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ORIGINAL PAPER

Potential impact of climate warming on the recruitment of an economically and ecologically important species, the European lobster (*Homarus gammarus*) at Helgoland, North Sea

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Abstract A laboratory-based study was performed to assess the impact of climate warming on the recruitment of the endangered population of the European lobster (*Homarus gammarus*) at Helgoland (North Sea, German Bight). Egg-bearing females collected in situ just after spawning in late summer were subjected to various seasonal temperature regimes. Regimes with elevated temperatures (mild winters) resulted in a strong seasonal forward shift of larval hatching. Hatching took place at significantly lower temperatures than under regimes with normal winters. Experiments on larval development across a range of constant temperatures showed that no successful larval development occurred at temperatures below 14°C. Larval survival increased from 9% at 14°C to 80% at 22°C, while duration of larval development decreased correspondingly from 26 to 13 days. We hypothesize that an ongoing warming of the North Sea will strongly affect the recruitment success of the Helgoland lobster, mainly resulting from a decoupling of the seasonal peak appearance of larvae from optimal external conditions (temperature, food availability) for larval development.

Introduction

The waters of the southern North Sea are warming at a rate greater than on the global scale (Belkin 2009), and therefore responses of marine communities to climate change may be expected to be more evident in this geographical area than in many others. At Helgoland (North Sea, German Bight), surface water temperature (annual mean) has risen by almost 1.5°C since 1962 (Wiltshire et al. 2008, for the period up to 2005), and warming has been most pronounced in winter (e.g. Franke et al. 1999). Climate change scenarios predict an ongoing warming, with a further increase in North Sea water temperature by 2–3°C over the 21st century (IPCC 2007).

Associated with rising water temperatures, the structure and function of marine communities are already changing and will be even more strongly affected by climate change in the coming decades (IPCC 2007). Recent regional changes driven by climate include phenological shifts (e.g. Greve et al. 1996, 2004; Edwards and Richardson 2004) and changes in species distribution patterns (e.g. Southward et al. 1995; Beare et al. 2004; Perry et al. 2005; Franke and Gutow 2004). Furthermore, as species usually do not respond to climate changes in exactly the same way, decoupling of interspecific relationships according to Cushing's match–mismatch hypothesis for predator–prey relationships (Cushing 1975) may become a frequent phenomenon of grave consequence for the functioning of ecosystems (e.g. Edwards and Richardson 2004).

The subtidal cliffs of Helgoland (an area of about 35 km^2) harbour a small, isolated population of the European lobster (*Homarus gammarus*) which is separated from neighbouring populations on similar hard-bottom areas by some hundred miles of soft bottoms. As top regulator and keystone species, the lobster is essential for the maintenance of the high species diversity of the local hard-bottom community. Up to the 1930s, there was an important lobster fishery at Helgoland, yielding up to 50 tons per year (Klimpel 1965). Since a dramatic decline in landings in the

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1950s and 1960s, the numbers of lobsters landed per year have been fluctuating at an extremely low level of only a few hundred individuals per year (Goemann 1990; Schmalenbach 2009). As no fishery-independent data on lobster abundance are available from past decades, we do not know to what extent the population actually declined. The reasons for the collapse of the Helgoland lobster stock are also not known in detail; they may include habitat destruction, extensive fishing pressure and anthropogenic pollution of the North Sea waters by oil spills and industrial wastes (Klimpel 1965; Anger and Harms 1994; Harms et al. 1995; Walter et al. 2008). Legislative regulations issued in 1981 and 1999 may have prevented an extinction of the local population but to date have not resulted in a significant recovery of the population.

The annual reproductive cycle of female lobsters at Helgoland is characterized by late summer mating and spawning, followed by a 9- to 11-month period of embryonic development which spans the winter time and culminates in larval release during a hatching season ranging from late May to August, with a peak in July when water temperature usually ranges around 16°C (e.g. Mehrtens 2008). In both the European lobster (*H. gammarus*) and the American lobster (*Homarus americanus*), the embryonic development duration (time from spawning to larval hatching) as well as the larval development duration (time from larval hatching to metamorphosis with recruitment to the benthos) is mainly governed by the temperature regime experienced by incubating females and larvae, respectively (Perkins 1972; Branford 1978; MacKenzie 1988; Charmantier et al. 1991; Charmantier and Mounet-Guillaume 1992; MacDiarmid and Saint-Marie 2006).

