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Effects of temperature on the moulting and locomotory activity of hatchery-reared juvenile lobsters (Homarus gammarus) at Helgoland (North Sea)

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ORIGINAL ARTICLE

Effects of temperature on the moulting and locomotory activity of hatchery-reared juvenile lobsters (*Homarus gammarus*) at Helgoland (North Sea)

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Abstract

Optimized release conditions of hatchery-reared juvenile lobster (*Homarus gammarus*) can reduce loss in the field. The effect of seasonal temperature on the behavioural and physiological activity of lobsters was examined, observing the timing of moulting and locomotory activity in juvenile lobsters maintained at increasing temperatures under standardized laboratory conditions. The juveniles of three different year and size classes mostly moulted when a threshold temperature between 12 and 14°C was reached. In addition, the locomotory activity of lobsters showed significant responses to seasonal temperatures between 12 and 15°C in the dark-phase. The knowledge about the temperature-dependent activity of lobsters may be helpful to explain behaviour in the field and in assessing the chances of a future large-scale stock enhancement programme.

Key words: Homarus gammarus, *locomotory activity, moulting activity, temperature*

Introduction

The fishery for the European lobster (*Homarus gammarus* (Linnaeus, 1758)) at Helgoland (North Sea, German Bight) was important during the 1920s and 1930s with catches of up to 80,000 animals (38 t) per year. Since the 1980s, annual landings have remained at only a few hundred lobsters (Schmalenbach et al. 2011). In 2010, the catch per unit effort (CPUE) averaged 0.03 (numbers of lobsters per pot lift) (Schmalenbach 2011). The reasons for this decline in the lobster population may be a combination of habitat destruction, fishing pressure and anthropogenic pollution of North Sea waters. Legislative regulations in 1981 and 1999 may have prevented an extinction of the local stock. These regulations included a ban on landings of berried females, a no-catch protection area, a closed season of 1.5 months in the late summer and a minimum landing size of 85 mm carapace length (CL). However, we suspect that these regulations to date are not sufficient to ensure the recovery of the population, which still remains below the critical threshold necessary for a recovery at a large scale (Schmalenbach et al. 2011). At the Marine Station at Helgoland a lobster rearing facility was established in 1997. During a pilot project from 2000 to 2009, the rearing conditions of juvenile lobster were improved as a basis for a possible large-scale stock enhancement programme to increase the local lobster population (Schmalenbach et al. 2009, 2011). Accordingly, juvenile lobsters were released into the wild after reaching a CL of about 15 mm, considering that larger lobsters demand more space, rearing time, and require more costs generally. Small lobsters are shelter-bound with preference to rocky sites, where they can hide from predators, digging holes in gravel, sand and softer sediments between boulders, where they spend most of their time especially as juveniles and during moulting (e.g. Cooper & Uzmann 1980; Lawton & Lavalli 1995). Juvenile lobsters seek hiding places directly after release. During this phase the risk of predation is high. The survival of released juvenile lobsters in the wild may be influenced by the presence of sufficient

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shelter, suitable substratum, abundance of competitors and predators, and the release techniques as the transportation conditions, time of release and seasonal water temperature (Van der Meeren 1993, 2000; Schmalenbach et al. 2011).

Seasonal changes in temperature affect the behavioural and physiological activity of *Homarus* spp. Migration speed and distance, and accordingly catchability, of adult lobsters is related to seasonal changes in temperature (McLeese & Wilder 1958; Koeller 1999) and several other environmental variables (light, wave height, current velocity, turbidity) (Ennis 1984; Karnofsky et al. 1989; Smith et al. 1998, 1999, Moland et al. 2011a). Furthermore, locomotory activity of nocturnal lobsters of *Homarus* spp. may depend on their size, sex and specific behavioural patterns (foraging, moulting, mating, dominance and territorial behaviour) (Branford 1979; Lawton 1987; Karavanich & Atema 1998; Mehrtens et al. 2008; Schmalenbach et al. 2011). So far, field studies that quantified movement in adult lobsters reported no significant differences in home ranges between lobster size and sex (Scopel et al. 2009; Moland et al. 2011b).

