectively. Our mean growth rate observed for males was 0.41 mm/day and was 0.76 mm/day for females at 22.3 °C (July 23rd) which are also higher than the most literature values, indicating that the autumn peak is related to the previous winter eggs production where the first mass immigration waves appeared. We also had the advantage to use our data to evaluate the new method established by Perger and Temming (2012). By applying their method 65 % and 89 % of the variances were explained at different temperatures as well as different size classes for males and females respectively which, however, strongly support the

new method. Also, combining both IGR and Perger and Temming methods make possible to measure the onset of field shrinkage (poor condition) the present study. However, need to evaluate the new method in order to clarify the method reliability when frozen samples used instead of live samples as Perger and Temming (2012) speculated. Thus, within **Manuscript 3**, we used frozen samples (-20 °C), from April to November 2010, to apply the parameters estimated (slope, intercept, minimum condition for males and females separately) by IGR and Perger and Temming (2012) growth methods (manuscript 2). In general, except when new recruits have been arrived, low growth rates (poor condition) were observed in both spring and autumn seasons, while higher growth rates values were observed during summer which indicating better nutritional situation during summer season (good growth). The annual length frequency distribution results indicating that two new recruitments have been observed first one was at 15th of June while the second one was at 23rd of July. We also used the length frequency distribution which, however, clearly suggested a short residence time; larger shrimps, are missing from the field, had left after period of two to 3 weeks to deeper water zone after the first new recruitment. The immigration of smaller individuals, with strong immigration waves in June and July, and emigration of larger individuals could be demonstrated during the study period as well as spring and summer immigrations.

Among the numerous studies on growth of *C. crangon* (L.), there are no studies on the nutritional requirement are available, except for one study carried out by Regnault (1977). Hence, in **Manuscript 4**, the aim was to provide information on how *C. crangon* reacts to an artificial pellet diet, which was optimised based on experience from shrimp aquaculture. Here, we evaluated the effects of artificial formulated diet on growth performance, body composition and survival of brown shrimp *C. crangon*. Field growth was estimated simultaneously based on IGR method and used as a reference in the present work during summer 2011. No significant differences ($p \leq 0.05$) in crude protein content of the final body composition between the control group (moult experiments) with group experiments and individual experiments for and between sexes were observed. Although a significant increase of the fat content at the end of experiments was observed for both individual and group experiments, the results of chemical composition analysis, energy levels and dry matter does not supporting the results from length growth rates; growth rates were not improved by artificial feeding as expected. The artificial diet were formulated and optimized based on the carnivore's peanied shrimps which contain the important components such as crude protein

from different two resources, lipids, cholesterol, different minerals and vitamins. In contrast, growth rates were dramatically lower than those of the reference groups sampled from the field. This indicates that some components, rather than that the important components that easily degrade are essential such as essential fatty acids (St. John, 1991)

However, the results from the reference experiments applying the IGR method revealed some additional important aspects of the *in situ* growth. For the first time we were able to show considerably shorter intermoult periods (6 days) in females than males (11 days). Female shrimp produced slightly lager mean moult increments (2.8 mm) than males (2.5 mm) which led in combination with the different intermoult periods to substantially different growth rates (Females 0.46 mm/day, males 0.22 mm/day).

GENERAL INTRODUCTION

Shrimps are an important component in the fauna of estuarine and coastal waters. The Caridea represent the dominant natant decapods crustacean group in the temperate region that replace the Penaeidea in the Southern latitudes (Allen, 1966). Overall there are about 2000 species of natant decapods in Europe of which about 1650 are Carideans (Smaldon, 1979).

Brown shrimp *Crangon crangon* is common species that tolerates a broad range of temperatures (Caudri, 1937; Weber and Spaargaren, 1970; Van Donk and de Wilde, 1981) and of salinities (Hagerman, 1970a; Gelin et al., 2001; Cieluch et al., 2005). It is distributed in many temperate European estuaries and coastal waters in the Eastern Atlantic from the White Sea to Portugal and Morocco, in the North Sea, in the Baltic Sea (Dornheim, 1969) up to the fjords of Finland, in the Mediterranean (Labat, 1977) and the Black Sea (Ebrenbaum, 1890; Dore and Frimodt, 1987; Luttikhuizen et al., 2008).
While the highest temperature tolerable is between 25-30°C (Berghahn, 1983) and the lower salinity limit is to be set to about 5 psu, apart from the low salinities and high temperatures hydrographical restrictions only exist due to low oxygen contents (Haefner-Jr., 1971; Hagerman, 1970b; Hagerman and Vismann, 1995).

Brown shrimp *C. crangon* is a shallow water species (Modlin, 1980; Hanamura and Matsuoka, 2003; Nakaya et al., 2004; Clifford and Moran, 2006), which inhabits sandy and shallow coastal areas (Boddeke et al., 1991; Beyst et al., 2001), sandy mud and muddy substrata mainly restricted from 0 up to 50 m (Lloyd and Yonge, 1947; Allen, 1966). The majority of the brown shrimp populations mainly limited between 10 to 20 m water depth in the German Coastal area (Tiews, 1970) but Wollebaek (1908) has observed *C. crangon* in the areas as deep as 120 m in winter, which, however, is based most likely on few individuals observed.
The brown shrimp plays an important role in the ecosystem functioning both as a prey (Pihl, 1985; Henderson et al., 1992; Del-Norte Campos and Temming, 1994; Walter and Becker, 1997) and as a predator (Pihl and Rosenberg, 1984; Van der Veer et al., 1991, 1998; Ansell and Gibson, 1993; Oh et al., 2001; Amara and Paul, 2003). Besides being ecologically significant, it supports an important commercial fishery off the coasts of Germany, Holland, Denmark and Belgium (Smaldon, 1979; Boddeke, 1989) and the total landing values varied

between 50 to 100 million Euro (Polet, 2002; ICES, 2006). Consequently, numerous studies have been conducted on various aspects of *C. crangon* biology.

In general, life history of caridean shrimps follows the sequence starting with eggs attached to females, larval stages (5-11), and a juvenile stage before reaching the final stage, adults (Ehrenbaum, 1890; Havinga, 1929; Lebour, 1931; Gurney, 1982).

The onset of the maturity appears to be at a size of between 35 and 40 mm total length and seems to be more temperature-dependent than age, that indirectly high temperature speeds growth and then size (Meredith, 1952; Oh and Hartnoll, 2004). The size at sexual maturation threshold differs for males and females, whereby males become mature at a smaller sizes ranging from 22 to 43 mm in contrast to females which mature between 30 to 55 mm (Lloyd and Yonge, 1947; Boddeke, 1966; Muus, 1967; Schockaert, 1968; Meixner, 1970; Gelin et al., 2000; Oh and Hartnoll, 2004). Until now, and despite reports by Lloyd and Yonge (1947) and Yonge (1955) describing the occurrence of setae as an indicator for maturity, female shrimps were still considered mature (apparent mature) only when they are egg bearing and all previous calculations are based on that (Siegel et al., 2005 and 2008).

Previous studies suggest that different life stages prefer different water depth and that migration patterns are therefore also related to size (Spaargaren, 2000). However, migrations are mainly restricted to two distinct periods: autumn and spring migrations. The autumn migration is also called autumn-winter (Boddeke, 1976) and winter migration (Lloyd and Yonge, 1947). The reason for seasonal migrations is mainly related to relative differences in temperature between coastal and off shore waters (Boddeke, 1976; Lloyd and Yonge, 1947). When inshore waters warm up first in spring, females egg bearing migrate inshore from deeper waters. The same seasonal migration pattern is also connected to life cycle. In autumn the maturing adult shrimps move offshore to deeper waters where the females carry eggs through a prolonged period and do not reappear after egg release until the following spring (Lloyd and Yonge, 1947, Boddeke, 1976). Temming and Damm (2002) reported that particularly egg-carrying females are staying in deeper waters during winter.

The eggs released at the end of the winter period continue their development as pelagic larvae and are subsequently transported to the coastal regions (Daewel et al., 2011). According to simulation by Temming and Damm (2002) these larvae from the main immigration wave observed in large numbers in June at a mean size of 15 – 20 mm. As they grow they migrate again to deeper areas, resulting in a pattern of increasing average size with depth (Del Norte-Campos and Temming, 1998).

In the Wadden Sea, shrimps utilize the shallow intertidal areas as nursery, especially smaller size class (< 30 mm), where they find shelter from predation, enough food and high temperatures for fast growth (Boddeke et al., 1986; Beukma, 1992; Cattrijsse et al., 1997). Temming and Damm (2002) observed an invasion of the Wadden Sea tidal flats by *C. crangon* measuring the densities of 5-20 mm shrimp during the middle of June. The timing of the invasion seems to be mainly temperature driven and occurs later after cold winters (Beukma, 1992, Temming and Damm 2002).

C. crangon individuals larger than 30 mm were found to leave the intertidal nursery and invade subtidal areas (Janssen and Kuipers, 1980; Kuipers and Dapper, 1981). They start to reach this length in the beginning of July, with most individuals reaching this size in August. It is debatable whether this June-cohort has reached the commercial size (50mm) by September. However, fisheries maximum is consistently observed in autumn (ICES, 1996; Boddeke, 1982). Hence a major discussion is still under debate: are spring settlers recruiting to fisheries in autumn? What is the contribution of the summer generation? This discussion was initiated by Boddeke (1976) who considered summer reproduction to yield the recruits to autumn commercial caches of the same year. In contrast, Kuipers and Dapper (1984) suggested that winter reproduction sustains the following autumn fisheries through heavy spring settlement. Campos et al. (2010) simulated the growth trajectories from 5 mm to 50 mm (fisheries size) and found that the maximum growth under optimal food conditions at the Wadden Sea temperature conditions revealed that males would take 1.5 years and females just 1 year from settlement to fisheries size. Therefore, females, which make up the bulk of commercial landings, to become available to the fisheries in autumn, must have settled in the Wadden Sea during the previous autumn, one year before, and hence probably arose from summer generation. Consequently, according to Campos et al (2010), it is not the summer brood from the current year as Boddeke (1976) claim, nor the previous winter generation as Kuipers and Dapper (1984) suggested, but the summer generation from previous year which represents the major contribution to autumn peak in fisheries. Until now, studies on growth still speculating maximum growth and then apply model predictions to analyse the life history in the field (Kuipers and Dapper, 1984; Temming and Damm 2002; Hufnagl and Temming, 2011b). Such growth model should be considered with caution, as long as the assumptions about *in situ* growth conditions have not yet been validated. However, under field conditions still no reliable growth data from shrimps in the Wadden Sea are available and any decision between the alternatives described before is totally dependent on accurate growth determination of *C. crangon*.

The first attempt was initiated by Perger and Temming (2012) to estimate the growth rate for brown shrimp *C. crangon* in the Wadden Sea based on dry weight condition. Perger and Temming (2012) estimated high growth rates for females brown shrimps as 0.44 mm/d for 27.5 mm total length for June and as 0.35 mm/d for July at 37.5 mm. However, only few laboratory studies with ad libitum feeding regimes have reported comparably high values (Dalley, 1980; Meixner, 1969 and Hufnagl and Temming 2011a).

The interpretation of a dry weight-based condition factor in crustaceans is, however, complicated by the discontinuous growth of the exoskeleton and hence the length of the individual as described before. The discrete moult events imply that dry weight will increase steadily during the intermoult period while length remains constant. During this phase, water content of the animal will decrease steadily, and consequently, the dry weight condition factor will increase (Rey-Rassat et al, 2004). During the actual moult, the length increases rapidly due to uptake of water, while the total dry weight is reduced by the weight of the exuviae. Immediately after the moult, the body is characterised by maximum water content and a theoretical minimum in dry weight condition for non-starving crustaceans. Based on the previous state, Perger and Temming (2012) suggested new method as an extension of the instantaneous growth rate (*IGR*) assuming that the dry weight of the moulted individuals that measured directly after moulted represent the cumulative food intake and is hence related to the food intake of the previous intermoult period.

It is still doubtful whether the standard methods applied so far, i.e. estimates based on shifts in length-frequency distributions, especially with larger shrimps, over time are applicable, although the study by Del-Norte Campos and Temming, (1998) was able to show such shifts in cohort. Due to continuous immigration and emigration movements, unstandardized method to estimate *in situ* growth rates between sexes at different size classes, size frequency distributions alone can not provide and reflect population growth.

We therefore initiated the present study with an aim of filling the gaps in our knowledge of *C. crangon* population with more focus on its population structure and the growth conditions in the field taking in considerations the different aspects described before.

So far, our objectives were distributed into 4 manuscripts.

In the first one our objectives were:

- To describe the population structure of *C. crangon* during winter by using new maturity indicator “setae”,
- To study the general spatial distribution and variability of the species along the Wadden sea mainly in the shallow and deeper areas,
- To analyze sex-specific pattern in dependence of total length, water depth region and
- To investigate egg development stages.

While in the Second manuscript we generally intended:

- To apply the IGR method established for Krill to measure growth components; addressing the effects of size, temperature and season which has so for not been tested before with *C. Crangon* and
- To evaluate the new method developed by Perger and Temming (2012) to estimate the *in situ* growth of *C. crangon*, with a focus on the effects of gender and temperature.

In addition, the aims for the third manuscript were:

- To, again, evaluate the new method developed by Perger and Temming (2012) but with more emphasize on year around samples,
- To track the cohort shifts based on length frequency distribution and
- To gain more information about the new recruitments and migrations.

Last, but by no means least, in manuscript 4 our objectives were:

- To identify the best protein/carbohydrate/fat composition of artificial food needed to generate high growth rates of brown shrimp in the laboratory.
- To, mainly, provide information on how *C. crangon* reacts to the complete replacement of natural and live feed by artificial generated food.
- To estimate growth performance based on chemical body composition and energy levels.

- To compare laboratory growth rates against field growth rates of *C. crangon* derived from the instantaneous growth method for males and females for only one size class which have not done before with brown shrimp.

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MANUSCRIPT 1

Population structure of *Crangon crangon* (L.) in the Wadden Sea during winter 2009/2010.

Abstract

Distribution patterns, population structure and condition of the *Crangon crangon* population during winter especially with regard to sex differences is not well known so far. Thus length frequency, abundance distribution, sex ratio, egg bearing females and dry weight condition were analysed from a 2009/2010 Wadden Sea winter survey. For the analysis the survey area was partitioned into three zones Eastern (Dutch), Central (German) and Northern (Danish) Wadden Sea. Based upon the previous mentioned parameters two groups of stations were identified using hierarchical cluster analysis. Group 1 consisted of samples situated in sub-tidal areas (> 20 m) water depth while the second mainly included the samples from shallow waters (≤ 20 m). Factors determining the spatial distribution were depth (less abundance in deeper areas), size (smaller animals in shallow areas) and sex (males in more shallow areas). Small (≤ 40 mm) males and females had similar dry weight conditions while big females were heavier than similar sized males. Size of female at maturity was determined from the proportion of ovigerous females (apparent mature) and females with setae at the endopodite (mature). The size at which 50% of females were mature was lower than the size determined based on apparent mature females. This indicates that setae are developed prior to egg development. Sex ratio was a function decreased with size in all cases examined.

Introduction

The brown shrimp *Crangon crangon* (Linnaeus, 1758) is highly abundant in European coastal and estuarine areas between 45° N and 57° N, characterized by strong tidal movements and sandy to muddy substrata (Tiews, 1970). In most areas it is the dominant mobile epibenthic species (Pihl and Rosenberg, 1982; Amara and Paul, 2003, Boddeke, 1996). Due to its abundance, *C. crangon* is an important prey for juvenile and adult fish (Tiews, 1970; Beukema, 1992; Del Norte-Campos and Temming, 1994; McLusky and Elliott, 2004) and also an important predator of the benthic and epibenthic zooplankton (Plagmann, 1939; Reise, 1977 and 1979; Pihl and Rosenberg, 1984; Beukema, 1992; Del Norte-Campos and Temming, 1994; Oh et al., 2001). Hence, it plays an intermediate role in the flow of energy between the trophic levels.

Through its predation of invertebrates (Kamermans and Huitema, 1994; Beukema and Dekker, 2005) and interference with settlement of juvenile fish (Wennhage and Gibson, 1998), this species has an impact on the structure and function of the in- and epifaunal animals in the costal waters (Kuipers and Dapper, 1981; Evans, 1983 and 1984; Pihl and Rosenberg, 1984; Pihl, 1985) which reflects its importance in estuarine systems.

Brown shrimp undergoes seasonal migration between in- and offshore located habitats. In summer it congregates in large numbers in warm shallow waters, frequently at depths from 0.5 to 5.0 m as reported by Żmudziński and Ostrowski, 1990 in Gulf of Gdańsk, while usually preferring depths of 20-40 m during winter (Boddeke et al., 1976; Siegel et al., 2005). Furthermore shrimps of different size and maturation status display different migration behaviour and prefer different water depth as briefly outlined below. Previous studies demonstrated that there are two spawning periods within the reproductive season of this species, one from winter to early spring and in summer with potential for continuous breeding during this period (Ehrenbaum, 1890; Havinga, 1930; Lloyd and Yonge, 1947; Meredith, 1952; Henderson and Holmes, 1987; Oh and Hartnoll, 2004).

Some studies have reported three spawning periods (Havinga, 1930; Tiews, 1954). This difference could reflect effects of latitude, resulting in different incubation periods (Meredith, 1952; Kuipers and Dapper, 1984).

In spring after hatching offshore, pelagic larvae migrate are drifted to coastal waters (Van Donk and De Wilde, 1981), developing to benthic post-larvae that invade estuaries and shallow intertidal inshore areas where abundant food sources are available (Beukema, 1992). Juveniles mainly settle during early summer and can be observed until October (Amara and Paul, 2003) in the shallow coastal areas (< 20 m) while adults are assumed to migrate back to the sea in autumn with decreasing temperatures (Boddeke, 1976). In contrast to these avoidance reactions of low temperatures similar behaviour has been reported for the Mediterranean Sea and the Atlantic coast for high temperatures (Labat, 1977; Crivelli, 1982). Therefore, migration movements during summer into deeper located areas seems to be an escape from excessively high temperatures comparable to observations reported by Berghahn (1983 and 1984) who reported a "mass exodus" of *C. crangon* from the intertidal towards deeper water when the water temperature increased above 27°C.

There are several detailed studies on aspects of reproductive biology of *C. crangon*. It generally has two reasonably discrete spawning periods within the breeding seasons (Ehrenbaum, 1890; Lloyd and Yonge, 1947; Meredith. 1952; Tiew, 1970; Henderson and Holmes, 1987). Kuipers and Dapper (1984) compiled data on latitudinal variations in the spawning season and concluded that the life cycle of *C. crangon* in the western Wadden Sea is mainly dependent on winter egg production which is in line with recent findings by Hufnagl and Temming (2011). Females carry the eggs attached to their abdomen and eggs spawned during winter are generally larger than those spawned during summer (Boddeke, 1982). Furthermore, egg development lasts 3.5 to 13 weeks depending on water temperature. Although Lloyd and Yonge (1947) and Yonge (1955) already described the occurrence of setae as an indicator for maturity, all studies on the reproductive biology and breeding pattern until now have only been based on the presence or absence of eggs; occurrence of ovigerous females. Using the setae on the endopodites of the first pleopods as indicators that egg extrusion is imminent has not been studied in the Wadden Sea so far.

Male length at maturity is not well studied but seems to range between 22-43 mm total lengths. Between 30-55 mm total length females become mature at a slightly larger size than males (Lloyd and Yonge, 1947; Tiews, 1954; Boddeke, 1966; Muus, 1967; Meixner, 1970; Oh and Hartnoll, 2004). For larvae hatched during winter this size is normally reached within the first year of life (Hufnagl and Temming, 2011). Due to this annual life cycle studies on the level and variability in recruitment in *C. crangon* must therefore focus on the early life stages, early in the year (Berghahn, 1983). Recruitment seems to be successful in most areas and years, since over a wide latitudinal range, *C. crangon* is abundant in shallow coastal systems (Tiews, 1970; Pihl and Rosenberg, 1982; Kuipers and Dapper, 1984; Oh et al., 1999). At this stage, water temperature can be considered as an important abiotic factor that strongly affects timing of immigration and settlement of shrimp larvae (Beukema, 1992). Hence, at least in the northern North Sea recruitment is positively related to water temperature (Henderson et al., 2006). Besides temperature, river run off seems to influence recruitment, probably due to the effects on the productivity and growth of estuarine organisms (Henderson et al., 2006).

Temperature and size of the animal will influence metabolism whereas higher productivity will increase the available energy. These factors with likely relate to local events and therefore the role as an exogenous factor influencing spatial and temporal distribution of estuarine and marine crustaceans has been investigated (Bishop et al., 1980; Szaniawska and Wolowicz, 1984; Weisse and Rudstam, 1989; Taylor and Peck, 2004). For brown shrimp, previous studies suggest that different life stages prefer different water depth and that migration patterns are therefore also related to size (Spaargaren, 2000). Larger individuals move to deeper water (warmer levels) in winter (Boddeke, 1976; Boddeke et al., 1976; Muus, 1967; Henderson and Holmes, 1987; Siegel et al., 2005), while smaller shrimps (Temming and Damm, 2002) and ovigerous female (Lloyd and Yonge, 1947; Van der Baan, 1975) prefer shallow waters and are invading in large numbers in spring and summer. As they grow they migrate again to deeper areas, resulting in increasing average size with depth (Del Norte-Campos and Temming, 1998). Furthermore, migration differs with age and sex groups (Boddeke, 1976), which partly reflects also differences in reproductive cycle (Van der Baan, 1975; Boddeke, 1976; Kuipers and Dapper, 1981; Henderson and Holmes, 1987; Gelin et al., 2001a, b). Ovigerous females and fertile males are more sensitive to temperature (Boddeke, 1976; Boddeke et al., 1976) and prefer higher salinities at lower temperatures, while young shrimps seem to prefer lower salinities at higher temperatures (Broekema, 1942).

As previously stated the winter season is important as population strength of the same year's recruitment and adults is formed. Within this study we therefore focused on the winter 2010 Wadden Sea situation and investigated quantitative observations of spatial distribution patterns of *C. crangon*. The main objectives of the present effort were therefore to:

(a) describe the species population structure during winter by also using new indicators like setae that indicate maturity,

(b) study the general spatial distribution and variability of the species along the Wadden sea,

(c) analyze sex-specific pattern in dependence of total length, water depth region and
(d) investigate egg development stages.

Materials and Methods

Sampling

C. crangon were caught on an annually performed winter shrimp survey, by the research vessel Solea and a chartered shrimp boat from 5th to 31st January 2010. The sampling with two boats was necessary because the draft of the research vessel Solea makes it impossible to fish in shallow regions. The latter areas were covered by a chartered commercial shrimp boat. Both ships were equipped with an identical 7 m small meshed beam trawl (20 mm stretched mesh) with rubber rolls but without tickler chains attached to the shoes of the beam. The 30 min tows were carried out with the prevailing tidal current at a towing speed of approximately three knots. The total abundance per 30 min trawling, water temperature and depth of the different water zones and regions were documented (Table 1.1).

Subsamples of 200 g *C. crangon* per station were deep frozen aboard (in separated bags) at -20°C for later analysis.

In total 38 stations mainly distributed along the German Wadden Sea coast were examined (Figure 1.1). For later analysis stations were separated into three zones: the Eastern (EWS), Central (CWS) and Northern Wadden Sea (NWS), respectively.

Population structure

Samples were defrosted and total length (*TL*) was determined for each individual using a USB camera (UI-1485LE 2560x1920 pixels) equipped with a Pentax C3516-M lens. *TL* was measured to the nearest mm by reanalysis of the taken pictures applying a Matlab routine (The Math works, Inc., Natick, MA). *TL* was measured from tip of the rostrum to the end of the telson. Male and female shrimps were distinguished on the basis of external characteristics (Figure 1.2) of the first pleopod by analyzing presence or absence of the appendix masculine (Lloyd and Yonge, 1947). For each sampling station, males and females were sorted into 5 mm length classes for further analysis. Gender and the existence of setae (Lloyd and Yonge, 1947, their Figure 4) or attached eggs were recorded. Females with eggs attached or existence setae were considered as mature animals. Eggs were carefully stripped from pleopods using fine forceps and any setal material was removed and directly classified into un-eyed or eyed eggs (see later section for more detailed description), enumerated and then fixed in 4%

formalin for further examinations. Shrimp were then immediately freeze-dried for 24h and weight to the nearest 0.1mg by electronic digital balance (Satorius ± 0.0001g).

To estimate the population structure, the length frequency distributions of *C. crangon* were sorted into 5 mm and 1mm total length classes and data were analyzed by using PASW Statistics software package Version 18. The differences in the size frequency distributions of population between sexes were determined by the Kolmogorov-Smirnov two-sample test. Student's *t*-test was used for comparison of the mean total length of males and females. Size frequency distributions of *C. crangon* in 5-mm and in 1-mm interval were plotted for each site (EWS, CWS, NWS) and sex (male, female without eggs, female with eggs) in both shallow and deep water area.

Dry weight condition index

Body weight itself is often inadequate as a condition index, but scaling by morphological measurements can markedly improve its value. Assuming that a heavier animal of a given *TL* is in better condition, dry weight condition (*K*) for males and females separately was calculated as:

$$K_i = DW_i \, / \, TL_i^b \tag{1}$$

where *DW* is dry weight in mg; *a* and *b* constants derived from the commonly used length-dry weight relationship which was calculated for males and females separately applying the criteria suggested by Le Cren (1951):

$$DW = a \text{ x } TL^b \tag{2}$$

Parameters were estimated by fitting a nonlinear model in PASW statistics 18 software package.

To evaluate dry weight condition variations in the morphometric *TL-DW* relationship at different locations and water depths in the Wadden Sea, *DW* were averaged into two *TL* classes: 30 mm (all shrimps < 40 mm) and 50 mm (shrimps > 40 mm) to reduce the influence of scaling (different exponents: *b*). According to this criterion the new dry weight was calculated for males and females separately as:

$$DW_i^*{}_{30} = K_i \text{ x } 30^b \tag{3}$$

$$DW_{i\ 50}^{*} = K_i\ x\ 50^b \tag{4}$$

where DW_i^{*} is new calculated dry weight (mg); K_i from equation (1).

Female size at maturity

Length at first sexual maturity was calculated based on two different criteria by applying (*i*) the presence of setae as a proxy for maturity (referred to as mature) and (*ii*) by taking the presence of attached eggs (referred to apparent mature). The last criterion was calculated for the purpose of comparison with data from other studies on *C. crangon* that used "apparent maturity" as proxies. Female length at sexual maturity (*TL50*) is defined as the length at which 50% of the female shrimp stock has attained sexual maturity and was estimated fitting the logistic equation:

$$P = 1 / (1+ exp^{-k \text{ x } (TL\ -\ TL50)}) \tag{5}$$

where P = estimated proportion of shrimps and k = coefficient.

Egg stages

Wehrtmann and Kattner (1998) described five stages of egg development: stage I: eggs recently produced; uniform yolk, no eye pigments visible "from transparency to white colour"; stage II: eye pigments barely visible "white"; stage III: eyes pigment visible; and the embryo is fully developed "yellow". Additionally, two later developmental stages were determined: stage IV: large eyes, eggs elongated, abdomen and appendages free from head "brown"; stage V: before hatching or hatching, setae of tail fan out of eggs "dark brown". Here the first two stages were combined and considered as un-eyed eggs while the last three stages were accounted as eyed eggs (Figure 1.3). The embryonic state of the egg was determined under a camera microscope (OLYMPUS DP 10 – DF PLAN 0.5x).

Cluster analysis

Hierarchical clustering is the major statistical method for finding relatively homogeneous clusters of cases based on measured characteristics which successively join the most similar observations. This method was used because it processes a small space distorting effect, uses more information on cluster contents than other methods, and has been proved to be an extremely powerful grouping mechanism. For sample classification, hierarchical cluster analysis has been applied to study the interrelations between the 12 variables (shrimp numbers, mean TL, abundance and condition K, each for males (Males), females without eggs (Female^{--}) and ovigerous females (Females^{++})) examined by using Ward’s method. The method was applied to normalized data using squared Euclidean distances as a measure of similarity. Calculations were carried out using the PASW Statistics 18 software package.

Results

Cluster analysis

Two main groups can be distinguished from the dendrogram (complete linkage) of samples obtained by the cluster analysis method (Figure 1.1). The first group is composed of deeper water stations (>20 m), while the second group comprises mainly the shallow water stations (≤ 20 m).

The shallow areas are characterized by low water temperature and high abundance of shrimps. Highest abundance was determined for an Eastern Wadden Sea shallow area (29169 individuals/30 min trawl). Big shrimps were generally located in deeper water (Table 1.2) with the lowest abundance observed in the northern Wadden Sea area with 974 individuales/30min trawl.

Length frequency distribution and sex ratio

Length frequency distributions of *C. crangon* for the whole study area were expressed as relative portion of males and females in each 5 mm length class and also as individual numbers in 1 mm and for the defined shallow and deep areas (Figures 1.4 and 1.5). Overall, total number of individuals analysed for this study was 2465 (42.9%) for male and 3278 (57.1%) for female shrimps, respectively. The mean *TL* was 45.3 ± 7.1 mm (± sd) and 50.7 ± 9.2 mm (± sd) for male and female shrimps, respectively. Minimum and maximum male *TL*'s were 15.4 mm and 68.0 mm and 18.2 mm and 83.7 mm for female shrimps, respectively. The mean *TL* of female shrimps was 5.4 mm longer than that of male shrimps (Table 1.1 and Figure 1.6).

In the Northern Wadden Sea area in total 575 (41.7%) male and 805 (58.3%) female shrimps were analyzed, respectively. Mean *TL* was 44.9 ± 6.7 mm (± sd) and 52.4 ± 8.6 mm (± sd) for males and females, respectively. Minimum and maximum male and female *TL* was 27.2 mm and 65.7 mm and 27.1 mm and 83.7 mm, respectively. Mean female *TL* was 7.5 mm longer than male *TL*.

In the Central Wadden Sea area, a total number of 1257 male (48.3%) and 1347 female (51.7%) shrimps was analyzed, respectively. Mean *TL* was 45.4 ± 7.3 mm (± sd) and 50.0 ± 9.1 mm for male and female shrimps, respectively. The minimum and maximum male *TL* was 15.4 mm and 67.0 mm, and 18.2 mm and 79.9 mm for female shrimps, respectively. The mean total length of female shrimps was 4.6 mm longer than that of the male shrimps. While in the Eastern Wadden Sea area, total number of individuals analysed for this study was 633 (35.9%) for male and 1126 (64.1%) for female, respectively. Mean *TL* was 45.5 (±7.2) mm and 50.4 (±9.5) mm for males and females, respectively. Minimum and maximum male *TL* was 23.7 mm and 68.0 mm, and female *TL* 23.2 mm and 79.4 mm, respectively. Mean female *TL* was 4.9 mm longer than male *TL* (Table 1.1). A significant size difference was apparent between males and females (Kolmogorov-Smirnov test, $p<0.001$). The sex ratio (female /male) was 1.4, 1.1 and 1.7 in the Northern-, Central- and Eastern Wadden Sea, respectively. The overall sex ratio was 1.4 female to male.

Abundance distribution

Spatially, density differences among strata (North, Central and East), as well as between water depths were apparent (Table 1.1 and Figure 1.7). High abundances of male and female (both with and without eggs) *C. crangon* were observed in the Eastern and Central stratum with 34182 and 25744 indviduals/30 min trawl, respectively. Shrimp biomass always displayed a distinct distribution with depth and highest abundances occurred in shallow water areas with 29169 individuals/30min trawl in the Eastern part of the Wadden Sea followed by the Central Wadden Sea area with 15310 individuales/30min trawl.

The overall number of females bearing eggs was higher in the shallow than in the deeper areas with highest abundance on the Northern shallow area of the Wadden Sea (355 individuals/30min trawl). A similar pattern was observed in the Central and Easter Wadden Sea areas (Table 1.2, Figures 1.1 and 1.7).

Length-dry weight relationship

All three *TL-DW* regressions (males and females and combined sexes) and potential fit indicated that the body weights are positive allometric growth of total lengths that the slope values (*b* parameters) are greater than 3 (Table 1.2). No significant ($p>0.001$) sex-specific condition differences between small animals were found when all shallow areas, or all deep areas were combined (Figure 1.8) e.g. the condition of small males and females averaged in the 30 mm length class were comparable.

In contrast, there are highly significant sex-specific differences between the larger animals. The condition of big males and females differs considerably ($p<0.001$) and big females (without eggs) were generally heavier than males at the same size. Subsequent dry weight conditions (*K*) in the studied areas varied between a minimum value of $K = 0.86$ in the Eastern Wadden Sea deep zone and $K = 1.13$ in the Central Wadden Sea area when combining males and females (Table 1.2). However, considerable differences occurred between the three water regions and between the depth strata within one region (Table 1.2).

Size at sexual maturity

In general, the TL_{50} values calculated via setae (mature) were lower (9 to 18 mm) than the TL_{50} values calculated based upon only ovigerous females. As general pattern, the TL_{50} values were approximately 5-10 mm larger in shallow areas (<20 m) than in areas >20 m water depth with one exception in the Northern Wadden Sea area (Figure 1.9).

The overall TL_{50} for mature females was 58.51 mm (*TL*) in the Eastern Wadden Sea shallow area while the smallest mature females encountered was 47.38 mm in the Central Wadden Sea >20 m area. The largest apparent mature female was 74.16 mm and the smallest was 64.79 mm in the Central Wadden Sea shallow and Eastern Wadden Sea deep area, respectively.

Discussion

Cluster analysis

Multicomponent statistical analysis is a mathematical technique applied frequently to many problems and has several advantages over graphical approaches as it takes more data into consideration. Cluster analysis enables relations among samples to be interpreted in terms of simpler relations that provide an insight into the underlying structure of the data set based on similarity (Matalas and Reiher, 1967; Everitt, 1993). It refers to a set of techniques designed to classify observations so members of the resulting groups are similar to each other but distinct from other groups. On the other hand, cluster analysis may be thought of as a useful way of objectively organizing a large data-set into groups on the basis of a given set of characteristics. This can ultimately assist in the recognition of potentially meaningful patterns. However, all possible combinations concerning the classification method (single, average, centroid and complete linkage) and the measure of similarity criteria (Eucledean, Square Eucledean, Pearson and Square Pearson) produced the same two groups (shallow and deep) of samples as represented in the results section.

Length-frequency distribution and Sex ratio

In this study we analyzed spatially the brown shrimp population structure of the Wadden Sea in January 2010. In general we found that abundance and size of the animals decreased with increasing water depth, that females without eggs can be found closer to the shore in contrast to males which are generally located more offshore. Females carrying eggs were also located offshore but generally eggs of more inshore situated females showed a higher development stage. Based on cluster analysis these patterns could be confirmed. Further the western Wadden Sea was more productive than the Central and Northern Wadden Sea likely due to the fact that due to drift from the western areas in the North Sea to support the more eastern parts with larvae.

In general, the relative portion of males gradually decreased with increasing body size and thus males dominate the smaller length classes while the females dominate the bigger length classes. This is in line with earlier finding from the German Wadden Sea by Tiews (1954) and Hufnagl et al. (2011) and Martens and Redant (1986) at the Belgian coast. *C. crangon* above 55 mm total length (*TL*) thus are almost exclusively females. Based upon our findings it can be stated that big animals of both sexes preferably spend the winter in deep water, with more males in the offshore areas.

The present study demonstrated that, sex ratio is a function of size in all cases examined. A deviation from the 1:1 sex ratio, in the over all sites, is apparently widespread in marine crustacean (Wenner, 1972). Thus, different hypotheses have been raised to illustrate such phenomenon e.g., higher mortality rates of males (Meredith, 1952), sexual different in growth (Tiews, 1954; Meixner, 1970; Henderson and Holmes, 1987; Hufnagl et al., 2010), migration (Boddeke, 1976) or sex transition from males to females by Boddeke (1966). Martens and Redant (1986) and Siegel et al. (2008) stated that sex change may occur and when happened, the percentage of males changing into secondary females would be very small to effect on the sex ratio. Thus, sexual transition can be considered as uncommon pattern in *C. crangon*. Hufnagl et al. (2010a) estimated the potential maximum egg contribution by secondary females to the population to be 4% with less than 1% of the total eggs produced by one cohort of males and females of brown shrimp *C. crangon*.

Abundance and size distribution

Depth was found to be the main factors explaining the spatial size distribution of *C crangon* shrimp. Small and medium sized shrimp were common in shallow area. Medium and large shrimp were more common in the Eastern part of the study area (Table 1.1). A similar pattern is apparent when comparing depth distributions for male and female shrimps separately: large animals (males and females) are more abundant in deep water zones. Depth dependent size differences have been reported earlier (Janssen and Kuipers, 1980; Del-Norte Campos and Temming, 1998) and might indicate lower tolerance of larger shrimps to extreme hydrographical situations like strong salinity and temperature gradients in shallow intertidal areas. Additionally predator and prey interaction likely play an important role. Ovigerous females were mainly found in deeper areas. Unique for the winter situation is that water temperatures in deeper areas are higher and more stable. This might be favourable for a constant ovary and egg development. However, this pattern of migration (sex dependent seasonal migrations) has also been recognized for the Severn Estuary and the Bristol Channel by Henderson and Holmes (1987). They have been suggested that this was to avoid the inshore and lower salinity parts of the estuary during the winter, while Lloyd and Yonge (1974) attributed it to the avoidance of cold waters rather than low salinities.

In the present study, ovigerous females were not distributed according to depth that shallow water included highest portion of eyed eggs (Table 1.1) which about to hatch. These females may have been migrated to the shallower areas to release their eggs or to the deeper water (other mature females) for gonad and eggs development thus it occurred at all depths.

Overall, it seems that water temperature has affected the *C. Crangon* distribution in a way that higher temperatures in deep water (3.7 ± 1.5°C) resulted in low mean total shrimp abundance (5474 individual/30min trawl) and the presence of bigger animals.

The opposite is true for small animals which are abundant in shallow zones characterized by colder water (1.6 ± 1.2°C) where 19164 individual/30 min trawl mean total abundance were collected. Small animals probably stayed in shallower water for two reasons, either because energetically they cannot handle a migration into deeper water or the colder water allows them to keep up reduced metabolic rates to save energy during the period of lower food availability.

In the present study the total number of egg bearing females is higher in shallower areas than in deeper areas, however, the share of females bearing eggs is higher in deeper areas than in the more shallow ones (Table 1.2) which can be expected as it is well known that bigger animals are usually found in the deeper waters, which was also confirmed by this study. A comparable distribution was also reported by Siegel et al. (2005), however, in their study the maximum water depth was 15 m. The reason for egg bearing females being located in deeper areas has been discussed before and might be related to the fact that a more constant or higher temperature is needed for egg development. The rate of development can be accelerated; larvae hatch earlier and are already developed at the start of the plankton bloom. Furthermore an earlier start of the larval stage before predation due to increasing temperatures and therefore increasing consumption of predator's increases might favour survival.

According to Tiews (1954), mating and spawning occurs in water shallower than 20 m and the females oviposit and migrate seaward to release their larvae (Henderson and Holmes, 1987) where the conditions are favourable where warmer water and decreased predation are more conducive to development (Hench et al., 2004). This finding was not really supported in our study when using the portion of eyed eggs (Table 1.1) where both the abundance of ovigerous females and the share of eyed eggs are higher in the shallow water area than in the deeper one except in the Northern Wadden Sea area. An onshore migration of animals carrying higher developed eggs might be the reason. Further studies focussing on the relation of egg development, temperature and water depth are needed.

Nevertheless, our results clearly show that the Eastern Wadden Sea zone is most productive (total abundance) area with 58.5% and followed with Northern Wadden Sea zone and (27.0%). The reason might be that due to the generally anticlockwise water currents and drift in the North Sea the eastern areas are supported by eggs from more western located spawning grounds.

Total length-dry weight relationship and condition index

Body condition was intimately related to animal's health and quality (Peig and Green, 2009) and has been widely clamed to be an important determinant of fitness. A wide range of morphological, biochemical or physiological metrics have been proposed as condition indices (Stevenson and Woods, 2006). Here, we are only concerned with condition indices based on the relationship between body mass and length measurement, whose ultimate goal is to interpret variations of body mass for a given size as an attribute of the individual's well-being. In the present study, the recurrent positive allometric growth ($b>3$) for shrimps was in agreement with previous studies (e.g. Łapińska and Szaniawska, 2005) where females are heavier (value of b is higher as well as K values) than males with increasing total length (Oh et al., 1999). Similar growth patterns were reported for other crangonids e.g. *A. dentata* (Couture and Filteau, 1971), *C. septemspinosa* (Haefner, 1972), *C. nigricauda* and *C. franciscorum* (Krygier and Horton, 1975), *N. antarcticus* (Bluhm and Brey, 2001), and *Philocheras trispinosus* (Labat, 1984).

There are differences in condition between big females and males in the shallow and deep water areas. Bigger shrimp have better condition (heavier) in shallow water especially near the River Basin Districts (RBD) areas (Figure 1.8). There it is generally colder but more productive in comparison to the deeper areas. This could be related to the weight of their gonads, as either mainly animals with well-developed gonads aims to migrate to the deeper water or well-fed shrimps has been reached during the survey.

Perger and Temming (2012) determined dry weight condition of freshly moulted, laboratory reared female brown shrimps. Their observed values were restricted to a narrow range of physiological optimal values which can be used in the present study as a reference for the interpretation of condition values in the field. As described by Perger and Temming (2012), values >1 indicate well-fed females that have not moulted recently while values <1 indicate poorly fed females. A considerable condition difference (Table 1.1) can be found between the studied areas, though, no considerable difference can be found between different depths within the Wadden Sea subareas examined here. Generally females in the Wadden Sea were well nurtured according to the previous criteria suggested by Perger and Temming (2012) with one exception in the Eastern Wadden Sea deep water area where the condition was slightly lower (0.93) than the limited value stated by them.

Hufnagl et al. (2010b) examined animals of both sexes regarding the nutritional condition (dry weight, RNA/DNA and caloric content). Their samples were collected in very shallow areas with a push net at about 1 m water depth and in a power station inlet at about 8 m water depth. Their mean dry weight condition values are slightly lower than the mean values observed in our study. The difference might have several reasons like the generally colder temperatures in 2010 than in 2006-2007 or the differences in water depth and locations. This could result from the highest total catch, as the bigger amount of animals also needs more nutrition on average (Table 1.2).

Additionally, the shrimps seem to just have begun with the period of nutrition shortage (food scarcity). An earlier start of nutrition shortage was recognised with minimum condition value at the Eastern Wadden Sea deep zone (0.86), compared to the others; hence the existed animals would began to starve. However, the dry weight condition seems to be quite independent of the water depth, generally, since the averages only change marginally (negligible) with changing water depth (Table 1.2).

Size at sexual maturity

Until now, female shrimps were considered mature (apparent mature) only when they are egg bearing and all calculations are based on that (Siegel et al., 2005 and 2008). One novelty in this study is that females are regarded as mature once they developed setae on the first pair of pleopod. The setae are likely to be developed shortly before the time of bearing eggs (Yonge, 1955), which has been not considered in previous studies. It is examined if the modification of criteria changes the calculation of the mean maturation length of females significantly, so that it would be necessary to reconsider the general mode of distinction of female shrimps.