In recent years, a number of occasional field findings have suggested a trend to earlier lobster larvae hatching. We hypothesize that increased temperatures in the German Bight over the winter half-year accelerate the embryonic development in the Helgoland lobster population, resulting in a significant seasonal forward shift of larval hatching. In this case, lobster larvae could run the risk of being released into environmental conditions, which are suboptimal or even detrimental for their development and thus for the population's recruitment success. When hatching much earlier in the year, larvae might become exposed to water temperatures, which (despite the general warming trend) are still too low for an optimal larval development. Furthermore, food might still be too poor due to a possible asynchrony in the seasonal forward shifts in food demand and food supply (primary production).

In the present paper on the European lobster at Helgoland, we examined the potential impact of the predicted future rise in North Sea water temperature by 2°C (IPCC 2007) on the timing of larval hatching and on successful recruitment of lobster larvae to the benthos community at Helgoland. Lobster larvae are extremely rare in plankton hauls at Helgoland (Greve et al. 2004), because the larvae may be near the bottom where they are inaccessible (Ennis 1973a). Under laboratory conditions, newly hatched larvae of *Homarus gammarus* only stayed at the surface for a short time before orienting to deeper layers (Schmalenbach and Buchholz 2010). Consequently, any study on the effects of temperature on the timing of larval hatching and recruitment of larvae to the benthic community has to rely on laboratory experiments.

Materials and methods

The study was carried out in the years 2005 to 2008 at the Marine Station on Helgoland. Lobsters were supplied by local fishermen from the rocky subtidal around the island of Helgoland (German Bight, North Sea; 54°11.3′N, 7°54.0′E).

Embryonic development duration and seasonal hatch timing

The first part of the study was designed to assess temperature effects on the duration of the embryonic development and thus the seasonal timing of larval hatching. Ovigerous (i.e. egg-bearing) females (mean total length and SD: 32 ± 2 cm; mean weight and SD: 1.30 ± 0.30 kg) were captured in September/October 2005 ($N = 7$), 2006 ($N = 8$) and 2007 ($N = 18$). Only specimens were considered which had spawned no more than 3 weeks before capture (eggs in prenaupliar condition). The animals were placed individually into tanks (49 × 79 cm), filled with running sea water to a depth of 20 cm (average salinity of 31 psu) and maintained, until larval hatching in the following year, under the natural LD-cycle and a temperature regime that closely followed the seasonal changes in ambient water temperature (see below). The lobsters were fed (ad libitum) a mixture of easily accessible small fish (*Pholis gunnellus*, *Myoxocephalus scorpius* and *Pleuronectes* sp.) and crustaceans (*Carcinus maenas*, *Crangon* sp. and *Liocarcinus* sp.).

The rate of embryonic development was not tracked through the incubation period. For each ovigerous female, only the beginning and the end of the period of larval hatching (usually spanning no more than a fortnight) as well as the water temperature at hatching were recorded. For each study period (2005/2006, 2006/2007, and 2007/2008) means of the seasonal hatch date, the embryonic development duration (from capture immediately after spawning to larval hatching) and the hatch temperature were calculated. In addition, the cumulative degree–days (dd) or 'heat sum', i.e. the sum of daily (laboratory)

temperatures for the period from capture of ovigerous females in September/October to larval hatching in the following year (2006, 2007 and 2008), were determined. As embryos upon capture were already up to about 3 weeks old (estimated mean: 10 days), field water temperatures for a 10-day period before capture were added in order to get dd-estimates ($dd_{adj.}$) for the complete period of embryonic development from egg extrusion to larval hatching.

The sea surface temperature (SST) at Helgoland was measured every workday as part of a long-term monitoring programme at 'Helgoland Roads' (Wiltshire et al. 2008). The shallow water body at Helgoland is well mixed by tidal currents throughout the year, so that SST is a reasonable proxy both for the near-bottom temperature experienced by ovigerous females in situ and for the temperature of the water entering the supply system of the Marine Station.

The water temperature in the flow-through laboratory tanks was measured daily. The data tracked closely with the SST. However, as a result of the mode of construction of the sea water supply system in the Marine Station, water temperatures which the animals experienced in the laboratory were on average 2.4°C (2005/2006), 2.9°C (2006/2007) and 3.1°C (2007/2008), respectively, higher than SST (Fig. 1). In 2005/2006, SST was relatively low (see results); the thermal laboratory set-up for this year may be considered as proxy of a 'normal' annual temperature regime for recent years. The laboratory set-ups of 2006/2007 and 2007/2008 (when SST was rather 'normal'), however, may be regarded as proxies of the climate change scenario for the end of this century.