Pre-moult induction and preparation for moulting are controlled by the endocrine system, which in turn responds to internal (age, nutritional state, health) and external (food, temperature, photoperiod, lunar cycle) cues. Temperature is the primary environmental regulator for moulting processes, and generally, juvenile lobsters moult more than once a year and grow more rapidly when the water is warming (Aiken 1980; Fingermann 1987; Waddy et al. 1995; Ferrero et al. 2002; Wahle & Fogarty 2006).

The first part of the study was designed to examine the timing of the first moults in three different size classes of juvenile lobsters (one-, two-, and three-year-old lobsters) maintained at a temperature regime that closely followed the seasonal temperature changes. In the second experiment, one-year-old lobsters were maintained at different constant temperatures to determine the threshold temperature of locomotory activity in darkness and light.

This laboratory study was designed to give an insight into how lobster activity may be influenced under laboratory-controlled conditions and should help to interpret and assess the ability of released hatchery-reared lobsters to seek successful hiding places for survival and growth in relation to temperature and with regard to habitat-specific factors.

Materials and methods

The laboratory experiments were carried out in the years 2006–2008 at the Marine Station on Helgoland.

Origin of animals and maintenance

Ovigerous (i.e. egg-bearing) female lobsters (*Homarus gammarus*) were captured by local fishermen in the rocky subtidal zone around the island of Helgoland (German Bight, North Sea; 54°11.3′N, 7°54.0′E). The juvenile lobsters used in the experiments were raised in the laboratory from the eggs of wild captured ovigerous females as reported by Schmalenbach et al. (2009). The animals were placed in rectangular frames with separate compartments. The frames were partitioned in 200 compartments (9×7 cm, height of water level: 7 cm). Lobsters larger than $\sim$15 mm and $\sim$30 mm in carapace lengths were separated in bigger compartments with 48 and 24 compartments, respectively, per frame (19×10 cm and 19×19 cm, respectively; height of water level: 10 cm). Each frame was placed in a flat tank covered with a light shield and a sprinkler. The sprinklers provided a constant flow of fresh seawater into each compartment. The bottom of the compartments was made of nylon gauze (300-μm mesh size). The lobsters were maintained under the natural light–dark cycle, at temperatures that closely followed the seasonal changes in temperature and at a salinity of ca. 31‰. The animals were fed *ad libitum* with a mixture of crustaceans (newly hatched *Artemia franciscana* (Kellogg, 1906), minced crabs of *Cancer pagurus* (Linnaeus, 1758) and *Carcinus maenas* (Linnaeus, 1758), and live juvenile isopods *Idotea emarginata* (Fabricius, 1793)). A short piece of a PVC tube provided shelter. Bottom substrate was avoided because it would cause contamination and further cleaning efforts. The combination of the different diets and the shelters in the lobster boxes stimulated the development of crusher claws in 95% of the specimens (Schmalenbach et al. 2011). The crusher claw is important for intraspecific competition for shelter, food and mates (Van der Meeren & Uksnøy 2000). Furthermore, the lobsters were allowed to eat their shed exoskeletons after moulting. The specimens were controlled for moults, and the minimum and maximum water temperature was recorded daily.

The lobsters used in this study were released at Helgoland within the mark–recapture programme (Schmalenbach 2009; Schmalenbach et al. 2011).

Moulting activity

Animals of three different size classes (one-, two- and three-year-old lobsters; Table I) were reared in single compartments with running seawater maintained at a temperature regime that closely followed the seasonal temperature changes. The temperature

Table I. Age, number (*N*), carapace length (CL) and weight of juvenile lobsters (*Homarus gammarus*) used for the moulting experiments. The first moults of lobsters for each year class and study year (2006, 2007 and 2008) were documented during the seasonal changes in temperature from the lowest to the highest water temperature in year, i.e. from 1 March to 1 August (see Figure 2). The threshold temperature (V50), with the coefficients of determination (*r*2), is the estimated temperature at which the half of the lobsters had moulted the first time (see Figure 3). Data are given as means and standard deviations (SD).