A successive increase in proportion of mature females with increasing *TL* was observed. The size at 50% maturity of female *C. crangon* is comparable to previous studies (Lloyd and Yonge, 1947; Meredith, 1952; Tiews, 1954; Oh and Hartnoll, 2004), but also larger (Siegel et al., 2008) or smaller sizes (Wollebaek, 1908; Havinga, 1930; Henderson and Holmes, 1987) have been recorded. Variable TL_{50} values were determined for the different zones as well as for the different depth strata. This indicates considerable spatial migration of mature females which as reported by Tiews (1970) or spatial differences in development due to differences in nutrition. In comparison to Siegel et al. (2005 and 2008) we extended the analysis of TL_{50} to different water depth. Siegel et al. (2008) reported TL_{50} values between 62.0 mm and 55.4 mm for winter and spring respectively. Their TL_{50} winter value was higher than our value when considering egg bearing (apparent mature) animals and especially when using presence of setae (mature) as maturation proxy. Since their sampling reached up to 15 m water depth only data from shallow water zones were compared. The variation partly originates from the different criteria used to estimate the size at maturity but for mature female's difference in growth rate between areas is likely the more important factor. However, the diagram of the three different water zones (Figure 1.9) shows that the "mature" females reach the TL_{50} earlier than "apparent mature" females. This means that setae are developed by mature females prior to development of eggs as reported on *C. crangon* (Lloyd and Yonge, 1947), *C. vulgaris* (Ehrenbaum, 1890), *Leander longirostris* (Gurney, 1923) and *Palemoninae* (Sollaud, 1923).

Table 1.1: Overview of population structure of brown shrimp *C. crangon* in various subareas studied in the Northern-, Central- and Eastern Wadden Sea during the winter 2010.

Subareas	Depth	Temp. °C	Sex	N	Mean TL ± sd	Mean DW ± sd	Abundance*
NWS	**Shallow**	**0.7**	Male	334	42.29 ± 6.35	127.93 ± 62.74	6097,16
			Female^{--}	569	49.86 ± 7.26	245.48 ± 123.57	6558,71
			Female^{++} (2.9)	54	63.89 ± 7.48	506.84 ± 223.95	355,15
	Deep	**2.1**	Male	241	48.49 ± 5.34	187.71 ± 75.78	692,56
			Female^{--}	140	54.50 ± 6.75	313.75 ± 144.26	223,11
			Female^{++} (24.1)	42	65.24 ± 6.94	514.84 ± 209.13	58,27
CWS	**Shallow**	**1.7**	Male	927	44.96 ± 6.83	149.91 ± 76.06	9472,49
			Female^{--}	1000	49.03 ± 8.32	221.06 ± 138.62	5519,98
			Female^{++} (8.8)	90	60.74 ± 7.28	408.94 ± 165.11	317,90
	Deep	**4.7**	Male	330	46.48 ± 8.36	165.02 ± 81.02	7150,74
			Female^{--}	215	47.20 ± 8.39	199.69 ± 129.33	3204,95
			Female^{++} (5.8)	42	64.34 ± 6.17	509.02 ± 166.79	78,58
EWS	**Shallow**	**2.4**	Male	393	43.18 ± 7.40	142.82 ± 94.76	10502,50
			Female^{--}	870	47.03 ± 7.18	196.45 ± 108.09	18478,02
			Female^{++} (50.7)	32	63.31 ± 6.27	529.82 ± 186.55	188,74
	Deep	**4.2**	Male	240	49.38 ± 4.71	185.52 ± 61.27	3881,00
			Female^{--}	116	58.56 ± 7.24	358.20 ± 147.71	1005,04
			Female^{++} (7.8)	108	65.14 ± 5.75	472.43 ± 170.50	127,00

N, sample size measured; TL, total length in mm; DW, total dry weight in mg; sd, standard deviation

**number of individuals per 30 min trawl*

Number between brackets is the percentage of eyed eggs

Table 1.2: Length-dry weight parameters of *C. crangon* of the subareas studied in the Wadden Sea during winter 2010.

	Northern Wadden Sea (NWS)			**Central Wadden Sea (CWS)**			**Eastern Wadden Sea (EWS)**		
	Combined	**Male**	**Female**	**Combined**	**Male**	**Female**	**Combined**	**Male**	**Female**
a	0.00039	0.00086	0.00038	0.00040	0.00088	0.00039	0.00047	0.00066	0.00046
b	3.3853	3.1404	3.3622	3.3269	3.1968	3.3762	3.3238	3.2172	3.3174
r^2	0.9373	0.9467	0.9226	0.9391	0.9439	0.9352	0.9338	0.9341	0.9367
K^{*}	0.98	1.03	1.11	1.13	1.03	0.97	0.97	0.99	1.0
K^{**}	0.91	1.01	1.06	1.12	1.01	0.99	0.86	0.91	0.93

a and b, parameters of the total length-dry weight relationship; r^2 *coefficient of determination*

K^{*} *= Shallow water*

K^{**} *= Deep water*

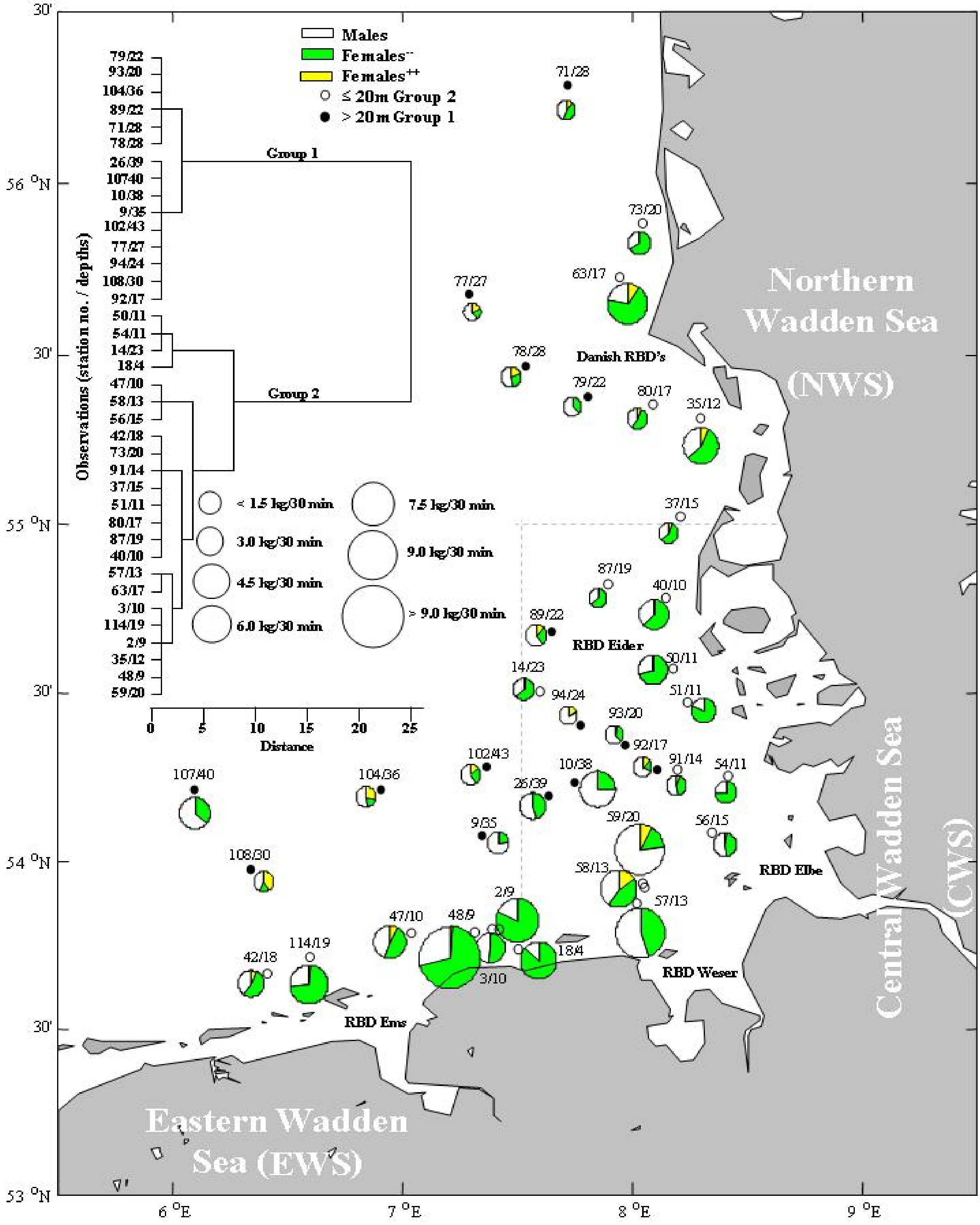


Figure 1.1: Map of fishing locations were studied; size of the circle, represents the individuals of *C. crangon* per sampling station in 30 min trawl; colours represents relative portion of shrimps; RBD, river basin district. Dendrogram based on agglomerative hierarchical clustering (Ward's method) mainly based on length distribution, sex and abundance.

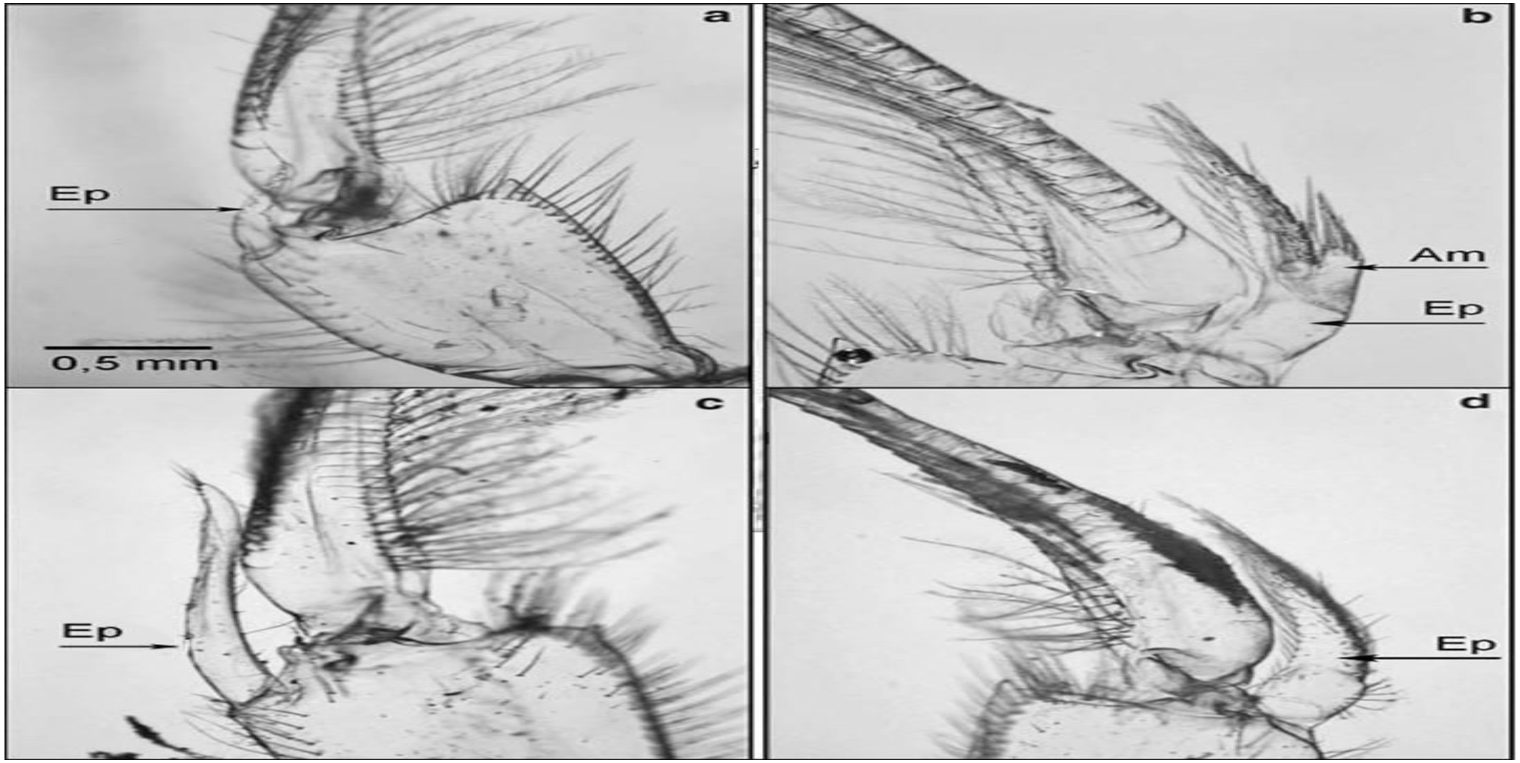


Figure 1.2: External reproductive organs of brown shrimp *C. crangon*. First pleopod (a) and second pleopod (b) of a male and first pleopod (c) and second pleopod (d) of a female brown shrimp. Endopodites (Ep) and appendix masculine (Am) (Schatte and Saborowski, 2006).

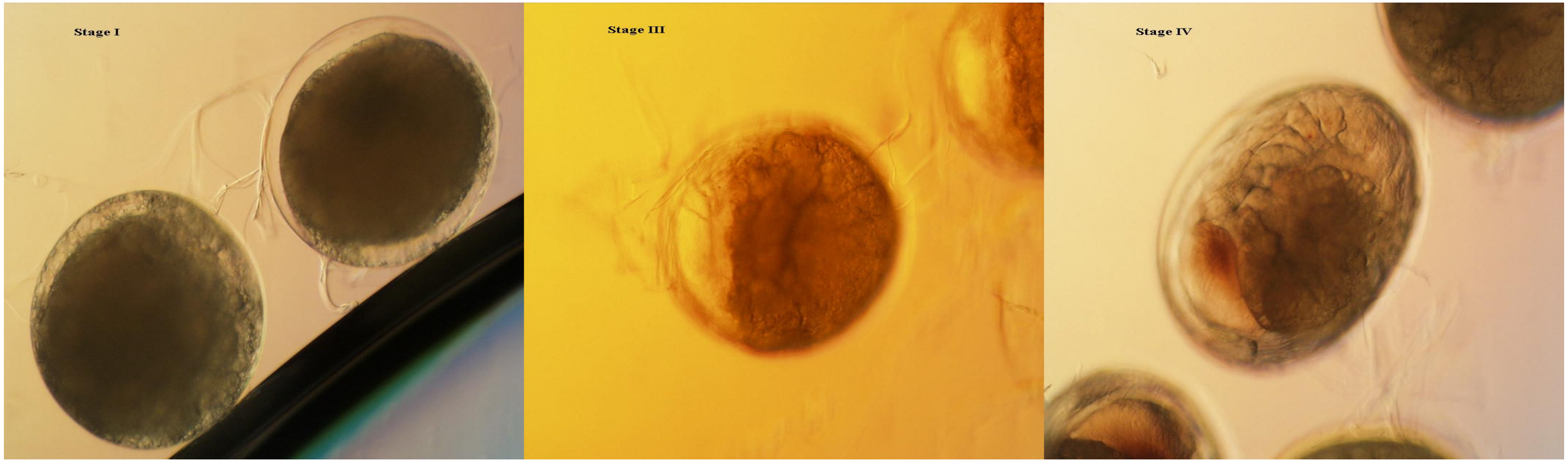
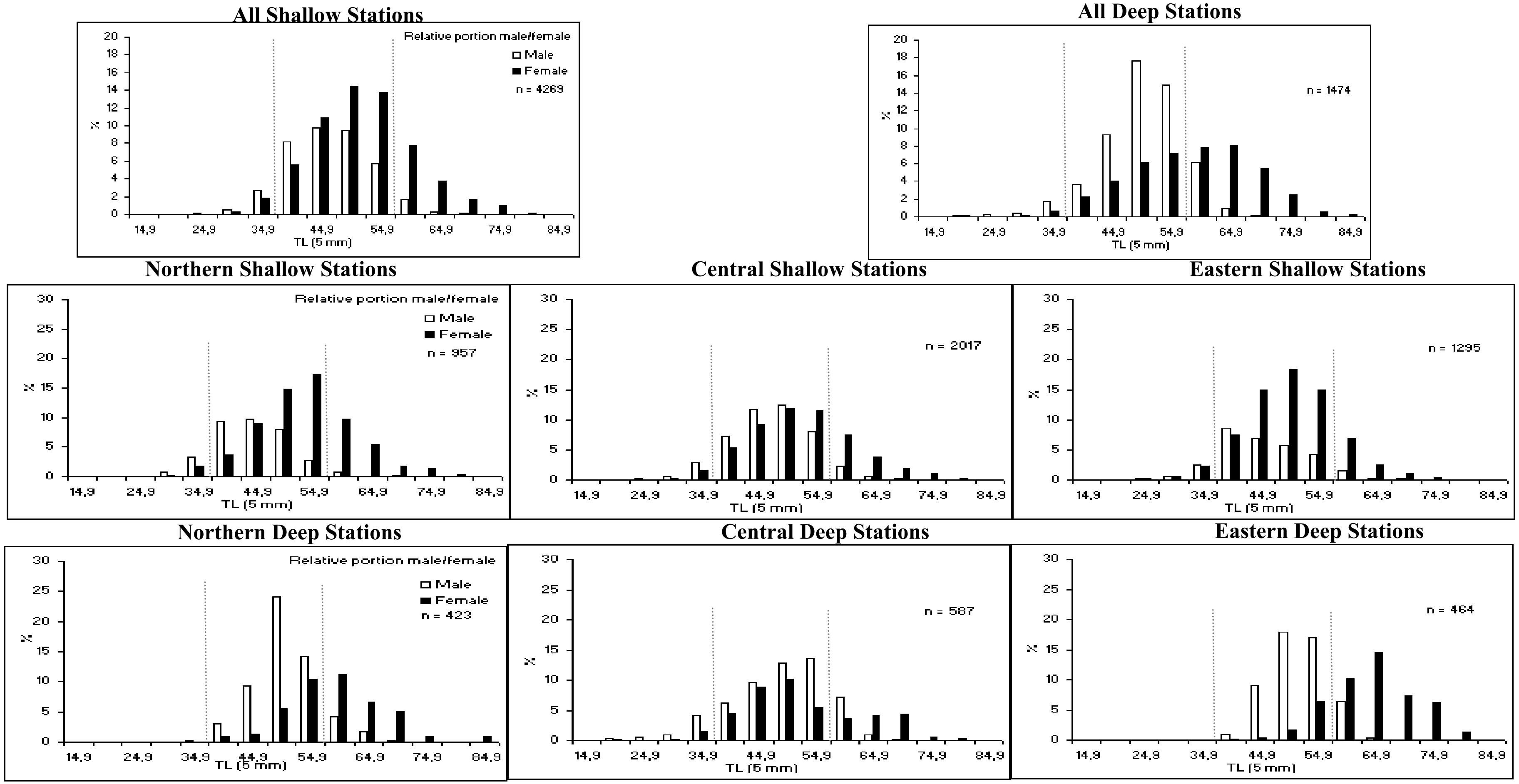


Figure 1.3: Brown shrimp *Crangon crangon* (L.) eggs in different stages of development.



All Shallow Stations

All Deep Stations

Northern Shallow Stations

Central Shallow Stations

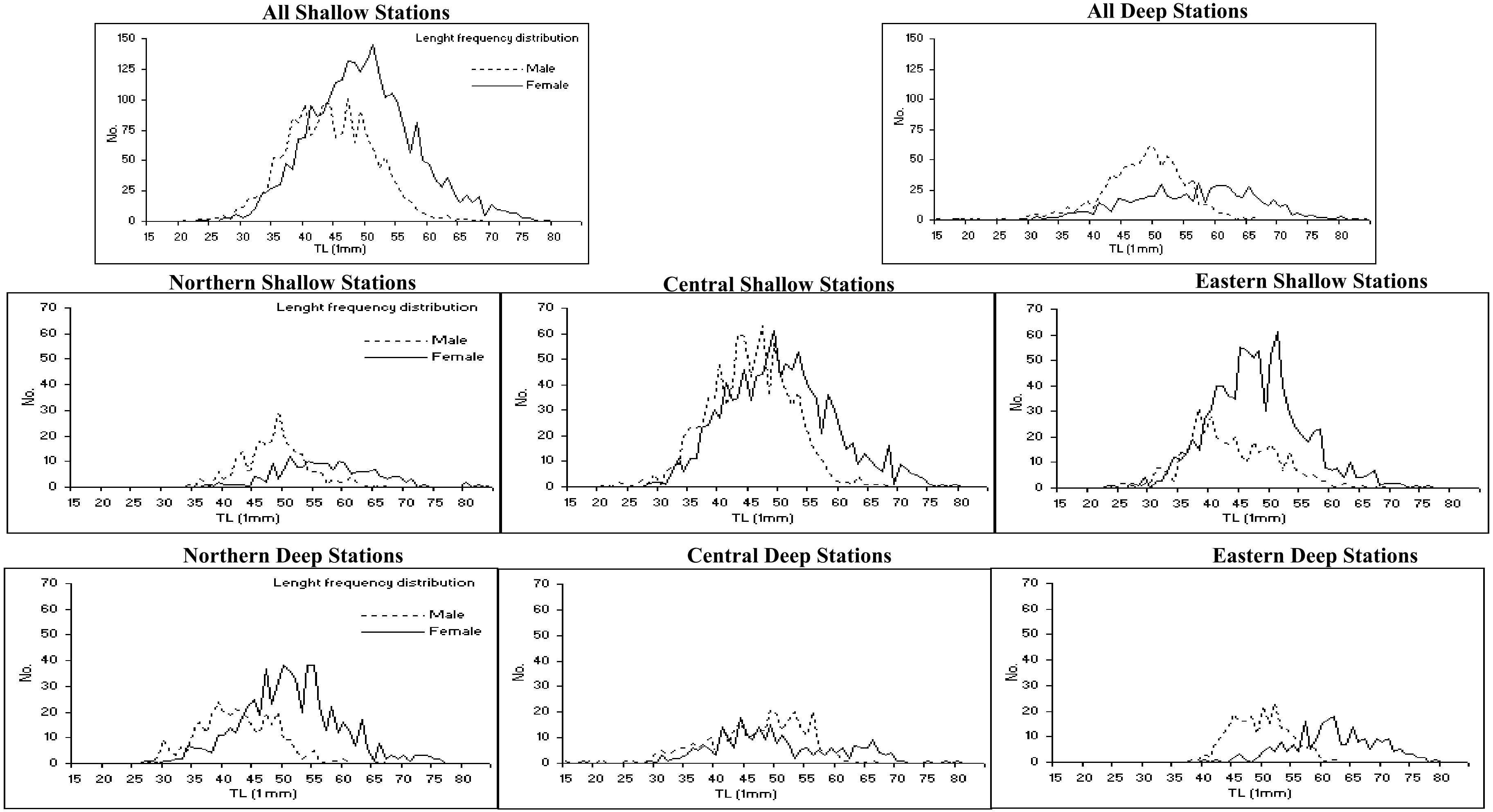
Eastern Shallow Stations

Northern Deep Stations

Central Deep Stations

Eastern Deep Stations

Figure 1.4: Histogram represents the relative portion of males and females brown shrimp in 5 mm length class collected from different locations within the distributional range of shrimp in the Wadden Sea during January 2010, vertical line presented the total length class limits (small, medium and large respectively).


All Shallow Stations

All Deep Stations

Northern Shallow Stations

Central Shallow Stations

Eastern Shallow Stations

Northern Deep Stations

Central Deep Stations

Eastern Deep Stations

Figure 1.5: Histogram represents the numbers of males and females *C. crangon* in 1mm total length class collected from different locations within the distributional range of brown shrimp in the Wadden Sea during January 2010.

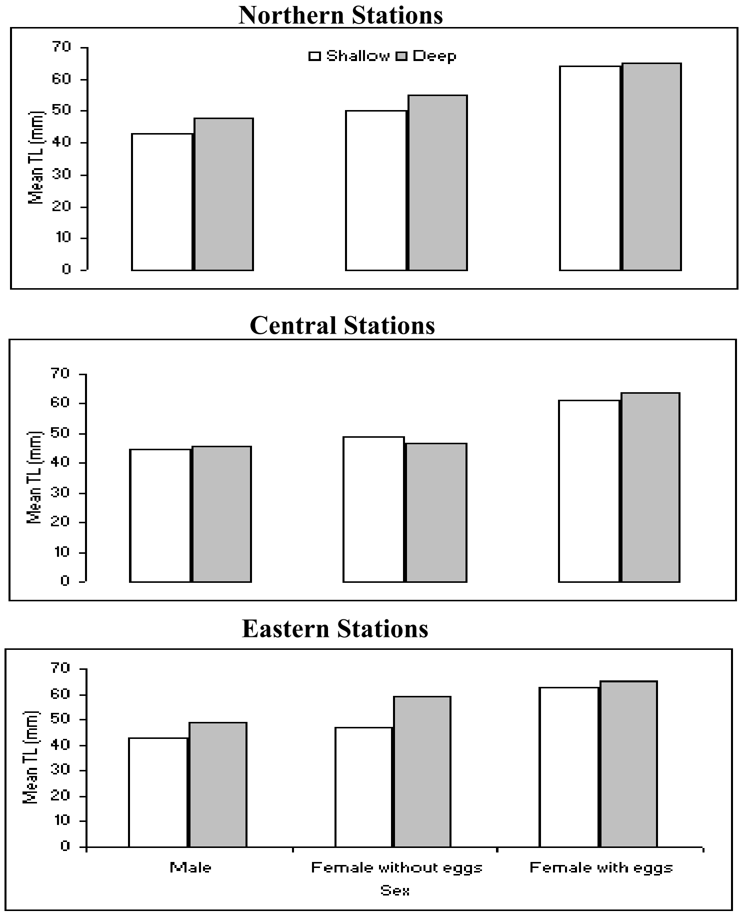


Figure 1.6: Spatial size distribution (*TL*) of males and females brown shrimp *C. crangon* with and without eggs collected from the Wadden Sea.

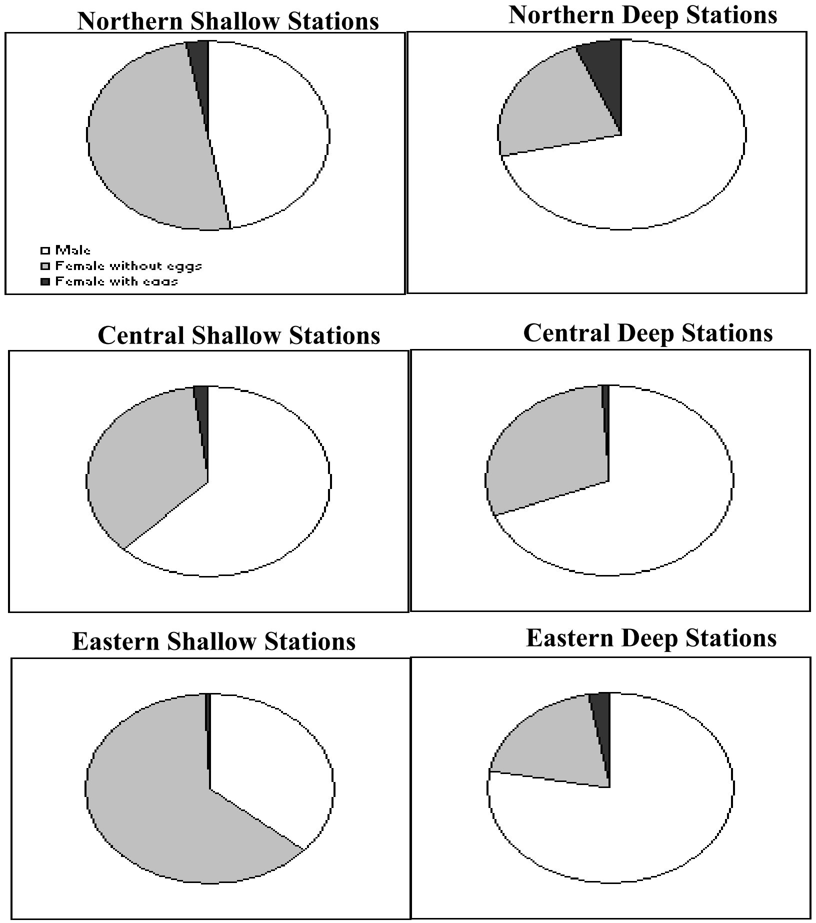
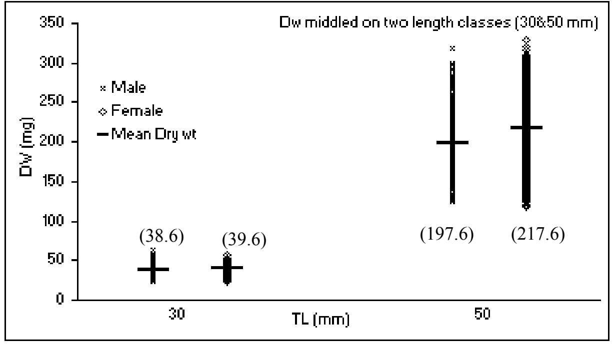
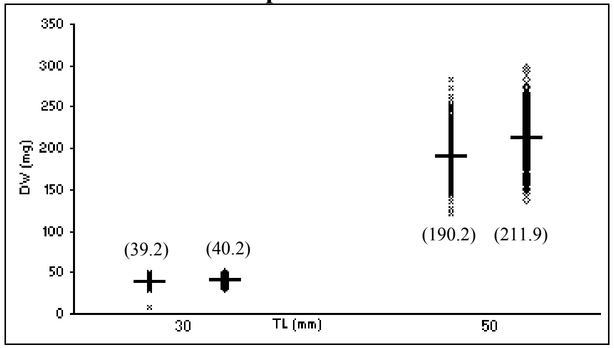


Figure 1.7: Numbers of males, females of *C. crangon* without eggs and females with eggs counted during 30 min trawl period at sampling stations (shallow, deep) for the Wadden Sea during January 2010.

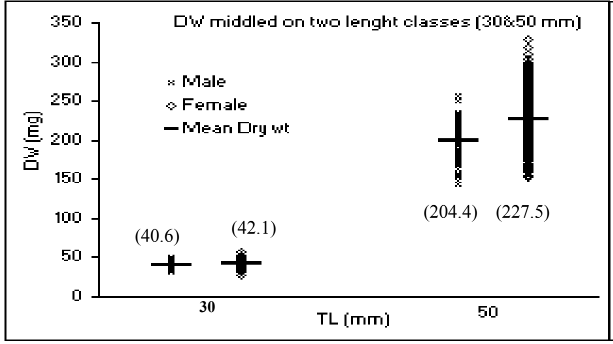
All Shallow Stations



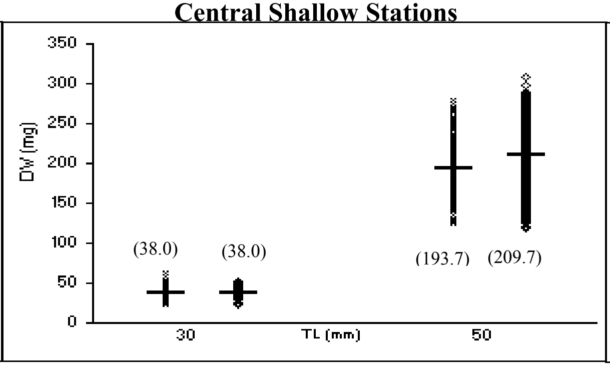
All Deep Stations



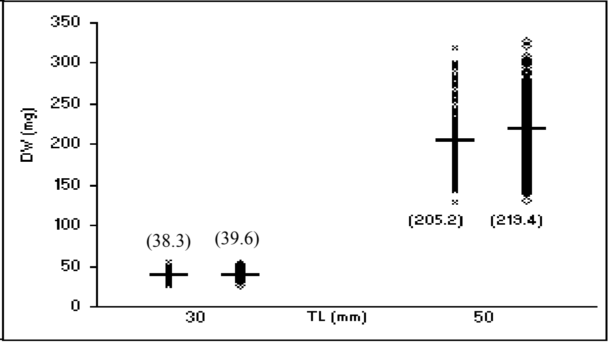
Northern Shallow Stations



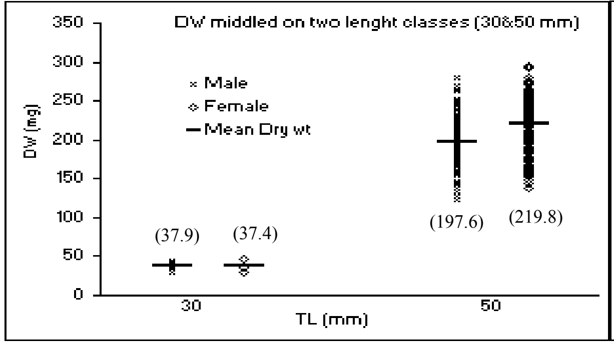
Central Shallow Stations



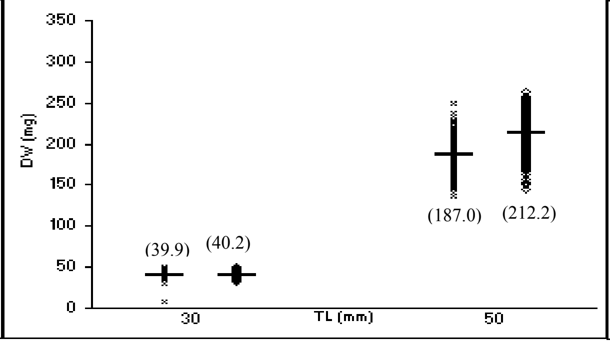
Eastern Shallow Stations



Northern Deep Stations



Central Deep Stations



Eastern Deep Stations

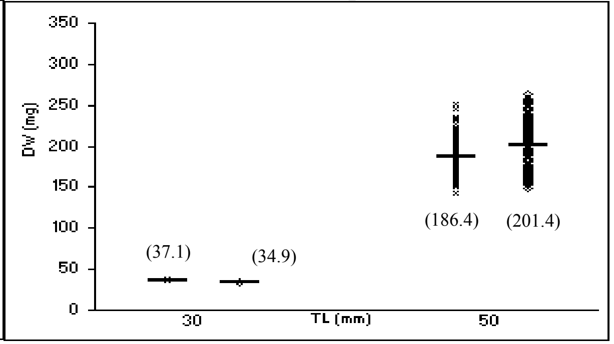


Figure 1.8: Dry weight of brown shrimp caught from different areas in the Wadden Sea, numbers between brackets represent the mean dry weight (mg).

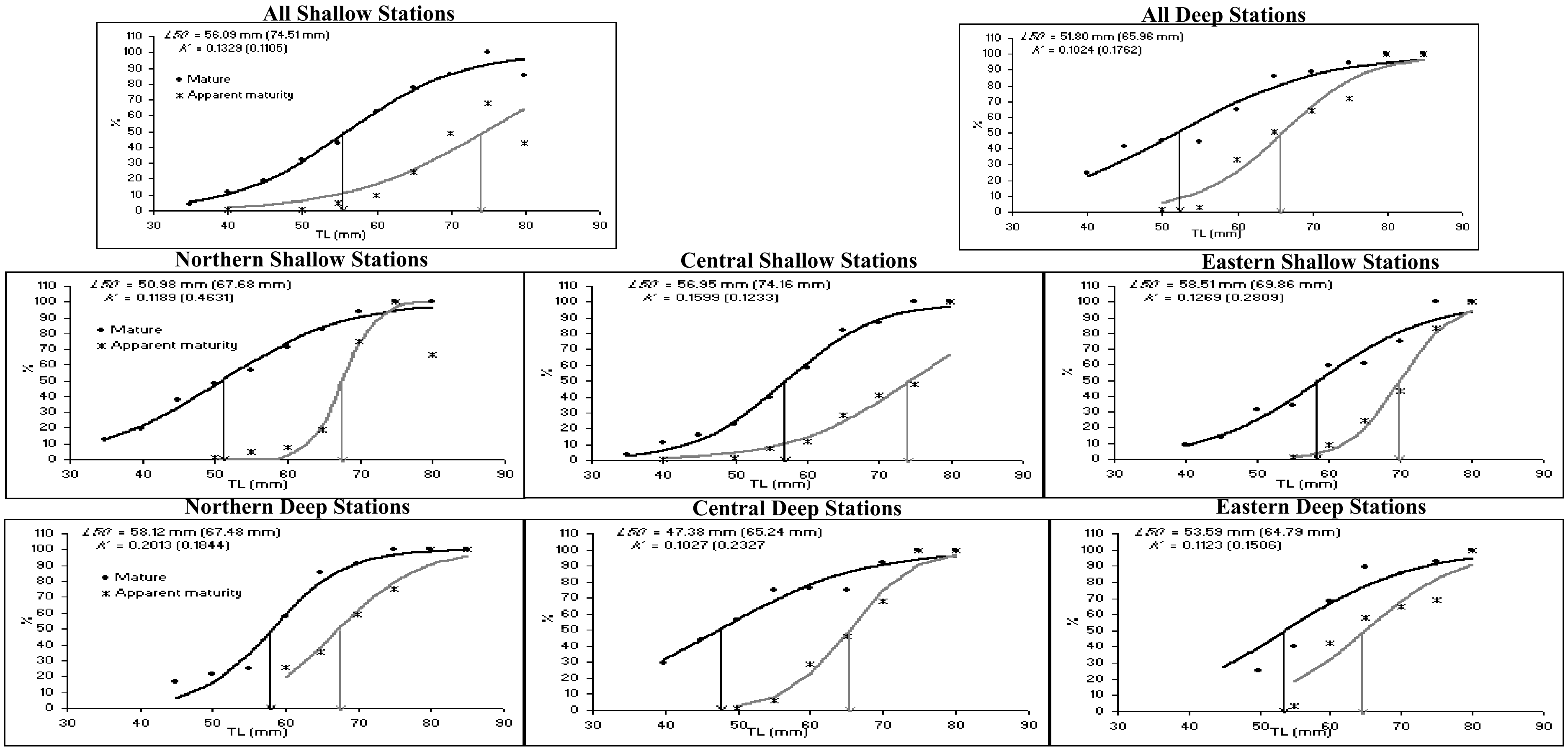


Figure 1.9: A logistic function fitting the proportion of mature based on setae (black line) and apparent mature based on (gray line) females of brown shrimp to total length; arrows correspond to a proportion of 50% of mature and apparent mature females are indicated (50% of the apparent mature between brackets).

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MANUSCRIPT 2

Short-term observations on growth and moulting of brown shrimp *Crangon Crangon* (L.).

Abstract

In situ growth rates of brown shrimp *Crangon crangon* in the German Wadden Sea off Büsum were measured during 2010. Growth rate was measured using the instantaneous growth rate (IGR) method which involved measuring the changes in individual total length before and after moult (*L1* and *L2*). We used the IGR technique to determine the effects of sex, size class and temperature on *in situ* growth of brown shrimp. In the first two days following catch, we observed shortest intermoult period (5 days) and larger moult increments (3.34 mm for males and 6.28 mm for females) than the values recorded before. Our mean growth rates observed for males was 0.41 mm/day and was 0.76 for females at 22.3 °C (July 23rd) which are also higher than the most published literature values under field and laboratory conditions, indicating that the autumn peak is related to the previous winter eggs production. We have also the advantage to use our date to evaluate the new method established by Perger and Temming (2012). By applying their method described 65% and 85 % of the variances (r^2) at warm temperatures and 24% and 92% of the variances were described at cold temperature as well as different size classes which, however, strongly support the new method. Also, combining both IGR and Perger and Temming methods will make possible to measure the onset of field shrinkage, poor growth, in upcoming suggested studies.

Introduction

The brown shrimp *C. crangon* is one of the common and highly abundant species in European estuaries playing an important role in the ecosystem functioning. In fact, brown shrimp is both a prey of fish, crustaceans and shorebirds (Pihl, 1985; Henderson et al., 1992; Del-Norte Campos and Temming, 1994; Walter and Becker, 1997) and predator of meiofauna and early stages of fish and bivalves (Pihl and Rosenberg, 1984; Van der Veer et al., 1998; Oh et al., 2001; Amara and Paul, 2003). Besides ecologically significant, it is also a valuable fisheries resource, especially in the North Sea where it has a market value between €50-100 million (ICES, 2006).

In the Wadden Sea, shrimps utilize the shallow intertidal areas as nursery, especially smaller size class (< 30 mm), where they find shelter from predation, enough food and high temperatures for fast growth (Boddeke et al., 1986; Beukma, 1992; Cattrijsse et al., 1997). Temming and Damm (2002) observed an invasion of the Wadden Sea tidal flats by *C. crangon* measuring the densities of 5-20 mm shrimp during the middle of June. The timing of the invasion seems to be mainly temperature driven and occurs later after cold winters (Beukma, 1992, Temming and Damm, 2002).

C. crangon individuals larger than 30 mm were found to leave the intertidal nursery and invade subtidal areas (Janssen and Kuipers, 1980; Kuipers and Dapper, 1981). They start to reach this length in the beginning of July, with most individuals reaching this size in August. It is debatable whether this June-cohort has reached the commercial size (50mm) by September. However, fisheries maximum is consistently observed in autumn (ICES, 1996; Boddeke, 1982). Hence a major discussion is still under debate: are spring settlers recruiting to fisheries in autumn? What is the contribution of the summer generation? This discussion was initiated by Boddeke (1976) who considered summer reproduction to yield the recruits to autumn commercial caches of the same year. In contrast, Kuipers and Dapper (1984) suggested that winter reproduction sustains the following autumn fisheries through heavy spring settlement. Campos et al. (2010) simulated the growth trajectories from 5 mm to 50 mm (fisheries size) and found that the maximum growth under optimal food conditions at the Wadden Sea temperature conditions revealed that males would take 1.5 years and females just 1 year from settlement to fisheries size. Therefore, females, which make up the bulk of commercial landings, to become available to the fisheries in autumn, must have settled in the Wadden Sea during the previous autumn, one year before, and hence probably arose from summer generation. Consequently, according to Campos et al. (2010), it is not the summer brood from the current year as Boddeke (1976) claimed, or the previous winter generation as Kuipers and Dapper (1984) suggested, but the summer generation from previous year which represents the major contribution to autumn peak in fisheries. Until now, studies on growth still speculating maximum growth and then apply model predictions to analyse the life history in the field (Kuipers and Dapper, 1984; Temming and Damm, 2002; Hufnagl and Temming, 2011b). Such growth model should be considered with caution, as long as the assumptions about *in situ* growth conditions have not yet been validated. However, under field conditions still no reliable growth data from shrimps in the Wadden Sea are available and any decision between the alternatives described before is totally dependent on accurate growth determination of *C. crangon*.

The first attempt was initiated by Perger and Temming (2012) to estimate the growth rate for brown shrimp *C. crangon* in the Wadden Sea based on dry weight condition. Perger and Temming (2012) estimated high growth rates for females brown shrimps as 0.44 mm/d for 27.5 mm total length for June and as 0.35 mm/d for July at 37.5 mm. However, only few laboratory studies with ad libitum feeding regimes have reported comparably high values (Dalley, 1980; Meixner, 1969 and Hufnagl and Temming, 2011a).

Due to the rigid exoskeleton, growth of *C. crangon* is irregular and takes place by various moultings, whereby the exoskeleton is released, an increase in body volume occurs and a new soft skeleton is formed that hardens in a few days (Smaldon et al., 1993). Crustaceans do not exhibit continuous growth; rather, in these animals, growth is discrete and biphasic. Their rigid exoskeleton limits external growth to the brief moulting events (Hartnoll, 1982). Thus growth of shrimp is difficult to estimate reliably because no direct method of ageing is available.

