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Growth in the brown shrimp *Crangon crangon*. II. Meta-analysis and modelling

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ABSTRACT: Existing laboratory and field data on growth were combined, reanalyzed and discussed to generate a holistic temperature-, length- and gender-dependent growth rate (G , mm d⁻¹) model for North Sea region brown shrimp *Crangon crangon* (L.). Length (L , mm) and temperature (T , °C) dependent growth rates of *Crangon crangon* are highly variable within and among studies but decrease with L and increase with T . Applying general nonlinear regression, mean growth was derived as $G = 0.02421 \cdot T - 0.00115 \cdot e^{0.08492 \cdot T} \cdot L$ ($r^2 = 0.860$). Applying quantile regression (75th percentile), a growth model describing growth of the fastest growing fraction of the population was derived as $G_{\max} = 0.03054 \cdot T - 0.00104 \cdot e^{0.09984 \cdot T} \cdot L$ ($r^2 = 0.857$). Female growth rates were higher than male growth rates and were similar to G_{\max} . In a simulation, G and G_{\max} were used with seasonally varying temperature to generate monthly length trajectories (cohorts). Further, length-based mortality was included and the fraction of each cohort attaining minimal commercial size was calculated. May cohorts (5 mm initial length), representing spring recruitment, grew to 50 mm by November if G was used. Application of the fast growth model (G_{\max}) allowed for the same length to be reached 2 mo earlier. We conclude that the autumnal peak in adult abundance in the North Sea is most probably due to recruitment from the spring cohort of the same year. Our results suggest that the previous year's summer cohort contributes little to this autumnal peak because of high cumulative and overwintering mortality.

KEY WORDS: Growth rates · Life cycle · Recruitment · Commercial fishing · Size-at-age · Moulting

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INTRODUCTION

The breeding season of the common brown shrimp *Crangon crangon* (L.) (Caridea: Decapoda) extends throughout the year along the Dutch and German coasts (Kuipers & Dapper 1984), with the highest and lowest numbers of egg-bearing shrimps being observed from February to July and September through October, respectively (Neudecker & Damm 1992, Siegel et al. 2008).

Eggs can be classified into summer (April to September) and winter eggs (October to March; Havinga 1930). Egg types differ according to size, dry mass, carbon content (Paschke et al. 2004) and larval hatch size (Boddeke 1982), with values in all cases being lower for summer eggs. Additionally, intermoult periods are shorter and number of gravid females are higher during summer, increasing the number of summer eggs in relation to winter eggs (Temming & Damm 2002).

Crangon crangon passes through up to 6 different planktonic zoeal stages that end in a benthic stage of ~5 mm total length (L) (Gurney 1982, Criales & Anger 1986). Highest abundances of postlarval/early juvenile *C. crangon* are observed on the flats and intertidal areas in late spring and early summer (May to June). At this stage, the L of juveniles is ~7–20 mm (Beukema 1992, Temming & Damm 2002).

The abundance of adult shrimps is highest during September and October (Maes et al. 1998, Henderson et al. 2006), corresponding with a peak in commercial catches (ICES 2010). The latter, if standardized for effort, can be used as an index of adult abundance, as catches are landed throughout the year. Commercial beam trawls retain shrimps >45 mm and landings are sieved to a minimum size of ~50 mm. Since females grow larger than males (Tiews 1970, Hufnagl et al. 2010a), the majority of the commercially exploited

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shrimps (>50 mm) are adult females (Tiews 1954, Martens & Redant 1986).

While Temming & Damm (2002) have shown that the spring recruitment most likely originates from the winter egg production of the previous winter, it is still not clear whether this spring recruitment generates the autumn peak of adult density. This uncertainty mainly originates from differences in reported growth rates from both laboratory and field studies. The different hypotheses assign the autumn peak in adult density either to shrimps from the same year's spring recruitment (Kuipers & Dapper 1984), the same year's summer recruitment (Boddeke & Becker 1979) or the previous year's summer recruitment (Campos et al. 2009a).

Boddeke & Becker's (1979) hypothesis obviously requires the highest growth rates followed by the life cycle model of Kuipers & Dapper (1984). The latter concept was based on laboratory growth data obtained by M. Fonds (unpubl.), but these rates were too low to connect the maximum juvenile abundance in spring with the maximum landings per unit effort (LPUE) in autumn, as discussed by Beukema (1992). Berghahn (1991) calculated that higher temperatures experienced by juveniles dwelling in tidal pools would allow for higher growth, which might close this gap. However, the data obtained by M. Fonds were not separated by gender, and will therefore likely underestimate the most relevant female growth. Finally, based on new growth experiments and results of a dynamic energy budget model (DEB), Campos et al. (2009a) suggested that >1 yr is needed to reach adult size. Their study shifts the important egg production period towards the previous years' summer.

Growth estimates in shrimp are difficult to obtain because no reliable aging method exists (Hartnoll 2001). Thus, growth information only originates from either laboratory observations, or field studies following the progression of length modes. Growth rates of *Crangon crangon* are highly variable not only within, but also among studies. Reported rates of 20–30 mm shrimps at 20°C varied from around 0 mm d⁻¹ (Edwards 1978), to >0.2 mm d⁻¹ (van Lissa 1977), to 0.5 mm d⁻¹ (Dalley 1980) (see also Fig. 1).

In a previous study, Hufnagl & Temming (2011, this volume) determined growth rates of 20–60 mm shrimps at 5 to 25°C and observed that not only temperature and *L*, but also gender and catch date, significantly influenced growth. Female shrimps grew faster than male shrimps. Shrimps from the earlier catch (May) grew slower than shrimps from the later July sampling. Hufnagl & Temming (2011) assumed that shrimps from the earlier catch were older overwintering individuals (although of similar length) than shrimps collected later, as the first recruitment peak of juvenile shrimps occurred after the May sampling. The

growth performances of the 2 groups (collected at different dates) were significantly different, with growth rates being lower for the most likely older, but comparably sized shrimps. For the faster growing, younger group, distinct gender- and temperature-specific growth patterns were observed. Due to this unexpected cohort effect, however, a large part of the study revealed only suboptimal growth rates and the data representing optimal growth remained incomplete with regard to the coverage of size, gender and temperature. Many earlier studies suffer from similar problems due to either suboptimal growth in part of the experiments, or a focus on only a few size classes or temperatures as in the case of field studies tracking cohorts.

This brought us to the idea of combining all these data sources to allow the parameterization of a full growth model based on a combined, literature based, meta data set. Since mortality in *Crangon crangon* is known to be very high (Tiews & Schumacher 1982, del Norte-Campos & Temming 1998, Hufnagl et al. 2010b), one focus of the growth model should be on maximum growth. The idea was that slowly growing individuals will not contribute substantially to the adult population because of high cumulative mortality during a prolonged period of growth to adult size. Analysis was attempted in 2 ways: (1) analyzing gender-specific data and taking mean female growth as a proxy for fast growth, and (2) conducting percentile regression to describe the 75th percentile instead of the mean growth. The first approach is based on observations by Meixner (1969), Campos et al. (2009b), and Hufnagl & Temming (2011) showing that female growth is significantly faster than male growth. The justification for the second approach is that all studies can be included, but the effect of males and poorly growing shrimp fed with inadequate prey sources can be eliminated.

If the likely growth rates of the relevant parts of the population, i.e. fast growing individuals, can successfully be described from such an analysis, it should also be possible to determine the most likely life cycle scenario. For this purpose, the growth trajectories of the different season cohorts can be calculated in combination with ambient seasonal temperature data. The clarification of the life cycle has an applied aspect, because there is a tendency to increase boat sizes and extend fishing operations during winter (Salz & de Wilde 1990, Berghahn 1991). If the Kuipers & Dapper (1984) version of the life cycle would be confirmed, such an intensified winter fishery should be monitored for any potential negative effects on recruitment.

The specific objectives of this study are therefore to (1) combine and analyze published temperature-, gender- and length-dependent growth data, (2) develop and parameterize comprehensive models of mean and

maximum growth with size, temperature and gender as explanatory variables, (3) analyze whether specific methods (field vs. laboratory) or treatments cause bias in the growth data set, and (4) describe the growth trajectories of different season cohorts in combination with seasonal ambient temperatures and mortality estimates to clarify the life cycle of *Crangon crangon* in the North Sea.

MATERIALS AND METHODS

In total, 36 studies containing growth and/or moult information on *Crangon crangon* were accessed (Table 1, see Fig. 1). The focus of this study is on the greater North Sea region between 5°W, 14°E, and 48° and 60°N. Twenty-five different growth studies were performed in this region. No genetic differences were observed for the North Sea (Luttikhuisen et al. 2008) and the population can be regarded as genetically mixed based on general ocean circulation patterns in combination with extended larval drift periods. Some studies were performed outside this defined North Sea region, e.g. in the Baltic (Dornheim 1969), in the Mediterranean Sea (Labat 1977), off Portugal (Viegas et al. 2007, Campos et al. 2009b), and in the Bay of Biscay (Lagadère 1982). These studies are also listed in Table 1 but were not used to parameterize the growth model. Besides regional separation from the North Sea, Baltic Sea brown shrimp also permanently experience salinities <16 and the effect of this low salinity on metabolism and growth is unclear. Three studies contained only information on moult increment or on intermoult period but not on growth rates (Lloyd & Yonge 1947, Regnault 1979, Schatte & Saborowski 2005).