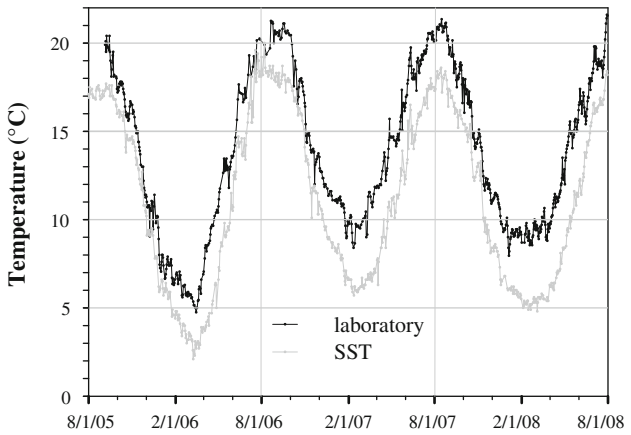

Fig. 1 Daily water temperatures in the field (surface water temperatures SST at Helgoland Roads) and in the laboratory over the three successive 1-year study periods from 1 August to 31 July (2005–2008)

Larval survival and development duration

The second part of the study was designed to quantify temperature effects on larval survival and larval development duration (time from larval hatching to metamorphosis with recruitment to the benthic life style). Intermoult periods and survival rates of the larval stages (Zoea I, II and III) were determined across a range of constant post-hatch temperatures. Newly hatched larvae (Zoea I) were collected from the tanks in the morning, as larvae usually hatch at night, following an endogenous rhythm (Ennis 1973b). All trials (eight treatments with 45 replicates each) were started at virtually the same time: From a large pool of actively swimming larvae, which had hatched over night from nine ovigerous females, larvae were randomly selected, and 45 were allocated to each of eight thermal treatments relevant to climate change scenarios: 11, 12, 13, 14, 15, 16, 20 and 22°C. This choice includes both lower and higher temperatures than those (16–17°C) experienced recently by lobster larvae at Helgoland.

Starting at a pre-hatching temperature of about 16°C, the larvae were step-by-step acclimated to the respective culture temperature within 24 h to avoid temperature shocks or thermal stress. The larvae were individually reared in 80-ml cylindrical plastic bowls under identical conditions (salinity of ca. 31 psu, LD 12:12 h) except for temperature. Every day, food (about 30 freshly hatched nauplii of *Artemia* sp. per lobster larva; cysts from Sander's Brine Shrimp Company) was added, and the medium was changed. Water temperature, salinity and the number of moulted and dead animals were recorded daily. The experiments were run until the larvae had either died or had moulted to the fourth stage (first juvenile stage). For each larval stage (Zoea I, II and III), the intermoult period and the survival rate were plotted against culture temperature.

Statistics

Statistical analyses were performed following Sokal and Rohlf (1995). Data are presented as means and standard deviations (SD) of replicates. A Mann–Whitney *t*-test (GraphPadPrism 3.0) was applied to test for differences between two temperature cycles, mean hatch dates, hatch temperatures and durations of embryonic development under different thermal conditions at a significance level of $\alpha = 0.05$. To test for differences in intermoult periods of larval stages, a two-factorial ANOVA with the independent factors temperature (eight levels) and larval stage (I, II and III) followed by a Tukey's multi-comparison test at a significance level of $\alpha = 0.05$ was performed using the computer program Statistica 7.1 (StatSoft). Non-linear regressions with fitted parameters and coefficients of determination (r^2) were analysed using SigmaPlot 9.0.

Results

Embryonic development duration and hatch timing with seasonal temperature

Daily temperature data for both the field (SST) and the laboratory, spanning three successive one-year periods from 1 August 2005 to 31 July 2008 are given in Fig. 1. The mean SST across the period 1 August 2006 to 31 July 2007 was significantly higher than the means of SST across the other one-year periods studied, mainly due to a mild winter (Table 1). Although a mild winter was also characteristic of the period 2007/2008, the mean SST across this period did not differ significantly from that across the period 2005/2006 with a 'normal' winter. The differences in mean SST between the periods were 1.6°C (2006/2007 vs. 2005/2006), 1.3°C (2006/2007 vs. 2007/2008) and 0.3°C (2005/2006 vs. 2007/2008). Mean water temperatures in the laboratory in which the ovigerous females were exposed to during incubation were significantly different among the three study periods (13.1°C in 2005/2006, 15.2°C in 2006/2007 and 14.1°C in 2007/2008) and exceeded those in the field by 2.4, 2.9 and 3.1°C, respectively (Table 1).