However, the biphasic nature of crustacean growth can be used as a foundation to develop a more appropriate model of crustacean growth. The growth pattern can be modelled by combining predictions of the amount of growth per moult with estimates of the frequency of moulting (moult rate) (Hiatt, 1948). Such approaches are termed moult process models (Smith, 1997). Such moult process models have been created for several crustaceans, e.g., Alaskan king crab (*Paralithodes camtschatica*), American lobster (*Homarus americanus*), Dungeness crab (*Cancer magister*), Blue crab (*Callinectes sapidus*), Antarctic krill (*Euphausia superba*), Brown shrimp (*C. crangon*) (McCaughran and Powel, 1977; Fogarty and Idoine, 1988; Wainwright and Armstrong, 1993; Brylawski and Miller, 2006; Atkinson et al., 2006; Hufnagl and Temming, 2011b; Perger and Temming, 2012).

Growth rates are dependent on temperature, sex, size of animal and food quality and quantity. Temperature and food supply have generally been considered as the main extrinsic factors affecting growth in crustacean. A number of studies have examined the effect of temperature on growth in crustacean (Hartnoll, 2001; Hufnagl and Temming, 2011a). In the laboratory, maximum growth has a positive relationship with increasing temperature and an inverse relationship with shrimp size (Tiews, 1954; Meixner, 1969; Rochanaburanon, 1974; Hufnagl and Temming, 2011a). However, juvenile shrimps show maximum growth at about 25 °C (Van Lissa, 1977) and compared to adults, juveniles show a faster growth and are more tolerant to high temperatures (Van Donk and De Wilde, 1981).

Other studies have investigated the effect of food on crustacean growth (Caudri, 1939; Lloyd and Yonge, 1947; Board, 1957; Kurata, 1962; Forster, 1970; Heywood, 1970; Adelung, 1971; Knowlton, 1974; Chittleborough, 1975; Klein Breteler, 1975a and b; Cariales and Anger, 1986; Mohamedeen and Hartnoll, 1989; Salama and Hartnoll, 1992; Oh and Hartnoll, 2000; Schatte and Saborowski, 2005; Campos et al., 2009; Hufnagl and Temming, 2011a). Several authors have demonstrated that a reduction in food quantity decreases or prevents growth of *C. crangon* (Nouvel van Rysselberg, 1937; Tiews, 1954; Meixner, 1969). However, most of the studies on brown shrimp have used ad libitum feeding to investigate the maximum growth rates under optimum conditions (Campos et al., 2009; Hufnagl and Temming, 2011a).

Since live food, especial copepods, are very difficult to produce in sufficient quantities for large scale experiments, the investigation of *in situ* growth rates is a logical alternative to such laboratory studies. The most widely applied method to investigate *in situ* growth is to determine the change in the mean length of sampled population over time. However, difficulties arise when growth determined from data obtained from repeated field sampling of *C. crangon* mainly due to different cohorts sampled with mixed age at the same length (Kuipers and Dapper, 1981). Other factors bias the growth estimates like seasonal, size, gender and temperature dependent migrations (Pihl and Rosenberg, 1982; Berghahn, 1983; Taylor and Collie, 2003; Hufnagl et al., 2010; Hufnagl and Temming, 2011b).

A promising alternative to cohort tracking is the instantaneous growth rate (IGR) method, which was originally adapted for use in Krill by Quetin and Ross (1991) and Nicol et al. (1992). The method involves taking around 100 krill, measuring and maintaining them for 2-3 days in individual containers. The animals must be checked daily and any moulted individuals extracted from the experiments with the exuviae and the newly moulted individual measured to determine the percent change in length at moult as well as the daily moult rate.

Quetin and Rose (1991) and Nicol et al (1992) outlined a methodology for the measurement of instantaneous growth rates, based on growth increments and intermoult periods, and demonstrated both growth and shrinkage in freshly caught krill.

The daily moult rate can be estimated by dividing the total number of shrimp at the start of an incubation day by the number moulting per day. The intermoult period can be recalculated as the inverse of the moult rate. Dividing moult increment by the intermoult period gives the growth in length per day (Ross et al., 2000).

Basic premises of the technique are that: (1) the moulting number each day is relatively constant; (2) the growth increment is not affected by the incubation condition for several days post-capture (Nicol et al., 1992; Tarling et al., 2006); (3) the moult interval is not affected by incubation; (4) the changes in length increase or decrease, before and after moult reflect the feeding and growth conditions over the previous intermoult period. Since the IGR method has never been tested with brown shrimp, we therefore decided to test its potential on a larger scale.

Previous studies have always considered growth in terms of change in body length whereas estimates of increases in weight and elemental composition are more important with regard to the parameterisation of the energy budget and the protein content of *C. crangon*. Furthermore, the pattern of increase in weight may differ to increase in length, particularly in adults that may continue to put on weight without lengthening (Båmstedt, 1976; Boysen and Buchholz, 1984; Falk-Petersen, 1985).

Dry weight condition has been used previously to describe the nutritional condition of crustaceans (Nicol et al., 2000; Pérez-Castañeda and Defeo, 2002). The interpretation of a dry weight-based condition factor in crustaceans is, however, complicated by the discontinuous growth of the exoskeleton and hence the length of the individual as described before. The discrete moult events imply that dry weight will increase steadily during the intermoult period while length remains constant. During this phase, water content of the animal will decrease steadily, and consequently, the dry weight condition factor will increase (Rey-Rassat et al, 2004). During the actual moult, the length increases rapidly due to uptake of water, while the total dry weight is reduced by the weight of the exuviae. Immediately after the moult, the body is characterised by maximum water content and a theoretical minimum in dry weight condition for non-starving crustaceans. Based on these considerations, Perger and Temming (2012) suggested a new method as an extension of the instantaneous growth rate (IGR) assuming that the dry weight of the moulted individuals measured directly after moulted represent the cumulative food intake and hence growth of previous intermoult period. Their new method can be applied to describe the spatial growth variability based on large sets of data from surveys and as an indicator of the *in situ* growth. However, further tests to evaluate the new method and to investigate the effects of the environmental temperature and sex are needed (Perger and Temming, 2012).

The major objectives of the present study are:

1. To apply the *IGR* method to measure *in situ* growth components (intermoult periods and moult increments); addressing the effects of size, temperature and season which has so for not been tested before with *C. Crangon* and
2. To evaluate the new method developed by Perger and Temming (2012) to estimate the *in situ* growth of *C. crangon*, with a focus on the effects of sex, size, temperature and season.

Material and Method

Sampling and measurements

Brown shrimps were collected using a push net from the Wadden Sea off Büsum (54° 07' N and 08° 51' E) at about 10 to 100 cm water depth during very low tide. Carful capture of specimens was considered to avoid damage and stress of the shrimps. Sampling time was limited to maximum 10 min (Gamito and Cabral. 2003). To minimise handling stress, sex of the shrimp was not determined prior to moult.

Net dimension were 1.44 m width and 23 cm height with 1.8 mm mesh size. Samples were taken on 2010, temperature (°C) and salinity (PSU) were measured (Table 1.1). Live specimens were transported in 100 l box filled with aerated sea water to the Institute for Hydrobiology and Fisheries Science (IHF) laboratory, Hamburg, Germany, where the experiments are carried out starting within approximately two to three hours after catch.

At each experiment, the total lengths before (*L1*) and after (*L2*) moult were measured to the nearest 0.1 mm from digital images (USB camera UI-1485LE 2560 x 1920 pixels equipped with a Pentax C3516-M lens) applying a Matlab routine (The Math works. Inc., Natick. MA). Measurements were from top of the rostrum to the end of the telson. Shrimp dry weight after moult (*W2*), exuviae dry weight (*E1*) and ash free dry weight of exuviae (550 °C for 2 h) were determined to the nearest 0.1 mg by electronic digital balance (Satorius ± 0.0001 g). Male and female shrimps were distinguished (after moult) on the basis of external characteristics of the first pleopod (presence or absence of the appendix masculine (Lloyd and Yonge, 1947).

Laboratory maintenance

A set of 15 short term experiments were conducted in 2010. For each experiment, individuals were randomly collected from the catch and carefully measured; total length (*L1*, mm). All individuals were immediately placed depending on size either to perforated plastic bottles or tubes which were submerged in aquaria supplied with running artificial North Sea water. Flow rates of water were kept constant during the period of experiments providing 100% water exchange per day. Shrimps were maintained at ambient surface water temperature as measured in the field (± 0.5 °C) during sampling with the help of an electrical heater or cooler when needed, in a manner similar to that described by Nicol et al. (2000). Individuals were incubated in separated container for only two days. The system was artificially illuminated (10L: 14D). Due to the short duration and the fact that shrimp reduce or stop feeding prior to actual moulting (Dall et al., 1990; Quetin and Ross, 1991; Hufnagl et al., 2010-food limits), no additional food sources were added.

Experimental procedures

For two days, shrimps were checked every 6 h (6-h period standardized by authors) for the mortality and moults. If the shrimp had moulted the animal and the exuviae (*E1*) were removed and the new total length of the shrimp (*L2*) was measured, dry weight (*W2)* and *E1* were measured after freeze-drying for 24 h. While the observed increments (*Obs_INC*) can be estimated directly by subtraction of *L2* and *L1*, the predicted increments (*Pred_INC*) can be determined as suggested by Perger and Temming (2012) as follows:

$$Pred\_INC = L1 \text{ x } C1_{-E}{}^{1/b} - L1 \quad (1)$$

$$C1_{-E} = (W1-E1) / (a \text{ x } L1^{b}) \quad (2)$$

$C1_{-E}$ is the dry weight condition before moulting corrected for the weight of the exuviae.

Following the established morphometric relationships by Perger and Temming (2012), the *E1-L1* and *L2-W2* relationships for males and females were estimated as follows:

$$E1 = a_E \text{ x } L1^{\,bE} \quad (3)$$

where a_E and b_E are constant; *E1* in mg. *L1* in mm.

$$W2 = a \text{ x } L2^{\,b} \quad (4)$$

where *a* and *b* are constant; *W2* in mg. *L2* in mm

In order to minimize measurement biases, the same investigator carried out the measurements under the same working condition. The moult increment and the intermoult period were combined to estimate the *in situ* growth rate. We calculated the intermoult period (*IMP*) of an experiment using the inverse of daily moult rate (*MR*), which can be estimated by dividing the total number of shrimp at the start of the incubation, taking mortality in consideration, by the number moulting per day, as follows:

$$IMP = (N \times ip) / m \tag{5}$$

where N represents the total number of shrimps that were alive at the end of the experiment plus those that moulted during the incubation period (ip) which is 2 days in the present study and m is the number of shrimps that moulted. Thus individual growth rates can be also estimated by dividing the individual growth increment by the common *IMP*. Due to limitations in facilities, numbers of shrimps were too low and to minimize handling stress, for each size class, sex and temperature combined. The relationship between intermoult period, body length and temperature was described with the following equation:

$$IMP = \alpha \times L1^{\beta} \times e^{c \times T} \tag{6}$$

where α ; β and c are constants; T is temperature °C.

Dry weight condition indices

We apply the following equations to determine the dry weight condition without ($C2$) and with ($C1$) the mineral components of the exuviae for males and females:

$$C2 = W2 / (a \times L2^{b}) \tag{7}$$

$$C1 = W1 / (a \times L1^{b}) \tag{8}$$

where $W1$ is the individual dry weight of shrimps directly after moulted plus the exuviae dry weight.

Results

Morphometric characteristics

In laboratory experiments, a total of 15 moult experiments were conducted and 1906 individuals (Table 2.1) have been observed for two days. Individuals shrimp ranged from 19.5 mm to 62.5 with an average of 35.9±7.9 mm. Shrimps were sorted into six and seven size classes (4.9 mm) for males and females respectively (Table 2.2).

A total of 13 experiments revealed moult events with total of 158 males and 92 females (Table 2.2).

All shrimps were analysed after 6 h from the actual moult event (standardized by the author). Over all the experiments, the smallest individuals moulted were 21.4 mm and 24.7 mm for males and females respectively. While the largest animals moulted were 47.0 and 53.6 mm for males and females respectively.

$L2$-$W2$ relationship of the newly moulted individuals was estimated as:

For males:

$$W2 = 0.003966 \times L2^{2.722} \quad (9)$$

with $r^2 = 0.983$ and n = 158

For females:

$$W2 = 0.001939 \times L2^{2.931} \quad (10)$$

with $r^2 = 0.996$ and n = 92

The relationships between exuviae dry weight $E1$ and $L1$ were determined (Figure 2.2) as:

For males:

$$E1 = 0.001112 \times L1^{2.659} \quad (11)$$

with $r^2 = 0.828$

For females:

$$E1 = 0.000256 \times L1^{3.102} \quad (12)$$

with $r^2 = 0.947$

When compared for the same length, females were increasingly heavier than males with growing *L* (Figures 2.1 and 2.2).

Observed and predicted growth rate components (*INC* and *IMP*)

Animals were grouped into 1 cm size classes (Table 2.3), to avoid the calculation of mean values from too small groups.

Observed moult increments: During the experiments, moulting events were restricted completely to hours of darkness. The maximum percentages of moulted shrimps recorded were 16 % at 21.3 °C while only 1.6 % at 9.4 °C (Table 2.1). Among a total of 15 moult experiments has been conducted in this study, unsuccessful moults were observed in 2 moult experiments at 7.5 ± 0.2 °C.

The shortest mean moult increments for male brown shrimp was observed at 30 mm *L1* associated with 21.3 °C as 0.66 mm while shrimps reached higher mean increments of 3.34 mm at 14.7 °C in 20 mm length (*L1*).

For females, the shortest mean moult increments was observed at 40 mm length (*L1*) associated with 21.3 °C) as 0.53 mm while shrimps reached higher mean increments up to 6.28 mm at the highest field temperature measured (22.3 °C) at 30.0 mm *L1*.

In the present study, moult increments clearly increased with increasing size class (> 35 mm *L1* for both males and females (Figure 2.3), for example, moult increments for males in August 03rd were 1.24, 1.70 and 2.81 mm in 20, 30 and 40 mm length, while were 2.62, 2.94 and 2.97 mm in June 19th at 30, 40 and 50 mm size classes (Figure 2.3).

Predicted moult increments: A regression of predicted moult increments from equation 1 on the observed moult increments explained 65.1 % and 85.1 % of the variance in the data for males and females respectively for the warm temperature; between 18.8 to 22.3 °C (Figure 2.4). While for colder temperature (9.4, 14.7 and 15.9 °C), a regression of predicted moult increments from equation 1 on the observed moult increments explained 24.2 % and 92.6 % of the variance in the data for males and females respectively (Figure 2.5).

Observed intermoult period: When sex combined, the minimum intermoult period (5 days) was observed in 20 mm size class at 22.3 °C which is highest temperature measured in the field while the longest observed *IMP* was 44 day at the lowest temperature measured (9.4 °C) but with larger size class (40 mm *L1*).

Predicted intermoult period: A nonlinear regression relationship between intermoult period, body length and temperature was estimated based on Equation 6 and expressed as:

$$IMP = 0.59796 \times L1^{1.3851} \times e^{-0.10232 \times T} \tag{13}$$

with $r^2 = 0.943$

It shows that the moult interval is a function of *L* of premoult of the specimens and temperature.

Growth rates (*GR*)

The corresponding mean growth rate (*GR*, mm/day) observed for males and females separately based on the *IMP* (sex combined) and individual male and female *INC*. Male's growth rates varied from 0.03 mm/day at 40 mm size class in 14.7 °C to 0.41 mm/day at 22.3 °C in 20 mm size class (Table 2.3). While female's growth rates ranged between 0.03mm/day at 50 mm size class in 15.9 °C to 0.76 mm/day at 22.3 °C in 30 mm size class (*L1*).

Growth rate was clearly fluctuated between different seasons. In spring, low growth rate value was observed which associated with large increment and long intermoult period e.g. largest moult increment was 3.34 mm for males in length 20 mm at 14.7 °C with 14 day intermoult periods, which is considerably high comparable to the minimum intermoult period (6 days). Likewise for females in 30 mm size, the moult increment was 2.37 mm with intermoult period of 16 day at 15.9 °C. However, similar patterns can be seen during autumn season. In contrast, higher growth rates for both males and females were observed at summer season which associated with shortest intermoult period, 5 and 6 days for males and females respectively, as well as smaller moult increments when compared with previous example.

Dry weight condition indices of individuals before and after moult

The corresponding condition indices directly after moult (*C2*), calculated using the equation 8 based on *L2*-*W2* relationship, were estimated and represented for both males and females (Figure 2.6). *C2* varied between 0.89 and 1.11 with a mean of 1.00±0.054 and from 0.92 to 1.11 with a mean of 1.00±0.038 in males and females respectively; variation stated here after excluding the extreme values which considered as outliers in the present study (Figure 2.6). The share of total dry weight (mg) of the exuviae from the total animal dry weight on average to 15.9±1.1 % in males while in females was 17.3±2.3%. The share of mineral components of the exuviae dry weight (free ash dry weight) to the total dry weight of the exuviae in males was 52.2±10.2 % while contributed 54.7±8.1% in females.

Dry weight condition indices (*C1*) results were estimated based on equation 9, where a = 0.003966 and b = 2.722 for males and a = 0.001939 and b = 2.931 for females. The minimum observed values of dry weight condition indices just prior to moult (*C1*) were 1.127 and 1.148 for males and females respectively.

Discussion

Moult intervals (*IMP*) are shorter compared to other studies

In the present study, short moult intervals have been observed comparable to previous studies, 5 days for small size class (< 30 mm) at high temperature (22.3 °C) which, however, is shorter than the minimum intermoult period estimated by Hufnagl and Temming (2011a) as 7 days and also shorter than the 6 days for 25-29.9 mm for females brown shrimp by Perger and Temming (2012). In a meta-analysis of all literatures published, Hufnagl and Temming (2011a) revealed generally longer intermoult periods than those estimated in the present study. In fact, these long intervals reported by many authors could have been influenced by laboratory conditions such as food (see manuscript 4 and Plagmann, 1939; Meixner, 1966; Evans, 1984; Oh and Hartnoll, 2000; Campos et al., 2009; Hufnagl and Temming 2011a). Many authors demonstrated that longer incubation period reflects the laboratory rather field conditions which would prolong the mean moulting intervals (Dall et al., 1990; Quetin and Ross, 1991; Hufnagl et al., 2010; Perger and Temming, 2012). The prolongation of moulting intervals under such conditions may also result from individuals stopping food intake, supposedly as a consequence of inadequate food. It has been demonstrated repeatedly, that starvation leads to increased moult intervals or a complete halt of moulting.

Moult increments are larger than the increments observed in previous studies

In the present study larger mean increments were observed for female brown shrimp using *IGR* method (highest mean values of 3.34 to 6.28 mm for males and females respectively) when compared to other studies. As an example from the most comparable study from the same study area Perger and Temming (2012) found mean moult increments between 0.8 mm (45-49.9 mm, late July) to 2.4 mm increment (25-29.9 mm, mid June) for females *C. crangon*. In contrast in our study there were 3 samplings with mean increments above 3 mm and 6 samplings with mean increments between 2.4 mm and 3 mm. An additional 9 samples revealed mean increments of between 2 and 2.4 mm.

The study of Perger and Temming (2012) is, however, the only study with a comparable methodology. Most of the other work on brown shrimp growth refers to laboratory experiments. Only a few of these lab studies reports similar high values.

Hufnagl and Temming (2011b) estimated the maximum increments from laboratory experiments with groups indirectly, by multiplying estimates of G_{max} and moult interval. They estimated the maximum increments as 7 mm comparable to results from an earlier study by Meixner (1969).

First interesting finding in the present study is the presence of almost zero increments which is surprising based given that the majority of shrimp were growing well in the field, indicating overall good food supply. However, there seems to be also a certain degree of variation between individuals from the same sampling location, as was discussed by Perger and Temming (2012) and Hufnagl et al. (2010). Zero increments or even negative ones have been observed with *C. crangon* but under laboratory conditions by Campos et al. (2009) in Minho estuaries. Such shrinkage also was reported for Antarctic Krill species, where *IGR* method used in the present study was initially established for e.g. *Euphausia pacifica* (Lasker, 1966), *E. superba* (Ikeda and Dixon, 1982), *Meganyctiphanes norvegica* (Buchholz, 1985), *Thysanoessa inermis* (Dalpadado and lkeda, 1989), *Nyctiphanes australis* (Hosie and Ritz, 1989) in laboratory experiments.

Nicol et al. (1992) measured growth rates using the *IGR* methods under experimental conditions and stated that when food was restricted, individual krill began to shrink immediately and mean population growth rates decreased gradually, becoming negative after few days (> 2 days). Populations of krill which exhibited higher initial growth rates began to shrink later than those which had initially been growing more slowly (Nicol et al., 1992).

Second interesting finding in the present work is that shrimps larger than 35 mm total length, which are become mature, tend to increase their moult increments. Such phenomenon is quite very obviously with females rather than males due to few individual males that moulted in the present work. However, such results are contradicting our knowledge based on Von Bertalanffy growth function (VBGF); decreasing growth when increasing size. We speculate that such finding is due to that larger mature (between 34 to 40 mm length, more details about maturity in manuscript 1) shrimps tend to change their feeding behaviour (broadened). However, such assumption need to be investigated based on stomach contents for small and large brown shrimp size class, especially different feeding behaviour between immature and mature shrimps. Del-Norte Campos and Temming (1994) studied the stomach contents analysis for brown shrimp and found that smaller shrimps mainly feeding on meiofauna (0-24 mm length) and with increasing size shrimps tend to change their feeding behaviour toward molluscs and crustaceans even they start to eat the smaller *C. crangon*. Also such findings; larger increments with increasing length may be confirmed when applying the new method (Perger and Temming, 2012) with *in situ* data to predict the moult increments based on dry weight conditions.

Daily growth rate (*GR*)

In the present study, growth rate was clearly fluctuated between different seasons from low growth rate in early spring and autumn to higher ones during late spring and summer. In spring, low growth rate value was observed which associated with large increment and long intermoult period e.g. largest moult increment was 3.34 mm for males in length 20 mm at 14.7 °C with 14 day intermoult periods, which is considerably high comparable to the minimum intermoult period (6 days). Likewise for females in 30 mm size, the moult increment was 2.37 mm with intermoult period of 16 day at 15.9 °C. However, similar patterns can be seen during autumn season. In contrast, higher growth rates for both males and females were observed at summer season which associated with shortest intermoult period, 5 and 6 days for males and females respectively, as well as smaller moult increments when compared with previous example.

In situ growth measured with the instantaneous growth rate (IGR) method is assumed to represent the growth of the previous intermoult period (*IMP*). Generally, high growth rates in crustaceans can be achieved by either increase in moult frequency or by the production of larger increments.

In the present study, a decreasing trend in intermoult period with increasing temperature was observed (Table 2.3) which, however, reported and confirmed in previous studies (Hufnagl and Temming, 2011b for review) i.e. high *in situ* growth rates achieved here was due to increases in moult frequency associated with high temperature as well as production of larger increments with shorter intermoult period at low temperature. However, such high growth rates at high temperatures were reported only when live food provided (Meixner, 1969; Labat, 1977; Dalley, 1980; Hufnagl and Temming, 2011a) under laboratory experiments, while was lower growth rates were observed when shrimps were fed only nematodes in the early study conducted by Gerlach and Schrage (1969). The effect of food on growth was discussed in more detail by Hufnagl et al (2010).

In the present study, females grew faster than males but differences with size were dependent on (a) sex and (b) temperature.

(a) Growth in females was higher about twice or even three times than in males at the same size. For example, at 20 mm length, daily growth rate for males was 0.15 mm/day while it was 0.26 mm/day at 20.2 °C (August 11th). Likewise on July 23rd, daily growth rate for males was 0.22 mm/day while it was 0.76 mm/day at 22.3 °C. Additionally, in manuscript 4 females growth rate and moult interval was as double as male values, which support our findings here, and the explanation could be that female *C. crangon* can only be fertilized directly after moulting when the exoskeleton is soft (Boddeke et al., 1991); therefore, maturation and reproductive processes may trigger moulting independent of growth rates and recent feeding. Furthermore, the size-at-maturation threshold differs for males and females, whereby males become mature at a smaller size (22-43 mm total length) than females (30-55 mm total length) (Lloyd and Yonge, 1947; Boddeke, 1966; Muus, 1967; Meixner, 1970; Gelin et al., 2000; Oh and Hartnoll, 2004).

These differences between males and females growth rate are comparable to those in previous studies on *C. crangon* in both laboratory (Dornheim, 1969; Labat, 1977, Oh et al., 1999) and field observations (Lagardère, 1982; Campos et al., 2009; Hufnagl and Temming, 2011a). Not only with *C. crangon* but also similar growth rate differences between males and females were also reported for other crangonids e.g. *A. dentata* (Couture and Filteau, 1971), *C. septemspinosa* (Haefner, 1972), *C. nigricauda* and *C. franciscorum* (Krygier and Horton, 1975), *N. antarcticus* (Bluhm and Brey, 2001), and *Philocheras trispinosus* (Labat, 1984).

(b) Temperature has a great effect on brown shrimps' growth rate, as in other crustaceans (Hartnoll, 2001). Both juvenile and adult *C. crangon* are able to grow at least between 5 and 25 °C (Van Lissa, 1977). Generally, growth becomes faster with increasing temperature (Meixner, 1966; Tiews, 1954; Duran, 1997), but at highest temperatures growth may decline where it is associated with higher mortality (Hartnoll, 2001). However, such a decline at high temperature was clearly observed in the present study with larger animals (> 40 mm) and this fits with previous studies (Hufnagl and Temming, 2011a) while our results show that the optimal temperature for *C. crangon* appears to be around 22 °C, this estimation not fitted with the optimal temperature determined for *C. crangon* by Freitas et al. (2007) and Campos et al. (2009) which they suggested to be around 25 °C.

However, the *in situ* growth rate obtained in this study, 0.41 mm/day (20 mm) and 0.76 mm/day (30 mm) at 22.3 °C (July 23rd) for males and females respectively was higher than any other estimate reported in previous studies except the maximum growth rate reported by Campos et al. (2009) with 0.89 mm/day at 25 °C for females *C. crangon* in Northern Valosen estuaries under laboratory condition while her maximum value for males was 0.17 mm/day at 10 °C at 30-39 mm size class. For example, in field studies the estimates were found on the Isle of Man as 0.01 mm/day by Oh et al. (1999), 0.02 mm/day in the UK by Duran (1997), 0.03 mm/day in the Baltic and in Germany by Meyer (1936) and Dornheim (1939), 0.16 mm/day in France by Amara and Paul (2003), 0.23 mm/day in Germany by Del-Norte Campos and Temming (1998), 0.35-0.49 mm/day in The Netherlands by Kuipers and Dapper (1981 and 1984), Boddeke et al. (1986) and Cattrijsse et al. (1997). In laboratory, the daily growth rates estimated from Germany 0.02 - 0.14 (5-25 °C) by Gerlach and Schrage (1969), from France 0.03-0.17 mm/day (11.5-23 °C) by Lagardère (1982), in the Isle of man 0.57 mm/day (20 °C) by Dalley 1980, and in the German Wadden Sea off Büsum 0.8 mm/day (5-25 °C) by Hufnagl and Temming (2011). Such great variability found in growth rates estimates in field and lab as well as between sexes is suggested to be related to the variable conditions in these works such as temperature, food, size, different cohort sampled and regions.

However, high *in situ* growth rates observed in the present study infer that the winter egg production is causing the autumn peak of the following year. This finding confirmed and fitted with the previous studies by Kuiper and Dapper (1984) and Perger and Temming (2012). In contrast, Campos et al. (2010) concluded that the summer egg production leads to the subsequent autumn peaks based on the slow mean field growth rates estimated (more details about life cycle in manuscript 3).

Validation of IGR and Perger and Temming methods with data from both sexes and different temperatures

The instantaneous growth method (*IGR*) has been used for brown shrimp *C. crangon* for the first time to determine *in situ* growth component (moult increments and intermoult periods). In principle, the method appears valid for males and females and our study has indicated that there are considerable variations in the growth rate, as measured by the IGR, with size class, sex, food quality and seasonal effects.

The results, however, agree with estimates of brown shrimp *C. crangon* growth determined by different techniques and show patterns, e.g. faster growth by smaller individual, which, however, are predictable from other studies.

We also evaluated the method established by Perger and Temming (2012), as an extension for IGR method, based on dry weight for females exclusively and, additionally, we have used same model to estimate the increments for males as well as females which is, however, the first practical application of the new method with taking into consideration accurate length measurements (as suggested by Perger and Temming, 2012) which, however, standardized using digital images via camera system, especially established for the present work in a way that length measurement can be repeated later whenever needed. We fixed the time to measure the dry weight to be 6 h-period directly after moult to minimize the dry weight variations biased.

By applying the method established by Perger and Temming (2012), 65 % and 89 % of the variance in the observed increments could be explained with the model using length and dry weight of the shrimp before moult. We have restricted the analysis to data from temperatures between 18.8 and 22.3°C, which was closest to the 18°C in Perger and Temmings study (Figure 2.3). Meanwhile, when using the data from cold temperature between 7.3 t0 15.9 °C, 24.2% and 92.6% of the variance (r^2) was explained.

However, our findings clearly indicating that:

- The need to repeat the measurements annually (length and dry weight) when using Perger and Temming method; our exponent for females is lower than the one in Perger and Temming (2012) results to smaller moult increments when using their exponent in our data,
- We can use the same equation with females even with cold temperature (considering that results based on few data) that 92% of the variance was described,

- Males have different equation due to different body proportions at the same size in comparison with females as will as the data were more scattered (Figure 2.3a and 2.4a) due to their body composition (see manuscript 4), maturity (males become mature at smaller size than females) and
- The share of exuviae is comparable; 17.3±2.3 % and 16.8% for present study and Perger and Temming (2012) respectively.

In summery, the instantaneous growth method (*IGR*) has been used for brown shrimp *C. crangon* for the first time to determine the growth component. In principle, the method appears valid for males and females and our study has indicated that there is considerable variation in the growth rate with size, sex and seasonal effects. The results agree with estimates of brown shrimp *C. crangon* growth determined by different techniques and show consistent patterns, e.g. faster growth by smaller individual at warm temperatures, better growth of females compared to males and seem to confirm the cohort effect that Hufnagl and Temming (2011a).

Practical application for the new method established by Perger and Temming (2012) indicating that further work needed including a wide range of sizes at different maturity stages of brown shrimp *C. crangon* from different populations and could be coupled with measurements of the available food supply and of the physiological condition (temperature preferences) of the brown shrimps. Also the need to apply the method with year around frozen samples is also required.

Table 2.1: Experimental conditions, total numbers of brown shrimp *C. crangon* incubated and numbers of males and females reared and moulted under controlled laboratory conditions for 2 days moult experiment during 2010, laboratory temperature during the incubation period was same as field temperature ±0.5 °C. Date of capture is the started date for the experiment. *N* is shrimp numbers.

Experiment	Date	Field temperature °C	Total *N* animals	Total *N* moulted	*N* male	*N* female
EX1	15.06.10	15,9	122	9		9
EX2	19.06.10	14,7	123	17	9	8
EX3	23.07.10	22,3	82	19	11	8
EX4	27.07.10	20,2	128	9	7	2
EX5	31.07.10	18,8	131	13	8	5
EX6	03.08.10	19,4	133	34	24	10
EX7	06.08.10	19,3	137	38	26	12
EX8	11.08.10	20,2	137	16	12	4
EX9	14.08.10	21,3	137	40	26	14
EX10	17.08.10	21,3	137	35	27	8
EX11	21.08.10	19,8	63	10	4	6
EX12	15.10.10	11,9	144	7	3	4
EX13	25.10.10	7,7	137			
EX14	02.11.10	9,4	151	5	1	4
EX15	10.11.10	7,3	144			

Table 2.2: Mean total length (*L1*, mm) per size class and numbers of males and females that moulted during the success 13 moult experiments for males and females brown shrimp *C. crangon* during 2010. *N* is the shrimp numbers.

Size class	**20.0-24.9 mm**				**25.0-29.9 mm**				**30.0-34.9 mm**				**35.0-39.9 mm**				**40.0-44.9 mm**				**45.0-49.9 mm**				**50.0-54.9 mm**	
Sex	**Male**		**Female**		**Male**		**Female**		**Male**		**Female**		**Male**		**Female**		**Male**		**Female**		**Male**		**Female**		**Female**	
Experiment	***N***	***L1***	***N***	***L1***	***N***	***L1***	***N***	***L1***	***N***	***L1***	***N***	***L1***	***N***	***L1***	***N***	***L1***	***N***	***L1***	***N***	***L1***	***N***	***L1***	***No***	***L1***	***N***	***L1***
EX1											2	32.1							3	44.1			3	47.0	1	50.7
EX2					3	28.8			3	33.2			2	38.0	1	35.3	1	42.9					6	46.4	1	53.6
EX3	1	24.9			6	27.4	1	29.5	3	32.7	4	31.2	1	35.6	2	36.9			1	44.5						
EX4	3	23.2			2	27.0	2	27.0	2	32.4																
EX5					7	27.8	1	25.0	1	34.9	1	30.2			1	36.9			1	40.3			1	48.7		
EX6					10	27.4	1	28.2	9	31.4	1	30.5	4	37.2	3	36.5	1	43.3	2	44.5			2	45.6	1	52.6
EX7	5	23.5			13	26.7	5	27.0	7	31.4	5	31.7	1	37.6					2	41.2						
EX8					8	27.1	1	29.0	3	31.9	1	33.1	1	35.8	2	35.7										
EX9	2	23.4	1	24.7	14	27.6	4	27.5	6	32.0	5	31.9	1	37.0	2	35.6	3	44.6	2	40.0						
EX10	2	23.2			6	27.9	1	26.2	12	32.3	4	31.6	4	38.2	2	37.8	1	41.9	1	40.2	2	46.8				
EX11	1	24.9			1	28.3	2	29.6	2	31.7	3	30.7														
EX12									1	32.8	2	31.8	2	38.5	2	37.7										
EX14					1	29.9					1	34.4			1	39.8			1	41.7						

Table 2.3: *In situ* growth rate components (*Obs_INC*, mm and *IMP*, day) and subsequent growth rates (*GR*, mm/day) and numbers of males and females brown shrimp that moulted during the experiments in 2010 within 2 days incubation period using *IGR* method.

Size class	**20 mm**								**30 mm**								**40 mm**								**50 mm**			
Sex	**Male**				**Female**				**Male**				**Female**				**Male**				**Female**				**Female**			
Date	***INC***	***IMP***	***GR***	***N***	***INC***	***IMP***	***GR***	***N***	***INC***	***IMP***	***GR***	***N***	***INC***	***IMP***	***GR***	***N***	***INC***	***IMP***	***GR***	***N***	***INC***	***IMP***	***GR***	***N***	***INC***	***IMP***	***GR***	***N***
15.06.2010													2.37	16	0.14	5					2.21	23	0.10	3	0.88	29	0.03	1
19.06.2010	3.34	14	0.24	3					2.86	18	0.16	5	2.62	18	0.14	1	0.68	24	0.03	1	2.94	27	0.11	6	2.97	31	0.10	1
23.07.2010	2.39	6	0.41	7	1.36	5	0.26	1	1.70	8	0.22	4	6.28	8	0.76	3					2.96	12	0.25	4				
27.07.2010	2.06	6	0.33	5					2.26	9	0.24	2	0.99	8	0.12	1					1.73	16	0.11	1				
31.07.2010	1.74	9	0.20	7	1.29	8	0.15	2	2.28	12	0.19	1	1.48	10	0.15	2					2.05	15	0.14	1				
03.08.2010	1.24	8	0.15	9	0.78	8	0.10	2	1.70	11	0.16	12	1.65	11	0.16	5	2.81	15	0.19	1	1.60	15	0.11	1	1.34	20	0.07	1
06.08.2010	1.20	7	0.16	17	1.56	9	0.18	3	1.46	10	0.15	7	1.29	11	0.11	5					2.23	16	0.14	4				
11.08.2010	1.09	7	0.15	8	1.96	8	0.26	3	1.32	10	0.14	4	0.92	11	0.09	1												
14.08.2010	1.17	7	0.18	16	0.94	7	0.14	5	1.41	9	0.16	7	0.93	9	0.11	7	1.62	13	0.12	3	0.65	11	0.06	1				
17.08.2010	0.70	6	0.11	9	1.15	6	0.18	2	0.66	9	0.08	15	0.76	9	0.09	4	1.24	13	0.09	3	0.53	11	0.05	1				
21.08.2010	2.09	7	0.31	1	2.09	9	0.24	1	2.17	11	0.22	3	1.36	10	0.15	4												
15.10.2010	3.13	20	0.16	1					1.21	24	0.05	2	3.08	24	0.13	3												
02.11.2010	1.43	21	0.07	1									1.17	27	0.04	2					2.41	44	0.05	1				

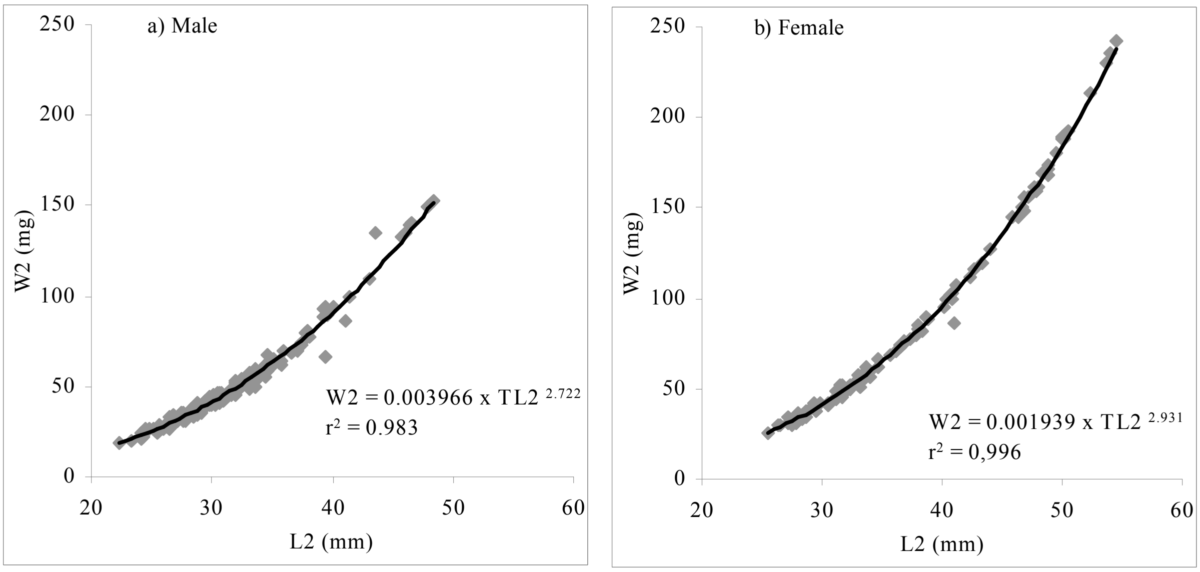

Figure 2.1: *L2*-*W2* relationships for moulted males (a) and moulted females (b) brown shrimp *C. crangon*. Each circle represents an individual.

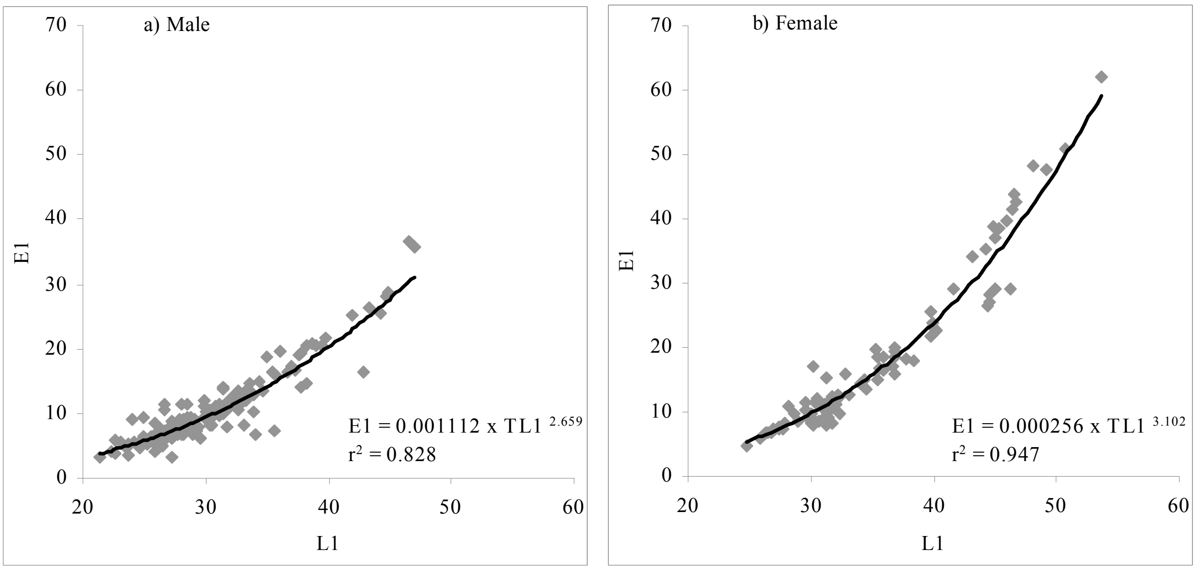

Figure 2.2: *L1*-*E1* relationship for moulted males (a) and moulted females (b) brown shrimp *C. crangon*. Each circle represents an individual.

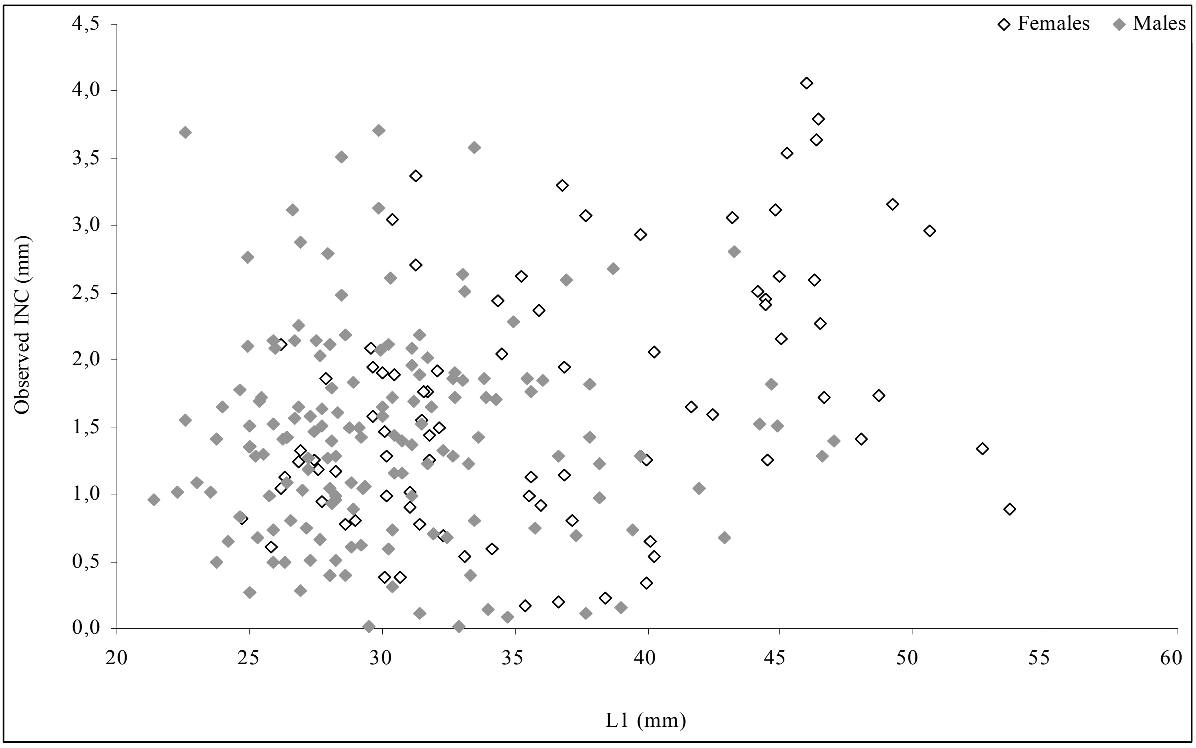

Figure 2.3: Observed moult increments of males and females brown shrimp *C. crangon* immediately after moult in relation to total length *L1* (mm). Each point represents an individual.