In 2 cases (Oh et al. 1999, Oh & Hartnoll 2000), carapace length was converted to L using a relationship stated in the article. In 2 other cases (Schockaert 1968, Henderson & Holmes 1987), growth rates were extracted from graphs using a MATLAB routine. For the conversion of wet weight growth (Edwards 1978) into length growth, the L -wet weight (ww) relationship

$$ww = 4.0625 \times 10^{-6} \cdot L^{3.084} \quad (1)$$

was used ($n = 8305$, $r^2 = 0.985$; Hufnagl et al. 2010a).

From studies on toxic or stress effects, only control groups were used in our analysis (Edwards 1978, Oh & Hartnoll 2000). Data from Gerlach & Schrage (1969) were not included in the growth model parameterization as temperature was uncontrolled and varied between 5 and 25°C in their experiments.

Growth rates determined for larval *Crangon crangon* (Criales & Anger 1986, Cattrijsse et al. 1997) were added to complete the review but values were also not used in the growth model as only juvenile and adult

growth is examined in our study. Growth of larvae is often not isometric, but this is one requirement of the von Bertalanffy growth model used in the actual study. Finally, the laboratory data presented in Hufnagl & Temming (2011) were added to the data set.

Growth function. The von Bertalanffy growth curve describes growth as the net effect of anabolism (Eq. 2, left term) minus catabolism (Eq. 2, right term)

$$\frac{dW}{dt} = H \cdot W^{\frac{2}{3}} - k \cdot W \quad (2)$$

where W = weight, k = catabolic constant, equivalent to % weight loss per unit time in starving individuals, and H = anabolic constant, which is related to food intake and synthesis of body mass. Transformation of Eq. (2) to length growth ($W \approx L^3$) leads to

$$\frac{dL}{dt} = E - K \cdot L \quad (3)$$

where L = total length, $K = k/3$, and E represents anabolism. Eq. (3) was expanded by Kuipers & Dapper (1981) with temperature (T) as an additional variable influencing E :

$$\frac{dL}{dt} = a + b \cdot T - K \cdot L \quad (4)$$

where a and b are constants. In this equation, $K \cdot L$ represents length dependent metabolism. However, metabolism generally increases exponentially with T . An exponential temperature term was therefore included into Eq. (4), replacing K with $c \cdot e^{dT}$:

$$\frac{dL}{dt} = a + b \cdot T - c \cdot e^{dT} \cdot L \quad (5)$$

where c and d are additional constants. Asymptotic length (L_{∞}) can be calculated from Eq. (5) as the length where growth is zero, i.e. $dL/dt = 0$:

$$L_{\infty} = \frac{a + b \cdot T}{c \cdot e^{dT}} \quad (6)$$

This equation shows that L_{∞} is inversely related to $K = c \cdot e^{dT}$ and directly proportional to anabolism. As the exponential term increases faster than the linear term, it can be deduced that from this formulation, L_{∞} decreases with increasing temperature.

Sensitivity of growth estimates to the inclusion of specific studies or methods. Specific data sets or methods could theoretically generate bias or variability in a model based on the whole data set. Field studies might for example systematically underestimate growth rates due to length dependent emigration or predation. Laboratory studies might underestimate growth due to poor food quality or stress. To test for a general effect of a method (field/laboratory), the data set was split according to the method used and the growth model (Eq. 5) was fitted independently to each subset.

Potential bias introduced by single studies was tested: of the whole North Sea data set made up of 25 studies, 1 to 4 randomly chosen studies were excluded from the data set and parameters a to d and their 95%

Table 1. Data from different authors who determined growth rates, moult intervals or moult increments of *Crangon crangon*: source (NB: sources not used for parameterizing our growth model are specified), method (cohort or laboratory experiments), temperature range of observed growth rates, observed length classes, range of observed growth rates, determined moult intervals, gender-specific growth rates, special treatments such as influence of starvation or light on growth rates, specific laboratory conditions, net used for cohort tracking and if net selectivity was included or not, ranking if distinct cohorts were observed or not, area where shrimps were caught, time of catch, and temporal and spatial sample resolution for cohort tracking

Source	Method	Temp. (°C)	Length (mm)	Growth (mm d ⁻¹)	Moult interval (d)	Gender sep.	Special treatment	Feeding	Laboratory conditions	Net selection; type of net	Distinct cohorts	Sample area	Year time	Sample resolution
Amara & Paul (2003)	Coh.	15–20	21–31	0.163	–	No	–	–	–	Yes according to (Kuijpers & Dapper 1981)	Only small size classes	La Canche France	Apr–Sep 2000	Good: weekly & tides resolved
Beukema (1992)	Coh.	8–12	10,15,22	0.20,0.63, 0.54	–	No	–	–	–	–	Medium	Balgzand Netherlands	Apr–Sep 1983–1991	High: 3 stations 40 cores
Boddeke (1976)	Coh.	16	60–63	0.11	–	No	–	–	–	–	–	–	–	–
Boddeke (1966)	Coh.	20	50	0.18	–	No	–	–	–	No	No graph	Netherlands	–	–
Boddeke et al. (1986)	Coh.	~20	23–67	0.22–0.48	–	No	–	–	–	No correction; push net + beam trawl	Medium	Netherlands	Jul–Oct 1984 + Mar 1985	High: from 4 depths; 8 hauls but low in time
Campos et al. (2009b) (not included)	Lab.	10–25	20–40	0.0–0.8	10–30	Yes	Latitudinal growth variation	<i>Mytilus</i>	Recirc. sand, l:d 12:12	–	–	Portugal, Norway	Apr–Sep 2005/2006	–
Cattrijsse et al. (1997) (not included)	Coh.	9–22	3–10 (post-larvae)	0.26–0.38	–	No	–	–	–	No correction; 5 m beam, 1 mm mesh	Only small sizes	Westerschelde, Netherlands	Mar 1990–Oct 1991	Medium, monthly
Caudri (1939)	Lab.	6–19	20–32	0.05–0.52	–	No	Differing salinities	<i>Mytilus</i> & algae	Stationary + sand and shells	–	–	–	Aug–Oct ~1937	–
Criales & Anger (1986) (not included)	Lab.	6–18	Larvae	0.01–0.14	3–18	No	Only Artemia, larvae, test of antibiotics	Artemia, rotifers, phytopl.	20 cm ³ , 30–32 psu, water change 2 d	–	–	Helgoland	~1986	–
Dalley (1980)	Lab.	20	7–26	0.17–0.57	3–4 (Larvae)	No	Light differences	Artemia + <i>Mytilus</i> (3 d)	2 l + sand, water change 3–6 d	–	–	Isle of Man	Jan + Feb	–
del Norte-Campos & Temming (1998)	Coh.	–	10–50	0.23	–	No	–	–	–	No correction; push net	Only small sizes	Germany	Apr 1991–Oct 1992	Medium: monthly
Dornheim (1969) (not included)	Coh.	2–17	10–74	0.03–0.14	–	Yes	–	–	–	No correction; push net	–	Baltic	May–Oct 1965	High: 1–4 mo ⁻¹
Edwards (1978) (only control group)	Lab.	10–20	25	0.02	13–47	No	Oil addition	Teleosts + <i>Crangon</i>	–	–	–	Scotland	Jul Aug 1976	–
Evans (1984)	Coh.	5 + 20	15–45	no	9–175	No	–	–	–	No correction; drop net	–	Swedish west coast	1976–1977	–
M. Fonds (pers. comm.)	Lab.	2–26	8–57	0.01–0.50	–	No	–	–	–	–	–	Netherlands	–	–
Gerlach & Schrage (1969) (not included)	Lab.	5–25	25–60	0.02–0.14	–	No	–	<i>Panagrellus</i> (5 d wk ⁻¹ 1–4 portions)	20 psu, water change 30 d	No correction; push net	–	Germany	Oct 1967, Jan Apr Sep 1968	–

Table 1 (continued)