Year class	Age (month)	*N*	CL (mm)	Weight (g)	Range of water temperature (°C)	Temperature range of first moults (°C)	Temperature at first moults (°C)	V50 (°C); *r*2
Study year: 2006								
1	8±3	173	12±3	1.2±0.8	4.7–21.4	4.8–20.5	11.8±2.8[a]	11.9; 0.9556
2	18±5	32	23±5	9±6	4.7–21.4	11.2–21.4	12.8±2.4[a]	12.2; 0.9623
3	30±2	27	31±4	21±6	4.7–21.4	11.7–15.7	14.3±2.0[b]	13.9; 0.9559
Study year: 2007								
1	13±1	31	14±1	1.0±0.6	9.0–19.6	9.2–19.2	13.5±2.4[a]	12.9; 0.9875
2	20±1	43	17±3	3±1	7.9–19.1	9.5–17.1	12.3±1.4[b]	12.1, 0.9709
3	34±3	32	30±3	16±4	7.9–19.1	8.0–16.6	12.8±2.5[a]	12.1, 0.9637
Study year: 2008								
1	12±1	29	14±1	1.6±0.5	6.4–19.1	9.7–17.4	12.6±2.7[a]	11.2; 0.9903
2	20±1	35	18±3	3±2	6.4–19.1	7.1–16.9	12.0±2.6[a]	11.7; 0.9884
3	33±3	41	30±3	17±4	6.4–19.1	11.3–13.3	12.5±0.6[a]	12.6; 0.9398

Different superscripts denote statistically significant differences for each study year (one-way ANOVA and paired comparison post-hoc test ($P < 0.05$)).

recorded reflected the sea surface temperature at Helgoland (Schmalenbach & Franke 2010), but as a result of the construction of the seawater supply system in the laboratory, water temperatures were on average 1–2°C higher than in the field.

The first moults of lobsters for each year class and study year (2006, 2007 and 2008) were documented during the seasonal changes in temperature from the lowest to the highest water temperature, i.e. from 1 March (5–8°C) to 1 August (19–21°C).

Locomotory activity

In this experiment, eight juvenile lobsters (mean CL and SD: 10.9±0.7 mm; mean weight and SD: 725±170 mg) were individually transferred to 10-litre basins and were acclimated to the first experimental temperature and light–dark cycle for a full week. Each day, food (freshly hatched nauplii of *A. franciscana* and live juvenile isopods *I. emarginata*) was added, and the water was changed.

The activity of lobsters was examined in a climatic exposure test cabinet (RUMED Rubarth Apparate 3001–3601, version D/30-36/02-2001) under an artificial 12 : 12 h light–dark cycle (light phase: start at 6 a.m.; dark phase: start at 6 p.m.) and to each of six different constant temperatures (3, 6, 12, 15 and 18°C). Light intensity was 0.2 μmol m^{-2} s^{-1} measured with a Quantum-Sensor LI-190SA, Licor Data Logger LI 1400.

The acclimated lobsters were individually transferred to 180-ml cylindrical glass bowls (diameter: 7 cm, area = 154 cm^2; height of water level: 4.5 cm). The bottom of the glass bowls was covered with natural shell sand (fill level: 1.5 cm; particle size: 1–5 mm) and a few stones (diameter: 1 cm). Furthermore, a short plastic tube (1.5 × 3.5 cm) provided shelter. Preliminary studies showed that lobster tended to be restless without substrate and shelter. The glass bowls were covered with a plastic cross to divide the bowl into four quadrants. The locomotory activity of lobsters was expressed as the number of crossings of the lines or centre of the bowl. The distance covered was calculated as the body length per crossing. One crossing was equivalent to a distance of 3 cm. A camera (AquaVu Underwater Viewing System MC 2X-120) was placed above the experimental basin and recorded the activity of the lobsters (Figure 1).

For each run of the experiment, the eight lobsters were acclimated to the experimental conditions for 2 h in the test cabinet. Video recording lasted 15 min per hour from 7 a.m. to 6 p.m. during the light phase, i.e. began 1 h after the change from ‘nighttime’ to ‘daytime’ and from 7 p.m. to 6 a.m. during the dark phase, i.e. 1 h after the change from ‘daytime’ to ‘nighttime’). The night activity was detected under red light. Red light did not disturb lobsters in their behaviour (Weiss et al. 2006).

After each light–dark cycle, the lobsters were acclimated to the next higher experimental temperature for a full week and observations were repeated as described above.