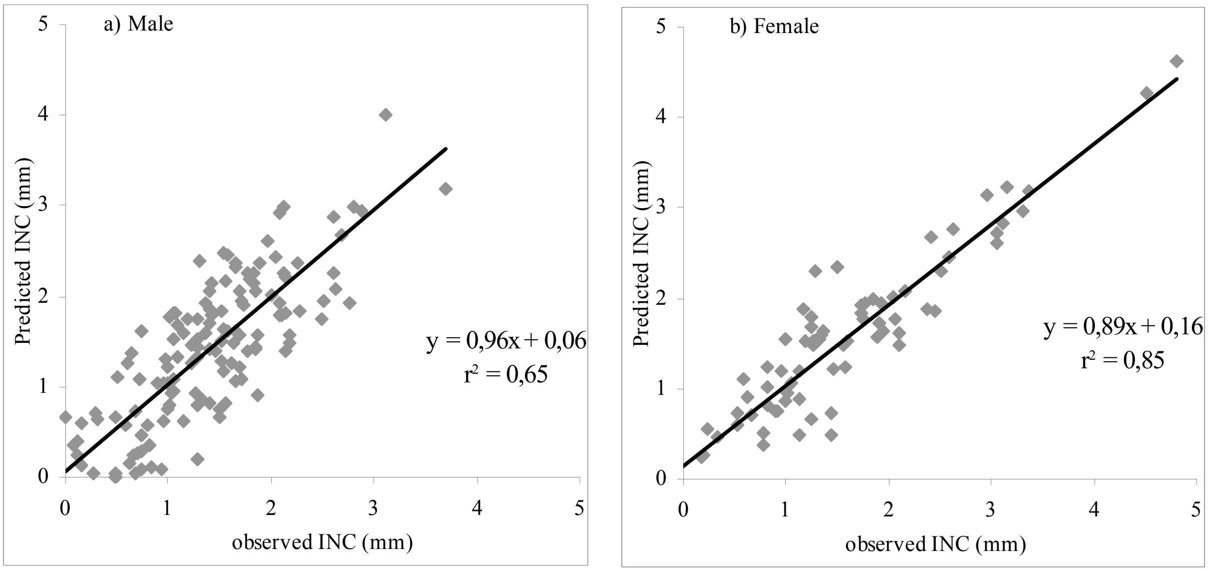

Figure 2.4: Regression of predicted increments on observed increments with warm temperatures (from 18.8 to 22.3 °C) of males (a) and females (b) *C. crangon*. Each circle represents an individual.

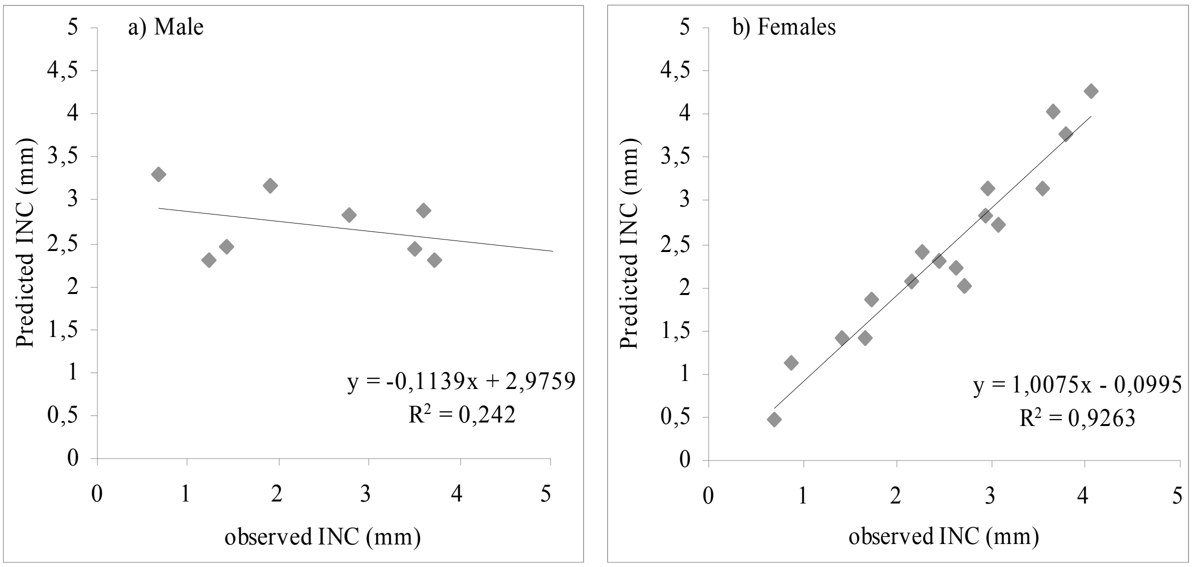

Figure 2.5: Regression of predicted increments on observed increments for cold temperatures (9.4, 14.7 and 15.9 °C) of males (a) and females (b) *C. crangon*. Each circle represents an individual.

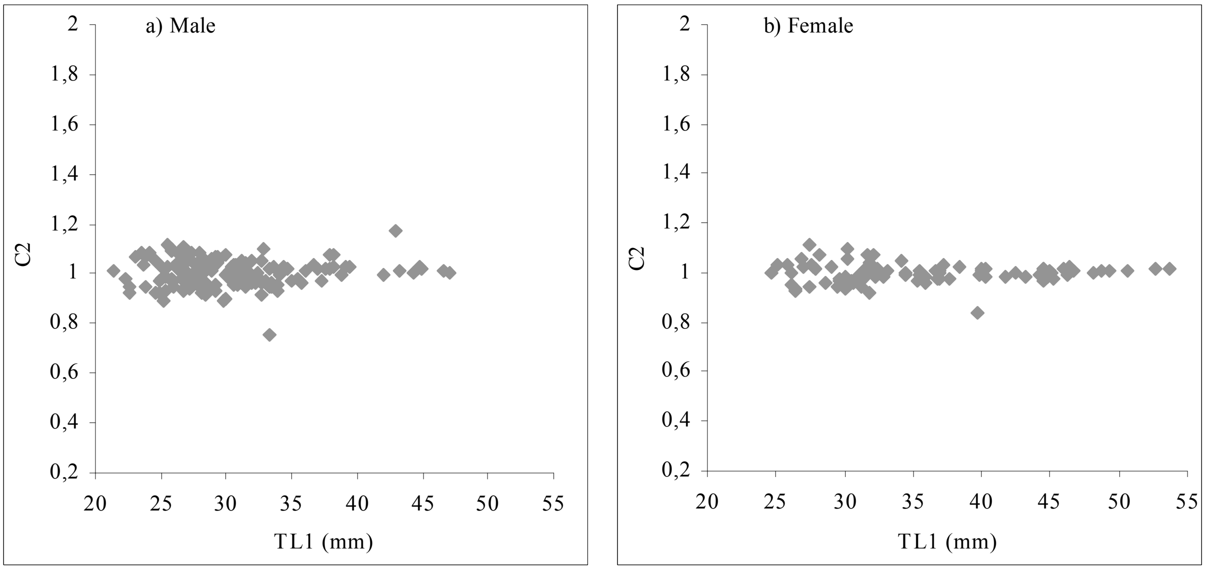

Figure 2.6: Dry weight condition (*C2*) of brown shrimp *C. crangon* directly after moulted under laboratory condition estimated from the constants presented in equation 8, where *a* = 0.003966 and *b* = 2.722 for males and *a* = 0.001939 and *b* = 2.931 for females.

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MANUSCRIPT 3

Observations on the population structure and growth of the shrimp *Crangon crangon* (L.).

Abstract

Extensively sampling, all year around from April to November, 2010 was conducted to contrast the laboratory growth parameters estimated based on both IGR and Perger and Temming (2012) methods with field growth inferred nutritional condition. Also we examined the morphological relationships between males and females of the Wadden Sea. In general and in contrast with summer 2010, except when new recruits have been arrived, poor growth condition observed in spring (beginning of sampling) as well as in autumn during (end of sampling), indicating better nutritional situation during summer. On the other hand, all the comparisons between the observed and expected distribution clearly suggested a short residence time; larger shrimps had left after period of two to 3 weeks to deeper water zone. The immigration of smaller individuals and emigration of larger individuals could be demonstrated during the study period.

Introduction

The common or brown shrimp *Crangon crangon* L. is an abundant epibenthic crustacean distributed over entire Atlantic coastal range from Norway to Morocco and throughout the Mediterranean and Black Seas. It especially favours shallow coastal and estuarine waters with sandy or muddy bottoms (Tiews, 1970).

Besides a key ecological role in costal ecosystems as prey species (Pihl, 1985; Henderson et al., 1992; Del Norte-Campos and Temming, 1994; Walter and Becker, 1997) and as predator (Pihl and Rosenberg, 1984; Van der Veer et al., 1991; Oh et al., 2001; Amara and Paul, 2003), brown shrimp is commercially exploited, especially in the North Sea.

As for other fishery resources, successful stock management requires knowledge of the population structure (Cadrin, 2000). In population structure, length is the basic measurement used to describe size and therefore, growth. Due to temperature preferences, previous studies suggest that different life stages prefer different water depth and that seasonal migration patterns are therefore also related to size (Lloyd and Yonge, 1947; Boddeke, 1976; Spaargaren, 2000).

Seasonal migrations occur in two distinct periods: autumn and spring migrations. Autumn migration is also called autumn-winter (Boddeke, 1976) and winter migration (Lloyd and Yonge, 1947). When waters start to be warmer in spring shrimps migrate inshore from deeper waters and autumn migration takes place usually in October when sea water has passed its annual temperature maximum (Boddeke, 1976). Moreover, such migration patterns are also connected to life cycle. Larvae are transported to shallow areas where the where they immigrate as early juveniles into the shallow intertidal waters of the Wadden Sea. The first immigration waves of 10–20 mm juveniles occur typically in mid June (Temming and Damm, 2002). The juveniles grow rapidly and move gradually offshore to deeper waters. During this period shrimp mature and are believed to move to even deeper off shore waters for spawning in winter (Hufnagl and Temming, 2011b).

This transition of new cohorts of growing juveniles through the different habitats in the Wadden Sea, namely shallow intertidal flats, small channels and deeper channels has been described earlier by Kuipers and Dapper (1981) and Del-Norte Campos and Temming (1998). In most studies the youngest juveniles between 5 and 15 mm have only been found in samples from the shallow intertidal flats (Temming and Damm, 2002). These can be found as early as

May and the shift of this peak can be tracked until June and sometimes even further until July. However, already in July new recruits of the smallest size may enter in a second wave the shallow intertidal areas. The peaks are often difficult to follow due to the transition from shallow to deep, but also possibly due to both sexes growing with different growth rates. With the aim to optimally resolve these immigration waves in this study a position at intermediate depth (shallow channel) was investigated with a high frequency of sampling dates. Furthermore and in contrast to all previous studies, the sexes were separated in all samples.

Perger and Temming (2012) suggested a new method as an extension of the instantaneous growth rate (IGR) assuming that the dry weight of an individual before the moulted represents the cumulative food intake of previous intermoult period. Perger and Temming (2012) applied the method on brown shrimp to estimate growth increments from *in situ* dry weight condition data. Their finding supported the idea of a standardized dry weight condition after moult that is adjusted during the moulting process by the regulated water absorptions, resulting in a length increase that is proportional to the accumulated dry weight. In Manuscript 2 we have verified that the new method can be used in both females and males to predict the observed increment from dry weight condition prior to moult. Therefore in this paper the aim was to apply the established equations to dry weight condition data from field caught shrimp, using two methods presented by Perger and Temming (2012). These data should complement the information from the repeated analysis of the sex specific size distributions.

Hufnagl et al. (2010) presented evidence higher shares of starving shrimp in field samples from the Wadden Sea. This analysis was based on dry weight conditions of shrimps after different starvation times under laboratory conditions. A weak point of this approach might have been the somewhat undefined initial condition of the shrimp in these starvation experiments. The method of Perger and Temming (2012) produces as a by-product a well defined reference dry weight condition (*C1* in Manuscript 2), which represents the lowest pre-moult condition of an individual, that had subsequently moulted, typically with a zero increment. Applying this criterion to the field sampled dry weight conditions allows a consistent analysis of the variable shares of starving individuals in different seasons and size classes.

To summarise, the main objectives of this study are:

(a) The analysis of the seasonal development of the population size structure for both sexes with a focus on immigration and emigration patterns,

(b) The application of Perger and Temmings *in situ* growth estimation method to seasonally resolved data of all size classes and both sexes and

(c) The identification of the share of starving individual.

Materials and methods

Collecting area and sampling

Live brown shrimps were collected using a push net from the Wadden Sea off Büsum (54° 07' N and 08° 51' E) at about 10 to 100 cm water depth during low tide. Sampling time was limited to maximum 10 min to minimize stress and damage of captured shrimps (Gamito and Cabral, 2003). Net dimensions were 1.44 m width and 23 cm height with 1.8 mm mesh size. Brown shrimp *C. crangon* collected at temperatures of 7.3 °C to 22.3 °C (Table 3.1). Samples were taken over eight months every 1-3 weeks from April, 2010 to November, 2010 depending on weather condition (Table 3.1). Per each sample date, subsample of shrimps were placed in a plastic bag (400 to 600 g/bag) and immediately transferred to Institute for Hydrobiology and Fisheries Science (IHF), Hamburg, Germany on dry-ice where the measurements were carried out. This technique was used to overcome biochemical changes (autolysis) through enzymatic decomposition of tissues (Mukundan et al., 1986; Schubring, 2002).

Morphometric measurements and Abundance

Samples were defrosted and only individual shrimp with complete rostrum have been manually straightened on millimetre paper (to remove the natural curvature of shrimp body). The measurements were defined (Figure 3.1) as follows:

- Total length (*TL*), from tip of the rostrum to the end of the telson.
- Carapace length (*CL*), distance from the posterior margin of orbit to the posterior edge of the carapace.
- Carapace width (*CW*), greatest width of the point of last dorsal rostral tooth.

To avoid bias due to measuring as well as more accurate procedures, individual lengths were measured to the nearest 0.1 mm applying a Matlab routine (The Math works, Inc., Natick, MA) using a USB camera (UI-1485LE 2560 x 1920 pixels) equipped with a Pentax C3516-M lens. Male and female shrimps were distinguished on the basis of external characteristics of the first pleopod (presence or absence of the appendix masculine (Lloyd and Yonge, 1947). Shrimp were then immediately freeze-dried for 24 h and weight was determined to the nearest 0.1 mg (*DW* mg) by electronic digital balance (Satorius ± 0.0001g).

Application of the Perger and Temming method to field data

Dry weight condition index (*CI*)

Dry weight condition ($C1$) for males and females separately was calculated as:

$$C1 = W1 / (a \times L1^{b}) \tag{1}$$

Then compared with the minimum $C1$ estimated for males ($C1\_MIN = 1.127$) and for females ($C1\_MIN = 1.148$) from laboratory experiments (manuscript 2).

Moult increment (*INC*, mm)

The predicted increment (INC) was determined as:

$$INC = ((W1 - E1) / a)^{1/b} - L1 \tag{2}$$

The calculations have been based on the constants derived from the moult experiments (for more details see moult experiments manuscript) which were:

For males: $W2 = 0.003966 \times L2^{2.722}$ (3)
with $r^2 = 0.983$

For females: $W2 = 0.001939 \times L2^{2.931}$ (4)
with $r^2 = 0.996$

while $W2$ defined as: $W2 = W1 - E1$ (5)
and the $L1$ - exuviae dry weight ($E1$) relationships were:

For males: $E1 = 0.001112 \times L1^{2.659}$ (6)
with $r^2 = 0.828$

For females: $E1 = 0.000256 \times L1^{3.102}$ (7)
with $r^2 = 0.947$

Intermoult period (*IMP*)

The estimated intermoult period (IMP) was determined based on the following nonlinear regression equation as:

$$IMP = 0.59796 \times L1^{1.3851} \times e^{-0.10232 \times T} \quad (8)$$

with $r^2 = 0.943$

where IMP in days, $L1$ in mm and T in °C.

The calculations have been based on the constants derived from the moult experiments (Equation 13 in manuscript2) for sexes combined.

Growth rate (*GR*)

Growth rates were estimated for each individual, sexes separated, based on both estimated moult increment (INC) and intermoult period (IMP) as:

$$GR = INC / IMP \quad (9)$$

where GR in mm/day, INC in mm and IMP in days.

Results

Size distribution

Length frequency distributions of brown shrimp *C. crangon* for the whole study area were expressed as relative portion of males and females in each 1-mm, 5-mm and 10-mm length class and also as numbers per 1-mm and 5-mm size class per 100 m^2 fished area for both males and females in the Wadden Sea off Büsum area for all combined and separated size classes.

Overall, total number of individuals analysed for this study was12430 individuals (Table 3.1), females dominated the catch with 56.2% (6986 individuals) while 43.8% were males with 5444 individuals.

Males were on average smaller (*TL* ranged from10.7 mm to 54.7 mm) than females (*TL* ranged from 12.2 mm to 78.0 mm), the mean *TL* was 30.4 ± 6.3 mm (± sd) and 35.5 ± 7.9 mm (± sd) for male and female shrimps, respectively. The mean *TL* of female shrimps was 5.1 mm longer than that of male shrimps (Table 3.1 and Figure 3.2).

A marked dramatically decrease in the mean total body size is firstly observed in June 15th; when mean *TL* dropped from 35.85 ±4.10 mm in June 3rd to 27.69± 6.77 mm in June 15th for males (Table .1 and Figure 3.3a) and from 43.70 ± 6.02 mm in June 3rd to 38.47 ± 9.78 mm in June 15th for females (Figure 3.3b). While the lowest mean *TL* for males was observed in July 15th with 24.44 ± 4.86 mm, the smallest mean *TL* for females was recorded about two weeks earlier (June 29th) with 26.68 ± 4.74 mm. A higher mean *TL* was observed in June 3rd and September 9th with mean *TL* of approximately 37.0 mm and 44.0 mm for males and females respectively (Table 3.1).

In the present study, the ratio between *CW*:*TL* were plotted on *TL* to investigate the deference's in body proportion between males and females, males and females grew constantly up to 26 mm *TL* (Figure 3.8). In contrast and when mean *CW*:*TL* ratio plotted on *TL*, the ratio is decreased in males but remained constant in females until point (34-35 mm) which the abdomen suddenly broadened (Figure 3.9) which is, however, indicating morphological shift between small and larger females.

The overall the relative portion of all males and females (all sampling dates combined) showed that the males dominated the smaller length classes with 64, 83, 62, 54 % for 15, 20, 25, 30 mm respectively while the females dominate the bigger length classes with 52, 61, 79, 92, 96 and 100% for 35, 40, 45, 50, 55 and 60 mm respectively (Figure 3.4 and Figure 3.5). Males and females of smallest size class (10 mm) have not been observed in the majority of the samples, specifically between April 30th until June 3rd and again from September 9th until November 2nd (Figure 3.5).

The overall mean *DW* (all sizes and sampling dates combined) of female shrimps was 50% heavier than that of male shrimps; the mean *DW* was 53.8 ± 30.8 mg and 101.0 ± 78.1 mg for male and female shrimps, respectively. Minimum and maximum male *DW*s were 4.5 mg and 250.9 mg and 4.6 mg and 1057.0 mg for female shrimps, respectively (Table 3.1). However, when data were separated according to sampling dates and size classes (Figure 3.6), the results clearly reveal that the small males and females in size classes 10 and 20 mm have the same mean *DW* (at the same length) regardless of season. In contrast, with increasing length the *DW* of females progressively exceeds that of males in the same size class reaching up to 150% of male dry weight in the 50 mm size class (Figure 3.6). It should be noted that the standard deviations (± sd) of means *DW* were not included in Figure (3.6) for better visualization and these can found in Table (3.2).

Morphometric characteristics

Specimens from all sampling dates were pooled by sex to determine relationships between *TL-DW*, *CL-TL* and *CL-CW*. The morphometric relationships equations computed for 5444 males and 6986 females as:

TL-DW relationships

For males: $DW = 0.003433\ TL^{2.7982\ (\pm 0.031)}$ (8)

with $r^2 = 0.962$

For female: $DW = 0.000950\ TL^{3.1909\ (\pm 0.029)}$ (9)

with $r^2 = 0.926$

***CL-TL* relationships**

For male: $TL = 4.8123\, CL^{1.0131\ (\pm 0.004)}$ (10)
with $r^2 = 0.953$

For female: $TL = 5.4909\, CL^{0.9367\ (\pm 0.006)}$ (11)
with $r^2 = 0.977$

***CL-CW* relationships**

For male: $CW = 0.7829\, CL^{0.9332\ (\pm 0.013)}$ (12)
with $r^2 = 0.950$

For female: $CW = 0.7030\, CL^{1.0021\ (\pm 0.007)}$ (13)
with $r^2 = 0.959$

TL-DW regression for males and females were significant (Kolmogorov-Smirnov test, $p<0.001$) and slopes significantly were differed between sexes. Females were increasingly heavier than males with growing *TL* (Figure 3.7).

Regressions of *TL* on *CL* were significant ($p<0.001$) for both sexes, total length scaled isometrically to *CL* in males and negatively in females (Figure 3.8). It shows that males body proportion change constantly (*CL*:*TL* ratio) but increased in females, i.e., in large females the *CL* (abdomen) were relatively shorter in comparison with the small one.
In contrast, the *CW*:*CL* ratio is decreased in males but remained constant in females until point which the abdomen suddenly broadened (Figure 3.9), indicating morphological shift between immature and mature females.

Sex ratio and abundance

The annual sex ratio of *C. crangon* showed temporal variations in the present study (Figure 3.10). In April 2010 the male: female ratio was close to 1:1, but in mid May, June and July 2010 significant bias toward females was observed in the larger size class (> 35 mm); male percentage dropped to about 25-35%. In August 2010 the sex ratio again showed 1:1 ratio. While the female fraction dominated the catch in September (76%), in October and November 2010 the male percentages were 50-56% (Figure 3.10).

Separating sex ratio by sampling date (Figure 3.11) shows that the length frequency distributions of both males and females have a strong peak in the 30 mm length class in the first sampling date (April 6th) until May 24th. While males brown shrimp still have their peak in the 30 mm length class on the June 3rd, meanwhile the female's peak was shifted toward 40 mm. New waves of smaller animals (males and females) started to invade the studied area with strong peak in the 20 mm size class on June 15th. Meanwhile, larger females (40 mm) still occupy the shallow water and males started to move to deeper water area on June 15th (Figure 3.11; 15.06.2010) and peaks are again shifted toward 30 mm size class. However, a skewed sex ratio in favour of females is observed all year around (2010) except on the sampling dates April 21st, June 3rd, August 17th and October 25th where males shrimp were dominated in the smaller (up to 30 mm) size classes (Figure 3.11).

The abundance of *C. crangon* was relatively low in the first half of the year (from April to June 2010). The highest abundance observed was 17.4 ind/m^2 in October (02.10.2010) while the lowest abundance recorded in the present study in April (06.04.2010) was 0.4 ind/m^2 (Table 3.1 and Figure 3.12; all size classes). While the small shrimps started in invade the area, with rise the temperature surface, the abundance also started to be increased about 3 times (Table 3.1) with first immigration wave between June 3rd and June 15th. The recruitment period of small shrimps (< 20 mm size class) in late July and September likewise corresponded to an increase in density in October (26.5 ind/m^2).

Application of the Perger and Temming method to field data

Predicted moult increment (INC): For each size classes and sampling date, field increments (*INC*, mm) determined as: (a) twice the mean of positive potential increments and (b) the intercept of the regression of potential increments on rank numbers as described by Perger and Temming (2012) and represents in Table (3.3 and 3.4) and Figure (3.14). As general pattern, mean *INC* of small shrimps (10 and 20 mm) was comparable while the mean *INC* of larger females was increased twice or even 3 times than males (Figure 3.14). For example, in 10 mm length class males have mean moult increment of 0.92 mm while females have 1.02 mm on July 23rd. Likewise on April 30th, males in 20 mm length have mean moult increment of 0.91 mm and females have 0.98. In contrast, male have mean moult increment of 0.99 mm on April 21st in 30 mm size class while females have twice mean moult increment than males with 1.88 mm at same date and size class. As in 30 mm length class, females reach mean of 2.83 mm moult increment while males have 0.26 mm at 40 mm length class in April 21st.

The potential increments calculated based on both methods were not identical. In general, the potential increments calculated by method (a) were larger than the calculated based on method b (Table 3.4). When applying method b to estimate the potential increments, we had negative increments at 40 and 50 mm length class with -0.14 and -0.74 mm respectively while the values in method a was 0.16 mm for the same length class. However such negative potential increments were not surprising due to the different way to estimate the potential between both methods as described by Perger and Temming (2012).

Predicted intermoult period (IMP): in the present study *IMP* (day) were calculated based on the parameters obtained from previous moult experiments (in manuscript 2) for sex combined, the following results were estimated to estimate the subsequent (*GR*) for both males and females. For males, the minimum mean intermoult periods (6-8 days) were observed in 10 mm size class between June 29th and July 31st while the temperature ranged between 18.8 to 22.3 °C, which is highest temperature measured in the field while the longest observed *IMP* was 39 day (April 21st) at the lowest temperature measured when males moulted (8.8 °C) but with larger size class (40 mm).
Similar patterns were observed for females, the shortest intermoult periods (5-7 days) were observed in 10 mm size class between June 29th and August 17th while the temperature ranged between 18.8 to 22.3 °C while the longest observed *IMP* was 60 day (November 10th) at the lowest temperature measured when females moulted (7.3 °C) but with 60 mm length (Table 3.5).

Estimated growth rate (GR): The corresponding mean growth rate (*GR*, mm/day) were estimated separately based on the *IMP* for both sexes combined and the potential increments based on method b, which was being more reliable (Perger and Temming, 2012), for each individual male and female separated. Again, it should be noted that both *IMP* and *INC* were calculated based on the parameters estimated as described in results method while more details in manuscript 2. So far, the minimum mean growth rate estimated for males was 0.01 mm/day mainly at 40 mm size class in the all sampling dates; individual males number varied between one individual in late July to 69 males in April 21st, while the maximum estimated was 0.32 mm/day at 10 mm length associated with 9.8 °C (May 14th). For females, growth rates was generally higher than in males with minimum of 0.02 mm/day at 60 mm length with 22.0 °C (July 15th) and a maximum mean value of 0.64 mm/day in July 15th which also associated with high temperature as 22.0 °C at 60 mm size class. As general pattern for both male and female brown shrimp, growth rates were lower in samples before June 15th and those taken in later summer than in samples of late spring and early summer.

Mean *GR*s (mm/day) in the present study were obviously fluctuated between different season as well as when new recruitments invade the studied area. For example, in spring and until first new recruitment observed on June 15th (samples between April 06th and June 15th), low mean growth rates were estimated (0.05, 0.09 and 0.06 mm) associated with longer *IMP* for males in 10 mm size class (Table 3.6). With increasing water temperature from 16.0 to 21.0 °C and the first new waves arrived, mean growth rates becomes twice than before; from 0.06 to be 0.14 next sampling date and achieving 0.32 mm with increasing individuals numbers (5, 30 and 128) in June 15th, June 29th and July 15th respectively. However, exactly similar patterns were observed for females brown shrimp at same sampling dates, same length class and temperatures. So far, similar trends can be seen in autumn for both males and females (Tables 3.4, 3.5 and 3.6).

In general and with increasing the size of both males and females, growth rates of females were almost twice or even 3 times than in males e.g. *GR* values in 20 mm length were 0.13 and 0.26 while in 30 mm size class values were 0.11 and 0.43 to achieve *GR* value of 0.50 in 40 mm length in June 29th for males and females respectively. Interesting observations that the higher mean growth values were associated with larger individual (30+ mm size class) females (Table 3.6).

Estimated dry weight condition (C1): For both males and females brown shrimp *C. crangon C1* was determined and compared with the *C1_MIN* and presented in Figure (3.13). In general, *C1* for both males and females varied not only between sampling date but also between size classes. For male brown shrimp, poor conditions were observed in the small size classes (10, 20 and 30 mm) during the first 4 sampling dates (April 06th, April 21st, April 30th and May 14th) as well as the last sampling date (November 10th) where minimum temperature measured with 9.0, 8.8, 12.3, 9.8 and 7.3 °C (Table 3.1). In addition, bad conditions have been also observed on July 15th where males have smallest *TL* with average of 24.44±4.86 mm; a newly incoming cohort of very small individuals arrived (Table 3.1). Generally males and females in larger size classes (40, 50 and 60 mm) have better condition except in the sampling dates May 14th and November 10th ((Figure 3.13a).

In females, the condition was generally better than in males of the same size classes and sampling dates. As in males, also females displayed poor conditions in the smallest size class (10 mm) in most sampling dates (Figure 3.13b; 10 mm). While for the 20 mm size classes, poor condition was observed on sampling dates June 03rd, July 15th and November 10th in 30 mm size class was on sampling dates July 15th and November 10th. Larger size classes (40, 50 and 60 mm) were generally in better condition than the smallest females brown shrimp (Figure 3.13b).

The overall share of individual shrimps (males and females separated into different size classes) classified as starving varied between 0.8 % in July 23rd to 100 % for males while in females varied between 1.3 % in July 31st to 100 % (Table 3.7). The portion of males classified as starving individuals estimated all year around are always higher than the one estimated for females except at small size class (10 mm) e.g. the share decreased from 53.8 to 20.0% in June 15th and June 29th directly after the new waves arrived.

Discussion

Recruitment waves and migration

Two distinct migration periods have been identified; autumn and spring migrations (Lloyd and Yonge, 1947; Boddeke, 1976). The seasonal migrations are believed to be related to differential developments in the shallow and deep waters temperature (Boddeke, 1976; Lloyd and Yonge, 1947). When shallow waters start to warm in spring shrimps migrate inshore from deeper waters and autumn migration takes place usually in October when coastal waters are rapidly cooling (Boddeke, 1976). This migration pattern is also connected to life cycle. Adult egg bearing females are usually found in deeper off shore waters, especially in winter, larvae are therefore released in deeper off shore waters. Subsequently larvae are transported by water currents to shallow areas where the juveniles grow up (Boddeke, 1976). The larvae from winter egg production reach according to Temming and Damm (2002) the intertidal Wadden Sea areas in middle June.

In the present study the pronounced decrease in the mean total length of the field samples (Figure 3.3) clearly revealed that a first immigration of new recruits occurred in late spring (between June 03rd and June 15th) while a second wave was recorded at 23rd of July. These dates correspond well with findings from earlier studies summarized in Temming and Damm (2002).

The first new wave which takes place before July 15th probably originates from the winter egg production as suggested by Temming and Damm (2002), while the second wave might originate from the first spring spawning events.. Temming and Damm (2002) developed and utilized an individual based model to investigate the relationship between the seasonal occurrence of juvenile immigration waves and the seasonal egg production. Their results indicated that the spring recruitment is related to winter egg production, with timing determined by winter water temperatures. Temming and Damm's (2002) model predicted the juvenile recruitment with time lag of about 3-6 weeks. The authors speculated that the deviation might be explained by ambient temperature experienced by the eggs and the larvae, which deviated from those assumed in the model. Daewel et al. (2011) later evaluated this hypothesis with a combined analysis of drift and temperature dependent development of larvae and juveniles. The results confirmed that a drift from warmer Dutch waters plays a significant role for the winter eggs and helps to explain the observed time lag between data and observations.

Janssen and Kuipers (1980) and Kuipers and Dapper (1981) showed that juveniles leave the tidal flats and invade the sub-tidal area at a length of 25-35 mm and significant number of juveniles leave the shallow intertidal in the beginning of July. Since our study area was located at an intermediate depth, the youngest juveniles between 5 and 25 mm were not consistently observed. Del Norte Campos and Temming (1998) analysed simultaneously very shallow tidal flat stations and tidal channel stations similar to the station of the present study. In their data both the recruitment of smaller shrimp and the subsequent shift of the youngest shrimp to the channels was evident.

We were able, based on the 1 mm total length frequency distributions, to identify a clear emigration pattern of larger shrimp (>40 mm) which were present between April and June, but then suddenly disappeared between the 15th and the 29th of June, at the same time when the first recruitment wave entered the area(Figure 3.16). These emigrating shrimps were mostly females, which are growing into the size of maturation and most likely participate in later summer spawning. In later months no clear emigration patterns are obvious, the somewhat similar size distributions rather suggest a steady situation of immigration, growth and emigration (Kuipers and Dapper 1981).

Temming and Damm (2002) further speculated that the main immigration wave in late spring might be responsible for the subsequent increase in commercial landings in autumn of the same year, but provided no quantitative analysis. In the meta-analysis study by Hufnagl and Temming (2011b), growth trajectories based on mean growth rates and ambient temperatures suggest that shrimps starting with 15 mm between May and July do not reach 50 mm prior to October. While these shrimps represent the main recruitment peak that is observed each year in the shallow intertidal areas of the Wadden Sea (Temming and Damm, 2002), the predicted growth rates are insufficient to explain the peak of commercial catches in September (see Fig. 6; ICES 2010). However, the match with the catch peak is much closer if maximum growth ($G_{\max}$) from quantile regression (75th percentile of the data used for the meta-analysis) or female growth is used for the predictions. However, most of the data used for this meta-analysis originate from laboratory trials and direct evidence for the occurrence of such high growth rates under *in situ* conditions were still missing so far. In the later sections our new data on *in situ* growth will be presented and discussed in the context of the understanding of the life cycle.

Sex ratio

Our data revealed a skewed sex ratio in favour of females with increasing length class, as was found earlier (Hufnagl et al., 2011a). Such a skewed sex ratio can theoretically have a number of different causes: (a) sex changes (Boddeke, 1966), (b) differential mortality (Tiews and Schumacher, 1982; Del Norte-Campos and Temming, 1998; Hufnagl et al. 2010b) and (c) lower growth of males (Lloyd and Yonge, 1947; Hufnagl et al., 2011a).

(a) Sex changes: Due to those observed changes in the sex ratio in relation to size, speculations about a possible sex change in *C. crangon* have been expressed and many papers have been published on that matter. Boddeke (1966) suggested that *C. crangon* is a protandric hermaphrodite, thus changing sex from male to female after reaching a certain size, while others (Meixner, 1969; Tiews, 1954; Lloyd and Yonge, 1947) did not observe any sex changes in their studies. Martens and Redant (1986) and Siegel et al. (2008) concluded that sex change may occur but assumed that the percentage of males changing into secondary females would be very small and have little effect on the sex ratio which, however, supporting our results. Thus, sexual transition can be considered as uncommon pattern in *C. crangon* (Wenner, 1972; Schatte and Saborowski, 2005). Hufnagl et al. (2010a) estimated the potential maximum egg contribution by secondary females to the population to be 4% with less than 1% of the total eggs produced by one cohort of males and females of brown shrimp *C. crangon*.

(b) Mortality rates: so far, sex specific mortality in *C. crangon* has actually not been investigated is mainly due to predation (Braber and de Groot, 1973; Daan, 1973; Tiews and Schumacher, 1982; Evans 1984; Del Norte-Campos and Temming, 1998; Singh-Renton and Bromley, 1999; Jansen, 2002; Hufnagl et al., 2010b) or even cannibalism (Regnault, 1976; Evans 1984, Pihl and Rosenberg, 1984; Henderson and Homes, 1989).

At the same size class, mortality of males and females is most likely equal. However, females differ in their spatial distribution and attain larger sizes than males (Meredith, 1952).

Maximum size reported for females is 95 mm (Tiews, 1954, 1970; Heerebout 1974), while males may reach a maximum size of 75 mm (Tiews, 1970) but both are rarely attained (Kuipers and Dapper, 1981). When migration patterns of males at the same size differed from those of females this may result in a different overlaps with predators. In the present study larger females tended to leave the shallow study area earlier in the year than males, the effect on predator overlap is however difficult to assets.

(c) The present study demonstrated that also under *in situ* conditions male's growth rates are significantly lower than female's growth rates. This confirms earlier findings from laboratory work (Meixner, 1969; Campos et al., 2009b; Hufnagl and Temming, 2011a). The actual differences between both sexes (25-50%) are even higher than those found in a meta-analysis (15-20%) of Hufnagl and Temming (2011b), therefore the conclusion of Hufnagl et al. (2010) is strongly supported, that these growth differences alone are sufficient to explain the observed size trend in the sex ratio of the field samples.

Growth differences between males and females

Hufnagl and Temming (2011a and b) performed growth studies on male and female shrimps and further reviewed the available literature on brown shrimp growth. Besides these studies there are only few other studies that analyzed in detail the differences between male and female growth rates. However, in all studies that took sex specific growth into account females were growing faster than males (Meixner, 1969; Labat, 1977; Lagardère, 1982, Oh et al., 1999). If these data are jointly analyzed females were on average 20% heavier than the males. This observed growth difference is common for many shrimps (Pauly, 1982, Baelde, 1994, Mehanna, 2000, Campos and Berkeley, 2003, Kim, 2004, Ragonese et al., 2004, Sainte-Marie et al., 2006) especially for those that do not have dominating males. *Crangon crangon* most likely follows a pure searching mating tactics which means that encounters at the right time (right after a female moult) lead to mating. In pure searching systems (Correa and Thiel, 2003) males are searching their mating partners and after a short act both partners separate immediately. There is generally no intrasexual competition (male-male) therefore males in these systems are smaller than females. Additionally female fecundity is generally correlated with female size (Bauer, 2006) which is not true for males. The higher the probability for a female is to reach a larger size, the higher the reproductive output becomes. Thus there is a permanent selection against slow growing females and for fast growing ones. Hufnagl and

Temming (2011b) could show that the number of shrimps reaching size of maturity is about 5 times higher for fast than for intermediate growing shrimps and their fast growth model (for the whole population) was comparable to their female growth model. The growth rates we observed here are even higher. There might be two reasons for the difference. Either the *in situ* measured growth rates are generally higher or 2010 was and extraordinary year where shrimps in general grew faster. The latter aspect is supported by above average landings per unit effort (LPUE) observed in late 2010 and early 2011 (ICES 2012). If growth was higher this would have directly translated into a higher catchable biomass of brown shrimp in autumn which is generally dominated by female shrimps (Siegel et al., 2009).

Changing body proportions with size

While small males and female brown shrimp have the same dry weight for large females the dry weight can reach up to 150% of that of males of the same length (Figure 3.7). The positive allometric weight growth for females found in this study is in agreement with previous studies (e.g. Łapińska and Szaniawska, 2005) where females are progressively heavier at the same length (value of *b* is higher) than males with increasing total length (Oh et al., 1999). Similar patterns were reported for other crangonids e.g. *A. dentata* (Couture and Filteau, 1971), *C. septemspinosa* (Haefner, 1972), *C. nigricauda* and *C. franciscorum* (Krygier and Horton, 1975), *N. antarcticus* (Bluhm and Brey, 2001), and *Philocheras trispinosus* (Labat, 1984).

Our results of the dry weight-total length relationships of males and females revealed that females started to be heavier than males from 35 mm on. At the same total length (>35 mm) females start to develop a wider carapace (Figure 3.9), while the males show rather the opposite pattern. However, previous morphometric relationships showed a general increase in only size of females when change from immature to sexual maturity stage (> 35 mm) as reported by Wollebaek, (1908), Meyer, (1935), Meredith, (1952) and Oh and Hartnoll, (2004). If the obvious increase in carapace widths/total length proportions (Figure 3.9) in the present study is actually related to sexual maturity can, only be verified by gonad histology. However, our finding can also be related to the pronounced growth differences between the sexes, especially for the larger individuals. Higher increments can only be produced, if the animal can store larger amounts of accumulated dry weight within the exoskeleton during the inter moult periods. A change in the body proportions yielding a wider body is exactly the mechanism to achieve this.

Application of the Perger and Temming method

Large females have higher growth rates and moult increments than males

One of the most surprising results of the present work is the repeated observation of large female shrimp having higher length growth rates than smaller females at a number of sampling dates between June and August. If the directly observed moult increments in Manuscript 2 are inspected for a confirmation of this result, it can be seen that larger females actually have a tendency to produce also larger increments, a pattern that is not found in males. Such results (for the females) are contradicting the assumptions of a growth trajectory following the Bertalanffy growth function (VBGF) where length growth steadily decreases with increasing size. It can not be concluded at this point that this is a general pattern, since theoretically the feeding situation of different size classes might have been untypically different in this year. One might alternatively speculate that this growth difference reflects a general ontogenetic difference in the feeding strategy of brown shrimp. However, such assumption need to be investigated based on stomach contents for small and large brown shrimp size classes, Del-Norte Campos and Temming (1994) studied the stomach contents analysis for brown shrimp and found that smaller shrimps mainly feed on meiofauna (0-24 mm length) and with increasing size shrimps tend to change their feeding behaviour towards molluscs and crustaceans including the smaller *C. crangon*.

Dry weight condition and starving shrimps

In the present study, we have applied the results from moulting experiments (presented in manuscript 2) to parameterize the Perger and Temming (2012) model .The resulting growth rates were low in April and May and started to increase only in June, at the time when also the new recruitment wave entered the area. This might be viewed as a support of the “cohort”-hypothesis by Hufnagl and Temming (2011a) according to which the overwintering cohort has lost its potential for high growth. However, in our field data it can be seen, that the strong increase in growth rates is not restricted to the smallest individuals, but actually includes also 40 mm size class in end of June. Since this is the first data set with such information, speculation should be done with great care; nevertheless, the results indicate that there may be rather a season effect than a cohort effect, which is responsible for the pronounced differences. After August, the observed growth rates are again declining rapidly, which is mostly an effect of longer intermoult periods due to decreasing temperatures.

Over all, the share of starving brown shrimp was slightly higher in males than females to reach 35% and 32% for males and females respectively. For both males and females the share of starving individuals was high during spring season with an average of 52% and 32% while reached the lower value during summer with mean of 25 and 20% for males and females respectively. The seasonal pattern was in general inversed to that of the growth rate confirming the pronounced differences between the seasons. Furthermore, in few sampling dates we observed highly share of the starved individuals as 100%. Hufnagl et al. (2010a) evaluated the condition of *C. crangon* in the Wadden Sea under laboratory conditions during 2005-2007 found that at least 25% of the shrimp population is food-limited (poor condition) while the food limitation was most pronounced in the period November until April, where up to 75% of the population exhibited signs of starvation or food limitation. Perger and Temming (2012) found that the share of starving female shrimps during 2007 varied between 15 and 33% (June 29th and July 29th) that their dry weight conditions were lower than the lowest value observed for moulting individuals in the laboratory (lowest than 1.166) during 2007.