	Coh.	3-23	35-66	0.00-0.10	14-144	No				Capture-recapture, power station	Medium	Bristol Channel	1980-1982	Medium: monthly
Henderson & Holmes (1987)						No	-	-	-		Medium			
Hufnagl & Temming (2011)	Lab.	5-25	20-60	0.0-0.8	8-60	Yes	Ad lib.	Zooplankton, polychaetes, algae	Recirc., 31.7 psu, 1 d 12:12	-	-	Germany, Büsum, Eider, Elbe	2006	-
Kuipers & Dapper (1981)	Coh.	7-19	15-30	0.12-0.35	-	No	-	-	-	Yes (van Lissa)	No	Netherlands	1976-1979	Monthly
Labat (1977) (not included)	Coh.	10-20	8-46	0.01-0.38	-	Yes	-	-	-	No correction; 5 mm net mesh size	Medium	France (Bages Sigean)	Apr. 1974 - Jul 1974	Low: 11 per 2 yr
Lagarère (1982) (not included)	Lab.	15-23	39-52	0.03-0.17	-	Yes	Noise	<i>Mytilus</i>	Flow through, 55 l + sand +nylon wool	-	-	France (La Rochelle)	April 1981	-
Lloyd & Yonge (1947)	Lab.	12	32-68	-	Increments	-	-	<i>Mytilus</i>	Sand, circulation	-	-	Bristol Channel	~1947	-
Meixner (1969)	Lab.	14	10-50	0.13-0.50	11-24	Yes	-	<i>Artemia</i>	0.5-5.5 l, 18-30 psu	Short catches	-	Germany	May June 1964	-
Meyer (1936)	Coh.	5-20	15-38	0.03-0.21	-	No	-	-	-	Placed nets (Stellhamen)	No graph	Germany	May 1930-Aug 1931	High: >4 mo ⁻¹
Oh & Hartnoll (2000) (only control group)	Lab.	15	35-45	0.06-0.10	10-55	No	Feeding daily or every 5 d	<i>Nephrops</i> + prawns	34 psu, compartments in 150 l tanks, flow through	-	-	Isle of Man	~2000	63 shrimps
Oh et al. (1999)	Coh.	av. 12	32-81	0.01-0.11	-	Yes	-	-	-	No correction; 1.5 (2) m beam trawl 3 (6) mm	Yes	Isle of Man	Apr 1995-Jul 1998	High: 5 transects every 2-4 wk
Regnault (1976)	Lab.	15-19	19-40	0.11-0.33	-	No	With & without substrate	<i>Carcinus maenas</i>	45-52 l, flow through	-	-	-	Jun-Oct 1975	-
Regnault (1979)	Lab.	19	25	No	10	No	Moult cycle	<i>C. maenas</i>	Standing aerated	-	-	France (Roscoff)	Jul	-
Regnault (1981)	Lab.	12-14	~40	0.20	-	No	Starv.	<i>C. maenas</i>	-	-	-	France (Roscoff)	-	-
Schatte & Saborowski (2005)	Lab.	5-16	26-39	No	23-46	Males	Obs. sex change	<i>Mytilus</i> + <i>Crangon</i>	Flow through, sand	-	-	Germany	Nov 2003	70 males
Schockaert (1968)	Coh.	1.1-15.5	45-65	0.00-0.17	-	No	-	-	-	-	-	Belgium	1962-1963	Medium: monthly
Tetard (1985)	Coh.	15-18	26-61	0.07-0.40	-	No	-	-	-	-	Yes	France, Manche-est	Jul 1977 Sep 1982	Low: monthly in summer
Tiewis (1970)		5,10,15	35,73	No	15-28	No	-	-	-	-	-	-	-	-
Uhlig (2002)	Lab.	16-17	20-40	0.20-0.56	13-14	Yes	-	Plankton, <i>Nereis</i> , smelt, <i>Mytilus</i>	Flow through	-	-	Germany	Jul 2000	-
van Leeuwen (1975)	Coh.	14	43-51	0.13	-	No	-	-	-	-	-	-	-	-
van Lissa (1977)	Lab.	10-25	13-44	0.06-0.27	-	No	-	<i>Mytilus</i>	30 psu	-	-	Netherlands	1977	-
Viegas et al. (2007) (not included)	Coh.	14-17	5-61	0.34	-	No	-	-	-	No correction; 2 m beam, 5 mm mesh	-	Portugal	Jun 2003-Aug 2005	Medium: monthly

confidence limits for a fit with Eq. (5) were estimated.

Model fitting to subsets of data. Growth models were determined based on all 25 North Sea studies. Both growth models (Eq. 4, no T - L interaction; and Eq. 5, with 2 temperature terms) were fitted to the data, applying nonlinear regression using the statistical program SPSS. The quality of the fit was evaluated using the r^2 , the 95% CIs of the parameters, and significance levels (p) of whether a parameter is significantly different from zero.

We combined all growth rates in 10 mm L (20, ..., 80 mm) and 5°C T (5, ..., 25°C) classes (Table 2). Fast growth (G_{\max}), here defined as the growth rate of the fraction of the population growing at rates between the median and maximum observed growth rate, was calculated based on these T - L groups. G_{\max} was estimated by quantile regression (Koenker & Bassett 1978) based on the 75th percentiles. In an alternative analysis, the growth model (Eq. 5) was fitted to the mean growth rate (of each T - L group) + 1 SD.

Based on Eqs. (4), (5) & (6), annual von Bertalanffy growth parameters K and L_{∞} were calculated assuming a mean North Sea temperature of 10°C (Eq. 7). In addition, the growth performance index $\Phi' = \log(K) + 2\log(L_{\infty})$ (Munro & Pauly 1983) was calculated to allow comparison of data with those of other species.

Only 7 studies separated growth rates according to gender and 3 of them were not from the greater North Sea region (Labat 1977, Lagardère 1982, Campos et al. 2009b). The number of gender-specific growth observations was too low to estimate all parameters of Eq. (5). Thus, the influence of gender on growth was tested by linear regression of male (dependent variable) and female (independent variable) growth rates reported for similar T and L classes.

Further, Eq. (5) with a fixed parameter d was fitted to male and female growth rates from North Sea studies that separated gender (Meixner 1969, Oh et al. 1999, Uhlig 2002, Hufnagl & Temming 2011 this volume), assuming that the temperature dependence of metabolism is not gender-specific. Parameter d was taken from the G_{mean} model and was therefore based on all 25 studies.

Application of the growth model to field temperature data. In this exercise, egg and larval development was not considered. Therefore, an initial L of 5 mm was chosen, representing youngest postlarval shrimp length (Criales & Anger 1986). Eq. (5) was used in com-

Table 2. Descriptive statistics of pooled literature data (temperature–total length classes): T = temperature class (5 includes 3 to 7°C, 10 includes 8 to 12°C, etc.), L = total length classes (e.g. 20 includes 15–24 mm), n = number of observations for that class; mean, median, minimum and maximum growth rates (mm d⁻¹), percentiles, SE and SD

T	L	n	Mean	Median	Min.	Max.	25th	75th	SE	SD
5	20	6	0.09	0.08	0.02	0.18	0.06	0.14	0.02	0.06
	30	6	0.07	0.06	0.05	0.11	0.06	0.09	0.01	0.02
	40	4	0.04	0.03	0.03	0.05	0.03	0.05	0.00	0.01
	50	2	0.03	0.03	0.00	0.06	0.00	0.06	0.03	0.04
	60	2	0.07	0.07	0.06	0.07	0.06	0.07	0.00	0.01
10	20	10	0.25	0.21	0.08	0.54	0.14	0.33	0.04	0.14
	30	11	0.16	0.15	0.02	0.33	0.08	0.25	0.03	0.09
	40	11	0.14	0.11	0.00	0.28	0.09	0.19	0.03	0.09
	50	4	0.10	0.08	0.05	0.18	0.05	0.16	0.03	0.06
	60	9	0.04	0.03	0.00	0.13	0.02	0.05	0.01	0.04
15	20	19	0.31	0.31	0.12	0.56	0.22	0.36	0.03	0.12
	30	26	0.29	0.27	0.03	0.52	0.19	0.41	0.03	0.13
	40	14	0.22	0.19	0.06	0.40	0.15	0.30	0.03	0.11
	50	13	0.16	0.13	0.03	0.36	0.09	0.26	0.03	0.10
	60	12	0.11	0.08	0.00	0.29	0.05	0.18	0.03	0.09
20	20	31	0.34	0.33	0.15	0.58	0.26	0.42	0.02	0.12
	30	31	0.24	0.21	0.02	0.55	0.16	0.31	0.02	0.11
	40	11	0.25	0.22	0.10	0.48	0.14	0.34	0.04	0.13
	50	3	0.18	0.17	0.07	0.31	0.07	0.31	0.07	0.12
	60	5	0.18	0.22	0.03	0.24	0.10	0.23	0.04	0.09
25	20	7	0.40	0.44	0.21	0.58	0.25	0.46	0.05	0.13
	30	6	0.31	0.36	0.13	0.40	0.18	0.39	0.05	0.12
	40	3	0.12	0.10	0.06	0.20	0.06	0.20	0.04	0.07
	50	2	0.11	0.11	0.10	0.12	0.10	0.12	0.01	0.02

bination with daily field temperature data, to calculate growth in the field. This was done in a stepwise fashion, starting with 5 mm total length and adding to each daily step the growth increment (Eq. 5) calculated with the corresponding temperature (Eq. 7). The new length ($L_{\text{new}} = L_{\text{old}} + G$) for each day was then used for each subsequent iteration. Negative growth rates were set to zero in the calculation to avoid shrinking. For each start of a month, one cohort of animals was started with 5 mm length, and length trajectories were generated.

