STUDIES ON THE DEVELOPMENTAL CONDITIONS OF THE EUROPEAN LOBSTER (*HOMARUS GAMMARUS* LINNAEUS, 1758) AT THE ROCKY ISLAND OF HELGOLAND (GERMAN BIGHT, NORTH SEA)

Dissertation

zur Erlangung des Doktorgrades
des Departments Biologie
der Universität Hamburg

vorgelegt von

ISABEL SCHMALENBACH

aus Hilden

Hamburg 2009

Genehmigt vom Department Biologie
der Fakultät für Mathematik, Informatik und Naturwissenschaften
an der Universität Hamburg
auf Antrag von Herrn Professor Dr. F. BUCHHOLZ
Weiterer Gutachter der Dissertation:
Herr Professor Dr. H.-D. FRANKE
Tag der Disputation: 26. Juni 2009

Hamburg, den   10. Juni 2009

Professor Dr. Jörg Ganzhorn
Leiter des Departments Biologie

CONTENTS

GENERAL INTRODUCTION

Lobsters belong to the invertebrate Subphylum Crustacea, which encompasses functionally very diverse marine groups such as barnacles, krill and crabs, as well as freshwater and terrestrial taxa. The order Decapoda contains most of the commercially important species including the European lobster (*Homarus gammarus* Linnaeus, 1758). *Homarus* species have been used as models in many biological fields, play important ecological roles, and much of their life history has been well studied although many ecological details are still little known, especially in view of fishery and population management.

In the following introductory chapters an overview is given of the life history of *Homarus* species, the geographical distribution of the European lobster, the European lobster fishery, and the usage of *Homarus* in aquaculture and stock enhancement. Furthermore, descriptions of the habitat of the Helgoland lobster population, the Helgoland lobster fishery and management are followed by an overview of previous studies at Helgoland, and lastly I give an outline of the dissertation.

Life history

The life histories of *H. gammarus* and *H. americanus* (H. Milne Edwards, 1837) show a close match. Morphology, physiology, behaviour and ecology of lobster are described in Holthuis (1974), Cobb and Phillips (1980), D'Abramo and Conklin (1985), Lawton and Lavalli (1995) and Cobb and Castro (2006).

Reproduction and embryonic development

The onset of functional maturity in females (presence of eggs under the abdomen) varied among populations and occurred approximately after 4 growing seasons in *H. gammarus* (Manuscript II). Comeau and Savoi (2002) and Mehrtens (2008) described one-year and two-year reproduction schemata: Females could spawn in successive years; they could moult/mate and spawn in the same year and/or females could moult/mate one year before spawning. Furthermore, females could spawn every two years with moulting and spawning in the same and/or alternating years.

In general, spawning and mating occurred in the female lobsters in late summer, followed by a 9- to 11-months period of embryonic development (e.g. Mehrtens, 2008). Fecundity ranges from about 1,000 to 26,000 eggs. The eggs change colour as they develop. At first they are dark (egg stage 1) until they begin to turn yellow as the embryo develops, consumes the yolk and finally becomes visible through the transparent outer layer (egg stage 4; Figure 1).

Figure 1 Egg stages 1 and 4 of female lobsters (*Homarus gammarus*).

Temperature is the main factor influencing the embryonic development in both *Homarus* species (Templeman, 1936a; Perkins, 1972; Branford, 1978; MacKenzie, 1988; Charmantier et al., 1991; Charmantier and Guillaume, 1992; MacDiarmid and Saint-Marie, 2006). Endogenous components are in further control of the timing of larval hatching (Ennis, 1973; Morgan, 1995; Manuscript II). Hatching occurs over several nights in batches of a couple of hundreds at a time. Pre-larvae are released into the water column by a shake of the female's tail and pleopods, and soon after hatching they moult to the first larval stage and begin their planktonic phase which ranges from late May to August.

Larvae

The larval phase comprises three Zoea stages which were morphologically described by Nichols and Lawton (1978) (Figure 2).

Figure 2 Larval stages (I, II and III) of the lobster *Homarus gammarus*. Pictures: Sandra Götze, 2009.