The repeated finding of substantial amounts of starving individuals in the same area during 2005-2007 and in 2010 (Hufnagl et al 2010, Perger and Temming 2012, this study) based on different methods, strongly supports the idea that growth conditions are not always optimal in this most important brown shrimp nursery and points at stronger density-dependent food limitation in parts of the year. However, these results, especially the long starvation trials conducted by Hufnagl et al (2010) indicate also that this species is quite adapted to coping with extended periods of food limitation.

Growth rates in comparison with other growth studies

The estimated growth components as well as subsequent growth rates results were quite similar to the results based on the *IGR* method (manuscript 2). The general pattern in both data sets was, that before the new waves of smaller individuals arrived, long intermoult period were associated with small increments resulting in poor growth. During the late spring and summer periods both methods confirmed large increments combined with short intermoult periods resulting in very high growth rates, especially for female shrimp.

For males, mean growth rates ranged between 0.01 mm/day (mainly at 40 mm size class) to 0.32 mm/day with smaller length class (10 mm at 22.3 °C). For females, growth rates ranged from 0.03 mm/day at 10 mm length (9.8 °C) to mean growth rates of 0.65 mm/day. These values confirm, that even the highest values observed in experiments, are actually occurring under *in situ* conditions. On the other hand also very low growth rates were observed in early spring and autumn, which are comparable with similar results from other studies. For example, in field studies the following estimates were found off the Isle of Man: 0.01 mm/day by Oh et al. (1999), 0.02 mm/day in the UK by Duran (1997), 0.03 mm/day in the Baltic and in Germany by Meyer (1936) and Dornheim (1939), 0.16 mm/day in France by Amara and Paul (2003), 0.23 mm/day in Germany by Del-Norte Campos and Temming (1998), 0.35-0.49 mm/day in The Netherlands by Kuipers and Dapper (1981 and 1984), Boddeke et al. (1986) and Cattrijsse et al. (1997).

In laboratory studies, the daily growth rates estimated from German waters as 0.02-0.14 mm/day (5-25 °C) by Gerlach and Schrage (1969), from France as 0.03-0.17 mm/day (115-23 °C) by Lagardère (1982), in the Isle of man 0.57 mm/day (20 °C) by Dalley 1980, and in the German Wadden Sea off Büsum 0.22-.44 mm/day (5-25 °C) by Hufnagl and Temming (2011).

The high *in situ* growth rates observed in the present study finally show that the June peak of juvenile immigrants with approximately 25 mm can actually grow to commercial size of 50 mm by September and thus support the peak of commercial landings. Since Temming and Damm (2002) and Daewel et al. (2011) have already shown, that this June peak in recruitment originates from Winter eggs, we can now also concluded that peak of the autumn fishery is mostly based on the winter egg production. This finding confirms the theories about the life cycle of Kuiper and Dapper (1984), Temming and Damm (2002) and Perger and Temming (2012). It is less clear, if Boddeke's (1976) version of the life cycle is falsified with these results. If growth rates of large females are consistently high during summer, the second wave of recruits originating from the first spring recruitment (summer eggs) may actually also contribute to the second phase of the autumn peak. In contrast, the life cycle version of Campos et al. (2010), who concluded that the summer egg production of the previous year leads to the subsequent autumn peaks, suffers from the main weakness that total mortality rates in brown shrimp are too high to allow a significant portion of these recruits to survive (Hufnagl et al., 2010).

Table 3.1: Population structure (all size classes combined) of males and females brown shrimp *C. crangon* L. in the Wadden Sea off Büsum from April to November 2010.

Sampling Date No	**Date**	***T***	**Density***	**Sex**	***N***	***TL* ± sd**	***CL* ± sd**	***CW* ± sd**	***DW* ± sd**
1	06 Apr.	9.0	0.4	Male	101	30.88 ± 5.66	6.12 ± 1.15	4.32 ± 0.76	53.33 ± 25.24
				Female	116	34.04 ± 6.73	6.89 ± 1.51	4.91 ± 1.05	80.62 ± 58.69
2	21 Apr.	8.8	1.6	Male	980	31.40 ± 6.07	6.38 ± 1.21	4.40 ± 0.79	58.17 ± 31.50
				Female	754	36.38 ± 7.11	7.51 ± 1.58	5.29 ± 1.14	102.64 ± 66.90
3	30 Apr.	12.3	0.9	Male	139	31.64 ± 5.51	6.22 ± 1.12	4.44 ± 0.72	58.95 ± 32.28
				Female	263	37.28 ± 7.80	7.57 ± 1.77	5.55 ± 1.32	115.44 ± 73.04
4	14 May	9.8	1.8	Male	98	31.05 ± 4.92	6.18 ± 0.99	4.38 ± 0.67	49.72 ± 22.29
				Female	305	37.36 ± 6.43	7.63 ± 1.52	5.54 ± 1.08	109.38 ± 62.85
5	24 May	13.8	0.9	Male	162	31.65 ± 4.37	6.50 ± 0.89	4.61 ± 0.55	61.37 ± 23.09
				Female	238	38.58 ± 6.78	8.16 ± 1.58	5.84 ± 1.15	125.95 ± 73.16
6	03 June	16.0	1.0	Male	154	35.85 ± 4.10	7.19 ± 0.84	5.00 ± 0.51	84.04 ± 25.19
				Female	243	43.70 ± 6.02	9.17 ± 1.42	6.61 ± 1.04	179.63 ± 77.05
7	15 June	15.9	3.1	Male	169	27.69 ± 6.77	5.63 ± 1.36	4.00 ± 0.88	46.16 ± 32.15
				Female	302	38.47 ± 9.78	8.04 ± 2.15	5.76 ± 1.53	142.01 ± 99.48
8	29 June	21.7	1.6	Male	189	24.94 ± 3.06	5.15 ± 0.64	3.62 ± 0.43	31.50 ± 11.62
				Female	211	26.68 ± 4.74	5.49 ± 1.03	3.93 ± 0.73	43.13 ± 34.58
9	06 July	22.3	0.7	Male	160	24.82 ± 4.80	5.11 ± 0.95	3.63 ± 0.69	31.46 ± 17.34
				Female	240	27.05 ± 6.26	5.49 ± 1.38	3.97 ± 1.01	47.20 ± 52.16
10	15 July	22.0	0.8	Male	628	24.44 ± 4.86	5.17 ± 1.04	3.56 ± 0.71	25.73 ± 14.21
				Female	1065	30.87 ± 5.99	6.51 ± 1.35	4.53 ± 1.01	56.90 ± 50.92
11	23 July	22.3	9.4	Male	181	24.47 ± 4.64	5.07 ± 0.96	3.62 ± 0.67	33.89 ± 16.92
				Female	221	30.26 ± 6.31	6.26 ± 1.40	4.50 ± 0.99	65.81 ± 46.44
12	31 July	18.8	5.9	Male	368	28.32 ± 5.03	5.81 ± 1.04	4.12 ± 0.72	46.36 ± 20.54
				Female	594	32.98 ± 6.11	6.84 ± 1.35	4.93 ± 0.98	79.82 ± 48.14
13	11 Aug.	20.2	3.1	Male	164	29.56 ± 5.21	6.11 ± 1.06	4.17 ± 0.72	52.58 ± 24.95
				Female	236	32.77 ± 7.34	6.90 ± 1.67	4.77 ± 1.23	82.18 ± 66.68
14	17 Aug.	21.3	7.3	Male	316	31.11 ± 5.46	6.28 ± 1.16	4.41 ± 0.76	60.19 ± 28.06
				Female	267	35.98 ± 7.03	7.44 ± 1.61	5.29 ± 1.17	105.35 ± 65.58
15	09 Sep.	13.9	6.2	Male	107	36.77 ± 5.65	7.52 ± 1.20	5.07 ± 0.79	89.93 ± 38.69
				Female	343	41.25 ± 7.88	8.65 ± 1.87	6.04 ± 1.39	152.96 ± 98.72
16	02 Oct.	11.9	17.4	Male	153	35.01 ± 6.17	7.02 ± 1.31	4.72 ± 0.88	79.27 ± 40.53
				Female	247	40.74 ± 9.10	8.43 ± 2.15	5.83 ± 1.59	153.89 ± 124.35
17	25 Oct.	7.7	9.1	Male	501	34.05 ± 4.63	6.79 ± 0.99	4.60 ± 0.67	72.55 ± 27.30
				Female	452	38.63 ± 6.04	7.93 ± 1.40	5.46 ± 1.04	121.06 ± 67.84
18	02 Nov.	9.4	4.8	Male	138	35.24 ± 4.93	7.00 ± 1.10	4.74 ± 0.70	80.17 ± 32.74
				Female	262	39.83 ± 7.36	8.15 ± 1.69	5.79 ± 1.37	146.27 ± 94.80
19	10 Nov.	7.3	1.7	Male	736	32.64 ± 4.78	6.46 ± 1.01	4.45 ± 0.67	53.88 ± 23.59
				Female	627	37.17 ± 5.60	7.55 ± 1.32	5.27 ± 0.98	103.08 ± 63.62

T, temperature (°C); *N*, sample size measured; *TL*, total length in mm; *CL*, carapace length; *CW*, carapace width; *DW*, dry weight in mg; sd, standard deviation

* number of individuals per m^2

Table 3.2: Mean dry weight (*DW* ± sd) separated into different size classes per catching date of males and females brown shrimp *C. crangon* L. collected in the Wadden Sea off Büsum from April 2010 to November 2010. Numbers without standard deviation (± sd) indicate that only individual shrimp has been measured.

Size class	**10 mm**		**20 mm**		**30 mm**		**40 mm**		**50 mm**		**60 mm**	**70 mm**
Sex	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Female**	**Female**
Date	***DW* ± sd**	***DW* ± sd**	***DW* ± sd**	***DW* ± sd**	***DW* ± sd**	***DW* ± sd**	***DW* ± sd**	***DW* ± sd**	***DW* ± sd**	***DW* ± sd**	***DW* ± sd**	***DW* ± sd**
06.04.2010	10.2 ± 1.2	7.8 ± 3.9	31.3 ± 9.9	31.6 ± 9.7	65.7 ± 13.7	76.6 ± 20.1	125.0 ± 17.3	143.8 ± 36.6		403.0 ± 43.8		
21.04.2010	11.8 ± 1.9	13.1 ± 2.7	30.9 ± 9.7	34.3 ± 9.6	71.1 ± 16.8	81.9 ± 22.5	125.9 ± 21.5	165.4 ± 35.7	235.4	291.4 ± 37.4	560.0 ± 128.7	
30.04.2010		13.4	34.9 ± 8.2	34.6 ± 9.2	67.4 ± 15.6	83.8 ± 25.5	116.8 ± 10.0	176.5 ± 39.6	226.4 ±24.1	290.2 ± 32.5		
14.05.2010			30.7 ± 7.4	36.4 ± 8.3	60.2 ± 11.8	84.7 ± 23.9	108.8 ± 11.2	172.5 ± 41.9		266.8 ± 36.2	467.0	
24.05.2010			42.3 ± 7.0	44.8 ± 9.4	69.2 ± 15.4	85.7 ± 20.5	127.1 ± 20.4	171.8 ± 37.5		290.3 ± 47.6		
03.06.2010			37.1 ± 9.6	34.3 ± 11.8	80.3 ± 14.9	97.9 ± 22.9	131.1 ± 16.6	187.3 ± 37.9		294.9 ± 30.5	566.0	
15.06.2010	13.6 ± 3.2	11.7 ± 2.0	29.4 ± 8.5	31.9 ± 10.2	82.0 ± 18.0	104.0 ± 23.2	126.6 ± 18.2	191.2 ± 38.9		291.1 ± 32.6		1057.0
29.06.2010	15.4 ± 2.7	15.1	30.2 ± 7.5	32.6 ± 9.6	60.7 ± 10.7	75.8 ± 21.9	111.4	198.5 ± 33.5				
06.07.2010	12.5 ± 2.8	13.3 ± 3.6	31.1 ± 9.2	33.0 ± 11.8	57.2 ± 7.1	72.2 ± 21.9	150.5	253.3 ± 29.4		373.3 ± 47.7		
15.07.2010	9.4 ± 2.0	9.6 ± 2.2	25.5 ± 8.6	29.9 ± 9.6	51.7 ± 7.6	65.4 ± 19.9		156.0 ± 39.1		345.0 ± 63.4	485.0	
23.07.2010	15.0 ± 2.2	10.1 ± 0.9	34.2 ± 10.0	36.6 ± 11.1	65.0 ± 11.8	84.2 ± 20.6		188.1 ± 29.3		313.7		
31.07.2010	12.9 ± 1.9	12.7 ± 3.1	35.7 ± 10.8	37.0 ± 10.1	66.5 ± 12.4	83.3 ± 21.6	104.9	161.9 ± 34.8		277.6 ± 16.9		
11.08.2010	12.9 ± 3.2		38.4 ± 9.7	35.6 ± 9.3	71.3 ± 18.3	80.1 ± 24.8	121.1 ± 7.8	183.0 ± 39.1		316.8 ± 31.7		
17.08.2010	13.1 ± 2.6	9.5 ± 0.1	39.6 ± 9.2	39.7 ± 9.8	71.9 ± 16.3	84.8 ± 20.7	139.1 ± 20.5	172.9 ± 37.1		311.5 ± 62.8		
09.09.2010		10.8	39.1 ± 8.1	40.6 ± 9.2	75.4 ± 16.4	83.5 ± 20.4	139.1 ± 25.4	172.4 ± 38.8	211.5	327.8 ± 56.4	531.0 ± 0.0	
02.10.2010			39.2 ± 7.7	39.1 ± 9.9	74.1 ± 18.3	80.8 ± 20.0	129.6 ± 22.2	168.4 ± 38.5	231.6 ± 23.9	347.9 ± 64.1	538.1 ± 90.6	
25.10.2010	11.6		40.3 ± 8.0	39.8 ± 6.9	73.0 ± 16.8	87.3 ± 21.1	122.9 ± 13.3	159.7 ± 29.2		334.8 ± 71.8	473.3 ± 19.7	
02.11.2010		12.2	39.7 ± 5.6	37.6 ± 9.1	74.5 ± 15.8	88.6 ± 25.4	129.5 ± 24.0	178.9 ± 46.9	238.9	351.2 ± 46.0	475.8 ± 41.3	
10.11.2010	11.8 ± 1.3	9.4 ± 1.9	30.2 ± 7.6	36.8 ± 9.3	58.5 ± 14.1	80.6 ± 24.2	114.0 ± 22.8	167.4 ± 40.7	227.4	331.3 ± 44.3	500.0 ± 76.4	

Table 3.3: Mean estimated field increments, *INC* in mm, (twice the mean of all positive potential increments; method a) separated into different size classes per sampling date of males and females brown shrimp *C. crangon* L. collected in the Wadden Sea off Büsum from April 2010 to November 2010.

Size class (mm)	**10 mm**		**20 mm**		**30 mm**		**40 mm**		**50 mm**	**60 mm**	**70 mm**
Sex	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Female**	**Female**	**Female**
06.04.2010	0.88		0.98	0.90	0.77	2.31		3.66	6.21		
21.04.2010		0.75	1.06	1.43	0.99	1.88	0.26	2.83	4.35	7.43	
30.04.2010		1.41	0.91	0.98	0.60	2.39	0.22	4.81	5.83		
14.05.2010			2.25	0.80	1.32	2.90	0.07	3.57	3.82	1.04	
24.05.2010			0.99	1.40	1.03	2.77		2.80	4.72		
03.06.2010	1.05		1.24		0.62	2.77		4.28	5.69	3.16	
15.06.2010	0,70		1.02	1.99		3.08		4.74	3.89		6.65
29.06.2010	0.86	0.75	1.02	2.08	0.97	4.19		6.14			
06.07.2010	1.90	2.50	2.07	1.86	1.60	2.52		7.33	7.13		
15.07.2010	0.88	0.22	1.50	1.26	1.48	1.31		2.14	5.73	9.63	
23.07.2010	0.92	1.02	1.62	1.96	1.07	3.27		5.44	6.53		
31.07.2010	0.76	0.99	1.64	1.94	1.08	2.77	0.12	4.12	4.59		
11.08.2010			0.50	1.55	0.74	2.70	0.07	4.74	5.53		
17.08.2010		6.97	0.74	1.48	0.50	2.11		3.37	5.73		
09.09.2010			1.20	1.13	0.89	1.61	0.08	2.34	5.00	7.36	
02.10.2010			0.19	0.83	0.66	2.61	0.30	3.02	5.27	7.34	
25.10.2010			1.65	1.13	0.41	1.86		3.11	5.91	6.63	
02.11.2010		1.19		1.76		2.70		5.95	9.34	7.61	
10.11.2010				3.00		3.48		3.49	5.56	6.29	

Table 3.4: Estimated field increments in mm (method a and method b) separated into different size classes of males and females brown shrimp *C. crangon* L. collected in the Wadden Sea off Büsum from April 2010 to November 2010.

Sex	**Male**		**Female**	
Size class	**Method a**	**Method b**	**Method a**	**Method b**
10 mm	0,99	0,72	1,76	0,95
20 mm	1,21	0,72	1,53	1,01
30 mm	0,92	0,28	2,59	1,62
40 mm	0,16	-0,14	4,1	3,05
50 mm	0,16	-0,74	5,6	6,69
60 mm			6,28	4,83

Table 3.5: Estimated intermoult period (*IMP*, day) separated into different size classes per sampling date of males and females brown shrimp *C. crangon* collected in the Wadden Sea off Büsum from April 2010 to November 2010 based on the following parameters, that is, calculated from the *in situ* growth in previous manuscript; Equation 14 where α =5.7066; β = 0.7364 and c = - 0.09363.

Size class (mm)	**10 mm**		**20 mm**		**30 mm**		**40 mm**		**50 mm**	**60 mm**	**70 mm**
Sex	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Female**	**Female**	**Female**
06.04.2010	19		27	24	33	33		42	49		
21.04.2010		22	29	28	34	35	39	41	46	54	
30.04.2010		15	20	20	24	25	29	30	33		
14.05.2010			26	27	30	32	36	38	42	48	
24.05.2010			18	19	21	22	25	25	29		
03.06.2010	11		13		18	18		21	23	28	
15.06.2010	11		14	14		18		21	24		32
29.06.2010	6	7	8	8	9	10		12			
06.07.2010	6	6	8	8	9	9		12	14		
15.07.2010	6	6	8	8	10	10		12	14	15	
23.07.2010	6	6	8	8	9	10		12	13		
31.07.2010	8	9	11	11	13	13	16	16	18		
11.08.2010			10	10	12	12	14	14	16		
17.08.2010		5	9	9	11	11		13	14		
09.09.2010			18	18	21	22	24	26	30	33	
02.10.2010			23	22	26	26	29	31	36	40	
25.10.2010			31	32	38	39		45	52	57	
02.11.2010		20		27		33		38	44	49	
10.11.2010				34		42		47	54	60	

Table 3.6: Estimated growth rate (*GR*, mm/day) separated into different size classes per sampling date of males and females brown shrimp *C. crangon* collected in the Wadden Sea off Büsum from April 2010 to November 2010 based on observed *INC* and estimated *IMP* from the following parameters, that is, calculated from the *in situ* growth in previous manuscript; Equation 14 where α =5.7066; β = 0.7364 and c = - 0.09363 which presented in Table (3.4). Numbers between brackets are the individual's number.

Size class (mm)	**10 mm**		**20 mm**		**30 mm**		**40 mm**		**50 mm**	**60 mm**	**70 mm**
Sex	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Female**	**Female**	**Female**
06.04.2010	0.05 (4)		0.04 (35)	0.04 (25)	0.02 (59)	0.07 (71)		0.09 (16)	0.13 (2)		
21.04.2010		0.03 (5)	0.04 (384)	0.05 (139)	0.03 (509)	0.05 (382)	0.01 (69)	0.07 (204)	0.09 (22)	0.14 (2)	
30.04.2010		0.09 (1)	0.04 (58)	0.05 (53)	0.03 (71)	0.10 (105)	0.01 (8)	0.16 (92)	0.18 (12)		
14.05.2010			0.09 (43)	0.03 (40)	0.04 (50)	0.09 (166)	0.01 (5)	0,09 (93)	0,09 (5)	0,02 (1)	
24.05.2010			0,05 (62)	0,08 (19)	0,05 (93)	0,13 (129)	0,01 (7)	0,11 (68)	0,16 (22)		
03.06.2010	0,09 (13)		0,09 (9)		0,03 (126)	0,15 (64)		0,20 (136)	0,24 (38)	0,11 (1)	
15.06.2010	0,06 (5)		0,07 (105)	0,14 (76)		0,17 (56)		0,22 (145)	0,16 (20)		0,21 (1)
29.06.2010	0,14 (30)	0,11 (1)	0,13 (175)	0,26 (178)	0,11 (8)	0,43 (25)		0,50 (7)			
06.07.2010	0,32 (128)	0,42 (18)	0,27 (110)	0,24 (166)	0,18 (19)	0,27 (50)		0,59 (2)	0,52 (4)		
15.07.2010	0,15 (40)	0,03 (15)	0,19 (416)	0,15 (486)	0,15 (84)	0,13 (501)		0,18 (46)	0,41 (16)	0,65 (1)	
23.07.2010	0,16 (23)	0,18 (5)	0,20 (118)	0,25 (113)	0,11 (23)	0,34 (88)		0,47 (14)	0,50 (5)		
31.07.2010	0,09 (3)	0,11 (6)	0,15 (202)	0,18 (188)	0,08 (142)	0,21 (319)	0,01 (1)	0,26 (75)	0,26 (6)		
11.08.2010			0,05 (97)	0,16 (104)	0,06 (58)	0,23 (90)	0,01 (6)	0,34 (36)	0,34 (6)		
17.08.2010		0,28 (2)	0,09 (133)	0,17 (52)	0,05 (161)	0,20 (135)		0,27 (70)	0,40 (8)		
09.09.2010			0,07 (10)	0,06 (14)	0,04 (68)	0,07 (155)	0,01 (28)	0,09 (117)	0,17 (54)	0,22 (2)	
02.10.2010			0,01 (37)	0,04 (22)	0,03 (84)	0,10 (116)	0,01 (29)	0,10 (65)	0,15 (36)	0,18 (8)	
25.10.2010			0,05 (98)	0,04 (27)	0,01 (341)	0,05 (246)		0,07 (161)	0,11 (15)	0,12 (3)	
02.11.2010		0,06 (1)		0,07 (18)		0,08 (116)		0,16 (103)	0,21 (20)	0,16 (4)	
10.11.2010				0,09 (35)		0,08 (444)		0,07 (129)	0,10 (15)	0,10 (2)	

Table 3.7: Estimates of the share (%) of males and females (sex separated) brown shrimp *C. crangon* classified as starving individuals at different size classes during the whole study period in 2010 in the Wadden Sea off Büsum.

Size class	**10 mm**		**20 mm**		**30 mm**		**40 mm**		**50 mm**
Sex	**% Male**	**% Female**	**% Male**	**% Female**	**% Male**	**% Female**	**% Male**	**% Female**	**% Male**
06.04.2010	75.0	100.0	77.1	64.0	57.6	63.4	33.3	43.8	
21.04.2010	80.0	40.0	67.4	62.6	39.7	39.3	30.4	11.3	
30.04.2010			51.7	49.1	35.2	24.8	12.5	3.3	
14.05.2010			97.7	67.5	96.0	39.2	80.0	15.1	20.0
24.05.2010			9.7	21.1	11.8	19.4		1.5	4.5
03.06.2010				75.0	12.7	26.6		5.9	2.6
15.06.2010	53.8	100.0	20.0	15.8	2.3		12.5	0.7	
29.06.2010	20.0		14.9	21.3		8.0			
06.07.2010	36.7	11.1	40.0	26.5	47.4	4.0	100.0		
15.07.2010	100.0	86.7	99.8	81.1	100.0	66.5		30.4	
23.07.2010		60.0	0.8	13.3	13.0	3.4			
31.07.2010	4.3	66.7	11.9	32.4	25.4	8.5		1.3	
11.08.2010	33.3		8.2	37.5	15.5	14.4	16.7	5.6	
17.08.2010		50.0	3.0	25.0	13.7	3.0	13.3		12.5
09.09.2010		100.0	40.0	35.7	22.1	47.7	7.1	10.3	11.1
02.10.2010			45.9	59.1	32.1	60.3	3.4	15.4	
25.10.2010			41.8	59.3	17.3	24.0	3.3	6.8	
02.11.2010			29.4	38.9	10.2	31.9		3.9	
10.11.2010	75.0	100.0	95.2	82.9	95.9	61.5	85.7	9.3	

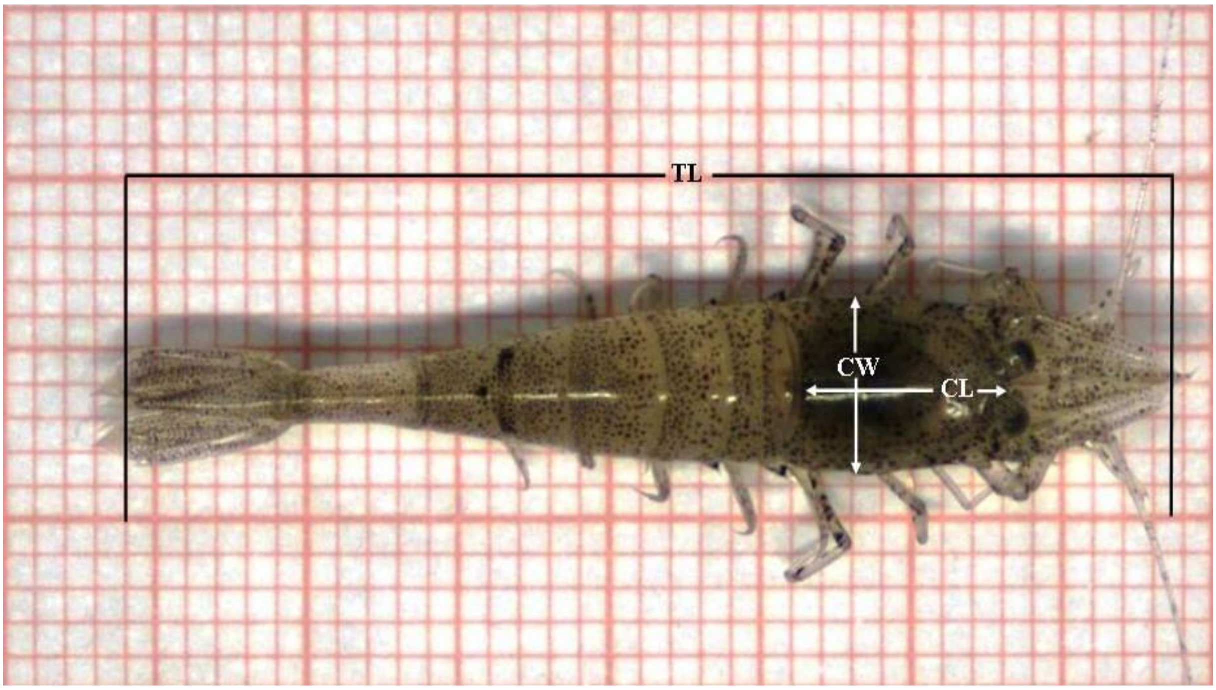


Figure 3.1: Morphometric measurements in brown shrimp *C. crangon* used in the present study; *TL* is total length, *CL* is carapace length and *CW* is width length.

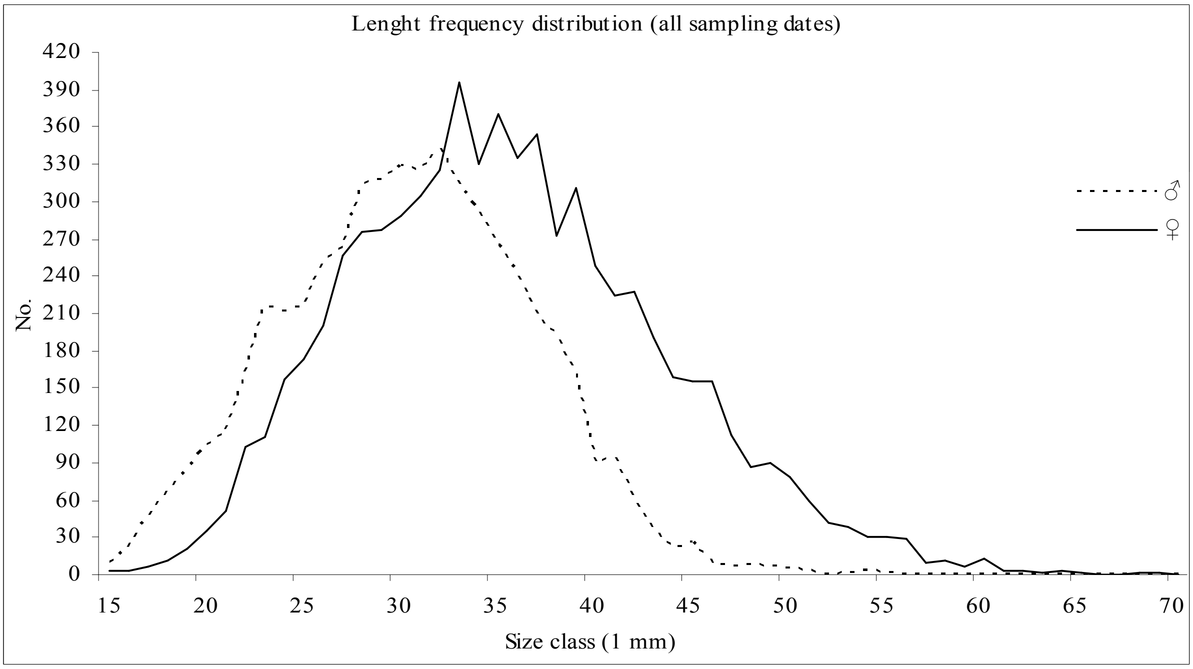


Figure 3.2: Length frequency distribution (numbers) of males and females brown shrimp *C. crangon* in 1 mm size class within the distributional range all year around during 2010.

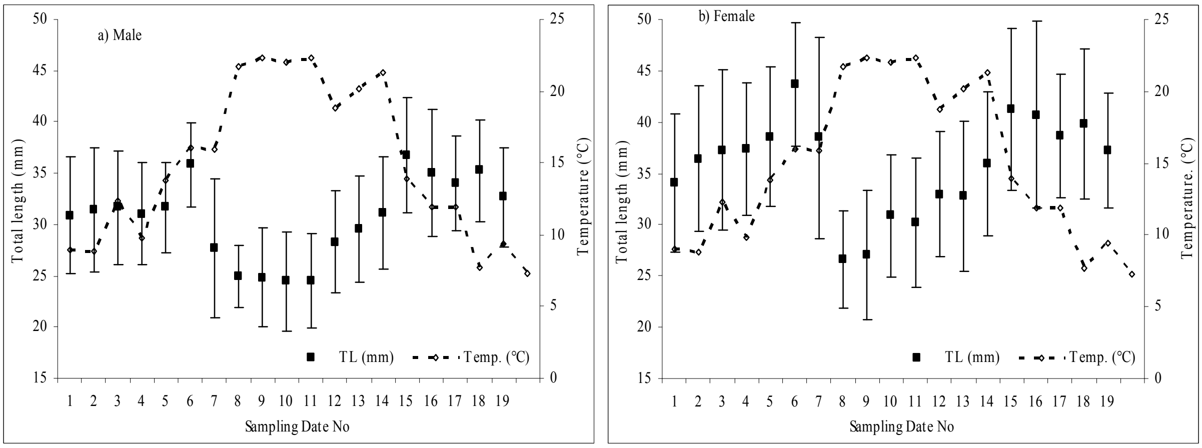


Figure 3.3: Mean total length of males (a) and females (b) brown shrimp *C. crangon* and temperature as measured in Büsum during sampling dates over sampling period 2010. Vertical bars represent the standard deviation (±sd).

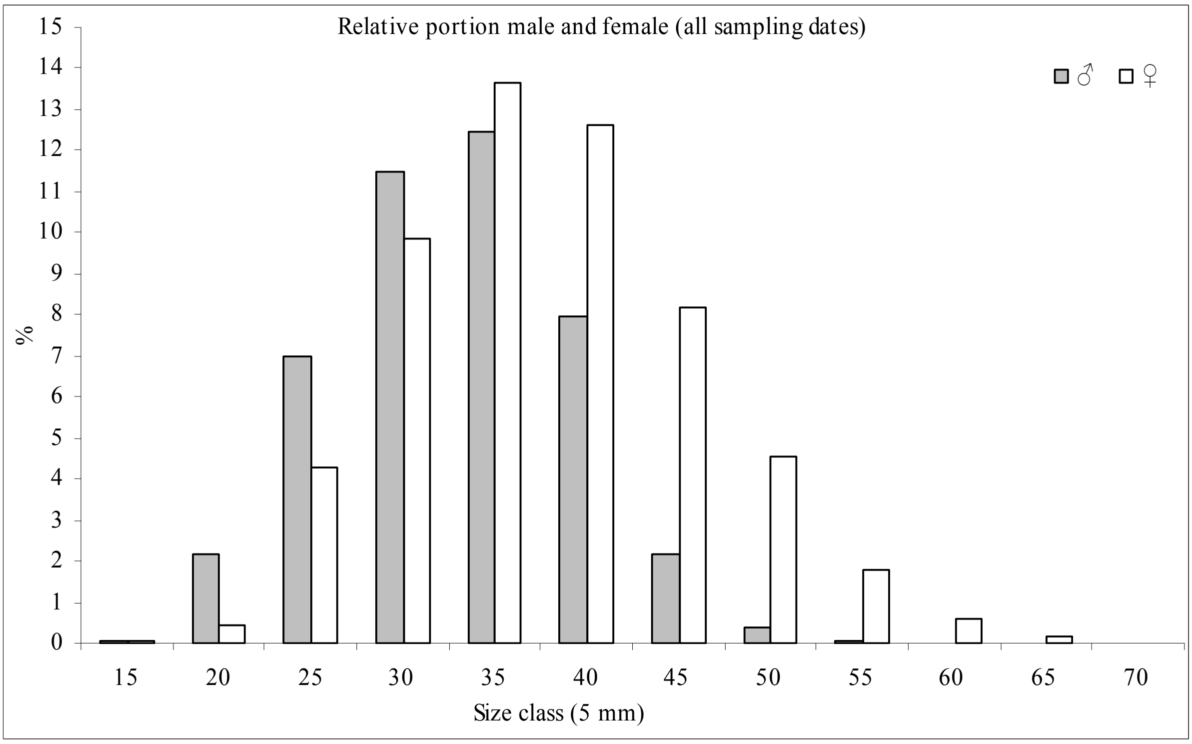


Figure 3.4: Histogram represents the relative portion (%) of males per size class/total shrimp numbers (gray columns) and females per size class/total shrimp numbers (empty columns) brown shrimp *C. crangon* in 5 mm size class for all sampling dates during 2010.

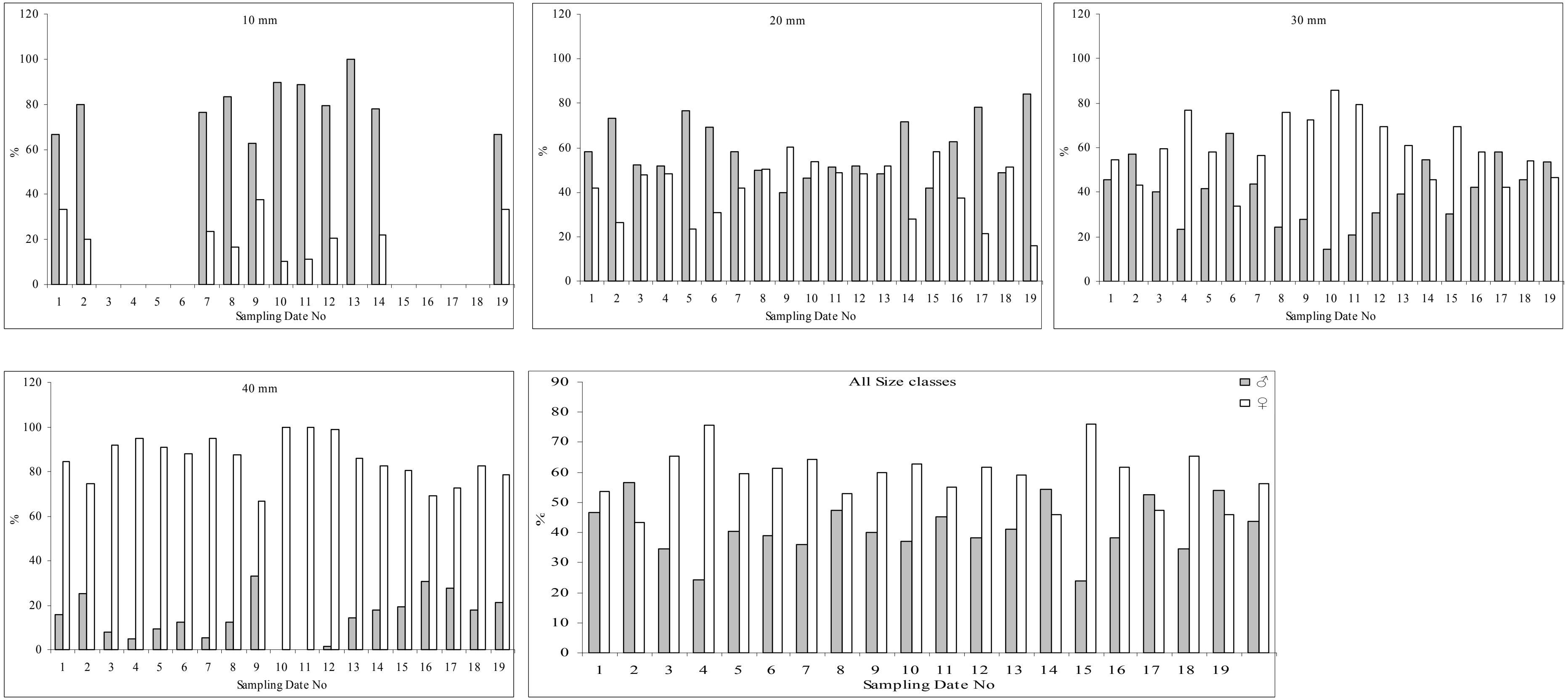


Figure 3.5: Histograms represent the relative portion (%) of males (gray columns) and females (empty columns) brown shrimp *C. crangon* separated into different size classes (10, 20, 30, and 40 mm) and combined size class per each sampling date (19 sampling date) during 2010 from the Wadden Sea off Büsum.

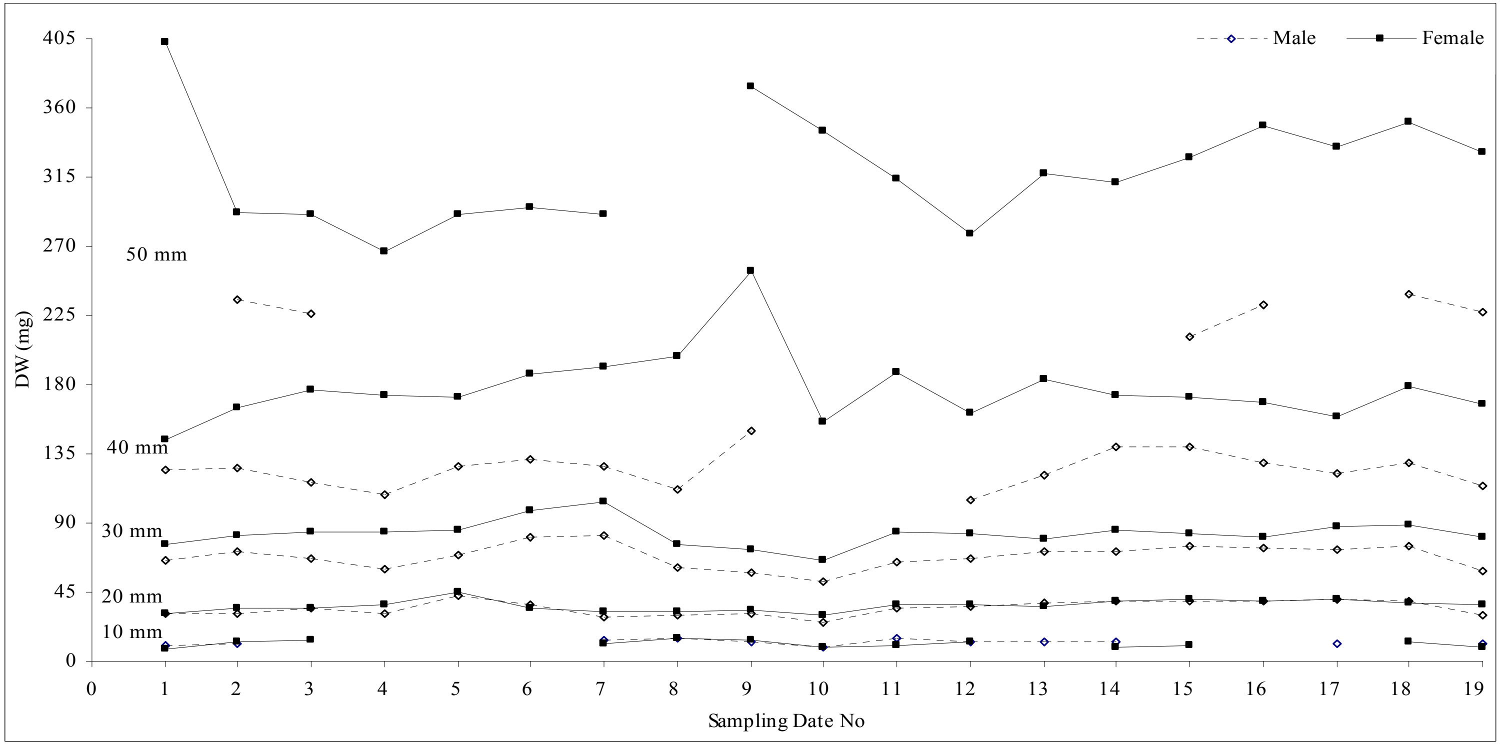


Figure 3.6: Mean dry weight (*DW*) of separated sex into males and females brown shrimp *C. crangon* as measured in Wadden Sea off Büsum during sampling dates (all year around) during 2010.

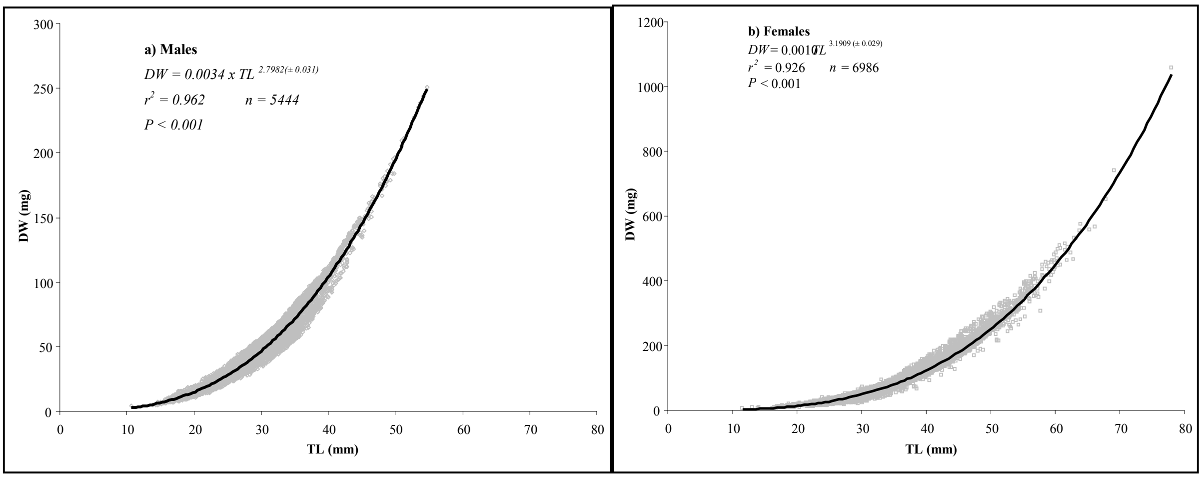


Figure 3.7: Total length-Dry weight relationship for males (a) and females (b) brown shrimp *C. crangon* collected from Wadden Sea off Büsum from April 2010 to November 2010 (all lengths combined) Each point represents an individual.