Daily temperatures were derived from temperature data measured in Büsum harbor, as a Wadden Sea point, and at the Weser light ship, as a near shore but open water point, applying the data presented by Temming & Damm (2002). The 2 geographical points were chosen as *Crangon crangon* dwell close to the shore but avoid low winter temperatures by migrating to deeper water (Boddeke et al. 1976, Pihl & Rosenberg 1982, Berghahn 1983). From each data series, the warmer of the 2 daily temperatures was chosen, to construct one temperature data set of likely temperatures experienced by *C. crangon*. This data set can be described by a sine function:

$$T_i = 9.8933 + 7.3877 \cdot \sin[0.01756 \cdot (i - 131.1761)] \quad (7)$$

where T_i = temperature at Day i and $i \in 1$ to 365.

Initial cohort size was set to 100 and a fraction of this cohort died each day. For adult shrimps >45 mm, an annual total exponential mortality rate of $Z = 5.3 \text{ yr}^{-1}$ was used to calculate the cohort size at the following day (N_{i+1}) based upon the present cohort size (N_i): $N_{i+1} = N_i e^{-Z/365}$. This z value represents the long term median (1956 to 2006) for adult North Sea brown shrimps (Hufnagl et al. 2010b). Mortality was applied daily, converting the annual rate into a daily rate by division with 365. Smaller shrimps most likely experience higher mortalities due to higher numbers of potential predators. Juvenile mortality can be up to 4× higher than the value determined for adult shrimps (del Norte-Campos & Temming 1998). The size effect on mortality was included into our calculations and Z for each size class <45 mm was determined according to Peterson & Wroblewski (1984). For example, a 15, 20 or 30 mm shrimp experiences a Z of 16.3, 14.4 or 10.6 yr^{-1} , respectively. This estimate is conservative in comparison to reported field measurements (Z up to 22 yr^{-1} ; del Norte-Campos & Temming 1998). Annual rates were again converted to daily rates by division with 365.

Moult interval and increment. Several studies reported data on moult intervals (intermoult periods) of brown shrimps (Table 1). In combination with data determined by Hufnagl & Temming (2011), a length- and temperature-dependent moult interval (MI) model was parameterized:

$$\text{MI} = a_{\text{MI}} \cdot TL^{b_{\text{MI}}} \cdot e^{c_{\text{MI}}T} \quad (8)$$

where a_{MI} , b_{MI} and c_{MI} are constants. Hufnagl & Temming (2011) found growth variability to be mainly determined by variable moult increments, whereas moult intervals were less variable at a given T and L .

Only a few authors (Table 1) reported data on moult increments. Fitting a T and L dependent function to these data was not possible. Maximum expected moult increments were therefore calculated as the product of the growth rate (Eq. 5, with the parameters for maximum growth) and the moult interval estimated using Eq. (8). Calculated values were compared to observed rates.

RESULTS

Crangon crangon growth was determined by modal progression analysis in 14 field studies, and through laboratory experiments in 11 studies (Table 1); 5 articles only reported moult intervals or increments, and 5 were performed outside the North Sea.

Most published studies examined growth rates at temperatures between 10 and 20°C. Growth variability was high both between and within studies (Fig. 1). At 15°C, growth rates varied between 0 and 0.6 mm d^{-1} or between 0 and 0.7 mm d^{-1} at 20°C (interstudy variability). Some authors (e.g. Schockaert 1968, Dalley 1980, Kuipers & Dapper 1981) observed growth rates in their studies that differed by >0.2 mm d^{-1} within one T - L class (intra-study variability). Highest mean growth rates of 0.57 mm d^{-1} were observed by Dalley (1980) at 20°C for a group of animals growing from 16.45 mm (mean) to 22.18 mm (mean) within 10 d (Fig. 1). Similarly, Uhlig (2002) observed mean growth rates of 0.52 (male) and 0.56 mm d^{-1} (female) for a group of 20 mm shrimps reared at field temperatures between 15.9 and 17.1°C.

Growth rates were maximum for *Crangon crangon* between 20 and 30 mm (Fig. 1) and decreased slightly towards the 10 mm class. With increasing size (>20 mm), growth rates decreased steadily. The length effect on growth rate increased with increasing temperature, and was less pronounced at low temperatures. Maximum growth rates at 10 to 25°C were ~6× higher than those observed at 5°C.

Growth rates for shrimps <10 mm (Fig. 1; Criales & Anger 1986, Dalley 1981) were <0.15 mm d^{-1} and less than the rates determined for 20 mm shrimps.

Splitting the data set into field studies and laboratory experiments did not indicate any differences with regard to either mean growth rates or growth variance, and parameter estimates were within the confidence limits of G in all cases (results not shown, but see Fig. 2 for comparison).

Parameter estimates were also not significantly influenced by single studies (Fig. 2) or by the exclusion of specific studies plus 1 to 3 additional randomly chosen studies. If single studies were omitted, the parameter estimates always remained within the 95% CIs of parameter estimates based on the whole data set (G). Maximum influence (10% deviation) on parameter b , which determines the temperature-dependent offset of the growth model, was observed if data from Hufnagl & Temming (2011) were excluded. Exclusion of growth rates determined by van Lissa (1977) and Tetard (1985) increased parameter c (which determines length-dependent growth) by 17 and 27%, whereas exclusion of Schockaert (1968), Oh et al. (1999) and M. Fonds (pers. comm.) decreased parameter c by 16, 21 and 15%, respectively. Exclusion of the latter 2 data sets increased parameter d (T effect on growth $\propto Q_{10}$) by 12 and 14%, respectively. Exclusion of the data of van Lissa (1977) and Tetard (1985) decreased parameter d by 11 and 10%, respectively. Parameter a was not significantly different from zero, regardless of which data set was excluded.