Dates of larval hatching, temperatures at larval hatching and durations of embryonic development showed marked changes among years correlated with the temperature regime (Table 2; Fig. 2). The mean date of larval hatching showed a significant shift forward or backward depending on the temperature regime experienced by the ovigerous females. When the mean water temperature over the incubation period was highest (14.6°C in 2006/2007), the mean date of larval release was 17 April, the mean water temperature at larval release was 13.3°C, and the mean duration of the embryonic development was 205 days. When sea temperature over the incubation period was lowest (11.5°C in 2005/2006), the embryonic development took significantly more time, resulting in a marked delay of larval release by 61 days on average (mean date of larval hatching: 17 June); correspondingly, the mean water temperature at larval release was significantly higher (16.0°C). In 2007/2008 when the temperature regime was between those of 2006/2007 and 2005/2006, the mean date of hatching, temperature at hatching and duration of embryonic development were also intermediate. The cumulative degree–days (dd) for the period of cultivation (sum of daily laboratory temperatures from the day of capture in late summer to the mean day of larval hatching) as well as the adjusted values (dd_{adj}) for the complete embryonic development did not vary significantly among the years (Table 2). The mean dd_{adj} for all periods of study was 2,772 ± 497.

Table 1 (A) Surface sea temperatures (SST) at Helgoland Roads and laboratory (culture) temperatures (T_L; means ± SD) for the three successive 1-year periods (1 August–31 July); (B) *P*-values of unpaired *t*-tests comparing single pairs of means

	SST (°C)	T_L (°C)
(*A*)		
2005/2006	10.7 ± 5.4	13.1 ± 5.2
2006/2007	12.3 ± 4.5	15.2 ± 4.0
2007/2008	11.0 ± 4.6	14.1 ± 4.2
	P	
(*B*)		
2005/2006 SST vs. 2005/2006 T_L	<0.0001	
2006/2007 SST vs. 2006/2007 T_L	<0.0001	
2007/2008 SST vs. 2007/2008 T_L	<0.0001	
2005/2006 SST vs. 2006/2007 SST	<0.0001	
2005/2006 SST vs. 2007/2008 SST	0.3376	
2006/2007 SST vs. 2007/2008 SST	<0.0001	
2005/2006 T_L vs. 2006/2007 T_L	<0.0001	
2005/2006 T_L vs. 2007/2008 T_L	0.007	
2006/2007 T_L vs. 2007/2008 T_L	<0.0001	

Larval survival and larval development duration with temperature

The intermoult periods increased significantly ($P < 0.001$) with larval stage (Zoea I, II and III) and decreased—in each larval stage—with increasing temperature (Table 3). The relation between intermoult period (y) and temperature T can be expressed by the following regression model (with m representing the 'slope' and $a = y$ for T approaching ∞):

$$y = \frac{a \times T}{m + T}. \quad (1)$$

The fitted regression curves and equations are shown in Fig. 3 along with the coefficients r^2 (all ≥ 0.89). The 'slope' of the regression curve is significantly steeper for Zoea III than for the Zoea I and Zoea II ($m = 11.3$ vs. -8.6 to -8.8; $P < 0.001$).

Homarus gammarus larvae developed successfully to the first juvenile stage only when the water temperature was 14°C or above. At 11, 12 and 13°C, most Zoea I moulted to Zoea II, and an increasing number also to Zoea III, but none was able to proceed further (survival time in Zoea III stage: 13.7 ± 2.1 days, $N = 6$ at 11°C; 13.3 ± 3.8 days, $N = 17$ at 12°C; and 11.0 ± 3.2 days, $N = 25$ at 13°C). For the temperature range, which allowed for a complete larval development, total larval development duration (TLD) decreased significantly with increasing temperature (from 26.3 days at 14°C to 13.5 days at 22°C, $P < 0.0001$; Table 3).