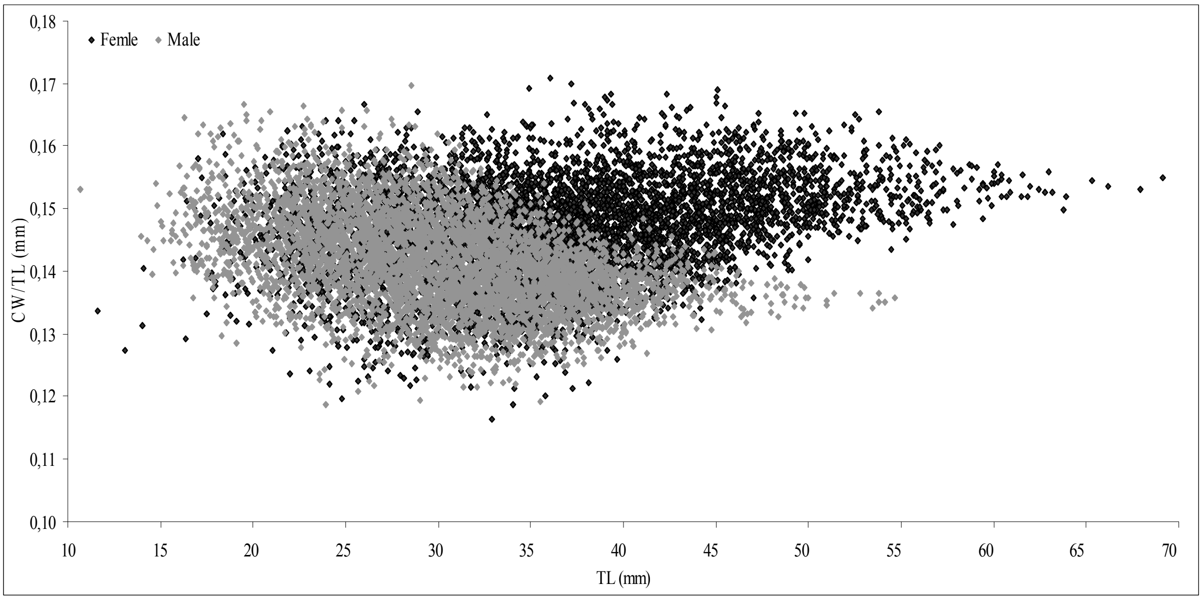


Figure 3.8: Carapace width divided by total length (*CW/TL*) on total length (*TL*) for males and females brown shrimp *C. crangon* collected from Wadden Sea off Büsum from April 2010 to November 2010 (all lengths combined). Each point represents an individual.

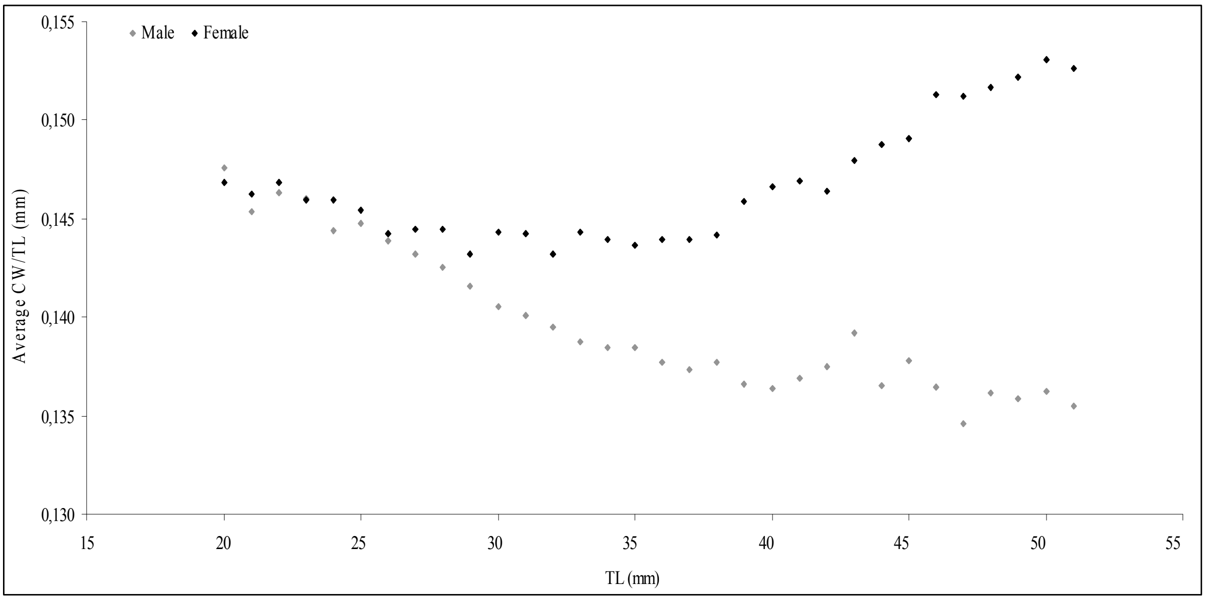


Figure 3.9: Average Carapace width divided by total length (*CW/TL*) on total length (*TL*) for males and females brown shrimp *C. crangon* collected from Wadden Sea off Büsum from April 2010 to November 2010 (all lengths combined).

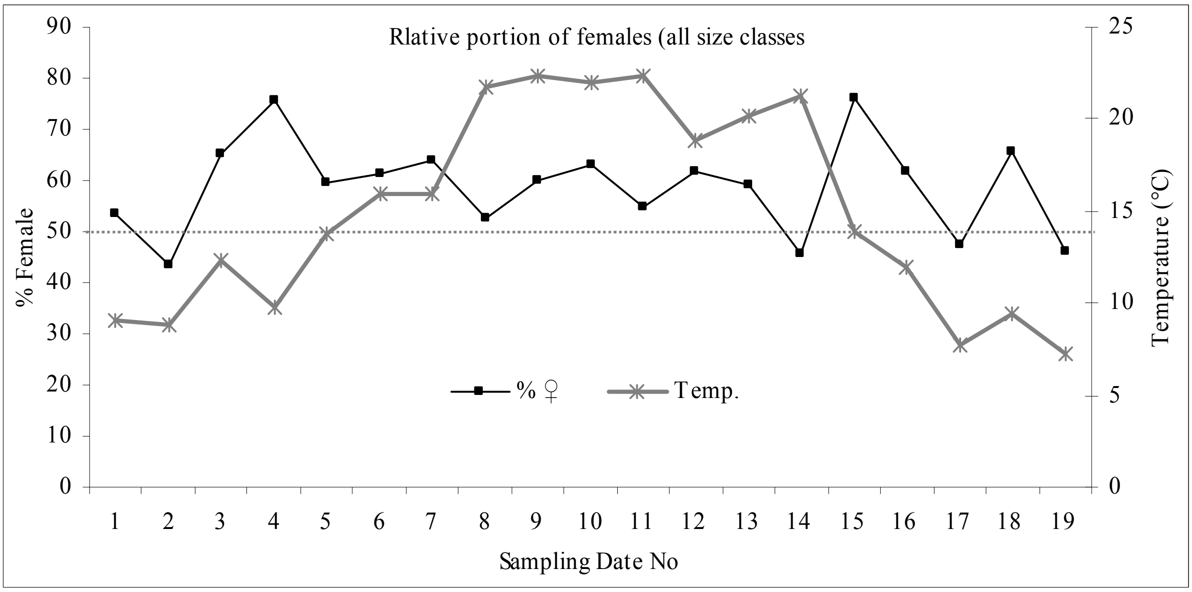


Figure 3.10: Variation of *C. crangon* sex ratio (% of female) at different temperature during study in 2010 in the Wadden Sea off Büsum. The dotted line represents equal sex ratio (1:1).

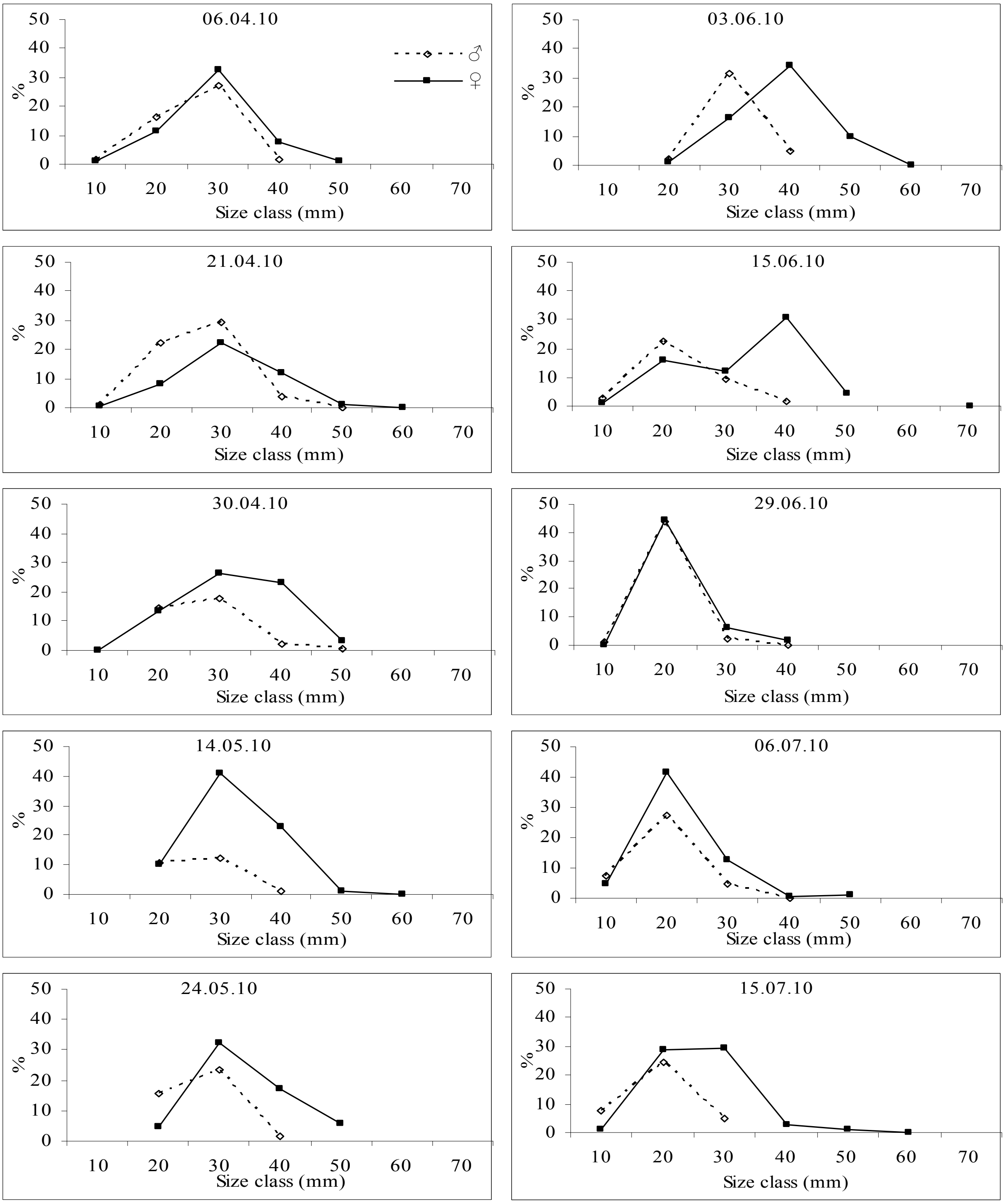


Figure 3.11: 19 Histograms represent the relative portion of all males (no of males per size class/total no of shrimps in the sample date) and all females (no of females per size class/total no of shrimps in the sample date) brown shrimp *C. crangon* collected from the Wadden Sea off Büsum during 2010.

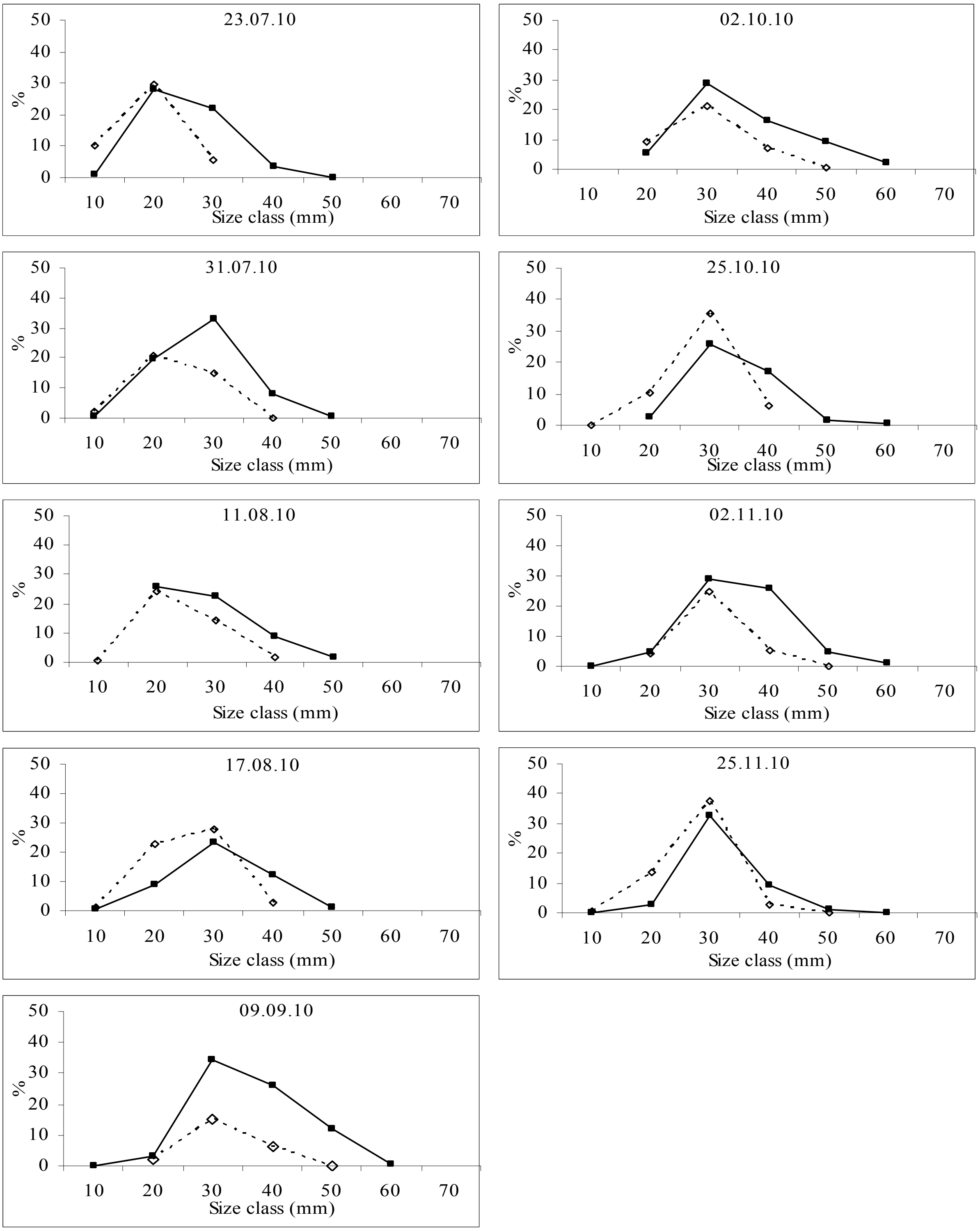


Figure 3.11: Continued.

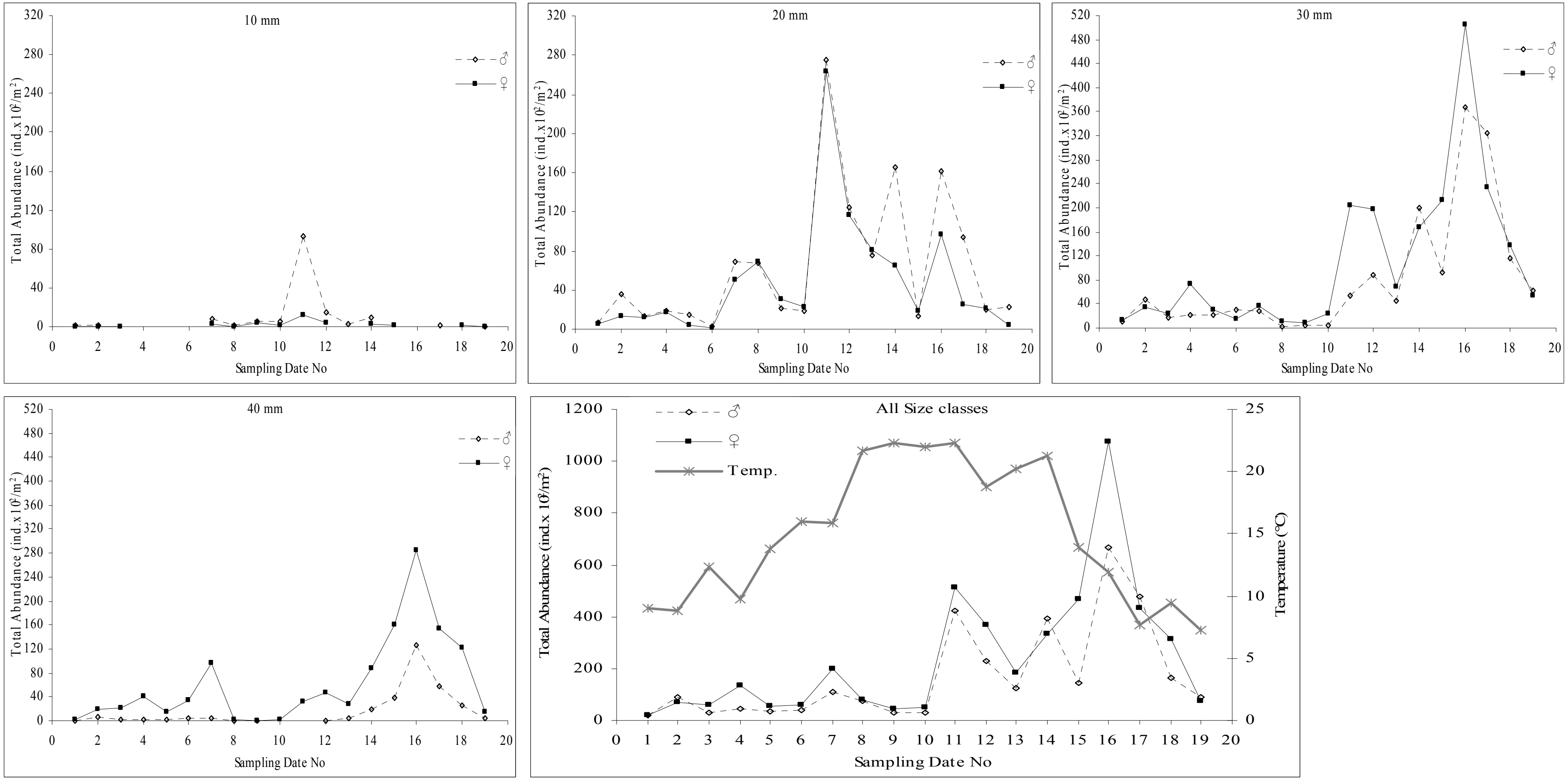
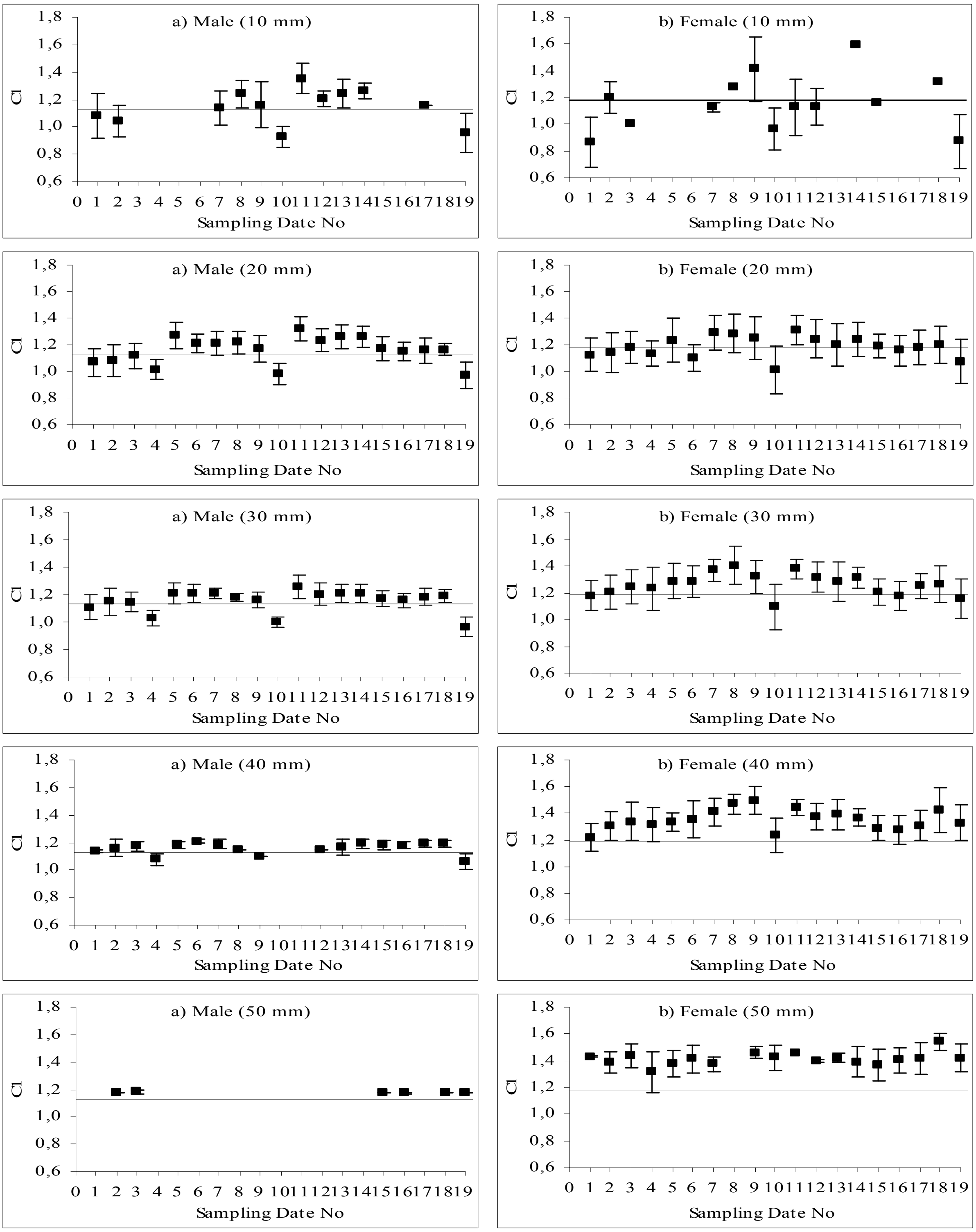


Figure 3.12: Annual temporal variations in the abundance (ind.x10^2/m^2) of males and females brown shrimp *C. crangon* separated into different size classes (10, 20, 30, and 40 mm) and combined size class together per each sampling date (19 sampling date) during 2010 from the Wadden Sea off Büsum. Note different scale between small (10 and 20 mm) and larger shrimps (30 and 40 mm).



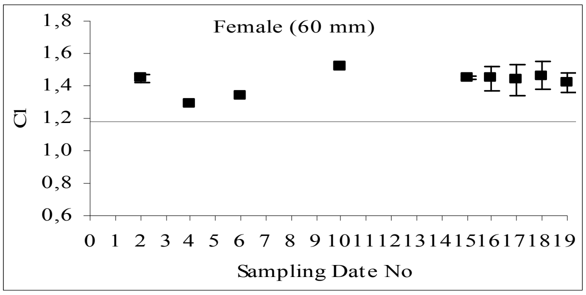


Figure 3.13: Variations in the mean condition indices (*C1*± sd) for different size classes in brown shrimp *C. crangon* males (a) and females (b) during 2010. The line represents the minimum *C1* as determent from laboratory experiments.

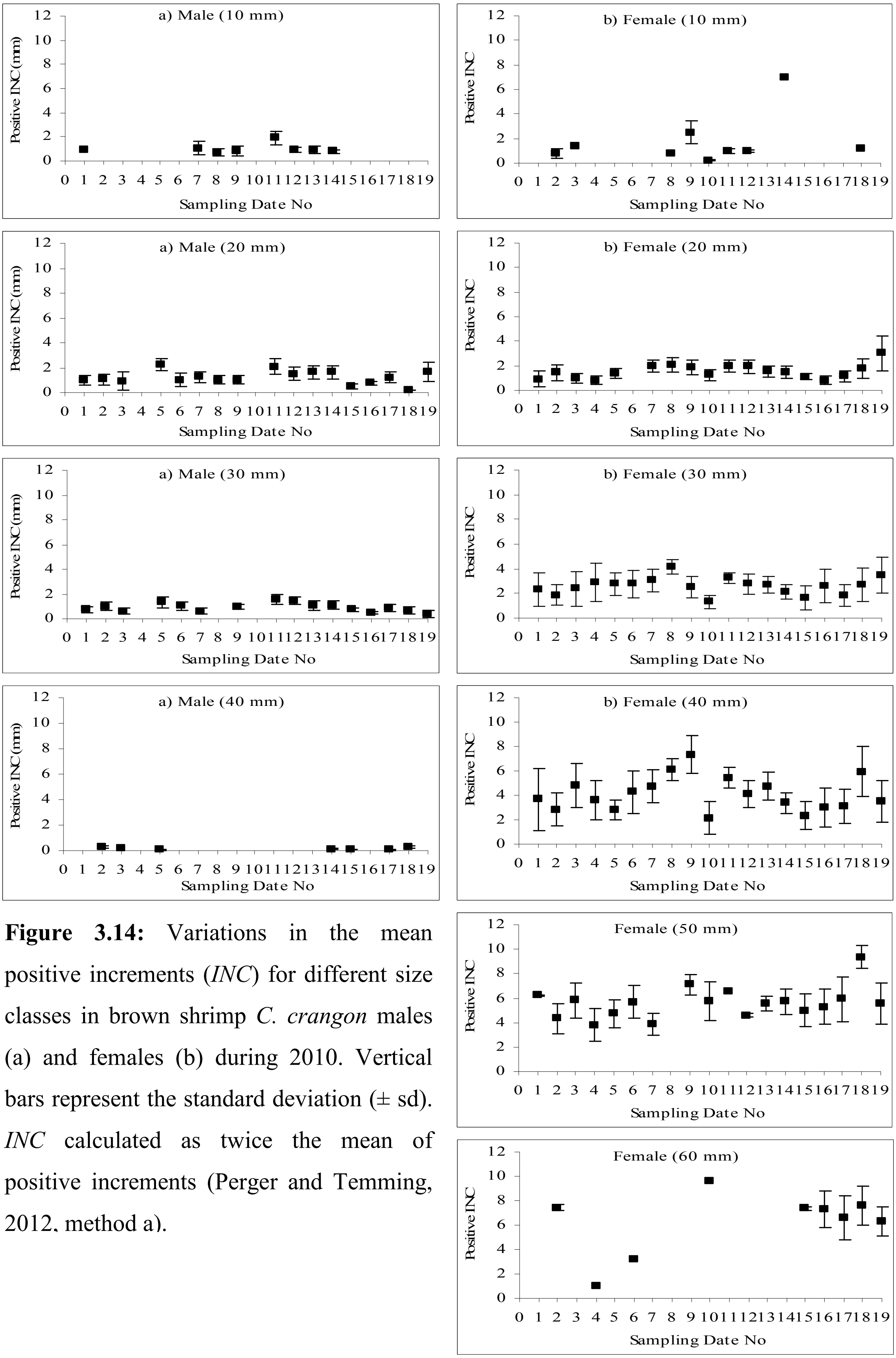


Figure 3.14: Variations in the mean positive increments (*INC*) for different size classes in brown shrimp *C. crangon* males (a) and females (b) during 2010. Vertical bars represent the standard deviation (± sd). *INC* calculated as twice the mean of positive increments (Perger and Temming, 2012, method a).

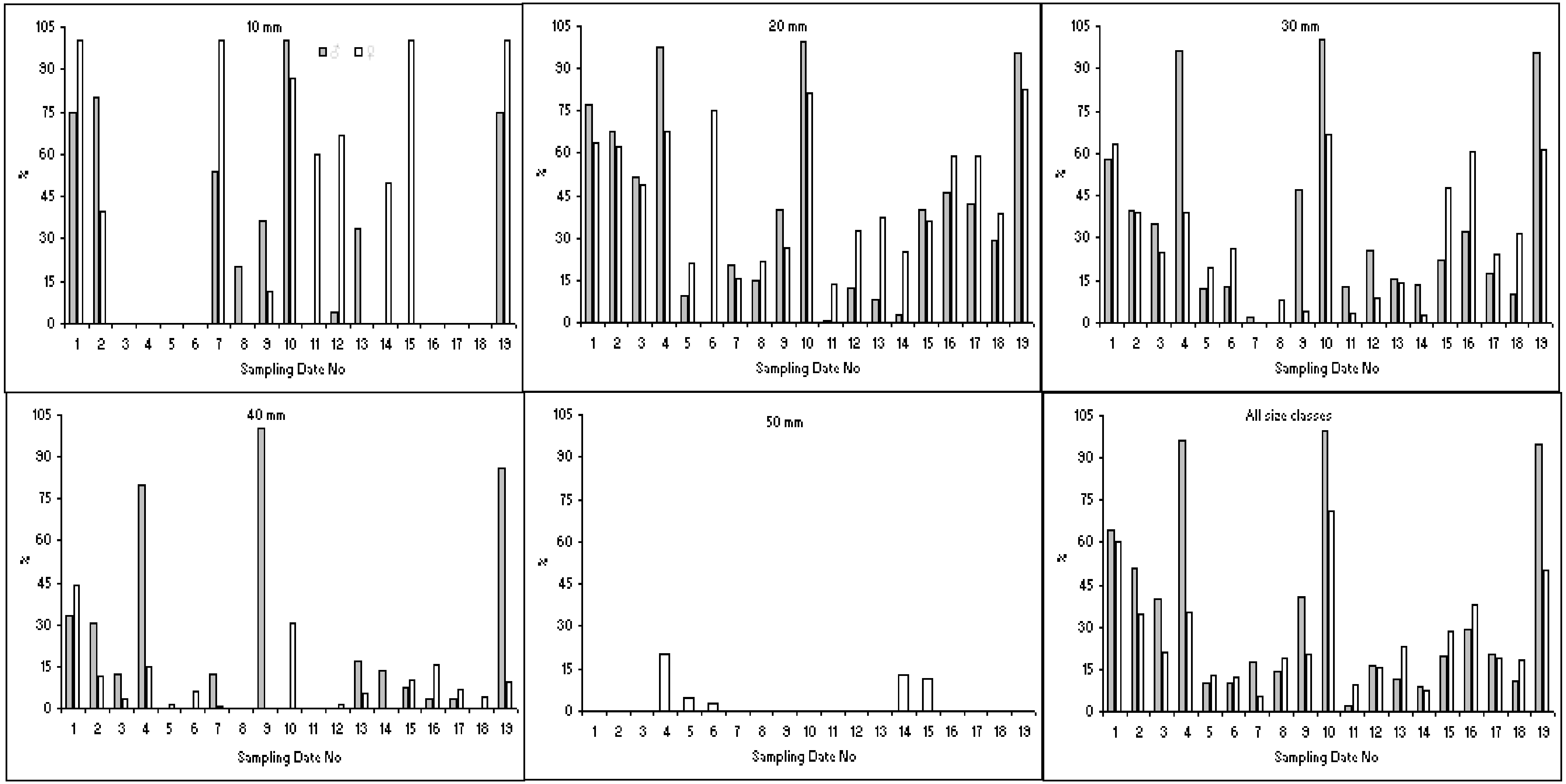


Figure 3.15: Histograms represent the share (%) of males (gray columns) and females (empty columns) brown shrimp *C. crangon* which classified as starving shrimps separated into different size classes (10, 20, 30, and 40 mm) and combined size class per each sampling date (19 sampling date) during 2010 from the Wadden Sea off Büsum.

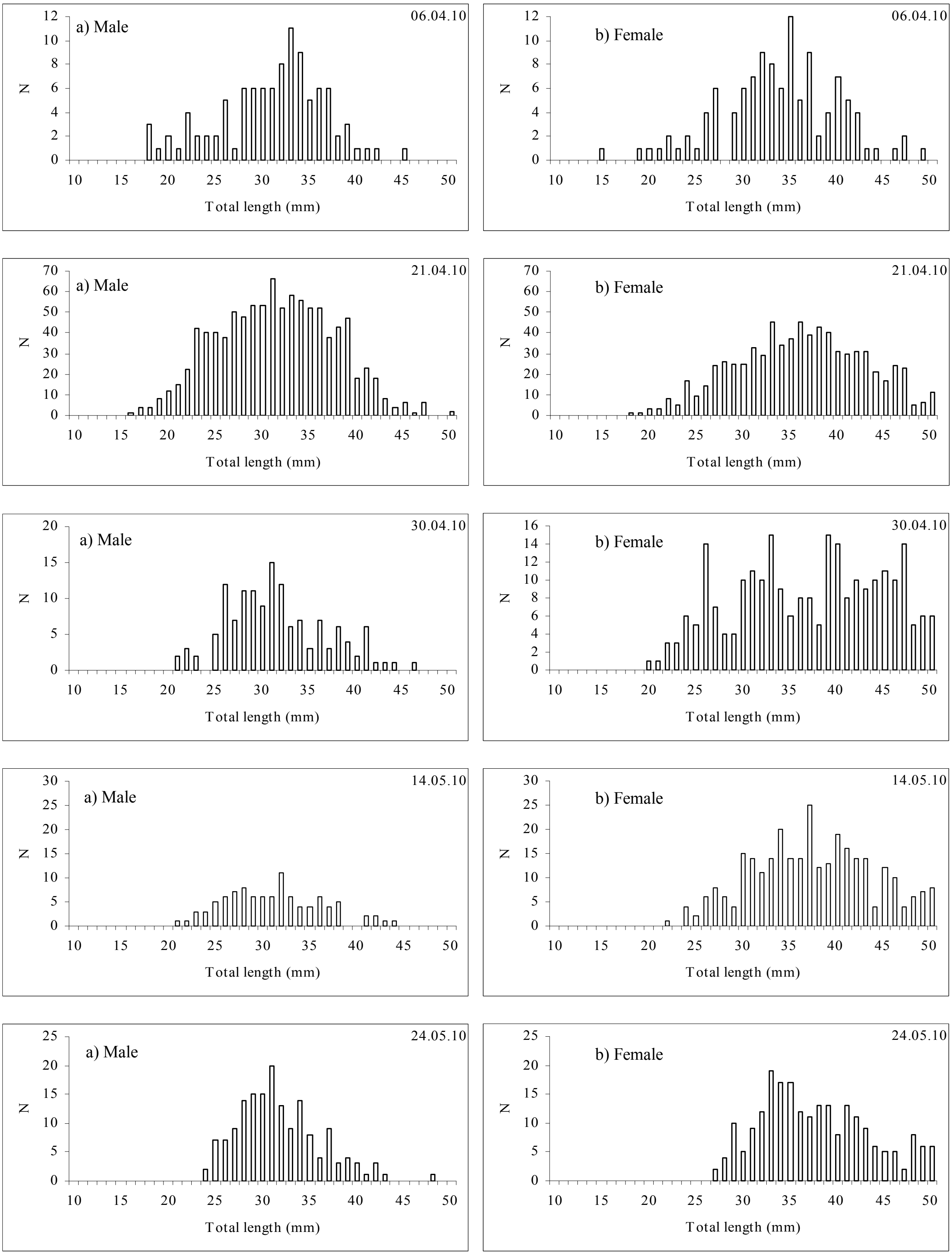


Figure 3.16: Total length (1 mm) frequency distribution (numbers) of males (a) and females (b) brown shrimp *C. crangon* collected in the Wadden Sea off Büsum from April to November 2010. Note the different Y-axes scale.

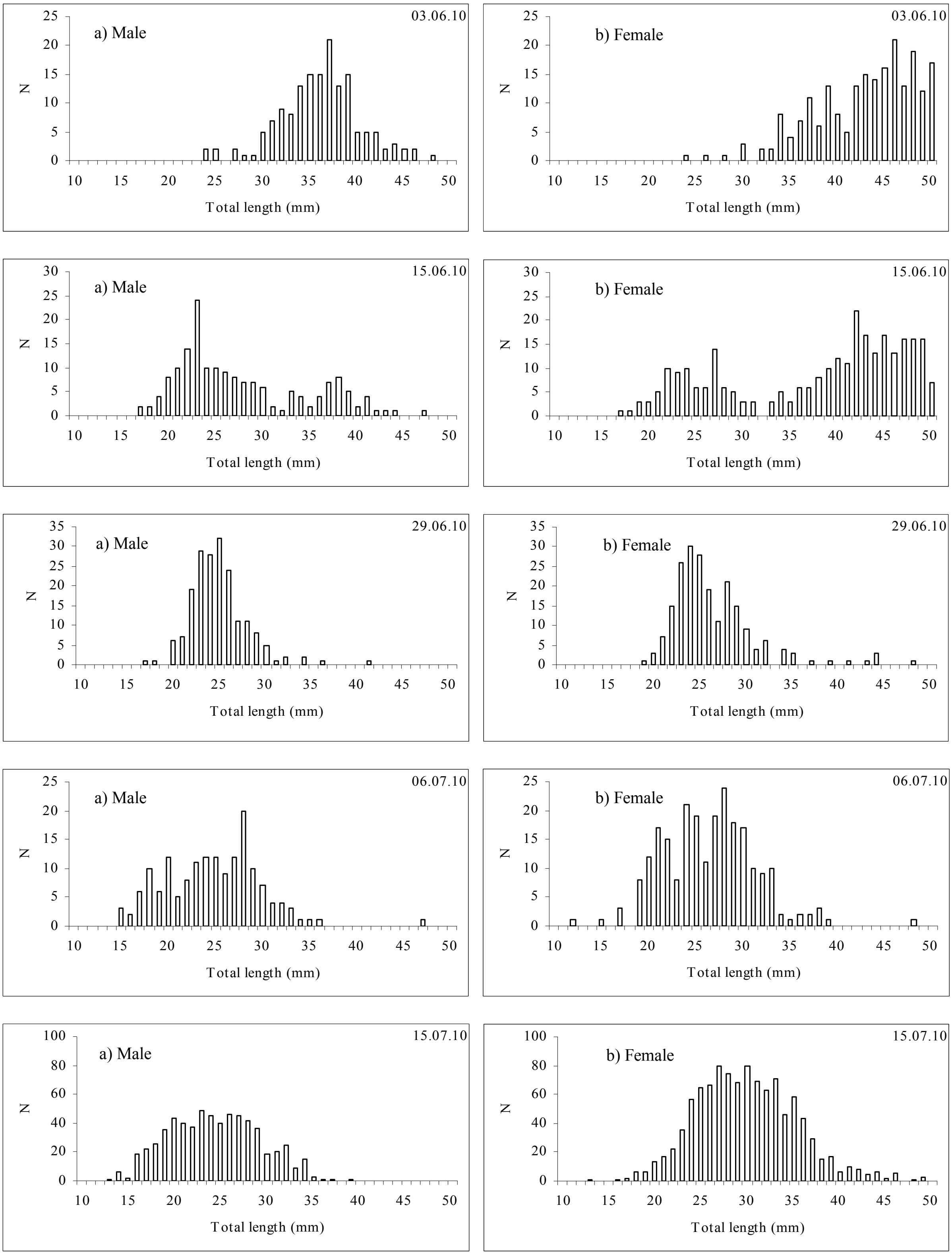


Figure 3.16: Continued.

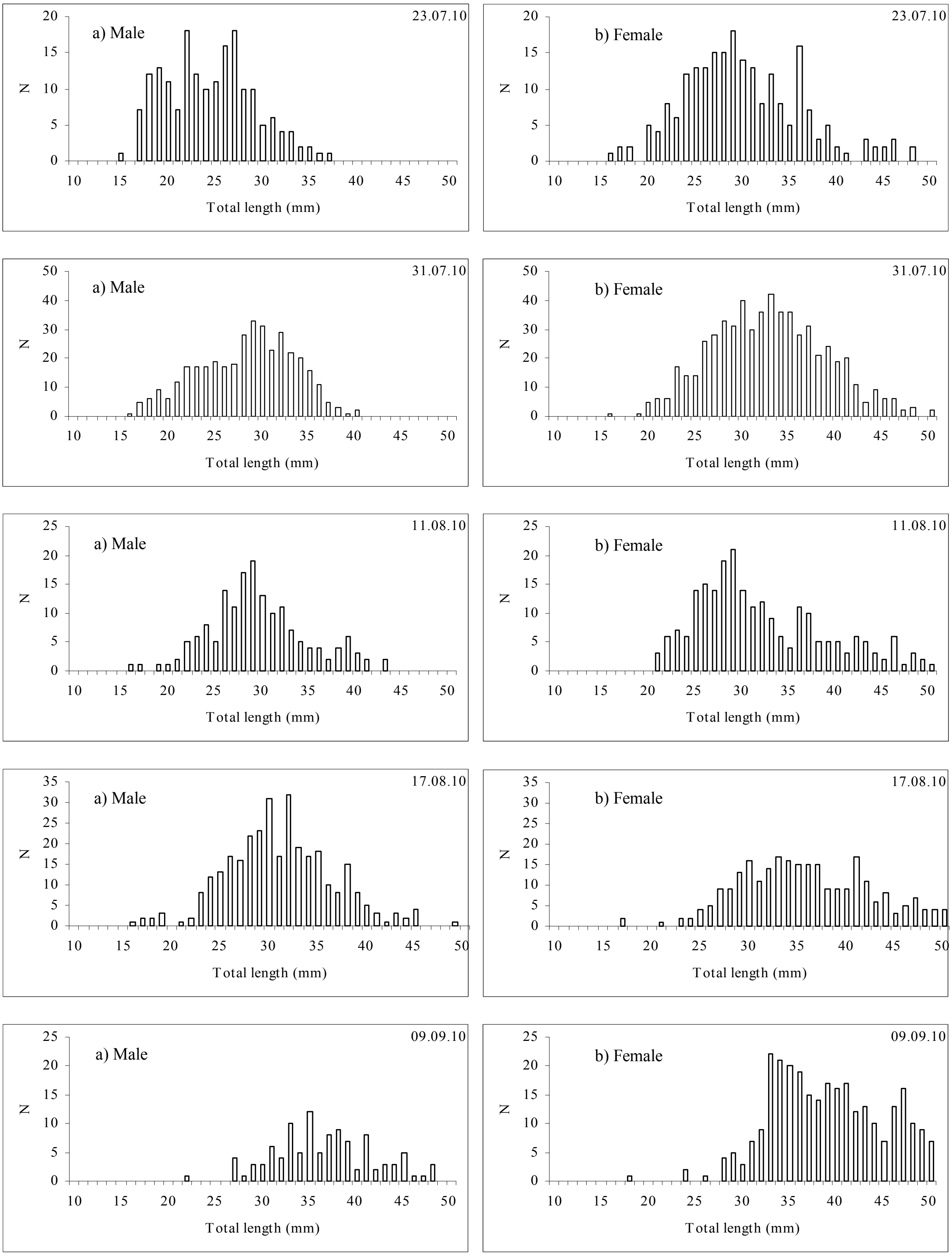


Figure 3.16: Continued.