The swimming capability of larvae increases during larval development (Ennis, 1995): Larvae of stage I use the six pairs of exopodites on the third maxilliped and the five thoracic limbs. Larvae of stage II additionally have four pairs of small pleopods ("swimmerets") on the second through fifth abdominal segments, and larvae of stage III have as well developed tail fan (uropods and telson) and enlarged swimmerets. The major swimming appendages of the pelagic larvae are the exopodite branches of the third maxillipeds, the chelipeds and the four pairs of pereipods (Neil et al., 1976). The larvae used their locomotive ability to move forward, backwards or upwards.

Lobster larvae are omnivorous, opportunistic feeders and their natural diet includes a large variety of phytoplankton and zooplankton (e.g. copepoda, decapoda larvae, gastropda larvae) (Ennis, 1995).

The larval recruitment is dependent on environmental factors such as current systems, pressure, the light-dark regime, temperature, predators, and food abundance; and on behavioural components such as swimming ability and the active orientation in response to these environmental factors (Ennis, 1983; Hudon and Fradette, 1993; Manuscripts II and III).

Juvenile and adult lobsters

Regular metamorphosis occurs at the moult from stage III to the post-larva and is accompanied by behavioural and habitat changes. Existing schemata of the benthic life cycle seem to differ among authors (Lawton and Lavalli, 1995). In the present work we used the terminology of Cobb and Wahle (1994), where the benthic life is divided into three phases. The *early benthic phase* (4-20 mm carapace length CL) is cryptic and the most habitat-restricted period of the life history. During the *adolescent phase* (20-50 mm CL) lobsters become more and more conspicuous. The *reproduction phase* is defined by the onset of sexual maturity.

Small lobsters and some adolescents use the interstitial spaces between heterogeneous rocks and boulders at the sea bed as burrows. Small lobsters are shelter-bound, they prefer to make their refuges in rocky sites, where they can hide in the crevices from predators (van der Meeren, 2000; Mehrtens et al, 2005), digging holes in gravel, sand, and softer sediments between boulders, where they spend most of their time (Karnofsky et al., 1989) especially in their early years and during moulting.

The growth and survival of juvenile lobsters in the wild is dependent on the abundance of predators and competitors, the presence of sufficient hiding places, the light regime, season and water temperature as well as on the carrying capacity of the habitat (Manuscript I).

Growth in adult lobsters differs between sexes. At maturity, males growth faster then females (e.g. Tempelman, 1933; Manuscript I). Furthermore, the timing of moulting is different between the sexes. Generally, males moult in spring while females moult after their larval hatching in late summer. Mating behaviours are described by Atema et al. (1979) and Atema and Voigt (1995) who suggested that the partners communicate chemically via sex pheromones. The pre-moult female selects and visits the largest male in its hiding place. After the female has moulted, mating happens, and thereafter it remains in the males`s shelter for about one week. Females can retain spermatophores for a long period of time before spawning and fertilisation will take place.

Geographical distribution

The typical habitat of the European lobster *H. gammarus* is rocky or coarse soft bottom with crevices, boulders and stones. The European lobster has a broad geographical distribution which extends along the North-East Atlantic coasts, from the cold waters at the Arctic Circle to the warm waters of Morocco, and it occurs at depths down to about 60 m (Figure 3).

In north Europe, the lobster occurs from northern Norway (Lofoten Island) to south-eastern Sweden and Denmark, where it is prevented from invading the Baltic Sea by low salinity and temperature extremes. The northernmost self-sustaining population is found in Tysfjord (68°15'N) in northern Norway. The distribution of the species extends south-wards along the European mainland, around the British Isles and to the Azores, reaching its southern limit of about 30° northern latitude on the Atlantic coast of Morocco. Although to a much lesser extent nowadays, the distribution also extends throughout the coastal and

Figure 3 Geographical distribution of the European lobster (*Homarus gammarus*). Map: Modified after Google Earth.

island areas of the Mediterranean Sea and its sub-seas, and the species has been reported from the westernmost end of the Black Sea in the region of the Straits of Bosporus (Dybern, 1973; Holthuis, 1974; Williams, 1988). Studies using molecular markers such as microsatellites, mtDNA and allozymes have shown that there is only a low level of overall genetic divergence among European populations of *H. gammarus* (Hedgecock et al., 1977; Jørstad and Farestveit, 1999; Ulrich et al., 2001).