Table 2 Date of larval hatching, temperature (laboratory) at larval hatching, duration of embryonic development, cumulative degree–days (dd) and adjusted degree–days (dd_{adj}) for the three successive periods of study

Year	Larval hatching		Embryonic development		
	Time (date ± day)	Temperature (°C)	Duration (days)	dd	dd_{adj}
(*A*)					
2005/2006	17 June 2006 ± 19	16.0 ± 2.2	258 ± 7	2,759 ± 128	2,923 ± 134
2006/2007	17 April 2007 ± 23	13.3 ± 1.3	205 ± 25	2,663 ± 351	2,809 ± 358
2007/2008	19 May 2008 ± 25	14.5 ± 2.3	219 ± 41	2,537 ± 610	2,697 ± 324
(*B*)					
2005/2006 vs. 2006/2007	<0.0001	0.0100	0.0001	0.5096	0.4431
2005/2006 vs. 2007/2008	0.0054	0.1599	0.3675	0.5923	0.6418
2006/2007 vs. 2007/2008	0.0106	0.1652	0.0231	0.3563	0.3898

(A) Means ± SD; (B) *P*-values of unpaired *t*-tests comparing single pairs of means

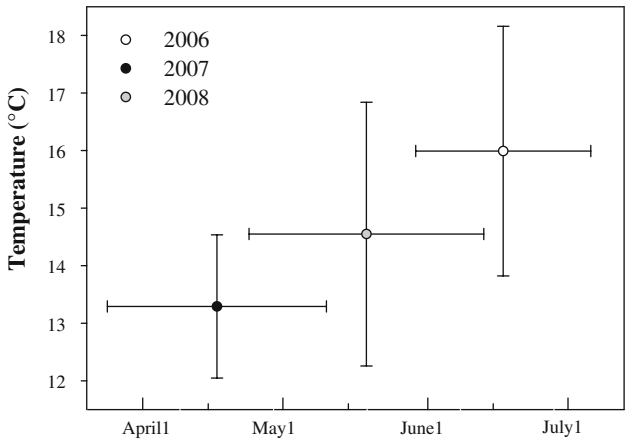

Fig. 2 Dates of larval hatching and temperatures (laboratory) at larval hatching (means ± SD) in 2006, 2007 and 2008

The survival rates of larval stages at different temperatures are given in Fig. 4. The percentage of larvae that reached the juvenile stage increased significantly from 9% at 14°C ($N = 4$) to 80% at 22°C ($N = 36$; $P < 0.0001$, χ-test). At all temperatures, the percentage of survivors decreased rather steadily over time (Fig. 5).

Discussion

The waters of the North Sea have been warming considerably in recent years (Wiltshire et al. 2008). There is much concern that this warming trend affects recruitment and productivity of commercially important marine species such as cod (e.g. Dippner 1997; Brander 2005). For both the European and the American lobsters, it has been suggested repeatedly that their recruitment success is modulated by the local sea temperature (Aiken and Waddy 1986; van der Meeren and Tveite 1998; Sheehy and Bannister 2002). The Helgoland population of the European lobster (*H. gammarus*) suffers from a dramatic decline about 40 years ago. The recent climate changes, although not responsible for this decline, might impose an additional

Table 3 Intermoult periods/stage durations (in days; means ± SD) of Zoea I, II and III and total larval development duration (TLD; in days; means ± SD) of *Homarus gammarus* at various temperatures

T (°C)	Stage duration						TLD	
	N	Zoea I	*N*	Zoea II	*N*	Zoea III	*N*	
10.6 ± 0.2	30	11.4 ± 1.0^{a}	6	13.7 ± 2.1^{a}		–		–
11.9 ± 0.0	38	8.4 ± 1.4^{b}	17	13.3 ± 3.8^{a}		–		–
12.7 ± 0.1	35	7.0 ± 0.7^{c}	25	11.0 ± 3.2^{a}		–		–
14.2 ± 0.3	42	6.5 ± 1.3^{c}	33	6.9 ± 2.4^{b}	4	13.5 ± 3.5^{a}	4	26.3 ± 3.8^{a}
14.7 ± 0.2	21	5.6 ± 0.5^{c}	11	9.5 ± 1.2^{a}	4	20.0 ± 4.6^{b}	4	35.3 ± 3.5^{b}
16.0 ± 0.3	44	4.4 ± 0.5^{d}	41	6.2 ± 1.0^{b,c}	30	9.2 ± 1.8^{c}	30	19.7 ± 2.0^{c}
19.9 ± 0.6	41	3.3 ± 0.7^{f}	36	4.7 ± 1.4^{c,d}	20*	6.4 ± 1.1^{d}	22	14.4 ± 1.5^{d}
22.0 ± 0.7	45	3.0 ± 0.0^{f}	42	3.7 ± 1.0^{d}	34*	7.1 ± 2.6^{d}	36	13.5 ± 2.8^{d}