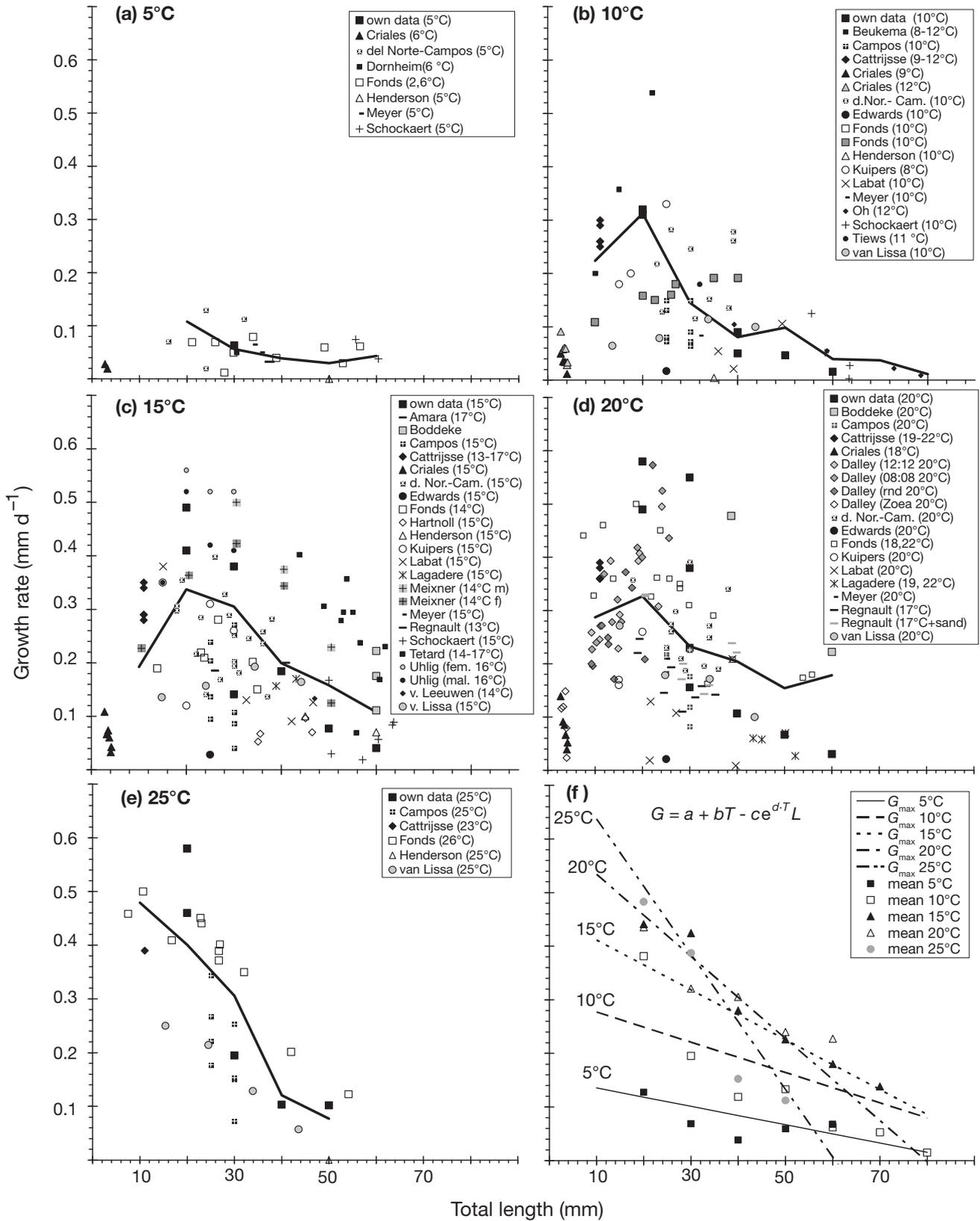
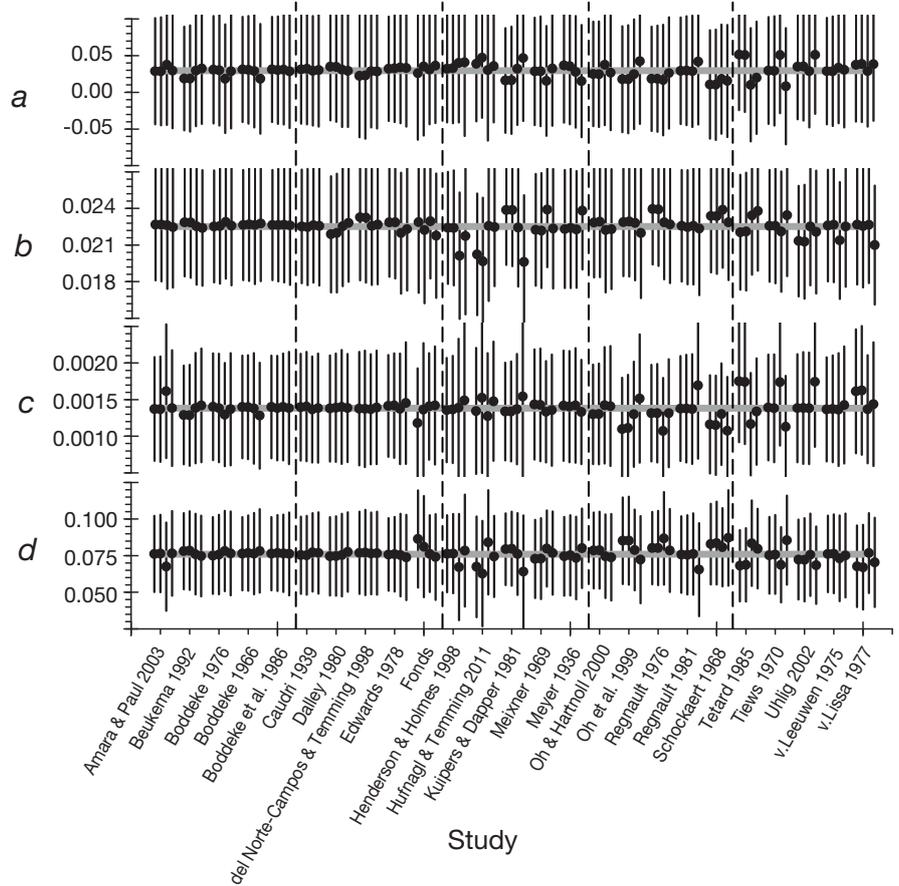


Fig. 1. *Crangon crangon*. Growth rates obtained from literature review and own data observed in the laboratory plotted according to length and temperature: (a–e) 5, 10, 15, 20, 25°C; and (f) results obtained by quantile regression. Points: 75th percentile of all North Sea studies; lines: model fitted to all data (Eq. 12)

Fig. 2. *Crangon crangon*. Growth model ($G = a + b \cdot T - c \cdot e^{dT} \cdot L$) sensitivity analysis for the influence of single studies. From top to bottom: parameters a to d . Dots: parameter estimates, and whiskers: confidence limits. For each study, 4 dots are shown: the leftmost describes the estimate when only the indicated study is taken out of the dataset, whereas the rightmost dots indicate the parameter estimates if 3 other randomly chosen studies are also left out



Growth models

All 25 North Sea studies were included in parameterizing the growth model since none of the studies influenced the parameter estimates significantly. The CIs for parameter a in Eq. (5) always included zero and was therefore omitted. Eq. (5) was fitted without this parameter. All remaining parameters were significantly ($p < 0.01$) different from zero. Both growth models (with and without the temperature interaction term) explained a high degree of variability within the data. A lower r^2 was calculated with temperature not acting on metabolism (Eq. 9; $r^2 = 0.74$) than with interaction (Eq. 10; $r^2 = 0.87$).

$$G = 0.197(\pm 0.057) + 0.011(\pm 0.002) \cdot T - 0.00435(\pm 0.0009) \cdot L \quad (9)$$

$$G = 0.02421(\pm 0.0021) \cdot T - 0.00115(\pm 0.0004) \cdot e^{0.08492(\pm 0.0144) \cdot T} \cdot L \quad (10)$$

Parameters obtained either from a fit to the mean growth rates +1 SD (Eq. 11, $r^2 = 0.85$), or by quantile regression (75th percentile Eq. 12, $r^2 = 0.83$), were comparable.

$$G_{\text{mean}+SD} = 0.03453(\pm 0.0042) \cdot T - 0.00121(\pm 0.0005) \cdot e^{0.10004(\pm 0.0144) \cdot T} \cdot L \quad (11)$$

$$G_{\text{max}} = 0.03054(\pm 0.0040) \cdot T - 0.00104(\pm 0.0005) \cdot e^{0.09984(\pm 0.0106) \cdot T} \cdot L \quad (12)$$

For both models, the parameter estimates of one model were included in the respective CIs of the other model. In the following analysis, only the parameters derived from quantile regression (Eq. 12) were used to describe fast growth.

Few North Sea studies (Meixner 1969, Oh et al. 1999, Uhlig 2002, Hufnagl & Temming 2011) separated growth rates by gender. Application of quantile regression or estimation of all parameters of Eq. (5) for a gender specific growth model was not possible. Therefore, parameter d from Eq. (10) was used and gender specific parameters b and c were determined by nonlinear regression. Eqs. (13) & (14) represent mean male ($r^2 = 0.67$) and mean female ($r^2 = 0.79$) growth rates, respectively.

$$G_{\sigma} = 0.03424(\pm 0.0083) \cdot T - 0.0020(\pm 0.001) \cdot e^{0.08777(\pm 0.0144) \cdot T} \cdot L \quad (13)$$

$$G_{\phi} = 0.04028(\pm 0.0077) \cdot T - 0.00193(\pm 0.0009) \cdot e^{0.08777(\pm 0.0144) \cdot T} \cdot L \quad (14)$$

Male growth rates were on average 83 % (± 0.024 SE, $r^2 = 0.935$) of female growth rates (Fig. 3) based on

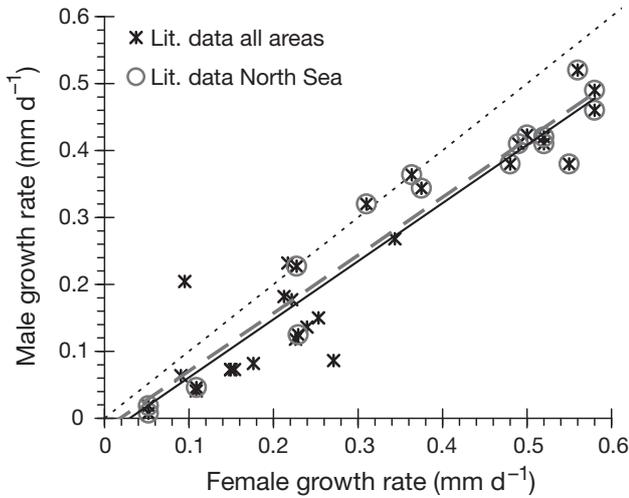


Fig. 3. *Crangon crangon*. Female and male growth rates (mm d⁻¹). Dotted line: line of perfect (1:1) agreement

North Sea data from Meixner (1969), Oh et al. (1999), Uhlig (2002), and Hufnagl & Temming (2011). If all studies reporting gender specific growth rates (previous references plus Labat 1977, Lagardère 1982, Campos et al. 2009b) were included, male growth rates would be 80.1% (± 0.028 SE, $r^2 = 0.883$) of female growth rates. For both data sets, intercepts were not significantly different from 0 and were therefore omitted.