Statistics

Statistical analyses were performed according to Sokal & Rohlf (1995). All data sets, presented as means and standard deviations (SD) of replicates, were examined for normal distribution and similarity

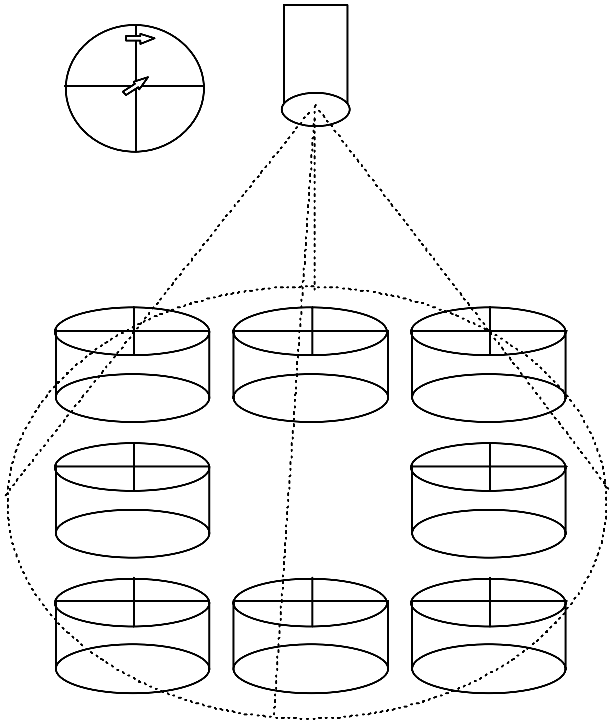

Figure 1. Top and side view of the experimental glass bowls. The bowls were partitioned by plastic crosses. The locomotory activity of lobster was expressed as the number of crossings of the lines or the centre of the bowl (see arrows). A camera was placed above the experimental basin and recorded the activity of the animals.

of variances using the statistical software package Statistica 7.1 (StatSoft Inc.). The data were subjected to one-way and two-way ANOVA followed by a Tukey's multi-comparison test at a significance level of $\alpha = 0.05$. Statistical differences ($P \leq 0.05$) of data sets in tables and figure were indicated by different letters. The relation between cumulative percentages of moulting lobsters and seasonal changes in temperature were expressed by the following three-parameter sigmoid function using the computer program SigmaPlot 9.0 (Systat Software, Inc.):

$$y = \frac{a}{1 + \exp\left(-\frac{(x - x0)}{b}\right)} \quad (1)$$

where a and b were the coefficients and x the temperature. The threshold temperature, V50, was the estimated temperature at which the half of the lobsters had moulted for the first time.

Results

Moulting activity

During the seasonal increase in water temperature from 5 to 21°C, the first moults of juvenile lobsters occurred at mean temperatures between 11.8 and 13.5°C (Table I, Figure 2). Similarly, analysis of

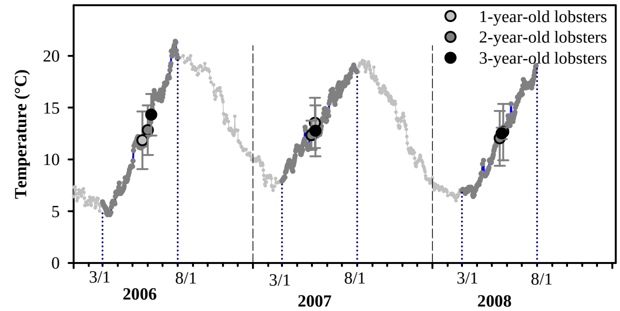

Figure 2. First moults per year (mean ± SD) of three year classes of juvenile lobsters (*Homarus gammarus*) in relation to time of years 2006–2008 and concomitant laboratory seawater temperatures.

cumulative moulting frequency showed that 50% of the lobsters had moulted between 11.9 and 13.9°C (Table I, Figure 3).