Different superscripts denote statistically significant differences [two-way ANOVA and paired comparisons post hoc test ($P = 0.05$)]

* Two more specimens each survived to the first juvenile stage but could not be considered here as their exact moulting dates were not known

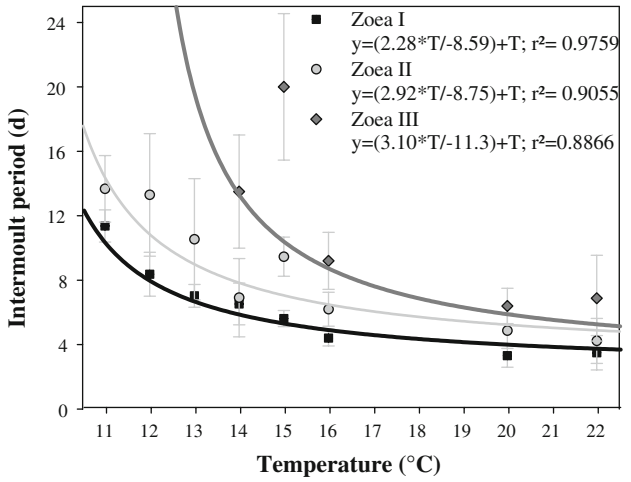

Fig. 3 Effect of temperature on intermoult periods (duration of the larval stages Zoea I, II and III) in the development of *Homarus gammarus* (days, means ± SD); non-linear regression with fitted parameters and coefficients (r^2)

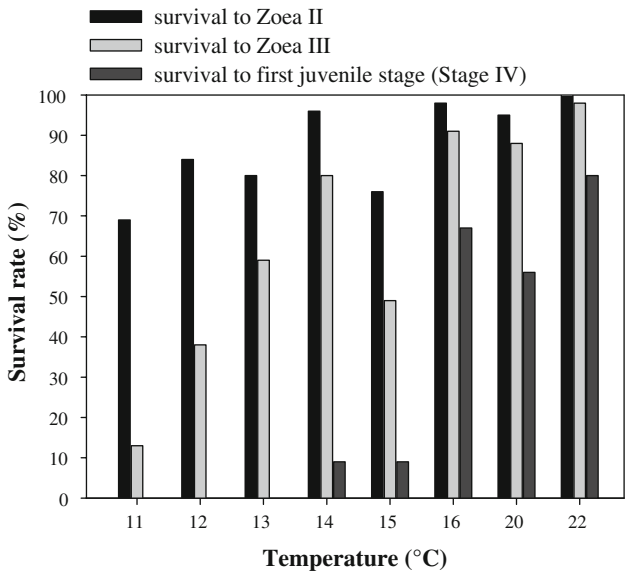

Fig. 4 Survival rates (%) for the larval stages of *Homarus gammarus* at different constant temperatures (initial $N = 45$ individuals per treatment)