The von Bertalanffy parameters K , L_∞ and the growth performance index Φ' were derived from Eqs. (9) to (14) (Table 3) based on the parameters determined for all growth models (G , G_{max} , $G_{mean+SD}$, G_\varnothing , G_σ). We

Table 3. Von Bertalanffy growth parameters K and L_∞ , growth performance index Φ' and Q_{10} for metabolism for mean and maximum, male and female growth models

	K (10°C)	L_∞ (10°C)	Φ'	Q_{10}
G no T interaction	1.59	70.57	3.90	
G plus T interaction	0.98	90.05	3.90	2.34
G_{max} mean + SD	1.20	104.94	4.12	2.72
G_{max} 75th percentile	1.03	108.20	4.08	2.71
G_\varnothing	1.70	86.07	4.10	2.34
G_σ	1.76	72.78	3.97	2.34

assumed a mean annual North Sea temperature of 10°C (Eq. 7). Highest Φ' of 4.08 to 4.12 were determined for G_{max} , G_\varnothing and $G_{mean+SD}$. Values for G and G_σ ranged from 3.90 to 3.97.

Moult interval and increment

Fitting Eq. (8) to the moult interval data obtained from previously determined experimental data (Hufnagl & Temming 2011) and literature values (Table 1) led to

$$MI = 5.7066(\pm 3.0514) \cdot L^{0.7364(\pm 0.1326)} \cdot e^{0.093363(\pm 0.01237) \cdot T} \quad (r^2 = 0.954) \quad (15)$$

with all parameters being significantly different from zero ($p < 0.01$). The theoretical maximum moult increment, which was calculated as the product of G_{max} and MI (Eq. 15), was greatest for *Crangon crangon* of $L = 30\text{--}40$ mm (Fig. 4). Maximum increments of 6 mm

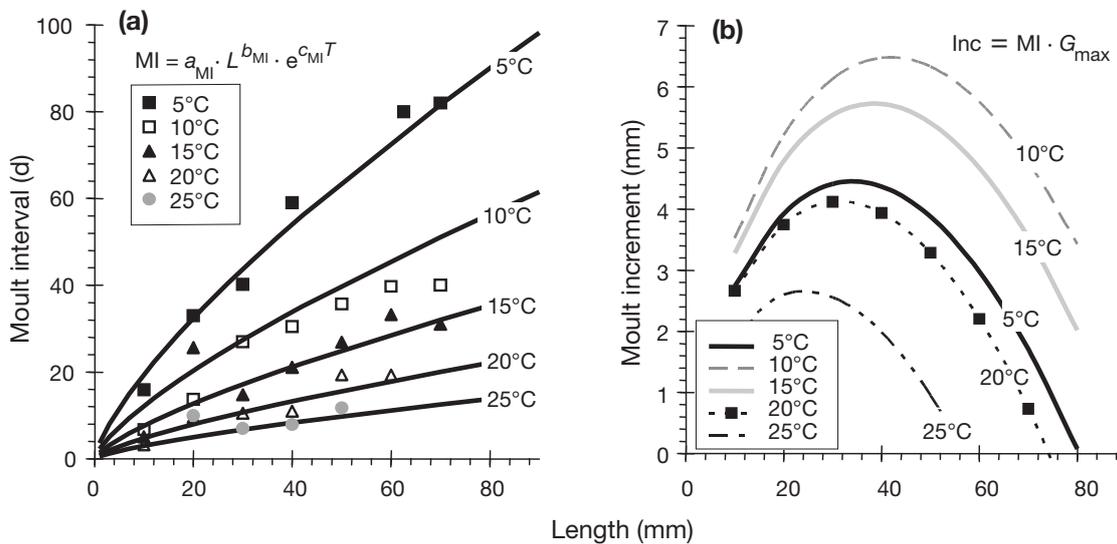


Fig. 4. *Crangon crangon*. (a) Mean moult intervals (MI; points) and Eq. (8) (lines) fitted to the data. (b) Theoretical moult increment (Inc) calculated as the product of the moult interval (Eq. 8) and the maximum growth (75th percentile quantile regression, Eq. 12)

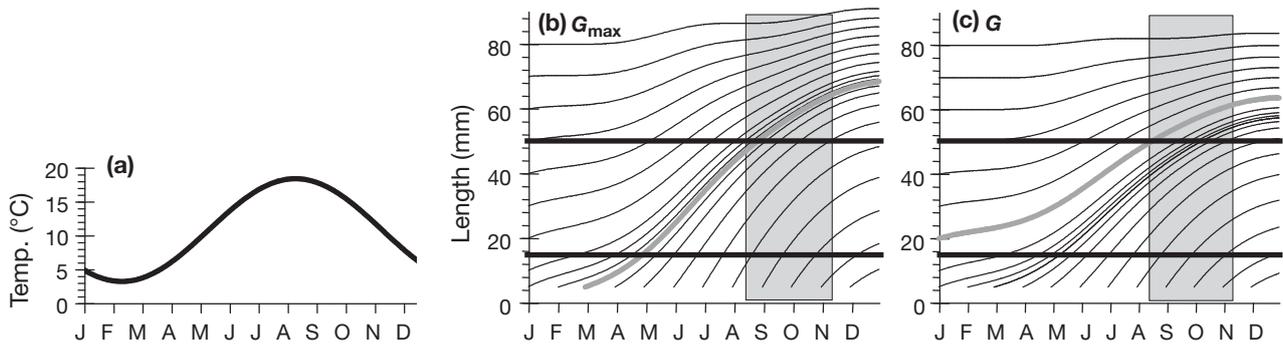


Fig. 5. *Crangon crangon*. Calculated length trajectories based on parameters derived for the different subsets and including water temperature (a) of the shallow North Sea at Weser light ship and Büsum. In all scenarios, animals start at 5 mm on each 1st day of the month. Length trajectories were calculated using (b) maximum growth (75th percentile quantile regression, G_{max}), and (c) mean growth (G). Horizontal lines: length at recruitment (15 mm) and minimum catch length (50 mm). Grey curve: first cohort reaching 50 mm in September. Grey boxes: autumn/winter fishing season

were calculated for 40 mm shrimps at 10°C, whereas smallest moult increments of 0–2 mm were predicted for a T of 25°C.

Application of the model

Applying seasonal North Sea temperatures (Fig. 5a, Eq. 7), most simulated shrimps recruiting at 5 mm in January to April reached 50 mm before September (Fig. 5b) when G_{max} was used. However, if trajectories were calculated using G (the model representing mean

growth, Fig. 5c), the 50 mm limit was reached 1 to 2 mo later.

Using G_{σ} (the model representing mean male shrimp growth), length trajectories were below those using G_{max} . Female length trajectories, which were calculated with G_{ϕ} , were comparable to G_{max} trajectories.

The LPUE maximum (Fig. 6 top; ICES 2010) observed between September and November represents shrimps >50 mm. Both cohorts from the previous winter egg production and the previous year’s summer egg production contribute to this adult biomass maximum (Fig. 6). However, the numerical importance of these components is controlled by the interaction between growth rates and cumulative mortality. For a typical fast growing (G_{max}) winter egg cohort starting at 5 mm in May, 1.3 % of the initial number reach 50 mm in September of the same year. However, if average growth (G) is assumed, the fraction attaining 50 mm is reduced to only 0.37 % and this 50 mm size is not reached before November. The same calculation for a typical fast growing summer egg cohort starting at 5 mm in August allows 1.1 % to reach commercial size in February. Of these shrimps, only 0.06 % contribute to adult biomass in September of the following year. With average growth, 0.06 % reach 50 mm in June and 0.022 % contribute to the adult biomass maximum in September of the following year.

DISCUSSION

Meta-analysis of growth data

High variability in growth was observed both within and between all studies analyzed. However, despite the scatter, general patterns can be derived: (1) small animals grow faster than large ones; (2) the L effect

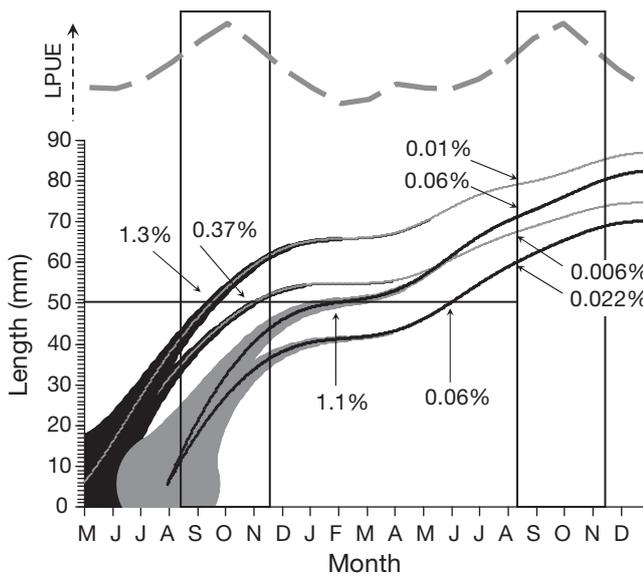


Fig. 6. *Crangon crangon*. Abundance and length. Comparison of May (winter egg hatched, black) and August (summer egg hatched, gray) juveniles assuming intermediate (lower lines) and fast growth (upper lines). Percentages indicate the fraction of shrimps left from initial cohort size upon reaching 50 mm or the period of high landings per unit effort (LPUE, Sep–Nov)

increases with increasing T ; and (3) high variability was observed in all T - L categories.