There were few significant variations in timing of first moults between the different year classes. In 2006, at a temperature range from 5 to 21°C, the one-year-old lobsters moulted firstly at 5°C, and in contrast, the two- and three-old lobsters moulted firstly at about 11°C. Furthermore, the mean moulting temperature of the three-year-old lobsters was significantly higher at 1.5–2.5°C than in the other year classes. In 2007, at a temperature range of about 8–20°C, the first moults in all year classes occurred at nearly the same temperature of 8–10°C. The mean moulting temperature of the two-year-old lobsters was significantly lower (0.5–1.5°C) than in the other year classes.

In 2008, at a temperature range from 6 to 19°C, the one-year-old lobsters moulted first at 10°C, the teo-year-old lobsters at 7°C, and the three-year-old lobsters at 11°C. There were no significant differences in the mean timing of moults between the three year classes.

Furthermore, there were no significant differences in timing of moulting between the three study years of each year class, except for the one-year-old lobsters between 2006 and 2007 and the three-year-old lobsters in 2006. In general, there is no trend in seasonal timing of moulting between the different year classes: first moults occur between 12 and 14°C (Figure 2).

Locomotory activity

Locomotory activity of juvenile lobsters depended significantly on temperature and dark–light phases. At each temperature, the activity of lobsters showed no significant effects ($P > 0.10$) recorded during the dark phase (7 p.m. to 6 a.m.) and the light phase (7 p.m. to 6 a.m.), respectively. The two-factorial analysis of variance with the independent factors night–day rhythm and temperature showed significant effects ($P < 0.0001$) in locomotory rhythm,

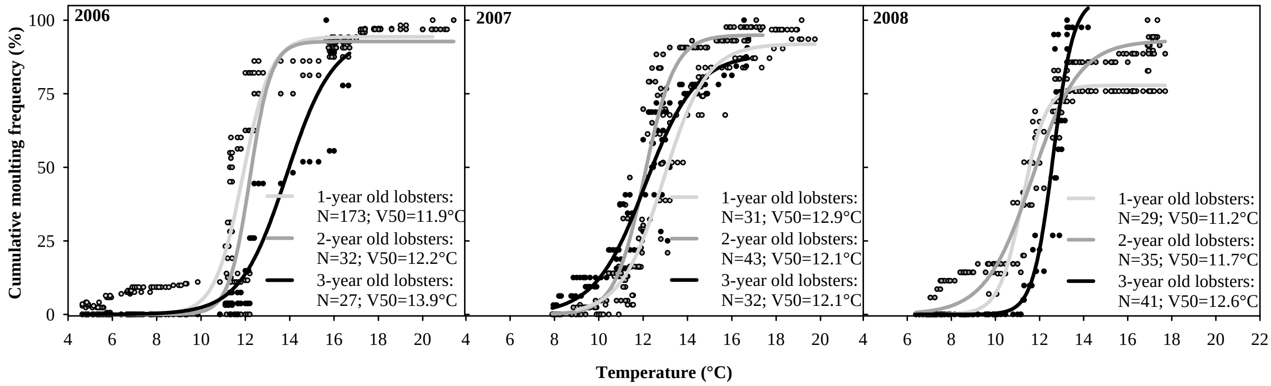

Figure 3. The relation between cumulative percentages of moulting one-, two-, and three-year-old lobsters (*Homarus gammarus*) and seasonal increase in water temperature in the years 2006, 2007 and 2008 significantly following the sigmoid equation.

except for 3°C (Table II). The locomotory activity of lobsters increased with increasing temperature (3–18°C) from 3.6 ± 1.4 to 11 ± 3.2 crossings in 15 min/h in the dark-phase by a factor of 3 and from 1.1 ± 0.7 to 6.0 ± 2.3 in the light-phase by a factor of 5.6. The total averaged distance lobsters covered in darkness was calculated per hour and averaged at 43 cm/h at 3°C and 132 cm/h at 18°C, and in light 13 cm/h at 3°C and 72 cm/h at 18°C. In the dark phase, significant differences ($P < 0.01$) in activities were shown between 12 and 15°C (Figure 4). In the light phase, the lobsters showed significant differences ($P < 0.05$) in activity between 15 and 18°C.

Discussion

The present study showed that water temperature is a significant factor influencing the moulting and locomotory activity of juvenile lobsters.