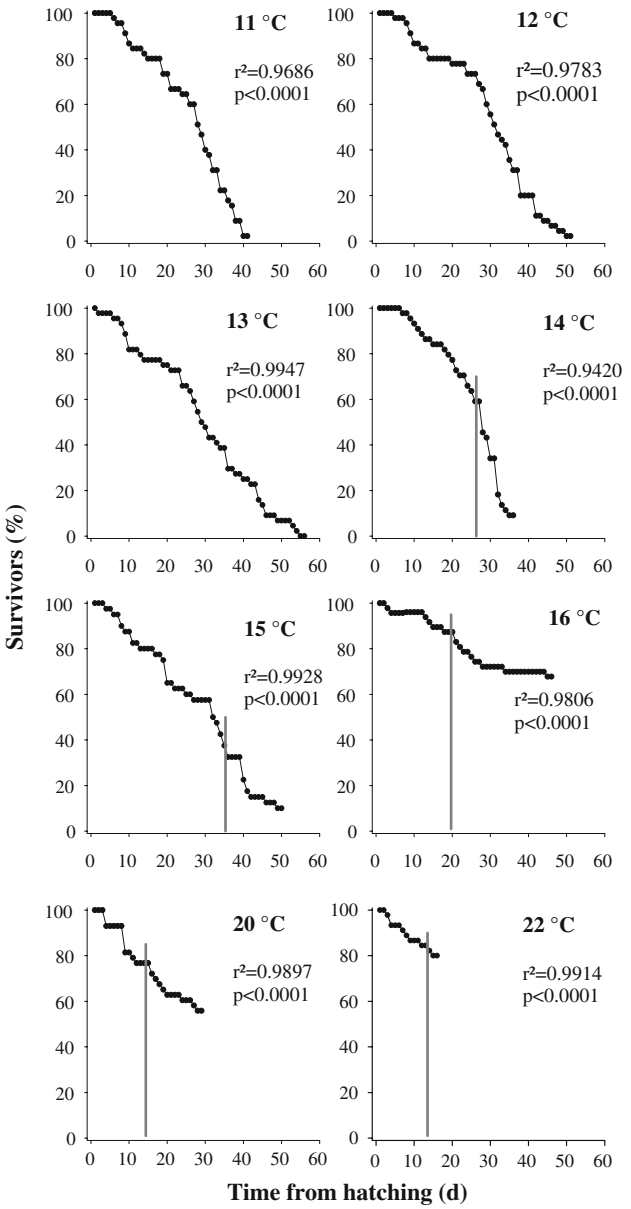

Fig. 5 Percentage of surviving lobster larvae over time. A complete larval development (i.e. moulting to the first juvenile stage) occurred only at temperatures of 14°C and above. *Vertical lines* represent mean times of moulting to the first juvenile stage

stress on the recovery of this endangered population. For an adequate assessment of the chances of a local lobster restocking programme, it is important to consider potential effects of climate warming on the population's recruitment.

Embryonic development/incubation period

The embryonic development of the European lobster usually spans 10 months or even more—from spawning in late summer/early autumn to larval release in early summer of the following year (e.g. Branford 1978, for the North Irish Sea; Mehrtens 2008, for Helgoland). Temperature regime strongly affects the duration of the embryonic development of lobsters and, thus, the date of larval hatching, but details are insufficiently known. In a study upon American lobsters kept under various constant temperatures (5–25°C), the time required from spawning to hatching increased exponentially with decreasing temperature (Perkins 1972).

The three successive one-year study periods from 1 August 2005 to 31 July 2008 showed clearly different temperature regimes, thus allowing for a study on how natural temperature cycles affect the timing of larval hatching in the European lobster at Helgoland.

There was a clear relationship between the mean temperature of the thermal regime on the one hand and the incubation time, the date of larval hatching as well as the temperature at hatching on the other hand. A high mean water temperature during incubation correlated with a reduced incubation time, an early date of larval hatching and a low temperature at hatching time. The cumulative degree–days for the incubation period, however, were not significantly different across the years of study (2005/2006, 2006/2007 and 2007/2008). This suggests that the incubation time under a fluctuating thermal regime may be largely similar to that under a constant temperature corresponding to the mean temperature of the former. The mean dd_{adj}-value of about 2770 thus represents a rough estimate for predicting the date of larval hatching under a given temperature regime. Applied to the field situations in 2005/2006, 2006/2007 and 2007/2008 (and taking 1 September as notional date of spawning), the mean dates of larval hatching would have been: 26 June 262006; 17 May 2007 and 21 June 2008.

In a number of brachyuran decapods, resting stages (periods of diapause) have been demonstrated in the embryonic development which cannot be shortened significantly by raising the temperature (Wear 1974; Petersen 1995; Moriyasu and Lanteigne 1998; Webb et al. 2007). By delaying larval release, resting stages may serve to synchronize larval development with optimal external condition e.g. food availability, which do not always change exactly parallel to the thermal regime. For instance, in the snow crab *Chionoecetes opilio*, the hatching of competent embryos is delayed; phyto-detritus acts as a chemical cue to synchronize larval hatching with optimal food supply (Starr et al. 1994). In lobsters, in contrast, there are at present no indications that the length of the incubation period is significantly influenced by other factors than the thermal history (Perkins 1972; own preliminary observations; Tong et al. 2000 and Moss et al. 2004 for spiny lobsters).