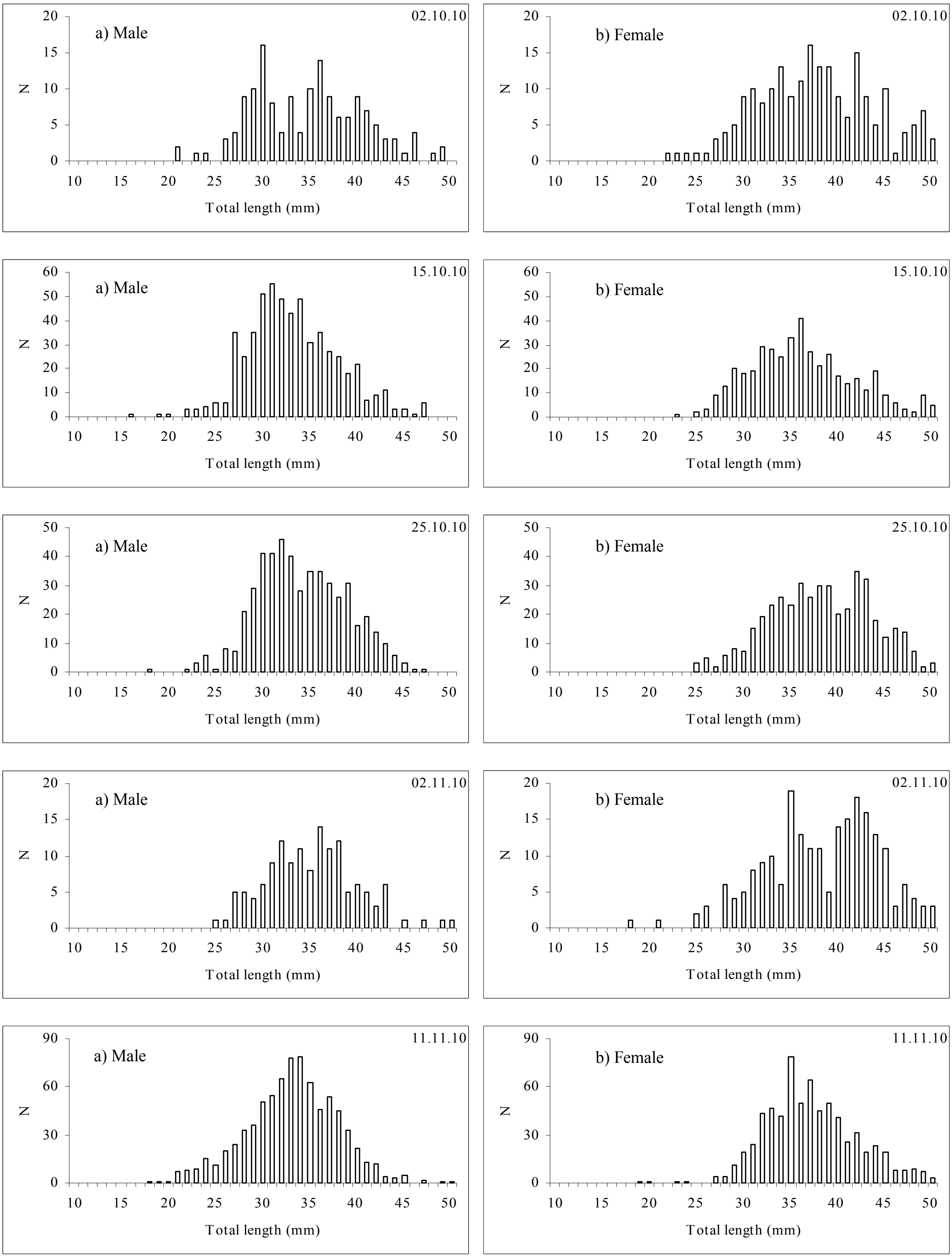


Figure 3.16: Continued.

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The effects of artificial diet on growth and body composition of brown shrimp *Crangon crangon* (Caridea, L. 1758) reared under laboratory conditions.

Abstract

Experimental diets were used in the present study to provide information on how brown shrimp *Crangon crangon* reacts to the complete replacement of natural and live feed by artificial generated food. *C. crangon* was raised in the laboratory at 17.6 ± 0.4 °C for 42 days to estimate its intermoult period and increase in body length (moult increments). Growth rates for males and females separated were then compared against field growth rates of *C. crangon* derived from the instantaneous growth method conducted in parallel with feeding experiments. Growth performance was measured as body composition and survival of brown shrimp. Besides food quality we also tested whether social effects like group or individual rearing affected growth. The results of this work were discussed in the context of further diet development and nutritional studies for brown shrimp *C. crangon*. In general, we observed shorter moult intervals, larger increments and higher growth rates comparable to previous studies. Female growth rate and moult interval were estimated as double than male values. While, no significant differences ($p \leq 0.05$) in crude protein content of the final body composition between the control group ME (moult experiments) with group experiments (GE) and individual experiments (IE) were observed for and between sexes were observed. For both, individual and group experiments, a significant increase of the fat content at the end of experiments was observed.

Introduction

Crangon crangon is example of a commercially important caridean whose productivity pales beside that of penaeid species because of its life history characteristics. Brown shrimp *C. crangon* is one of the smallest commercially fished shrimp species, with counts of 230-320 shrimps per pound. Commercially landed shrimps of > 50 mm thus weight only a few grams (Boddeke, 1989, this study). Brown shrimp grow and survive in habitats displaying a large temperature range between 5 and 30 °C (Lloyd and Yonge, 1947; Abbott and Perkins, 1977; M. Fonds, unpublished cited in Van Lissa, 1977; Kuipers and Dapper, 1981; Jeffery and Revill, 2002). Hence, *C. crangon* is distributed over a wide geographic area, in shallow ecosystems along the entire European coast, from the White Sea in the North to Morocco in the south and from the Mediterranean Sea till the Black Sea in the east. *C. crangon* support an important fishery in Europe, mainly the Southern North Sea and Wadden Sea and catches amount to over 30 000 tonnes per annum.

The growth of *C. crangon* is difficult to estimate reliably since no direct method of ageing is available. As with other crustaceans, growth is dependent on the sex and size of the animal as well as environmental factors like food quality and quantity, population density, light, temperature and salinity. However, in many studies these factors have not been considered resulting in a single deterministic growth figure for a species, which might not be truly representative.

Temperature and food supply have generally been considered the main extrinsic factors affecting growth in crustacean. Whereas a number of studies have examined the effect of size and temperature on growth in crustaceans (Hartnoll, 2001; Hufnagl and Temming, 2011b for review), less studies focused on the effect of food on growth which is especially true for the brown shrimp. In the laboratory, maximum growth has a positive relationship with increasing temperature and an inverse relationship with shrimp size (Tiews, 1954; Meixner, 1969; Rochanaburanon, 1974; Hufnagl and Temming, 2011a). However, juvenile shrimps show maximum growth at about 25 °C (Van Lissa, 1977) and compared to adults, juveniles show a faster growth and are more tolerant to high temperatures (Van Donk and De Wilde, 1981).

Other studies have investigated the effect of food on crustacean growth (Caudri, 1939; Lloyd and Yonge, 1947; Board, 1957; Kurata, 1962; Forster, 1970; Heywood, 1970; Adelung, 1971; Knowlton, 1974; Chittleborough, 1975; Klein Breteler, 1975a and b; Cariales and Anger, 1986; Mohamedeen and Hartnoll, 1989; Salama and Hartnoll, 1992; Oh and Hartnoll, 2000; Schatte and Saborowski, 2005; Campos et al., 2009; Hufnagl and Temming 2011a). While, several authors have demonstrated that a reduction in food quantity decreases or prevents growth of *C. crangon* (Nouvel van Rysselberg, 1937; Tiews, 1954; Meixner, 1969) fewer studies have reported whether sex is differently affected (Meixner, 1969; Lagardère, 1982; Campos et al., 2009; Hufnagl and Temming, 2011a) and none quantified the amount of food consumed.

Moreover, previous studies have always considered growth in terms of change in body length whereas estimates of changes in weight and elemental composition are more important with regard to the parameterisation of the energy budget and protein content of *C. crangon*. Furthermore, the pattern of increase in weight may differ from the increase in length. Particularly in adults may continue to put on weight without growing in length (Båmstedt, 1976; Boysen and Buchholz, 1984; Falk-Petersen, 1985).

While the analysis of growth rates in captivity requires extensive laboratory experiments under controlled food and temperature conditions, still lack of information on the growth of *C. crangon* under natural conditions (ICES, 2007; Campos and Van der Veer, 2008) to be used as reference. Recent studies showed that growth of brown shrimp is highly variable (review by Hufnagl and Temming, 2011) with food quality and quantity, rarely addressed, likely being one important factor describing it. Furthermore high growth rates are seldom observed in captivity and thus feed development for the on-growing of captive brown shrimp *C. crangon* is seen as one of the key steps to the successful establishment of viable experiments in the laboratory.

To date, controlled laboratory (indoors) experiments have relied only on the availability of natural and live food such as *Artemia* (Meixner, 1969; Criales and Anger, 1986), *Mytilus* (Campos et al., 2009), sprat and pellet fish food (Hufnagl and Temming, 2011a). These food sources and especially the often used brine shrimp or blue mussels have several beneficial characteristics: they are slow swimmers, available in different sizes and hardy enough for mass culture (Verischele, 1989). From a nutritional perspective, however, they are far from ideal as they show nutritional inconsistency depending on source, age and culture technique (Sorgeloos et al., 1986; Tucker, 1992), and they typically lack more fundamental nutrients (e.g. highly unsaturated fatty acids) which are necessary for growth and survivability of marine species (Southgate, 2003). Furthermore, the production of such foods are further associated with a need for skilled personnel, dedicated equipment and facilities, and a need for micro-algae culture as a food source for the live prey. On these bases, research into alternative diets is required before efficient and reliable techniques can be developed for crustacean species (Lavens and Sorgeloos, 2000; Holme et al., 2009). During the last decade, research into total replacement of life prey for crustaceans has attracted much attention (Holme et al., 2009 for review). However, the successful development of a formulated and artificial diet for crustacean requires an understanding of behavioural, physical (e.g. appropriate size, shape, water stability) and chemical features (e.g. balanced nutritional content) of the target species.

Integral to the development of feed for any species is the identification of their protein, lipid and energy requirements. Protein is required to provide the fundamental amino acids units for growth, while dietary lipid provides both essential fatty acids and most of the energy needed for the metabolic processes of growth (D'Abramo et al., 1997). Further energy can also be derived from metabolism of protein and dietary carbohydrates. In general, the identification of the protein and energy requirements for growth and development of animals allows the formulation of suitable diets from a range of ingredients (Tacon, 1990 and 1996).

Besides the food source also social behaviour and stocking density might affect growth and survival of shrimps. E.g. potential aggressive interactions or stress due to high stocking density might lead to increased mortality and lower growth rates. Also fighting for food can lead to severe injuries and increased mortality as well as increased growth of dominant animals while subordinate individuals may have disadvantages and suffer from lack of nutrients and/or inadequate essential component. This might also lead to increased cannibalism a known habit of brown shrimp.

Studies on the feeding habits of the brown shrimps generally classified *C. crangon* as opportunistic omnivorous/carnivorous nocturnal predator. Stomachs generally contained algae, polychaetes, gastropods, bivalves, amphipods, fish eggs and fish larvae (Plagmann 1939; Lloyd and Yonge, 1947; Pihl and Rosenberg, 1984). Feeding behaviour of *C. crangon* is similar to that of other crangonid shrimps such as *C. septemspinosa* (Price, 1962), *C. franciscorum* and *C. nigricauda* (Wahle, 1985), *C. affinis* (Kosaka, 1970; Hong and Oh, 1989) and *C. allmani* (Allen, 1960 and 1966). Based on this information, it can be assumed that *C. crangon* as a carnivore species, has both high-protein (Jones et al., 1993; Kumlu and Jones, 1995) and high-energy diets requirements (Jones, 1998) similar to that of other carnivorous crustacean like penaeid shrimps, *Penaeus japonicus* (Moe et al., 2004) and mud crab, *Scylla serrata* (Holme et al., 2009). Despite the numerous studies on *C. crangon* (L.), there are no studies known to the authors available that focus on the nutritional requirements except for the only one study carried out by Regnault (1977). He found that highest growth was obtained using food containing 60% of proteins for juveniles, while 30% was sufficient for older animals.

The major objective of this study was to identify the best protein/carbohydrate/fat composition of artificial food needed to generate high growth rates of brown shrimp in the laboratory. This will provide information on how *C. crangon* reacts to the complete replacement of natural and live feed by artificial generated food. Growth performance will be measured as body composition and survival of brown shrimp. Growth rates were then compared against field growth rates of *C. crangon* derived from the instantaneous growth method. The results of this work were discussed in the context of further diet development and nutritional studies for brown shrimp *C. crangon*.

Besides food quality we also tested whether social effects like group or individual rearing affected growth. Since the aggressive interaction between individuals has major influence on the animals' growth and survival; the interactions between the animals at high stocking densities led to increased mortality and lower growth rates. Also fighting for food can lead to severe injuries and increased mortality as well as increased growth of dominant animals while subordinate individuals may have disadvantages and suffer from lack of nutrients and/or inadequate essential component which lead to cannibalism. Thus, attempts to reduce the interactions between individuals have been made by using animals at the same size class as well as sex separated. These attempts were thought to decrease aggressive behaviour and increase the growth.

Materials and Methods

Sampling and measurements

Live brown shrimps (30.0-34.9 mm) were collected in the Wadden Sea in shallow coastal waters (about 10 to 100 cm water depth) off Büsum (54° 07’ N and 08° 51’ E) using a push net during very low tide. Short haul duration, carful capture and handling of specimens were considered to provide shrimps from damage and stress. Sampling time was limited to at maximum 10 min (Gamito and Cabral, 2003). Net dimension were 1.44 m width and 23 cm height with 1.8 mm mesh size.

Samples were taken in 2011 on August, 16th, August, 30th and September, 13th. On each sampling data Temperature (°C) and salinity (PSU) were measured. Live specimens were transported in a 100 l box filled with aerated sea water to the Institute for Hydrobiology and Fisheries Science (IHF) laboratory, Hamburg, Germany, where the experiments were started approximately two to three hours after catch.

At the beginning and at the end of the experiments, individual’s total length (*TL*, mm), and wet weight (*WW*, mg) were measured. *TL* was measured from top of the rostrum to the end of the telson to the nearest 1 mm using a USB camera (UI-1485LE 2560 x 1920 pixels) equipped with a Pentax C3516-M lens and a Matlab routine (The Math works, Inc., Natick, MA). *WW* and *DW* were determined to the nearest 0.1 mg using an electronic digital balance (Satorius ± 0.0001 g). Male and female shrimps were distinguished on the basis of external characteristics of the first pleopod (presence or absence of the appendix masculine (Lloyd and Yonge, 1947). Prior to the experiments, a sample of 48 individuals (24 males and 24 females) were randomly selected and stored at - 20 °C for both initial body size measurements and initial proximate body composition analysis.

While, at the end of the experiments, shrimp were immediately freeze-dried for 24 h and weight to the nearest 0.1 mg (dry weight: *DW*) by electronic digital balance (Satorius ± 0.0001g).

Tank system

The experimental tank systems consisting of 6 tanks were purpose-built for this study and situated in a water recirculation system at IHF-laboratory (KII). Each tank had 24 separated compartments (separated by removable partitions) in two columns a total surface area of 0.63 m^2 (61.0 cm x 103.5 cm) and a height of 21.0 cm (Figures 4.1 and 4.2). The whole tank was covered by a transparent plastic cover to allow eye observation and to prevent shrimps from escaping.

Flow rates and the exchange of water were kept constant during the period of experiments providing 100 % water exchange/day. Water temperature was kept at 17.6 ± 0.4 °C (mean ± sd) with the help of an electric heater and the system was artificially illuminated (10L : 14D). An overview and more details about the system components and the tank are available in Figures 4.1 and 4.2 respectively.

Reference group and moult experiment (ME)

Quetin and Rose (1991) and Nicol et al. (1992) outlined a methodology for the measurement of instantaneous growth rates (IGR), based on growth increments, and demonstrated both growth and shrinkage in freshly caught krill. We used this method to generate reference growth rates from the natural environment. The technique was also extended to examine the effect over time of feeding on the mean growth rate.

The IGR method allows a growth estimated that is highly related to the growth rate in the field (Perger and Temming, 2012). Animals are collected in the field, measured and stored individually in the laboratory. Those animals that moult within the first two days will likely show increments that they would have showed in the field as well and can thus be regarded as reference sample in our experiments.

Here live shrimps were randomly collected from the catch, separated into male (m) and female (f), measured and weighed and then placed into the individual compartments of the tanks (MEm and MEf). The tanks were maintained at 17.6 ± 0.5 °C, ambient surface seawater temperature as measured in the field during the sampling. No additional food source was added; thus allowing us to measure the growth rate using the instantaneous growth method (IGR) which is assumed to be representative of field condition.

Shrimps were checked every 6 h visually (6 h period was standardized by the author) for mortality and moults. If a shrimp had moulted both the animal and the exuviae were removed and the new *TL* of the shrimp was directly measured. The change in size at moult (moult increment) was noted and the growth rate (moult increment/intermoult period) was estimated. Only those shrimps that moulted within a short period after catch were considered as longer periods are biased by rearing conditions and begin to reflect laboratory rather than field condition (Quetin and Ross, 1991). Brown shrimp start to reduce and later even stop feeding prior to actual moulting (Dall et al., 1990). This period is about 2 days long and thus C. *crangon* have been incubated for only two days during the laboratory experiment.

The daily moult rate can be estimated by dividing the total number of shrimps at the start of an incubation day by the number of observed moult events per day. The intermoult period can be calculated as the inverse of the moult rate. Dividing moult increment by the intermoult period gives the growth in length per day (Ross et al., 2000).

Basic premises of the technique are that: (1) the moulting number each day is relatively constant; (2) the growth increment is not affected by the incubation condition for the 2 day period post-capture (Nicol et al., 1992; Tarling et al., 2006); (3) the moult interval is not affected by incubation; (4) the changes in length, increase or decrease, before and after moult reflect the feeding and growth conditions over the previous intermoult period.

Feeding experiment

Both individual (IE) and group (GE) feeding experiments for males (m) and females (f) were carried out over a six week period. One formulated diet (as described further down) was used in this study and animals were fed at a rate of 10 % wet weight once daily at 18:00 hours. Animals were individually measured (*TL* and *WW*) at the start of the experiment, then again biweekly and at the conclusion of the six weeks feeding study. In each tank, the total weight (Σ *WW*) and number of shrimps was measured biweekly to adjust the food ration according to the growth. Mortalities were recorded, and only animals that died during the first day were replaced with similar sized animals. All tanks were carefully cleaned on regular basis and uneaten food was removed daily. Exuviae of moulted animals were removed immediately to avoid providing a supplementary nutritional source and these moulting events were recorded. Animals that died during the experimental period were also removed and calculations were always based on the actual number of animals being alive on the time of measurement.

For the experiments where individual growth was considered (IE), a total of 48 *C. crangon* (24 males and 24 females) were distributed over 48 compartments in two tanks (one tank for each sex), with an average *WW* of 269.7 ± 37.3 mg and *TL* of 32.8 ± 1.6 mm for males and an average *WW* of 266.3 ± 30.0 mg and *TL* of 32.4 ± 1.3 mm for females, respectively.

In the group experiment (GE), a total of 48 *C. crangon* (24 males and 24 females) were equally distributed over two tanks stocking 12 shrimps per column with an average *WW* of 260.8 ± 30.6 mg and *TL* of 32.3 ± 1.1 mm for males and an average *WW* of 274.6 ± 34.2 mg and *TL* of 32.6 ± 1.4 mm, respectively .

The mean final *WW* per tank was determined by dividing the total weight in each tank by number of animals. Weight gains (*WG*), specific growth rate (*SGR*) and survival rate (*SR*) were calculated using the following equations:

$$WG = FBW\,(\text{mg}) - IBW\,(\text{mg}) \tag{1}$$

$$SGR = ((\ln FBW - \ln IBW) / \text{t}) \times 100 \tag{2}$$

$$SR = (\text{Final number of shrimp} / \text{Initial number of shrimp}) \times 100 \tag{3}$$

where:

FBW = Final body weight

IBW = Initial body weight

t = Time in days

The condition factors (K) were determined based on clusters of shrimps of one sex in the moult (ME), individual (IE) and group (GE) experiments as:

$$K = DW / TL^3 \tag{4}$$

where:

DW = dry weight (mg)

TL = total length (mm)

Experimental diet

The diet used in the experiments for this study was purpose-made to meet the macronutritional requirements of *C. crangon*. Because the dietary macronutritional requirements of *C. crangon* are unknown, the experimental diet was formulated based on 56 % crude protein (CP) and 12 % crude lipids (CL). These fractions are higher than the commonly recommended fractions used to cover the nutritional requirements for penaeid (Lovell, 1989; NRC, 1993) especially *P. japonicus* which is carnivore's species (Moe et al. 2004; Holme et al. 2009).

Semi purified diet was prepared from practical ingredients; fish meal, wheat-gluten, fish oil and wheat-starch. Fish meal and wheat-gluten were used to serve as protein sources (3:1 respectively). While fish oil used as source of lipids and wheat-starch for carbohydrates. The chemical analysis of each ingredient is presented in Table (4.1) and the approximate analysis of experimental diets composition is presented in Table (4.2).

The experimental diets of the study were prepared by individually weighing of each component and by thoroughly mixing the minerals, vitamins and CMC with wheat starch. This homogenous mixture was added to other components together with oil. De-ionized cold water (up to 30 % of the total amount) was added after the ingredient has been perfectly mixed, which was then extruded. The produced pellets were dried at room temperature for three days to about 10 % moisture then diet was stored until used.

Chemical and statistical analysis

At the end of the experiments and after the measurements, all shrimps per tank were combined blended, homogenized and stored at - 20 °C for subsequent analysis. The proximate composition of shrimp and diet samples were analysed (3 replicates per sample) for dry matter, crude protein, crude fat and ash content according to the Association of Official Analytical Chemists (1995). Dry matter was determined by gravimetric analysis following freeze-drying for 24 h. Crude protein (N % x 6.25) was calculated from the determination of total N applying the Kjeldhal method and crude fat by Soxhlet extraction. Ash content was calculated by gravimetric analysis following loss of mass on ignition at 550 °C for 2 h. Carbohydrate content was calculated as the dry matter difference remaining after the determination of crude protein, crude fat and ash content. Gross energy was calculated based on known energetic value of protein, fat and carbohydrate (Brett, 1973).

The obtained results were statistically analyzed using one-way analysis of variance (ANOVA) using SPSS version 18 statistics software package. Duncan's multiple range test was used to compare differences between means when significant *F*-values were observed ($p<0.05$).

Results

Growth indices and survival

Reference growth and moult experiments (ME)

From the field sampling a total of 144 shrimps (72 males and 72 females) were directly analysed. The average initial *TL* of the shrimps used in the present study was 34.6 ± 2.4 mm (mean ± sd) and 34.7 ± 2.6 mm for males and females, respectively. The final mean *TL* was 36.2 ± 1.8 mm and 37.6 ± 2.9 mm for males and females, respectively. The individual length increments observed during the two day period after capture ranged from 1.7 to 3.0 mm with a mean (± sd) of 2.5 ± 0.4 mm for males, and from 2.0 to 3.6 mm (min, max) with a mean (± sd) of 2.8 ± 0.5 mm, for female shrimps, respectively.

The shrimps' mean initial dry weights, as measured from the subsample stored prior to the experiments which have the same starting *TL*, were 69.9 ± 8.5 mg and 80.2 ± 10.6 mg for males and females, respectively. While the mean final dry weights, measured at the end of the experiments, were 69.8 ± 9.6 mg (from 54.7 to 89.9 mg) and 81.6 ± 17.9 mg (from 49.1 to 113.0 mg) for males and females, respectively.

Condition factors (*K* values) at the end of the experiments ranged from 0.5 to 2.0 and from 1.4 to 1.8, for male and female shrimps, respectively. The female mean *K* was 1.5 ± 0.1 whereas the male mean *K* was 1.2 ± 0.4. Field condition values for males and females ranged from 1.7 to 2.2 (2.0 ± 0.2) and from 1.7 to 2.3 (2.1 ± 0.2), respectively. However, the initial body size (*TL* and *WW*) and finale body size were not significantly different ($p \leq 0.05$) between males and females. During the experiments, survival rates of 98 % for male and 97 % for female shrimps were observed. Highly significant values were determined between weight gain of males and females. Females increased weight by 22.5 ± 7.5 mg and males by 16.9 ± 5.3 mg. Also the growth rates between the sexes showed highly significant differences ($p \leq 0.05$). The growth rates of females were higher (0.46 mm/day), approximately double, than those of males (0.22 mm/day, Table 4.3), while the intermoult period was shorter in females (6 days) than in males (11 days).

Individual feeding experiment (IE)

In the individual feeding experiment (24 males and 24 females), the initial mean total length was 32.9 ± 1.6 mm and 32.4 ± 1.3 mm for males and females, respectively. The mean final *TL* was 36.4 ± 2.7 mm and 36.6 ± 3.2 mm for males and females, respectively (Figure 4.3a). Individual length increments (start *TL* - end *TL*) ranged from 0 to 7.4 mm with a mean value of 3.3 ± 2.7 mm for males. Length increments of females ranged from 0 to 8.8 mm with a mean value of 4.3 ± 3.0 mm (Figure 4.4a)

Mean initial dry weights were 69.9 ± 8.5 mg and 80.2 ± 10.6 mg for males and females, respectively. Mean final dry weights were 86.4 ± 22.1 mg (from 48.1 to 121.9 mg) and 89.2 ± 31.5 mg (from 45.6 to 138.1 mg) for males and females, respectively.

Final condition factors (*K* values) at the end of the experiment ranged from 1.5 to 2.0 (mean ± sd: 1.8 ± 0.2) for males and 1.4 to 2.1 (mean ± sd: 1.7 ± 0.2) for females, respectively. In contrast the field condition values (*K*) for males and females ranged from 1.7 to 2.2 (mean ± sd: 2.0 ± 0.2) and from 1.7 to 2.3 (mean ± sd: 2.1 ± 0.2), respectively.

The initial wet weight ranged from 205.2 to 317.8 mg with a mean wet weight of 269.7 ± 37.3 mg and from 209.7 to 307.6 mg with a mean wet weight of 266.3 ± 29.9 mg for males and females, respectively. The final wet weight ranged from 212.3 to 459.5 mg with a mean wet weight of 342.5 ± 69.3 mg and from 232.0 to 538.2 mg with a mean wet weight of 370.9 ± 94.9 mg for males and females, respectively (Figure 4.3b).

The differences in final wet weight of shrimps were reflected by differences in specific growth rate (*SGR*, Table 4). After the 6-week period, the average *SGR* was with 0.79 and 0.57 $\%\cdot\text{day}^{-1}$ significantly higher ($p \leq 0.05$) for females than for males. In contrast to *SGR* survival was significantly higher for males (58%) than for females (42%).

However, initial body size (*TL* and *WW*), final *TL*, *DW* and GR were not significantly different ($p \leq 0.05$) between males and females. Final *TL*, *WW* (Figure 3), *SGR*, *WG* and *IMP* were significantly affected when compared with the instantaneous growth experiments (ME).

Group feeding experiment (GE)

The shrimps' initial *TL* (mean ± sd) in the group feeding experiments (24 males and 24 females) were 32.3 ± 1.1 mm and 32.6 ± 1.4 mm for males and females, respectively. The final *TL* ranged from 31.1 to 40.2 mm (mean ± sd: 36.5 ± 2.7 mm) and from 31.9 to 40.5 mm (mean ± sd: 36.9 ± 2.2 mm) for males and females, respectively (Figure 4.5a). The length increments (start *TL* - end *TL*) ranged from 0.8 to 8.9 mm with a mean value of 4.3 ± 2.4 mm for males and ranged from 1.4 to 7.6 mm with a mean value of 3.5 ± 2.5 mm (Figure 4.4b)

Condition factors (*K* values) at the end of the group experiments ranged from 0.8 to 3.2 (mean ± sd: 1.7 ± 0.7) for males and ranged from 1.5 to 3.4 (mean ± sd: 2.1 ± 0.7) for females, respectively. The field condition values (*K*) for males and females ranged from 1.7 to 2.2 (mean ± sd: 2.0 ± 0.2) and from 1.7 to 2.3 (mean ± sd: 2.1 ± 0.2), respectively.

The initial *WW* ranged from 204.6 to 325.0 mg with a mean wet weight of 260.8 ± 30.6 mg and from 202.0 to 349.6 mg with a mean wet weight of 274.6 ± 34.2 mg for males and females, respectively. The final *WW* ranged from 217.4 to 469.3 mg with a mean wet weight of 340.1 ± 75.4 mg and from 236.0 to 494.1 mg with a mean *WW* of 382.4 ± 62.1 mg for males and females, respectively (Figure 4.5b).

At day 42 the average specific female growth rate (0.79 $\%\cdot d^{-1}$) was significantly higher ($p \leq 0.05$) than the male growth rate (0.63 $\%\cdot d^{-1}$). Survival rate of male shrimps (58 %) was higher than for female shrimps (42 %).

While initial *TL*, initial *WW* and final *TL* were not significantly differed between males and females ($p \leq 0.05$), the final *TL*, *WW* (Figure 4.2), *DW*, *WG* and *SGR* were significantly affected by adding the artificial diets in both sexes where high significant values were observed in female shrimps (Table 4.4).

Protein and lipid contents

Data concerning the body composition at start and end of the individual and group experiments for males and females *C. crangon* are presented in Table (4.5). No significant differences ($p \leq 0.05$) in crude protein content (approximately 56 %) of the final body composition between the control group with GE and IE were observed for and between sexes were observed.

For both: individual and group experiments, a significant increase of the fat content at the end of experiments was observed. Values ranged from 4-6 % in males and 6-7 % in females, which is comparable to the field animals. The body fat contents (%) in the GE were 18.4 ± 2.3 and 17.5 ± 1.0 for males and females, respectively. This ratio is higher than the percentage reached in the IE (Table 4.5). These contents were higher than the fat content of the initial *C. crangon* group. However, no significant differences in the crude fat content (%) between the individual and the group experiment were observed.

Ash contents (%) at the end of both experiments (IE and GE) were not significantly different between males and females but were slightly higher in the control than in the feeding experiments. Dry matter content (%) at the end of the experiment was higher in the GE (85 %) than in the IE (82 %) and the control (81%).

At the end of experiments, the highest energy levels were reached in GE with a mean of 556.5 ± 9.0 and 545.2 ± 8.6 kJ 100 g^{-1} $shrimp^{-1}$ for males and females, respectively. The mean energy level calculated (kJ 100 g^{-1} $shrimp^{-1}$) for IE were 536.9 ± 8.1 and 539.4 ± 5.2 for males and females, respectively. However, the energy levels were increased significantly ($p \leq 0.05$) in the feeding experiments when compared to start energy levels with 514.5 ± 7.8 and 508.5 ± 6.3 kJ 100 g^{-1} $shrimp^{-1}$ for males and females, respectively (Table 4.5).

Discussion

Practical application

Previous studies on *C. crangon* suggested that four major factors affect the growth rate: temperature, body length, sex and food quality (Hufnagl et al., 2010a and 2010b; Hufnagl and Temming, 2011a). However, to minimize these effects that can under and/or overestimate the growth components' (moult increment and moult interval) the following standard protocol was established and applied in the present study.

The positive effects of temperature on growth were observed in previous studies (del Norte-Campos and Temming, 1998; Campos et al., 2009; Hufnagl and Temming, 2011a). Therefore, the present study has been carried out during the summer with narrow water temperature range, from 15.7 to 17.6 °C.

In general, growth decreased with increasing body length; small shrimps grow faster than larger ones (Kuipers and Dapper, 1981; del Norte-Campos and Temming, 1998; Hufnagl and Temming 2011a). Thus, individuals *C. crangon* with total length ranged between 30.0 to 40.0 mm were used in the present study.

The differences in growth observed between males and females of *C. crangon* could explain part of the growth variability reported in previous studies with mixed sexes (Hufnagl and Temming, 2011b).

The effects of feeding and food type have been extensively studied by several authors (Hufnagl and Temming, 2011b for historical review). These studies indicated that the feeding and food type have high impact on growth rate while no studies on artificial diets has been established (see introduction part). Hence, the present work was conducted to clarify whether brown shrimp *C. crangon* can be successfully reared under completely replacement of natural feed (effects of formulated feed).

In undertaking this study we had the advantages over Perger and Temming (2012) that aspect of accurate measurement of length before and after moult has been standardized using digital images via camera system which was especially established for the present work as described in the material and method part.

Moult Experiments (ME)

Moult intervals and body length increments

In the present study, short moult intervals have been observed comparable to previous studies (manuscript 3) or even shorter than the minimum intermoult period estimated by Hufnagl and Temming (2011a) as 7 days. In a meta- analysis of all literatures published, Hufnagl and Temming (2011a) showed higher (twice) intermoult periods than that estimated in the present study. In fact, these long intervals reported by many authors could be influenced by laboratory conditions such as suboptimal food condition (Plagmann, 1939; Meixner, 1966; Evans, 1984; Oh and Hartnoll, 2000; Campos et al., 2009; Hufnagl and Temming 2011a). However, our results support Perger and Temming (2012) who estimate that the same moult interval for females shrimps although they sampled only individuals from the slow growing overwintering cohort with several individuals with 0 mm or even low increment. Thus, it seems that moulting occurs even if there is no benefit for the individual when the moult increment is zero.

Only large increments for females shrimp (ranged from 2.0 to 3.6 mm/day) were observed in the present study compared to Perger and Temming (2012) with 0 to 3.4 mm increment per day, the reason is most likely cohort effects than laboratory effects; spring or summer cohort which translated to faster growth increments than the overwintering cohort.

Growth rates (*GR*)

In the present study, growth is measured with the instantaneous growth rate (*IGR*) method as changes in length during moult (moult experiment) which is assumed to represent the growth of the previous intermoult period (*IMP*). The *IGR* of freshly caught *C. crangon* that moulted during the first two days following collection was positive for sexes in all experiments. The obtained growth rates were as high as the results obtained in field studies by Beukema (1992) and Perger and Temming (2012). In the laboratory comparably high values were reported when live food provided (Meixner, 1969; Labat, 1977; Dalley, 1980; Hufnagl and Temming, 2011a) while was lower growth rates were observed when shrimps were fed only nematodes in the early study conducted by Gerlach and Schrage (1969). The effect of food on growth was discussed in more detail by Hufnagl et al (2010).

In addition, growth in females was higher than in males at the same size. This difference is comparable to those in previous studies on *C. crangon* both in the laboratory (Dornheim, 1969; Labat, 1977, Oh et al., 1999) and field observations (Lagardère, 1982; Campos et al., 2009; Hufnagl and Temming, 2011a). Similar growth differences between males and females were reported for other crangonids e.g. *A. dentata* (Couture and Filteau, 1971), *C. septemspinosa* (Haefner, 1972), *C. nigricauda* and *C. franciscorum* (Krygier and Horton, 1975), *N. antarcticus* (Bluhm and Brey, 2001), and *Philocheras trispinosus* (Labat, 1984).

Female growth rate and moult interval was estimated as double than male values. The explanation could be that female *C. crangon* can only be fertilized directly after moulting when the exoskeleton is soft (Boddeke et al., 1991); therefore, maturation and reproductive processes may trigger moulting independent of growth rates and recent feeding. Furthermore, the size-at-maturation threshold differs for males and females, whereby males become mature at a smaller size (22-43 mm total length) than females (30-55 mm total length) (Lloyd and Yonge, 1947; Boddeke, 1966; Muus, 1967; Meixner, 1970; Gelin et al., 2000; Oh and Hartnoll, 2004).

Feeding Experiments (IE vs. GE)

Effect of formulated diet on growth (body size)

When the components of crustacean growth (moult increment and moult interval) were analysed separately, it was apparent that both of these factors were affected by diet. The moult increments were lower during the feeding experiments than the *IGR* experiments. In addition, the intermoult period was longer than that in the moult experiments, resulting to low growth rate. Similar to low growth rates, the dry weight condition values (*K*) were lower in the feeding experiments than in moult experiments when used as reference.

Several authors observed growth rate of *C. crangon* reared under laboratory conditions when different natural feed were provided (Hufnagl and Temming 2011a for historical review). Hufnagl and Temming (2011a) indicated a significant food type effect during growth experiments, with live copepods being the optimal diet (0.2 - 0.3 mm/day). High growth rates were also observed in laboratory experiments when *Artemia nauplii* were provided with about 0.53 mm/day (Meixner, 1969; Dalley, 1980).

In the present study, the lower growth rates of *C. crangon* fed with artificial diet can be attributed to nutritional condition where still lack to some essential components which are not included in our diet especially with dramatically increased mortality overtime although higher nutrient requirements for comparable carnivores species were considered (Moe et al., 2004; Holme et al., 2009). Other reason can be due to stress caused by different factors such as handling, measurements and laboratory effects, however, no indication of higher mortality after such process.

However, the results indicates that the shrimps in the moult experiment were in better condition than the animals from longer feeding experiments under controlled laboratory conditions. Lower growth rates with group experiment were observed than the individual experiments. Similar results were observed by Regnault (1976). Contrary to the present results, high growth rate was observed with group shrimps by Hufnagl and Temming (2011).

Effect of formulated diet on body composition and energy

Interestingly, the results of chemical composition analysis show that both fat contents and energy levels of brown shrimp *C. crangon* reared within 42 days in the feeding experiments is higher compared to those animals analysed as field conditions proxy, while no reduction in protein content was observed. The results of chemical composition analysis, energy levels and dry matter does not supporting the results from length growth rates. However, the fact that the formulated diet did not improve growth rate indicates that some components, rather than that the important components such as crud protein from different two resources, lipids, cholesterol, different minerals and vitamins used which are optimized for carnivores shrimp, that easily degrade are essential, such as highly unsaturated fatty acids (St. John et al 2001) and still more work are needed to achieve higher growth rates that observed in the present work.

Table 4.1: Composition of the ingredients used in the experimental diet.

Ingredients (%)	Fish meal	Wheat-gluten
Moisture	6.09	8.75
Crude protein	68.52	76.28
Crude fat	11.11	4.60
Total carbohydrates	0.75	9.52
Ash	13.53	0.86

Table 4.2: Formulation and proximate composition of the experimental diets (diet as-fed basis).

Feed ingredient	Diet (g/kg)
Fish meal	613.2
Wheat-gluten	184.2
Wheat-starch	24.2
Fish oil	43.4
Mineral and vitamin premix *	50.0
Monocalcium phosphate	10.0
Cholesterol	10.0
Soy lecithin	10.0
Vitamin C (Stay-C)	5.0
Carboxyl Methyl Cellulose	50.0
Chemical composition (DM)	
Crude protein (g/kg)	542.4
Crude fat (g/kg)	122.7
Total carbohydrate (g/kg) **	137.9
Ash (g/kg)	122.0
Gross energy (MJ kg^{-1} diet^{-1}) ***	21.3

* Vitamin and mineral mixture supplement each kg contains: 4800 IU Vitamin A; 2400 IU Vitamin D; 40 g Vitamin E; 8 g Vitamin K; 4 g Vitamin B12; 4 g Vitamin B_2; 6 g Vitamin B_6; 4 g pantothenic acid; 8 g nicotinic acid; 400 mg folic acid; 20 mg biotin; 200 mg choline; 4 g copper; 0.4 g iodine; 12 g iron; 22 g manganese; 22 g zinc; 0.04 g selenium; 1.2 mg folic acid; 12 mg niacin; 26 mg D-calcium pantothenate; 6 mg pyridoxine HCl; 7.2 mg riboflavin; 1.2 mg thiamine HCl; 3.1 g sodium chloride; 65 mg ferrous sulphate; 89 mg manganese sulphate; 150 mg zinc sulphate; 28 mg copper sulphate; 11 mg potassium iodide; 1 g acid-washed diatomaceous earth silica.

** Total carbohydrates calculated as (100 - (moisture+protein+fat+ash)).

*** Calculated using gross calorific values of 23.63, 39.52 and 17.15 kJ/g for protein, fat and carbohydrate, respectively, according to Brett (1973).

Table 4.3: Directly observed measurements in laboratory experiment (moult experiments). The values represent the mean ± standard deviation (sd) of different treatment.

Measurements	Male	Female
Initial total length (mm)	34.6 ± 2.4	34.7 ± 2.6
Range (mm)	29.4 - 39.1	29.8 - 39.8
Initial wet weight (mg)	310.7 ± 59.2	325.5 ± 70.7
Initial dry weight (mg) *	69.9 ± 8.5	80.2 ± 10.6
Final total length (mm)	36.2 ± 1.8	37.6 ± 2.9
Range (mm)	33.1 - 39.7	32.4 - 42.8
Final wet weight (mg)	313.7 ± 42.0	365.6 ± 79.4
Final dry weight (mg)	69.8 ± 9.6	81.6 ± 17.9
Dry weight condition (mg/mm^3)	2.0 ± 0.2^a	2.1 ± 0.2^a
Moult interval (day)	11	6
Moult increment (mm)	2.5 ± 0.4	2.8 ± 0.5
Wet gain (mg)	15.5 ± 6.4^a	26.2 ±12.1^b
Moults (n/tank)	13 (72)	22 (72)
Survival (%)	98	97
Growth rate (mm/day)	0.22	0.46

Mean values (± sd), in the same row, sharing the same superscript are not significantly different ($p \leq 0.05$).

* Dry weight for shrimps from the same catch and size class.

Number between brackets is the total numbers of shrimps observed.

Table 4.4: Sex-week growth response and survival performance for brown shrimp *C. crangon* fed 56% protein and 12% lipid under laboratory conditions. The values represent the mean ± sd of different treatment.