Under laboratory conditions, half of the one-, two-, and three-year-old lobsters moulted within a narrow temperature window between 12 and 14°C in all three study years. At Helgoland waters, the surface water temperature normally reaches 12°C in June, increasing to about 18–19°C in August, decreasing thereafter; in November, the water temperature decreases to below 12°C (Figure 4). In 2006, at a temperature range from 5 to 21°C, the one-year-old lobsters moulted for the first time at 5°C, and in contrast, the two- and three-year-old lobsters moulted first at about 11°C. In the other study years, the temperature range was not lower than 6°C; here, all year classes moulted first at 7°C. Aiken (1977) reported that metabolic processes in lobsters accelerated within the range of 8–25°C. However, the timing of moulting varied by few weeks only depending on different seasonal temperature regimes (Templeman 1940). In another study, no moulting occurred at or below 10°C in lobster larvae (Schmalenbach & Franke 2010), and Aiken & Waddy (1976) reported that in lobsters held below 6°C the moult induction was blocked.

The laboratory results showed that the locomotory activity of lobsters increased with increasing temperatures from 3 to 18°C by a factor of 3 and 6 in the dark and light phase, respectively. This implies that

Table II. Locomotory activity of juvenile lobsters (*Homarus gammarus*) observed during the dark and light phases at six different constant temperatures. Eight replicate experiments were run. df, degrees of freedom; SS, sum of squares; MS, mean squares; F, variance ratio, *P*, probability of rejecting a correct null hypothesis ($P < 0.05$).

	Analysis of variance				
Source of variation	df	SS	MS	F	*P*
Main effects					
Dark/Light	1	5393	5393	168.5	< 0.0001
Temperature	5	4891	978	30.6	< 0.0001
First-order interactions					
Temperature × Dark/Light	5	464	93	2.9	0.0132

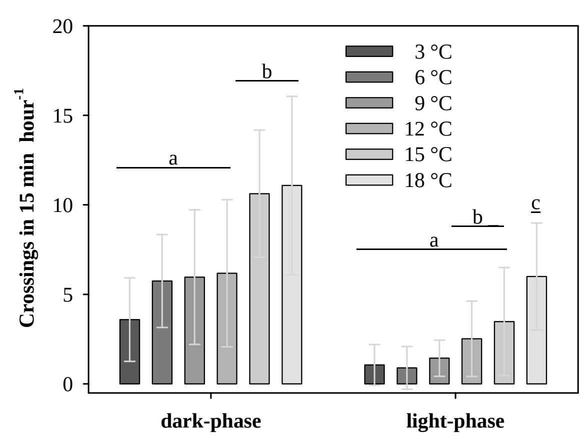

Figure 4. Locomotory activity of eight juvenile lobsters (*Homarus gammarus*) expressed as the number of crossings in 15 min/h (mean ± SD) at different constant temperatures during the dark and light phases, respectively. Different letters indicate differences in activity of lobsters during the dark and light phases (one-way ANOVA and paired comparison post-hoc test ($P < 0.05$)).

light may have more influence on locomotion than temperature. However, the activity was nearly the same at 15°C in the light phase as at 3°C in the dark phase. Furthermore, lobsters showed significant differences in activity between 12 and 15°C in the dark phase and also significant effects between 15 and 18°C in the light phase. Similarly, Cooke (2005) reported that *Homarus americanus* moved farther in the dark than in the light with two activity stages below and above 12°C. Furthermore, Jury (1999) and McLeese & Wilder (1958) found an activity threshold at about 10°C.

Temperature thresholds appear to be associated with several stages of the lobster life cycle at Helgoland. The timing of embryogenesis and larval hatch was strongly dependent on late winter and spring temperatures (Schmalenbach & Franke 2010). In juvenile lobsters first moults and enhanced locomotory activity started when a threshold between 12 and 15°C was passed independent of year class, which means also independent of size, underlining the importance of the temperature factor. In terms of size, however, an activity threshold was apparent at a total length of 75 mm (CL 27–34 mm), at which nocturnal locomotory activity and exploration behaviour in the laboratory increased. At the same time, the frequency of shelter visits decreased rapidly. Apparently, the larger lobsters were less dependent on the attainability of shelters and thus could more intensively explore and utilize their environment (Mehrtens et al. 2005). This size usually was reached under Helgoland rearing conditions at the end of the second year. Furthermore, in adult lobsters, a clear dependence of commercial catch rates and ambient seasonal temperature was noted (Schmalenbach unpubl.). Equally, a concomitant decrease was seen with the cooling of the sea temperature later in the year. Reports by the local fishermen corroborate that below 10°C pot placement ‘does not pay’ both in spring and autumn, indicating that such an activity threshold may exist in the field. Our corresponding laboratory experiments confirmed a similar activity–temperature relationship.