Larval development

The larval development of the European lobster comprises three Zoea stages (I, II and III). Stage IV is the first juvenile stage. The stages have been illustrated and described by Nichols and Lawton (1978). Charmantier et al. (1991) have reported on the morphological, anatomical, ethological and physiological changes which lobster larvae undergo during metamorphosis.

The present study demonstrated a strong effect of temperature on larval survival and duration of larval development. Intermoult periods increased with larval stage and decreased with increasing temperature. This largely conforms to the findings of Havinga (1929) who studied temperature effects within the range of 14 and 22°C. Effects of temperatures below 14°C have not been studied before. Our results show that stage-specific survival rates increased with increasing temperature. No moults occurred at 10°C and below (not reported here). At 11, 12 and 13°C, an increasing percentage of larvae moulted to Zoea II or even to Zoea III, but none was able to proceed to Stage IV. More advanced larval stage needs higher temperatures to proceed in development than do less advanced stages. Development to the first juvenile stage was only possible at temperatures of 14°C and above. The percentage of larvae that reached Stage IV increased from 9% at 14°C to 67% at 16°C, while the duration of total larval development decreased from 26 to 14 days. Optimal larval survival occurred within the temperature range of 16 and 22°C. The upper limit of thermal tolerance for incubation must be well above 22°C.

A temperature effect on stage-specific survival of larvae was also reported for the American lobster (*H. americanus*) by MacKenzie (1988). Unlike larvae of the European lobster, those of the American lobster can develop successfully at a temperature as low as 8°C (Templeman 1936). Furthermore, the temperature of optimal larval survival (11°C) was much lower in the American lobster than in its European relative (Caddy 1979).

Climate change and lobster recruitment

The duration of the embryonic development (and thus the date of larval hatching) as well as larval survival and the duration of the larval development of the European lobster has been shown to be strongly dependent on temperature. We hypothesize that an ongoing warming trend in the North Sea (increase in mean monthly temperatures throughout the annual cycle, but particularly in winter) will strongly affect the recruitment success of the Helgoland lobster.

The applied laboratory temperature regimes (Fig. 1) can serve as estimates of what lobsters at Helgoland may become confronted with in coming decades. Increased water temperatures during the incubation period will significantly accelerate the embryonic development, resulting in a clear seasonal forward shift of larval hatching. A forward shift in the annual peak abundance of pelagic larvae related to climate warming of the North Sea has been demonstrated in a number of benthic animal species including decapods (Edwards and Richardson 2004; Edwards et al. 2007).

At present, no information is available on how temperature may affect the date of mating and egg extrusion. A temperature-induced forward shift in hatching might be followed by a comparable shift in mating and spawning which would exacerbate the effect of temperature increase on the timing of hatching.

Associated with a forward shift in hatching, problems to lobster recruitment may arise in two different contexts:

1. The increase in water temperature will probably not keep pace with the forward shift in larval appearance. Consequently, larvae will start their development at lower seasonal temperatures and will need more time to metamorphosis. Under these conditions, larvae are expected to suffer from an increased temperature-dependent mortality. Furthermore, since the period of larval development is associated with the highest rate of stage-specific mortality, an increased duration of the larval period will probably result in an increased predator-induced mortality.
2. The survival of larvae is not only dependent on temperature; quality and abundance of food play an important role in bottom-up regulation. The natural diet of lobster larvae includes a wide variety of phyto- and mesoplankton such as calanoid copepods (Ennis 1995). Presently, larval hatching seems to coincide with optimal food conditions for larval development (e.g. Greve et al. 2006). A rapid climate change probably would decouple this phenological relationship, as not all trophic levels are expected to respond in just the same way and at just the same pace. For instance, diatom blooms seem to be relatively stable in time, largely independent of temperature (Edwards and Richardson 2004; Wiltshire et al. 2008).

Considering that the timing of larval release in lobsters is mainly governed by the thermal history, and lobsters do not seem to possess endogenous mechanisms to delay larval hatching after mild winters into periods of optimal external conditions for larval development, an increasing decoupling (mismatch) of larval peak appearance from optimal external conditions would reveal a serious problem for lobsters in a warming North Sea. The confluence of low abundance, rapidly changing environmental conditions and impacts of warming on the early life history leads to a concern over the future recruitment potential particularly of the lobster population at Helgoland.

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