Measurements	**Individual Experiment**		**Group Experiment**	
	Male	**Female**	**Male**	**Female**
Initial total length (mm)	32.5 ± 1.6	32.4 ± 1.3	32.3 ± 1.1	32.6 ± 1.4
Range (mm)	30.2 - 35.5	29.8 - 35.2	30.3 - 34.5	30.0 - 35.2
Initial wet weight (mg)	269.7 ± 37.3	266.3 ± 29.9	260.8 ± 30.6	274.6 ± 34.2
Final total length (mm)	36.4 ± 2.7	36.6 ± 3.2	36.5 ± 2.6	36.1 ± 2.2
Range (mm)	30.7 - 40.1	31.7 - 41.8		
Final wet weight (mg)	342.5 ± 69.3^{a}	370.9 ± 94.9^{b}	340.1 ± 75.4^{a}	382.4 ± 62.1^{c}
Final dry weight (mg)	86.4 ± 22.1^{a}	89.2 ± 31.5^{a}	81.4 ± 29.6^{a}	97.2 ± 24.7^{a}
Dry weight condition (mg/mm^{3})	1.8 ± 0.2^{a}	1.7 ± 0.2^{a}	1.7 ± 0.7^{a}	2.1 ± 0.7^{a}
Moult interval (day)	22	27	33	31
Moult increment (mm)	3.3 ± 2.7^{a}	4.3 ± 3.1^{a}	4.3 ± 2.1^{a}	3.5 ± 2.6^{a}
Weight gain (mg)	72.8 ± 27.3^{a}	106.6 ± 91.4^{b}	81.5 ± 26.2^{ab}	97.6 ± 24.7^{b}
Moults (n/tank)	14 (24)	10 (24)	15 (24)	12 (24)
Biweekly Survival rate (%)	92-83-58	75-54-42	88-71-63	79-71-50
Specific Growth rate (%/day)	0.57 ± 0.03	0,79 ± 0.01^{a}	0.63 ± 0.01	0.79 ± 0.02^{a}
Growth rate (mm/day)	0.16	0.16	0.13	0.13

Mean values (± sd) in the same row sharing the same superscript are not significantly different ($p \leq 0.05$).

Number between brackets is the total numbers of shrimps observed.

Table 4.5: Effects of the artificial diet on chemical composition of shrimp *C. crangon* in the different experiments (dry weight basis).

Ingredients (%)	**Initial body composition (Control)**		**Final Body composition (Individual)**		**Final body composition (Group)**	
	Male	**Female**	**Male**	**Female**	**Male**	**Female**
Crude protein	57.2 ± 2.1	57.2 ± 1.8	55.4 ± 3.0^{a}	55.7 ± 2.9^{a}	57.3 ± 0.6^{a}	56.3 ± 1.4^{a}
Crude fat	12.4 ± 1.4	11.1 ±2.6	16.0 ± 1.7^{a}	16.0 ± 2.4^{a}	18.4 ± 2.3^{a}	17.5 ± 1.0^{a}
Ash	12.1 ± 2.4	12.0 ± 1.3	10.8 ± 2.3^{a}	10.2 ± 1.8^{a}	9.8 ± 3.7^{a}	11.0 ± 2.1^{a}
Energy (kJ 100g^{-1} shrimp^{-1})	514.5 ± 7.8	508.5 ± 6,3	536.9 ± 8.1^{a}	539.4 ± 5.2^{a}	556.5 ± 9.0^{b}	545.2 ± 8.6^{b}

Mean values (± sd) in the same row sharing the same superscript are not significantly different ($p \leq 0.05$).

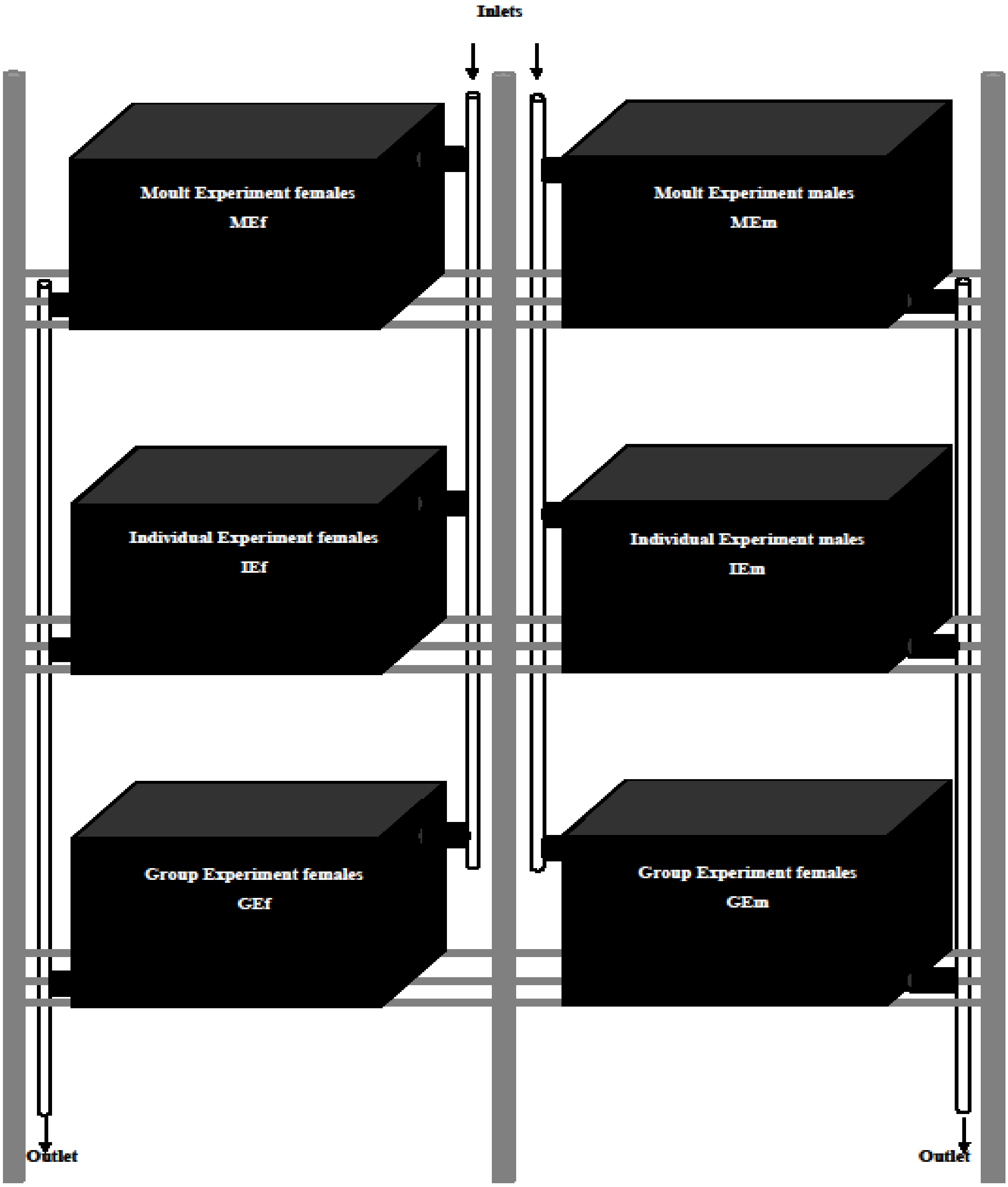

Figure 4.1: Schematic drawing of the system used for the experiments of the study.

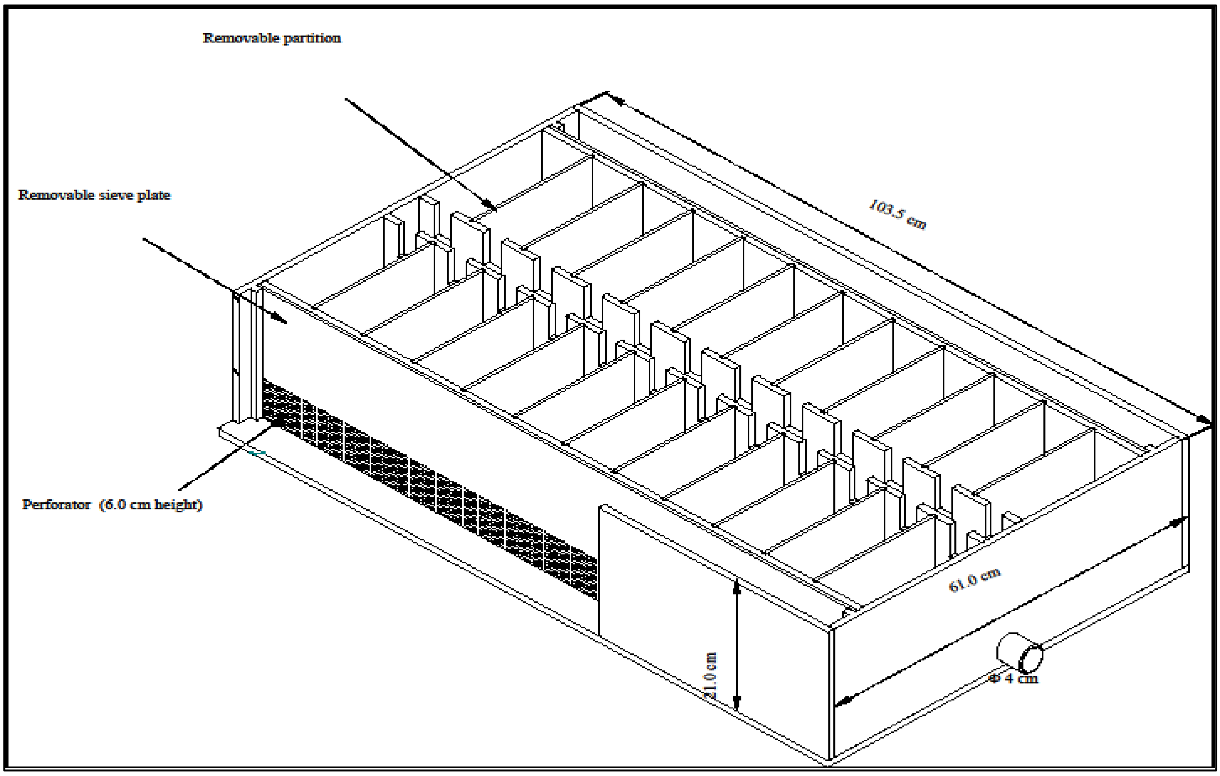

Figure 4.2: View of the experimental tank system used for this study.

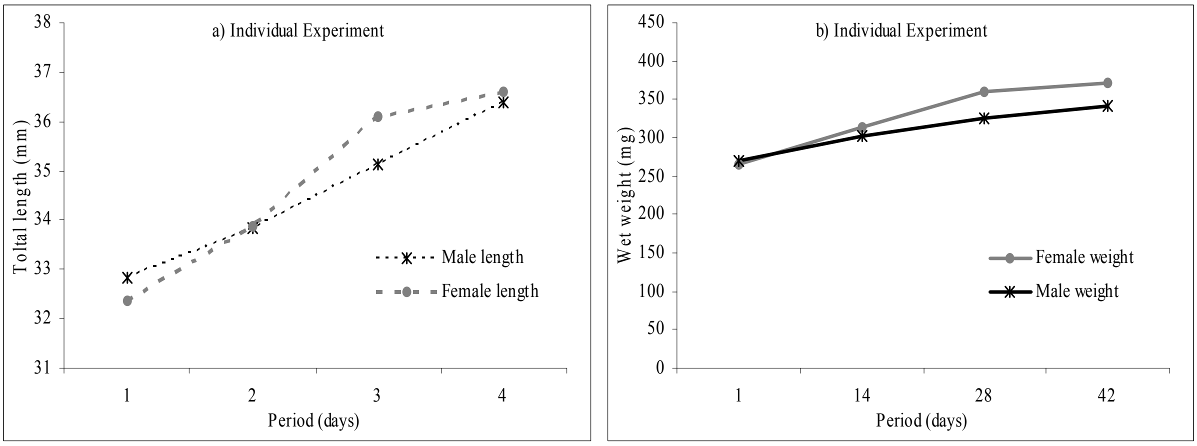

Figure 4.3: Changes in mean total body length (a) and weight (b) of males and females *C. crangon* fed on artificial diet for sex weeks in tank systems under controlled conditions in the individual experiments.

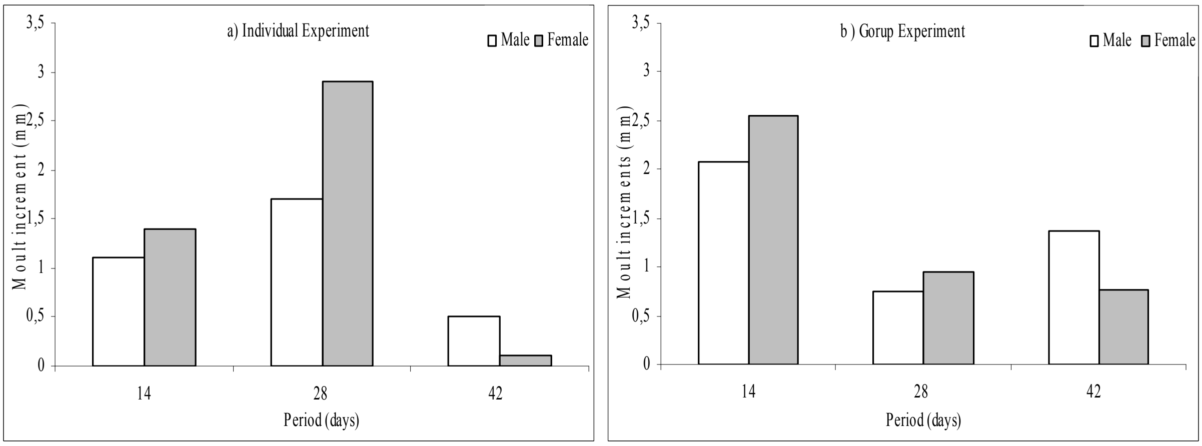

Figure 4.4: Changes in mean moult increments: individual experiments (a) and group experiments (b) for males and females *C. crangon* fed on artificial diet for sex weeks in tank systems under controlled conditions.

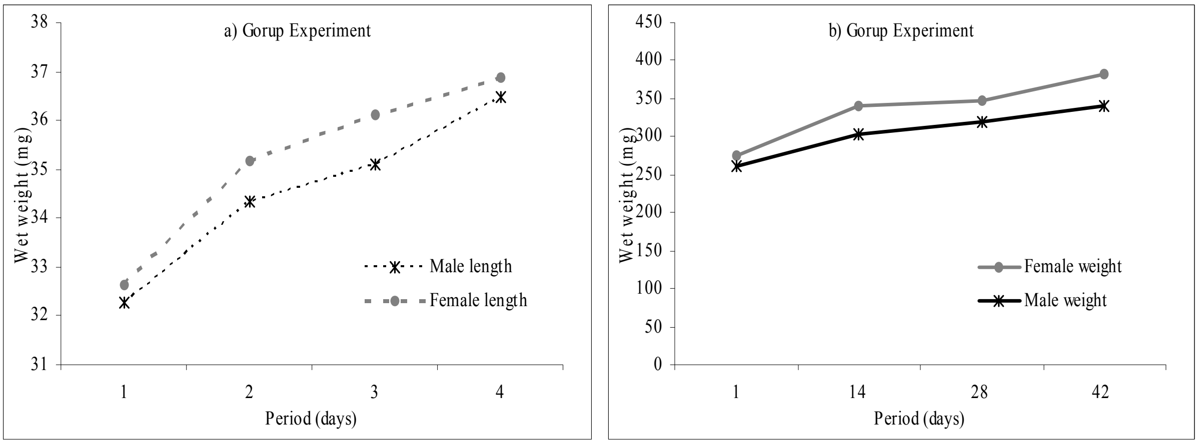

Figure 4.5: Changes in mean total body length (a) and weight (b) of males and females *C. crangon* fed on artificial diet for sex weeks in tank systems under controlled conditions in the group experiments.

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DISCUSSION AND CONCLUSION

Crangon crangon is commonly distributed as far north as the White Sea, in Russia, till Morocco in the south of Atlantic and also into the Mediterranean and Black Seas. This wide region differs greatly in environmental characteristics. Brown shrimp must then be able to cope with an extensive variety of ecological conditions especially of temperature, salinity, food quality and quantity observed in such vast geographic area. Besides ecologically important, the species is a very valuable fisheries resource in the North Sea. Although numerous studies at several levels were conducted, from the species physiology to ecological population dynamics and commercial fisheries and despite being so abundant and so extensively studied, still basic life history features like growth conditions and population dynamics are unclear. The aim of contribution was to identify the remaining gaps in knowledge and to try to fill in some of them.

Due to its commercial interest, the winter shrimp survey was established in 1991 to estimate the effects of the expanding commercial winter fishery on the shrimp stock. The survey was conducted annually in January on board RV ‘‘Solea’’ and covered the area of the German Bight beyond the 10 m depth contour. For the analysis, in the manuscript 1, the survey area during 2010 was partitioned into three zones Eastern (Dutch), Central (German) and Northern (Danish) Wadden Sea. Based upon the previous mentioned parameters two groups of stations were identified using hierarchical cluster analysis. Group 1 consisted of samples situated in sub-tidal areas (> 20 m) water depth while the second mainly included the samples from shallow waters (≤ 20 m). Factors determining the spatial distribution were depth (less abundance in deeper areas), size (smaller animals in shallow areas) and sex (males in more shallow areas). Here our mean findings were:

- Size and abundance of the animals decreased with increasing water depth,
- Females without eggs found to be closer to the shore in contrast to males which are generally located more offshore,
- Females carrying eggs were also located offshore but generally eggs of more inshore situated females showed a higher development stage,

- The relative portion of males gradually decreased with increasing body size and thus males dominate the smaller length classes while the females dominate the bigger length classes,
- The size at which 50% (TL_{50}) of females were mature (based on our new indicator "setae") was lower (between 9 to 18 mm) than the TL_{50} values calculated based upon only ovigerous females.

Here, our results clearly indicating depth dependent size differences which, however, have been reported earlier for shallower regions and other seasons (Janssen and Kuipers, 1980; Del Norte-Campos and Temming, 1998). This behaviour might indicate a lower tolerance of larger shrimps to extreme hydrographical situations like strong salinity and temperature gradients in shallow intertidal areas. Ovigerous females were mainly found in deeper areas. Unique for the winter situation is that water temperatures in deeper areas are higher and more stable. This might be favourable for a constant ovary and egg development. However, this pattern of migration (sex dependent seasonal migrations) has also been recognized for the Severn Estuary and the Bristol Channel by Henderson and Holmes (1987). They have suggested that this was to avoid the inshore and lower salinity parts of the estuary during the winter, while Lloyd and Yonge (1974) attributed it to the avoidance of cold waters rather than low salinities. Generally another aspect of the distribution of egg carrying shrimp in winter is important. The positions of these shrimp determine ultimately the drift paths of the pelagic larvae and hence the locations to which the subsequent juveniles will finally recruit (Daewel et al., 2011). This aspect is however quite complex, since migration routes do not only depend on temperature, which regulates the total duration of the pelagic phase, but also on the vertical migration patterns of the juvenile shrimp. This aspect is currently not fully understood.

Overall, it seems that water temperature has affected the *C. Crangon* distribution in a way that higher temperatures in deep water (3.7 ± 1.5°C) resulted in low mean total shrimp abundance (5474 individual/30min trawl) and the presence of bigger animals. While, the opposite is true for small animals which are abundant in shallow zones characterized by colder water (1.6 ± 1.2°C) where 19164 individual/30 min trawl mean total abundance were collected. Small animals probably stayed in shallower water for two reasons, either because energetically they cannot handle a migration into deeper water or the colder water allows them to keep up reduced metabolic rates to save energy during the period of lower food availability.

In the present study the total number of egg bearing females is higher in shallower areas than in deeper areas, however, the share of females bearing eggs is higher in deeper areas than in the more shallow ones. The reason for egg bearing females being located in deeper areas might be related to the fact that a more constant or higher temperature is needed for egg development. The rate of development can be accelerated; larvae hatch earlier and are already developed at the start of the plankton bloom. Furthermore an earlier start of the larval stage before predation due to increasing temperatures and therefore increasing consumption of predator's increases might favour survival. According to Tiews (1954), mating and spawning occurs in water shallower than 20 m and the females oviposit and migrate seaward to release their larvae (Henderson and Holmes, 1987) where the conditions are favourable where warmer water and decreased predation are more conducive to development (Hench et al., 2004). This finding was not really supported in our study when using the portion of eyed eggs where both the abundance of ovigerous females and the share of eyed eggs are higher in the shallow water area than in the deeper one except in the Northern Wadden Sea area. An onshore migration of animals carrying higher developed eggs might be the reason.

Perger and Temming (2012) determined dry weight condition of freshly moulted females under laboratory conditions during 2007. Their observed values were restricted to a narrow range of physiological optimal values which can be used in the present study as a reference for the interpretation of condition values in the field. As described by Perger and Temming (2012), values >1 indicate well-fed females that have not moulted recently while values <1 indicate poorly fed females. While a considerable condition difference can be found between the studied areas, there is no considerable difference found between different depths within the Wadden Sea subareas examined here. Most of the females were well nurtured according to the previous criteria suggested by Perger and Temming (2012). Bigger shrimp have better condition (heavier) in shallow water especially near the estuaries. There it is generally colder but more productive in comparison to the deeper areas. This could be related to the weight of their gonads, as either mainly animals with well-developed gonads aims to migrate to the deeper water or only well-fed shrimps have migrated out of the shallower regions.

Between 2005 and 2007, Hufnagl et al. (2010b) investigated the nutritional condition of males and females brown shrimp using different three methods; dry weight, RNA/DNA and caloric content. Their samples were collected in very shallow areas with a push net at about 1 m water depth and in a power station inlet at about 8 m water depth. The mean dry weight condition values were slightly lower in their study than the mean values observed in ours. In our study, shrimps seem to just have begun with the period of nutrition shortage (food scarcity). An earlier start of nutrition shortage was recognised with minimum condition value at the Eastern Wadden Sea deep zone (0.86), compared to the others. However, dry weight condition seems to be quite independent of the water depth, generally, since the averages only change marginally (negligible) with changing water depth.

One novelty in this study is that females are regarded as mature once they developed setae on the first pair of pleopod. Our results indicating that the "setae" are likely to be developed shortly before the time of bearing eggs as reported on *C. crangon* (Lloyd and Yonge, 1947), *C. vulgaris* (Ehrenbaum, 1890), *Leander longirostris* (Gurney, 1923) and *Palemoninae* (Sollaud, 1923). Timing of the development should be studied in the future under laboratory conditions to test the validity of this indicator as a true maturity index.

In the present study, sex ratio was a function decreased with size in all cases examined; the relative portion of males gradually decreased with increasing body size and thus males dominate the smaller length classes while the females dominate the bigger length classes. A deviation from the 1:1 sex ratio, in the over all sites, is apparently widespread in marine crustacean (Wenner, 1972) therefore different hypotheses have been raised to illustrate such phenomenon (manuscript 1). It seems that lower growth of males than females as observed in manuscript 2 and 4 is the main reason for such skewed sex ratio toward females at medium and large size (>30 mm total length). Thus, the growth trajectory under natural environment towards recruitment to fisheries has received some attention in the past, especially in the Wadden Sea. Here reproduction occurs throughout the year with more intense settlement in spring/summer and autumn (Boddeke and Becker, 1979), while fisheries maximum is consistently observed in autumn (ICES, 1996). Hence a major discussion is still under debate: are spring settlers recruiting to fisheries in autumn? What is the contribution of the summer generation? This discussion was initiated by Boddeke (1976) who considered summer reproduction to yield the recruits to autumn commercial caches. In contrast, Kuipers and Dapper (1984) suggested that winter reproduction sustains autumn fisheries through heavy spring settlement. In other words, For Boddeke *C. crangon* growth should be fast to enable to reach the commercial size in large numbers within about four months, from summer to autumn but for Kuipers and Dapper brown shrimp would require at least about nine months till recruiting to fisheries. The different perspectives mainly rely on growth rates under field conditions. However, until now great uncertainties exist about its population dynamics and life cycle, mainly because observed growth rates are highly variable both within and between different studies.

Therefore, to bring this dispute one step further would require clarification on the growth timeframe from settlement to commercial size which, however, still not addressed that no reliable growth rate data from shrimps in the Wadden Sea are available. Therefore, an alternatives were required to estimate the growth rates based on field rather laboratory growth. And for this the new method established by Perger and Temming (2012) was used. Perger and Temming (2012) suggested new method as an extension of the instantaneous growth rate (*IGR*) assuming that the dry weight of the moulted individuals that measured directly after moulted represent the cumulative food intake and hence growth of previous intermoult period. Here, we firstly evaluated the reliability of the new method, within manuscript 2, and then we applied it into a year around frozen samples in manuscript 3.

In manuscript 2, the *in situ* growth rates of brown shrimp *Crangon crangon* in the German Wadden Sea off Büsum were measured during 2010. Growth rate was measured using the instantaneous growth rate (*IGR*) method which involved measuring the changes in individual total length (*L*) before and after moult which is not done before with the brown shrimp *C. crangon*. We used the IGR technique to follow the individual growth components (intermoult period and moult increments) to determine the effects of sex (male and females), size class (small, medium and large shrimps) and temperature (from 7.0 to 22.0 °C) on *in situ* growth of brown shrimp. In manuscript 2 our main findings were:

- Moult intervals are shorter compared to other studies,

In the present study, short moult intervals have been observed comparable to previous studies, 5 days for small size class (< 30 mm) at high temperature (22.3 °C) which, however, is even shorter than the minimum intermoult period estimated by Hufnagl and Temming (2011a) as 7 days and also shorter than the 6 days for 25-29.9 mm for females brown shrimp by Perger and Temming (2012). In a meta-analysis of all literatures published, Hufnagl and Temming (2011a) revealed generally longer intermoult periods than those estimated in the present study. In fact, these long intervals reported by many authors could have been influenced by laboratory conditions such as food (see manuscript 4 and Plagmann, 1939; Meixner, 1966; Evans, 1984; Oh and Hartnoll, 2000; Campos et al., 2009; Hufnagl and Temming 2011a).

Many authors demonstrated that longer incubation periods reflect the laboratory rather field conditions and tend to prolong the mean moulting intervals (Dall et al., 1990; Quetin and Ross, 1991; Hufnagl et al., 2010; Perger and Temming, 2012). The prolongation of moulting intervals under such conditions may also result from individuals stopping food intake, supposedly as a consequence of inadequate food. It has been demonstrated repeatedly, that starvation leads to increased moult intervals or a complete halt of moulting.

- Moult increments are larger than the increments observed in previous studies,

By using IGR method, highest increments (mean of small groups) were found as of 3.34 to 6.28 mm for males and females respectively. As an example from the most comparable study from the same study area Perger and Temming (2012) found mean moult increments between 0.8 mm (45-49.9 mm, late July) to 2.4 mm increment (25-29.9 mm, mid June) for females *C. crangon*. The study of Perger and Temming (2012) is, however, the only study with a comparable methodology. Most of the other work on brown shrimp growth refers to laboratory experiments. Only a few of these lab studies reports similar high values. For example, Hufnagl and Temming (2011b) estimated the maximum increments from laboratory experiments with groups indirectly, by multiplying estimates of G_{max}, using their own and other studies data, and moult interval. They estimated the maximum increments as 7 mm comparable to results from an earlier study by Meixner (1969).

- The presence of zero increments which are surprising given that not always shrimp were growing well in the field,

Zero increments or even negative ones have been observed with *C. crangon* but under laboratory conditions by Campos et al. (2009) in Minho estuaries. Such shrinkage also was reported for Antarctic Krill species (Lasker, 1966; Ikeda and Dixon, 1982; Buchholz, 1985; Dalpadado and lkeda, 1989; Hosie and Ritz, 1989; Nicol et al., 1992) under laboratory experiments. Nicol et al. (1992) stated that when food was restricted, individual krill began to shrink immediately and mean population growth rates decreased gradually, becoming negative after few days (> 2 days).

- Shrimps larger than 35 mm total length tend to increase their moult increments,

Such phenomenon is more obvious with females rather than in males which, may be, due to few individual males that moulted in the present study in the larger size classes. However, our results are contradicting the general assumption of the von Bertalanffy growth model (VBGF) that is length growth is decreasing with increasing the size. We speculated that such finding is due to that larger mature (between 34 to 40 mm lengths) shrimps tend to change their feeding behaviour. However, such assumption need to be investigated based on stomach contents for small and large brown shrimp size class, especially different feeding behaviour between immature and mature shrimps. Del-Norte Campos and Temming (1994) studied the stomach contents analysis for brown shrimp and found that smaller shrimps mainly feeding on meiofauna (0-24 mm length) and with increasing size shrimps tend to change their feeding behaviour toward molluscs and crustaceans even they start to eat the smaller *C. crangon*.

- Growth rate varied strongly between seasons,

We observed lower growth rate values in early spring and autumn when compared with growth rate values in late spring and summer. In spring, low growth rate value was observed which associated with large increment and long intermoult period. Likewise, similar patterns can be seen during autumn season. In contrast, higher growth rates for both males and females were observed at late spring/early summer season which associated with shortest intermoult period, 5 and 6 days for males and females respectively, as well as smaller moult increments. Since these high growth rates occur in both smaller and larger (female) shrimp at the same time, this may be less like the effect of a new cohort, as speculated by Hufnagl and Temming (2011a), but rather the effect of improved seasonal feeding conditions.

- A decreasing trend in intermoult period with increasing temperature,

This finding which, however, was reported and confirmed in previous studies (Hufnagl and Temming, 2011b for review). High *in situ* growth rates achieved here were due to increases in moult frequency associated with high temperature as well as production of larger increments. However, such high growth rates at high temperatures were reported only in few laboratory studies so far, when live food provided (Meixner, 1969; Labat, 1977; Dalley, 1980; Hufnagl and Temming, 2011a) under laboratory experiments.

- Females grew faster than males at the same size

These differences between males and females growth rate have been reported in previous studies on *C. crangon* in both laboratory (Dornheim, 1969; Labat, 1977, Oh et al., 1999) and field observations (Lagardère, 1982; Campos et al., 2009; Hufnagl and Temming, 2011a). In the present study, however, the differences were more pronounced: growth in females was about twice or even three times higher than in males at the same size. It can be speculated that this is related to the size-at-maturation threshold, which differs for males and females, whereby males become mature at a smaller size (22-43 mm total length) than females (30-55 mm total length) (Lloyd and Yonge, 1947; Boddeke, 1966; Muus, 1967; Meixner, 1970; Gelin et al., 2000; Oh and Hartnoll, 2004). From our morphometric analysis we were able to find supporting evidence: females start to become wide at the size (approximately 35 mm) where growth trajectories begin to diverge. This increase in the body volume is a precondition for an increase in accumulated dry weight during an inter moult period, which in turn leads to a larger increment in the subsequent moult.

Likewise, temperature has a great effect on brown shrimps' growth rate, as in other crustaceans (Hartnoll, 2001). Both juvenile and adult *C. crangon* are able to grow at least between 5 and 25 °C (Van Lissa, 1977). Generally, growth becomes faster with increasing temperature (Meixner, 1966; Tiews, 1954; Duran, 1997), but at highest temperatures growth may decline where it is associated with higher mortality (Hartnoll, 2001). Such a decline at high temperature was observed in the present study with larger animals (> 40 mm) and this fits with previous studies (Hufnagl and Temming, 2011a) while our results show that the optimal temperature for *C. crangon* appears to be around 22 °C, this estimation contradicts the optimal temperature determined for *C. crangon* by Freitas et al. (2007) and Campos et al. (2009) which they suggested to be around 25 °C. However, in our results were also not able to separate the effects of seasonal food supply and temperature, so further investigations are required.

The maximum in situ growth rates obtained in this study, 0.41 mm/day (20 mm) and 0.76 mm/day (30 mm) at 22.3 °C (July 23rd) for males and females respectively were higher than any other estimate reported in previous studies except the maximum growth rate reported by Campos et al. (2009) with 0.89 mm/day at 25 °C for females *C. crangon* in Northern Valosen estuaries under laboratory condition while her maximum value for males was 0.17 mm/day at 10 °C at 30-39 mm size class. High in situ growth rates observed in the present study support the theory that the winter egg production is causing the autumn peak of the following year. This finding confirmed and fitted with the previous studies by Kuiper and Dapper (1984) and Perger and Temming (2012). In contrast, Campos et al. (2010) concluded that the summer egg production leads to the subsequent autumn peaks of the following year based on the slow mean field growth rates estimated. As has been discussed already by Hufnagl and Temming (2011b) this version of the life cycle is unlikely, since due to the very high mortalities of 5 – 6^{-y} hardly any shrimp will survive this very long period.

- Perger and Temming (2012) new method was valid for males and females,

We evaluated the method established by Perger and Temming (2012), and applied it for the first time not only to both sexes, but also to data sampled year round. Deviating from Perger and Temming, we standardized the length measurements using digital images. We fixed the time to measure the dry weight to a 6 h-period directly after moult to minimize the dry weight variations following from the mineralisation.

By applying the method established by Perger and Temming (2012), 65 % and 89 % of the variance in the observed increments could be explained with the model using length and dry weight of the shrimp before moult. We have restricted the analysis to data from temperatures between 18.8 and 22.3°C, which was closest to the 18°C in Perger and Temmings study (Figure 2.3). Meanwhile, when applying the model estimated from the warm data to the data from cold temperature between 7.3 to 15.9 °C, 24.2% and 92.6% of the variance (r^2) in the observed increments were explained in males and females respectively. In conclusion, our evaluations indicate:

a) The need to repeat the measurements annually (length and dry weight) when using Perger and Temming method. Unfortunately the exact parameter values estimated for the females differ between the two studies which suggest that some experiments have to be repeated in each year. Alternatively it has to be explored if the differences are due to too few individuals in the larger size classes.
b) We can use the same equation with females even with cold temperature (considering that results based on few data) that 92% of the variance was described,
c) Males have different equation due to different body proportions at the same size in comparison with females as will as the data were more scattered (Figure 2.3a and 2.4a) due to their body composition (see manuscript 4), maturity (males become mature at smaller size than females) and
d) The share of exuviae is comparable; 17.3±2.3 % and 16.8% for present study and Perger and Temming (2012) respectively.

In summary, the instantaneous growth method (*IGR*) has been used for brown shrimp *C. crangon* for the first time to determine in situ growth rates based on moult intervals and moult increments. In principle, the method appears valid for males and females but our study has indicated that there is considerable variation in the growth rate with size, sex and season. The results agree with estimates of brown shrimp *C. crangon* growth determined by different techniques and show consistent patterns, e.g. faster growth by smaller individual at warm temperatures, better growth of females compared to males and seem to confirm the cohort effect by Hufnagl and Temming (2011a).

Practical application for the new method established by Perger and Temming indicating that further work needed including a wide range of sizes at different maturity stages of brown shrimp *C. crangon* from different populations and could be coupled with measurements of the available food supply and of the physiological condition (temperature preferences) of the brown shrimps. Clearly more effort has to be allocated to the investigation of the moulting process at low temperatures.

Also the need to apply the method with year around frozen samples, therefore, within manuscript 3, we used the growth parameters estimated via new method (Perger and Temming, 2012) with samples from April to November 2010 inferred the *in situ* nutritional condition and our main findings were:

- Two main recruitment waves during late spring and summer

In the present study a pronounced decrease in the mean total length of the field samples clearly revealed that a first immigration of new recruits occurred in late spring (between June 03rd and June 15th) while a second wave was recorded at 23rd of July. These dates correspond well with findings from earlier studies summarized in Temming and Damm (2002).

Temming and Damm's (2002) model predicted the juvenile recruitment with time lag of about 3-6 weeks. The authors speculated that the deviation might be explained by ambient temperature experienced by the eggs and the larvae, which deviated from those assumed in the model. Daewel et al. (2011) later evaluated this hypothesis with a combined analysis of drift and temperature dependent development of larval and juveniles. The results confirmed that a drift from warmer Dutch waters plays a significant role for the winter eggs and helps to explain the observed time lag between data and observations.

- Emigration pattern of larger shrimp between April and June

Based on the 1 mm total length frequency distributions of males and females, we identified a clear emigration pattern of larger shrimp (>40 mm) which were present between April and June, but then suddenly disappeared between the 15th and the 29th of June, at the same time when the first recruitment wave entered the area (Figure 3.16). These emigrating shrimps were mostly females, which are growing into the size of maturation and most likely participate in later summer spawning. In later months no clear emigration patterns are obvious, somewhat similar size distributions rather suggest a steady situation of immigration, growth and emigration (Kuipers and Dapper 1981).

- A skewed sex ratio in favour of females with increasing length class

Such a skewed sex ratio can theoretically have a number of different causes: (a) sex changes (Boddeke, 1966), (b) differential mortality (Tiews and Schumacher, 1982; Del Norte-Campos and Temming, 1998; Hufnagl et al. 2010b) and (c) lower growth of males (Lloyd and Yonge, 1947; Hufnagl et al., 2011a). In combination with our results on growth, confirming very high *in situ* growth rates for the females and a pronounced growth difference between males and females, our results support the hypothesis of Hufnagl et al (2010) that these growth differences alone can account for the observed patterns of decreasing male share with size.

- Females grew faster than males (25-50%) faster than the observed in other studies

In all studies that took sex specific growth into account females were growing faster than males (see Hufnagl and Temming, 2011b for review). If these data are jointly analyzed females were on average 20% heavier than the males. *Crangon crangon* most likely follows a pure searching mating tactics which means that encounters at the right time (right after a female moult) lead to mating. In pure searching systems (Correa and Thiel, 2003) males are searching their mating partners and after a short act both partners separate immediately. There is generally no intrasexual competition (male-male) therefore males in these systems are smaller than females. Additionally female fecundity is generally correlated with female size (Bauer, 2006) which is not true for males. The higher the probability for a female is to reach a larger size, the higher the reproductive output becomes. Thus there is a permanent selection against slow growing females and for fast growing ones. Hufnagl and Temming (2011b) could show that the number of shrimps reaching size of maturity is about 5 times higher for fast than for intermediate growing shrimps and their fast growth model (for the whole population) was comparable to their female growth model. The growth rates we observed here are even higher. There might be two reasons for the difference. Either the *in situ* measured growth rates are generally higher or 2010 was and extraordinary year where shrimps in grew faster as a consequence of optimal feeding conditions. The latter aspect is supported by above average landings per unit effort (LPUE) observed in late 2010 and early 2011 (ICES 2012). If growth was higher this would have directly translated into a higher catchable biomass of brown shrimp in autumn which is generally dominated by female shrimps (Siegel et al., 2009).

- Changing body proportions with size as an indication for maturity

Our results of the dry weight-total length relationships of males and females revealed that females started to be heavier than males from 35 mm on. At the same total length (>35 mm) females start to develop a wider carapace, while the males show rather the opposite pattern. However, previous morphometric relationships showed a general increase in the width length relationship of females at the transition from immature to sexual maturity stage (> 35 mm) as reported by Wollebaek, (1908), Meyer, (1935), Meredith, (1952) and Oh and Hartnoll, (2004). If the obvious increase in carapace widths/total length proportions in the present study is actually related to sexual maturity can, only be verified by gonad histology. However, our finding can also be related to the pronounced growth differences between the sexes, especially for the larger individuals. Higher increments can only be produced, if the animal can store larger amounts of accumulated dry weight within the exoskeleton during the intermoult periods. A change in the body proportions yielding a wider body is exactly the mechanism to achieve this.

- Application of the Perger and Temming method

A surprising result of the present work is the repeated observation of large female shrimp having higher length growth rates than smaller females at a number of sampling dates between June and August as also shown in manuscript 2. If the directly observed moult increments in Manuscript 2 are inspected for a confirmation of this result, it can be seen that larger females actually have a tendency to produce also larger increments, a pattern that is not found in males. Such results (for the females) are contradicting the assumptions of a growth trajectory following the Bertalanffy growth function (VBGF) as described before.

In the present study, we have applied the results from moulting experiments (presented in manuscript 2) to parameterize the Perger and Temming (2012) model .The resulting growth rates were low in April and May and started to increase only in June, at the time when also the new recruitment wave entered the area.

Over all, the share of starving brown shrimp was slightly higher in males than females to reach 35% and 32% for males and females respectively. For both males and females the share of starving individuals was high during spring season while reached the lower value during summer. The seasonal pattern was in general inversed to that of the growth rate confirming the pronounced differences between the seasons. Furthermore, in few sampling dates we observed highly share of the starved individuals as 100%. Hufnagl et al. (2010a) evaluated the condition of *C. crangon* in the Wadden Sea under laboratory conditions during 2005-2007 found that at least 25% of the shrimp population is food-limited (poor condition) while the food limitation was most pronounced in the period November until April, where up to 75% of the population exhibited signs of starvation or food limitation. Perger and Temming (2012) found that the share of starving female shrimps during 2007 varied between 15 and 33% (June 29th and July 29th) that their dry weight conditions were lower than the lowest value observed for moulting individuals in the laboratory (lowest than 1.166) during 2007.

The repeated finding of substantial amounts of starving individuals in the same area during 2005-2007 and in 2010 (Hufnagl et al 2010, Perger and Temming 2012, this study) based on different methods, strongly supports the idea that growth conditions are not always optimal in this most important brown shrimp nursery and points at stronger density-dependent food limitation in parts of the year. However, these results, especially the long starvation trials conducted by Hufnagl et al (2010) indicate also that this species is quite adapted to coping with extended periods of food limitation.

The estimated growth components as well as subsequent growth rates results were quite similar to the results based on the *IGR* method. As general pattern and before the new waves of smaller individuals arrived, long intermoult period were associated with small increments resulting in poor growth. During the late spring and summer periods both methods confirmed large increments combined with short intermoult periods resulting in very high growth rates, especially for female shrimp.

For males, mean growth rates ranged between 0.01 mm/day (mainly at 40 mm size class) to 0.32 mm/day with smaller length class (10 mm at 22.3 °C). For females, growth rates ranged from 0.03 mm/day at 10 mm length (9.8 °C) to mean growth rates of 0.65 mm/day. These values confirm, that even the highest values observed in experiments, are actually occurring under *in situ* conditions. On the other hand also very low growth rates were observed in early spring and autumn, which are comparable with similar results from other studies (Hufnagl and Temming. 2011b for review).

The high *in situ* growth rates observed in the present study finally show that the June peak of juvenile immigrants with approximately 25 mm can actually grow to commercial size of 50 mm by September and thus support the peak of commercial landings.

Although the very extensive studies on *C. crangon* (L.), there are no studies on the nutritional requirement are available, except for a study carried out by Regnault (1977). Thus in manuscript 4, our aim was to provide information on how *C. crangon* growth reacts to the complete replacement of natural and live feed which is lacking or inadequate. Here, we evaluated the effects of the artificial formulated diet and aquarium effects on the growth performance, body composition and survivability of brown shrimp *C. crangon* where field growth has estimated based on *IGR* method and used as a reference in the present work during summer 2011. Generally, shorter moult intervals, larger increments and high growth rates were highly correlates to our findings in manuscript 2. Additionally, manuscript 4 added more information on the intermoult period, moult increment and subsequent growth rates for only size length group (32.5 mm) with high individual numbers for males and females which have not been investigated before which so far was not considered in manuscript 2. For example, female growth rate and moult interval were estimated as double than male values at the same length while the moult increments were almost the same (2.5 mm and 2.8 mm) for males and females respectively. However, high growth rates observed in both manuscripts were comparable to previous studies (manuscript 2 and 4).

While, no significant differences ($p \leq 0.05$) in crude protein content of the final body composition between the control group (moult experiments) with group experiments and individual experiments for and between sexes were observed. For both, individual and group experiments, a significant increase of the fat content at the end of experiments was observed. However, the fact that the formulated diet did not improve growth rate indicates that some components that easily degrade are essential, such as highly unsaturated fatty acids (St. John et al., 2001) and more studies are still required achieving this aim.

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Eidesstattliche Versicherung

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

Hamburg,