The negative effect of L on growth and of T on the slope (growth vs. L) can be interpreted in the context of the von Bertalanffy growth theory (von Bertalanffy 1934). The food-related term (anabolism) was expanded in our study with a linear T term following Kuipers & Dapper (1981). In addition, the catabolic term was expanded with an exponential T effect. With rising temperatures, the catabolic term increasingly approaches the anabolic term, resulting in decelerated growth especially for large shrimps. This means that at a certain point, the animal is unable to channel enough energy to further growth, and all energy gained is channeled into maintenance or reproductive processes. The same mechanism could also have been modeled with a growth function with 2 exponential temperature terms, for both anabolism and catabolism, but with a smaller exponential coefficient on the anabolic term.

The intersection of the growth function (Eq. 5; Fig. 1f) with the x-axis represents L_{∞} (asymptotic length), which is the equilibrium length of anabolism and catabolism. At constant temperatures, maximum L of 61 mm at 25°C and 108 mm at 10°C were predicted. This corresponds to field observations where populations dwelling at higher latitudes or in deeper water were found to reach larger sizes than related species in tropical regions (Gunter 1950, Angilletta et al. 2004).

Factors influencing growth

The parameter b , which mainly determines the intercept of Eq. (5) with the y-axis, is 40% higher for female ($b = 0.040$) than for male shrimps ($b = 0.035$). This translates into female growth rates being ~15% higher than male growth rates. A direct regression of male and female growth rates for comparable L and T classes indicated that male growth rates were 17 to 20% lower than female rates. The effect of gender on growth was discussed in more detail by Hufnagl et al. (2010a) and Hufnagl & Temming (2011). Reproductive investment of female crustaceans increases with L , whereas searching ability and agility of male crustaceans decrease with L (Bauer 2006). In pure-searching species where males display no guarding behavior, females reach larger sizes than males (Correa & Thiel 2003) and display higher growth rates.

T dependence, which is represented by parameter d in the growth model for all scenarios (G , G_{\max} , G_{σ} and G_{ρ}), varied between 0.0849 and 0.100. Parameter d can be converted into a Q_{10} value according to $Q_{10} = \left(\frac{e^{dT_1}}{e^{dT_2}} \right)^{\frac{10}{T_1 - T_2}}$. *Crangon crangon* Q_{10} values range

from 2.34 to 2.72, being comparable to values for other ectotherms (reviewed by Angilletta et al. 2004; lower quartile 1.1, upper quartile 2.8) and lower than values determined for *Crangon septemspinosa* (Q_{10} between 2.85 and 3.01; Taylor & Peck 2004).

Von Bertalanffy growth parameters K , L_{∞} and growth performance index Φ' were comparable to previous findings for *Crangon crangon*. L_{∞} and K values as determined by Tiews (1954), Tiews & Schumacher (1982), and Kuipers & Dapper (1984), respectively, ranged between $K = 0.7, 1.12$ and 0.95 ; $L_{\infty} = 110, 85$ and 78 ; and $\Phi' = 3.93, 3.91$ and 3.76 . Applying the Powell (1979) and Wetherall et al. (1987) methods to length-frequency distributions of several long-term survey data, Hufnagl et al. (2010b) determined $L_{\infty} = 79.3$ mm, assuming $K = 1.17$, corresponding to $\Phi' = 3.87$.

The T dependence of K is comparable to rates determined in starvation experiments (Hufnagl et al. 2010c), increasing exponentially from $K = 1.08$ at 9°C to $K = 2.29$ at 20°C. Brown shrimp growth performance indices determined in this study are high in comparison to other similar sized crustaceans like *Farfantepenaeus californiensis* ($\Phi' = 2.85 - 3.06$; López-Martínez et al. 2003), *Neocallichirus mirim* ($\Phi' = 2.79 - 2.84$), and *Callichirus major* ($\Phi' = 2.28 - 2.32$; Botter-Carvalho et al. 2007). The higher value determined for brown shrimp, in comparison to the named species, indicates a higher growth performance and might indicate a shorter life span.

Although T and L explained most of the observed growth variability, unexplained variation still remains. This might originate from several sources, but here we will focus on (1) bias in the cohort tracking data; (2) bias related to laboratory experiments or factors such as food and habitat; (3) gender-specific growth rates in studies without sex differentiation; and (4) effects of pre-feeding history or genetic variability.

(1) Cohort tracking

Crangon crangon spawns throughout the year except in late autumn (Kuipers & Dapper 1984, Neudecker & Damm 1992). Permanent recruitment leads to a mixing of slow-growing individuals from early cohorts with fast-growing individuals from later cohorts. This makes it impossible to follow the length modes of individual cohorts over prolonged periods. Furthermore, small individuals are observed in shallow water, whereas larger animals prefer deeper water and tidal gullies. Gradual disappearance of shrimps >20 mm (Beukema 1992) requires simultaneous sampling on the tidal flats and in deeper water. Since migration patterns are not only determined by L but are also related to age, gender, season and T (Boddeke

1976, Boddeke et al. 1976, Pihl & Rosenberg 1982, Spaargaren 2000), obtaining representative length compositions for the entire population is a difficult task requiring a large sampling effort.

In practical applications, growth rates of juveniles are most reliable because growth is fast and youngest cohorts are less affected by site dependent emigration into deeper water (del Norte-Campos & Temming 1998, Amara & Paul 2003). Cohort tracking of larger shrimp will only generate reliable growth estimates if a single recruitment event dominates in a local region and both emigration and immigration are unlikely to occur. Such a situation was analyzed on the northeast coast of France (Manche-est) by Tetard (1985) and their estimated growth rates are close to G_{\max} .

(2) Laboratory artifacts

Laboratory studies avoid many of the problems discussed for cohort tracking but generate other issues related to, e.g. prey composition, density or water quality. For *Crangon crangon*, especially food, group vs. individual rearing, health, noise and toxicity were examined.

Crangon crangon is an opportunistic omnivore (Pihl & Rosenberg 1984, Boddeke et al. 1986, Feller 2006). Feeding experiments indicated a significant food type effect, with live copepods being the optimal diet (Hufnagl & Temming 2011). Similar results were obtained in the laboratory when plankton or *Artemia salina* was provided as food (Meixner 1969, Dalley 1980, Uhlig 2002), whereas growth rates were lower when only *C. crangon* (Edwards 1978) or nematodes (Gerlach & Schrage 1969) were used. Uhlig (2002) observed that frozen smelt supports only slow growth of *C. crangon* (20 mm *L*: 0.25 mm d⁻¹), whereas fresh caught, live plankton doubled the growth rates of shrimps (20 mm *L*: 0.56 mm d⁻¹). The food type therefore seems to be important for high growth to occur.

The high densities of animals in laboratory vessels in comparison to those in the field might influence growth rates by creating stress. This induces higher energy consumption for activity, resulting in less energy available for growth. Onnen & Zebe (1982) described that tail flipping, a common escape mechanism in *Crangon crangon*, as very cost intensive. For *Penaeus esculentus*, feeding and walking increased oxygen consumption by 45% and active swimming by 130% (Blaxter & Southward 1991). Lower growth rates might therefore be a result of higher activity and metabolic costs.

Regnault (1970, 1976) observed that *Crangon septemspinosa* grew faster when isolated than when in groups, or when held on natural substrate than without substrate. Stress therefore influences growth and

growth variability, while shelter (sand) might compensate for stress or reduce activity. In Regnault's experiments, total length of isolated shrimps increased from 8 to 32 mm and that of grouped shrimp only from 8 to 18 mm. Contrary to Regnault's findings, high growth rates with group setups were observed by Hufnagl & Temming (2011), M. Fonds (unpubl.), and Uhlig (2002).

Tiews (1970) reported that animals with missing extremities grew slower over successive moults due to the added costs of limb regeneration. If animals do not get optimum food, aggressive interactions (leading to cannibalism) may increase, causing more injuries and therefore slowing growth rates. The regeneration effect could also partially explain the observed variability in laboratory experiments. Catching, treatment or shell diseases could also lead to injuries of shrimps, which then grow slower than their healthy conspecifics.

In summary, optimum conditions would be obtained by rearing small groups at low densities within tanks having natural substrate like sand or small gravel, and using a mixture of prey optimally including natural live zooplankton.

(3) Gender

Growth of female *Crangon crangon* in our analysis was ~15 to 20% higher than that of males. The differences in growth observed between genders could explain part of the growth variability reported in studies with mixed genders of shrimp. However, even in experiments where gender was registered and rearing conditions were close to the perceived optimum for this species, growth variation still existed. For example, females (20 mm *L*) reared in the same tank grew at minimum and maximum rates of 0.4 and 0.75 mm d⁻¹, respectively (Hufnagl & Temming 2011).