Optimum release conditions, such as the site and also the time of release (night or day, sea temperature) for juvenile lobsters are generally important for a successful restocking programme of lobster populations affording maximum protection and minimal predation pressure (e.g. Howard 1983; Mills et al. 2008). The critical phase for the survival of juvenile lobsters released into the wild is the first hour after release (Van der Meeren 2000). To avoid loss by predation after release, the locomotory capacity of lobsters should be high enough to quickly find a hiding place. The present study showed that lobsters were significantly more active at a temperature above 12°C. Furthermore, the metabolism of lobsters is higher at warmer temperatures, enhancing growth considerably compared to winter time. Preliminary additional studies have shown that the locomotory activity of juvenile lobsters was higher in the absence than in the presence of shelter, and activity increased more with increasing temperature without shelter (Schmalenbach unpubl.). Equally, adult American lobsters were more active without shelter than when shelter was provided (Krekorian et al. 1974). This indicates that increased activity may be related to shelter-seeking behaviour (Zeitlin-Hale & Sastry 1978). This increased activity could be useful for lobsters to quickly find appropriate hiding places after release. The predation and competition pressure of juvenile lobsters varied between different habitats and season. Van der Meeren (2000) suggested that release sites must be examined by previous monitoring of predatory crustacean and fish species and for sufficient shelters for lobsters. At Helgoland, the most abundant fish species and potential predators of juvenile lobsters in summer are visually oriented fishes such as shorthorn sculpin (*Myoxocephalus scorpius* Linnaeus, 1758), long-spined bullhead (*Taurulus bubalis* Euphrasen, 1786), and rock cook wrasse (*Centrolabrus exoletus* Linnaeus, 1758). To minimize the loss of lobsters by vision oriented fishes, juveniles should be released at night. At other locations, juvenile lobsters were released in winter when predators were less abundant than in summer (Van der Meeren 2000). In view of the choice of optimal release sites, the main competitor for food and shelter at Helgoland is the edible crab *Cancer pagurus* (Anger & Harms 1994). Since the 1980s, the population of the edible crab *C. pagurus* has increased with decreasing North Sea cod (*Gadus morhua* Linnaeus, 1758) stocks, which, since 1990, have been at levels at which the risk of stock collapse of the latter is considered to be high (Daan et al. 1994; Cook et al. 1997; Drinkwater 2005; Hannesson 2007). Preliminary data from SCUBA surveys indicate that the abundance and size of *C. pagurus* varied at possible lobster release sites (Schmalenbach unpubl.). Accordingly, the choice of optimum release sites should consider competition between the crab *C. pagurus* and lobster *H. gammarus* for food and shelter. Furthermore, transport conditions play an important role to avoid stressed lobsters (see Van der Meeren 1991). Consequently, a suite of different environmental factors of the respective habitats have to be considered to choose optimal release strategies at each location.

In conclusion, in view of enhancing a population, good knowledge of the environmental conditions and of behavioural characteristics is necessary, which should also include concern of the impact of the warming trend of North Sea waters on the early life history of lobsters (Schmalenbach & Franke 2010). At Helgoland, the specific habitat, the recruitment conditions and productivity of the lobster population may allow for a successful restocking programme, based on a mark–recapture study of hatchery-reared lobsters which indicated that released juvenile lobsters could sustainably increase the productivity of the local stock (Schmalenbach et al. 2011). Important criteria for success are optimum rearing and release conditions (locations, time and temperature), which reduce the loss of cost-intensive hatchery-reared juvenile lobsters. Accompanying management and conservation measures such as a ban on landings of all females to increase recruitment along with the establishment of no-catch control areas (see Hoskin et al. 2011) may further improve the stock status of the Helgoland lobster.

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