(4) Effects of pre-feeding history or genetic variability

Working with *Penaeus monodon*, Benzie (1997) reported that 10% of the growth variability in the progeny was determined by genetic factors. A similar study has not been conducted for *Crangon crangon*, hence no statement about maternal or paternal effects on growth can be made.

Several authors observed that genetic variability in the field is low and only differs between very remote places (Bulnheim & Schwenzer 1993, Beaumont & Croucher 2006, Luttkhuizen et al. 2008), which might lead to latitudinal differences in growth performance (Campos et al. 2009a). All studies analyzed and used

for the parameterization here were from the North Sea region where no genetic differences have been observed (Luttikhuisen et al. 2008). The high inter- and intrastudy variability (Fig. 1) might therefore eventually be explained not by regional genetic effects but by differences in individual genetic growth potentials.

Moult interval and increment

Maximum moult increments were deduced indirectly by multiplying estimates of G_{\max} and moult interval. Based on this calculation, maximum increments of 7 mm for a 40 mm shrimp were obtained. These values are comparable to values observed by Meixner (1969) and Hufnagl & Temming (2011). Translating these increments into wet weight (Eq. 1) would result in a maximum weight gain of 50% for 40 mm shrimps at 10°C and 100% for 20 mm shrimps at the same temperature. These values seem high but it should be taken into account that weight growth does not take place during the moult event but is a gradual process over the whole intermoult period. Due to the hard exoskeleton, weight growth is achieved by reduction of the water content and steady replacement of water with protein (Rosa & Nunes 2004). The observed increment is therefore only achieved by an uptake of water and subsequent expansion. Therefore, the 50 to 100% growth has to be distributed over the whole moult interval, reducing these values to a net wet weight growth rate of 1.5 and 4% d^{-1} , respectively. This is within the range of values for other crustaceans (e.g. blue crab: 1.5 to 9.3% d^{-1} ; Rice & Short 1989) and lower than rates observed for larval fish of comparable size (e.g. menhaden, fork length: 28–55 mm, mean \pm SD growth: $9 \pm 7\%$ d^{-1} ; Hettler 1976)

Approximately 95% of the observed variability was explained by T and L if Eq. (8) was fitted to T and L binned mean moult intervals. This indicates that feeding and habitat conditions influence moult intervals only to a minor extent and that moulting follows more regular, perhaps hormone controlled, patterns. Reasons are most probably maturation processes or avoidance of shell diseases and parasites as discussed by Buchholz et al. (2006) for krill.

Application of the growth model

Growth trajectories based on mean growth rates and ambient temperatures suggest that 15 mm shrimps in 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 & 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) or female growth is used for the predictions. This is in contrast to the growth hypothesis of Campos et al. (2009a) who assumed that the autumn landings maximum is connected to the previous year's summer recruitment. Due to high mortality rates, only a very small fraction of shrimps is actually left after 1 yr, hence it is unlikely that the recruitment of the previous summer augments the adult maximum in autumn of the current year.

High mortality rates are related to the high numbers of potential brown shrimp predators. Predators of adult shrimps are mainly cod and whiting (Daan 1973, Singh-Renton & Bromley 1999) and grey gurnard in deeper water (de Gee & Kikkert 1993). For juvenile shrimps, besides cannibalistic conspecifics (Regnault 1976, Evans 1984, Pihl & Rosenberg 1984), the gobiid *Pomatoschistus* sp., flatfish such as *Pleuronectes platessa*, *Platichthys flesus*, *Limanda limanda*, *Hippoglossoides platessoides*, and *Solea solea*, and other species such as *Agonus cataphractus*, and *Ciliata mustela* (Braber & de Groot 1973, Evans 1984, Jansen 2002) need to be included.

The current year summer eggs, which Boddeke & Becker (1979) identified as the main recruitment source, are also only contributing to a small extent to the autumn landings maximum of the same year. Assuming egg development times similar to the moult interval (Eq. 8) of ~30 d at summer temperatures of 10 to 15°C and $L = 55$ mm, larval developmental times according to Criales & Anger (1986) of an additional 30 d (between 10 and 15°C), and a summer egg period of mid April to mid September, larvae hatched from the first summer eggs will reach 5 mm in mid June. According to Fig. 5, only fast growing juveniles hatched from the earliest summer eggs (hatched in April, recruiting in June) of the present year will reach adult length between October and November, towards the end of the autumn catch peak.

According to the calculations shown in Figs. 5 & 6, the abundance of shrimps growing at G_{\max} and reaching commercial length is 4× higher than that of shrimps growing only at G due to higher cumulative mortality in the latter. Shrimps starting at 5 mm total length between January and June and growing at G_{\max} reach commercial length between September and November, whereas shrimps growing at G need 1 to 3 mo longer (Fig. 5). It can therefore be concluded that the fast growing shrimps are of vital importance for the autumn harvest and also for the population as they will carry the winter eggs from which the new cohort emerges.

The existence of high growth rates in nature is also supported by the results of the only field study where distinct cohorts of large shrimps were analyzed to have growth rates comparable to G_{\max} (Tetard 1985). Tetard (1985) sampled brown shrimps within a rather enclosed estuary where a single distinct spawning event happened, allowing the tracking of a single cohort over a longer time span without mixing effects.

The better fit of G_{\max} (which is almost equal to G_{ϕ}) with field observations in comparison to G might be because the larger size classes are dominated by females (Tiewes 1970, Martens & Redant 1986, Hufnagl et al. 2010a). However, even when only considering females, growth variability is still high.

One aspect that has not been taken into account here is that juvenile shrimps (<20 mm) might experience higher temperatures than assumed in the model. During low tide, when juvenile animals reside on tidal flats and in small pools (Berghahn 1983, 1991, Beukema 1992), growth might increase significantly due to warming, if sufficient food exists. A 5°C difference in ambient temperature experienced by shrimps <20 mm would lead to commercial length being reached 2 to 3 wk earlier. However, this result would not influence the previous conclusions about the importance of the winter eggs but might increase the proportion of shrimps growing at G that reach commercial length.

Based on the results of this study, the life cycle of *Crangon crangon* can be summarized as follows: the autumn peak in adult shrimp is dominated by females >50 mm. By winter, these shrimps have grown into the length class >60 mm. Within this length class, >90% of the female shrimps carry eggs in winter (Oh et al. 1999, Siegel et al. 2008). These females subsequently spawn the eggs for the recruitment peak of juveniles of ~15 mm L , in the following May or June (Temming & Damm 2002). Approximately 1.3% of these juveniles grow into the adult length class within summer and reach commercial length (>50 mm) in September, assuming G_{\max} . Approximately 0.37% of the shrimps growing at G (mean growth rate) reach adult length 1 mo later. Thus, the life cycle and the population is dominated by an annual cycle: hatch from winter eggs, recruitment into the shallow Wadden Sea areas in late spring, maximum growth during summer, marketable length in autumn and production of winter eggs.

These findings indicate that the summer recruitment is less important despite summer egg production being much higher (Temming & Damm 2002) than winter egg production. Temming & Damm (2002) calculated an egg production index based on the assumption that eggs are released after each moult. Due to the short moult intervals during summer, this assumption strongly influences their summer egg production estimate. Klęk-Kawińska & Bomirski (1975) assumed only

2 ovipositions during summer, which at least halves the abundance of the previous summer eggs. Further studies focusing on oviposition, gonad development and fertilization processes are therefore recommended to gain a better insight into summer and winter egg production rates.

If the egg production rates that we assumed here are correct, another explanation for the high summer egg peak could be that the life cycle might be different in other areas. *Crangon crangon* covers a large distribution area including the Black, Mediterranean, North and Baltic Seas as well as the Atlantic, whereas the present study mainly focused on the southern North Sea. Kuipers & Dapper (1984) reviewed latitudinal trends in spawning seasons and the work of Campos et al. (2009b) also indicates that latitudinal trends in growth performance might exist. However, gene flow within the North Sea is not hindered and no subpopulations were identified (Luttikhuisen et al. 2008). Hence, one adaptation mechanism for different temperature and feeding situations could be variability in growth and production. In more northern areas, production of summer eggs might be the most efficient strategy.

The demonstrated relevance of the winter egg production also implies that increased mortality of adult shrimps during winter might affect the commercial recruitment of *Crangon crangon*. The recently observed increase in the winter fishery, which is driven by high prices during this time, could theoretically reduce the spawning stock size. Such effects might presently be masked by the historically low level of key brown shrimp predators: cod and whiting preying on the adult stock in late autumn and winter (Welleman & Daan 2001). Recovery of the stock size of these predators in combination with increased winter fishing on egg-carrying females might negatively impact the brown shrimp population.

Future research should focus on the causes of the high individual growth variability observed in laboratory studies. The application of condition and growth proxies (e.g. RNA/DNA ratio) or the instantaneous growth rate method (Hart 2001) could reveal the extent of this variability under field conditions.

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