European fishery

Landings of the European lobster (*H. gammarus*) in Scotland, England and Wales (Bannister, 1986), Ireland (Browne et al., 2001; Tully et al., 2006), Norway (van der Meeren and Tveite, 1998), France, Sweden, Denmark and Spain (see Dow, 1980) have varied within the past 70 years between 1,700 and 3,500 tons per year (Figure 4).
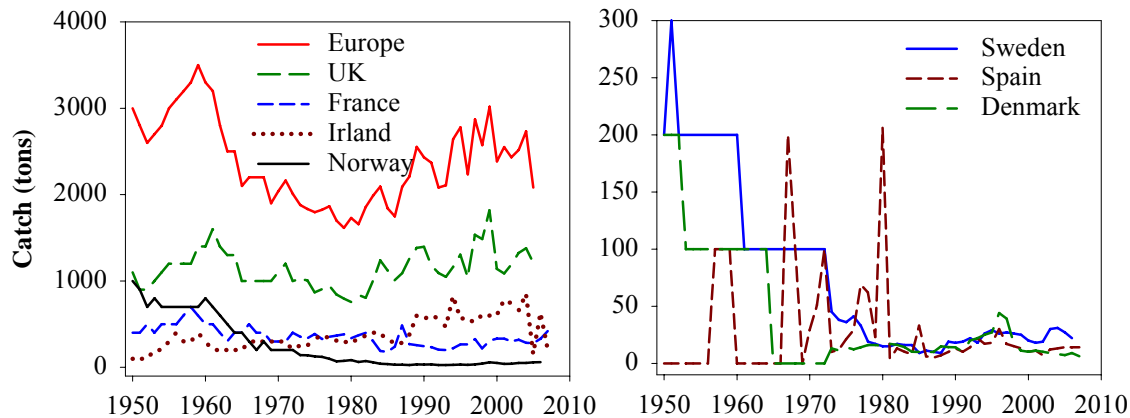

Figure 4 Total landings of *Homarus gammarus* in Europe (Fishery Statistics, 1950-2007).

Catches have declined in several countries from peak landings during the period from 1930 to 1975. The greatest reported declines have occurred in Denmark with 90 % (1933: 198 t; 1980: 15 t) and in Sweden with 95 % (1933: 299 t; 1980: 15 t) (Dow, 1980). In Norway, lobster landings per year severely decreased from about 1,000 t in the 1930s to about 50 t during the last 20 years (Agnalt et al., 1999). In Germany at Helgoland, landings declined by 98 % (1937: 41 t; 1970s: 1 t) (Klimpel, 1965; Goemann, 1980, Figure 6; Appendix: Table 1). However, in some countries the total landings stayed at the same level or even increased due to discovery of previously unexploited stocks (e.g. Scotland) or by an increase in fishing effort (e.g. Ireland 1940: 135 t; 1994: 715 t) (Bennet, 1980; Browne et al., 2001). Landings in Italy, Yugoslavia and Algeria fell to almost zero (Cobb and Castro, 2006).

The main lobster regulation measure used in Europe is the minimum landing size of 74-88 mm carapace length, which was chosen in relation to size at maturity. The landing of berried females is completely banned in Germany, in Spain and one area of Denmark (Limfjord), while in Portugal it is banned for a short period only. Closed seasons exist in

Portugal, Spain, Germany, Norway, and Sweden. Limiting fishing effort was attempted in Sweden. Capture by diving is banned in Ireland, Sweden, and Germany, mainly to prevent hobby fishing (Bennet, 1980; Ministerium für Landwirtschaft, 1981).

Aquaculture and stock enhancement

Both *H. gammarus* and *H. americanus* have been evaluated for their potential for aquaculture and stock enhancement since the middle of the 19th century (Aiken and Waddy, 1995; Nicosia and Lavalli, 1999; Wickens and Lee, 2002; Gendron and Sainte-Marie, 2006). Nicosia and Lavalli (1999) reviewed and summarized the literature on past and present homarid lobster culture, hatchery activities, stock enhancement programmes, and gave recommendations for the future use of lobsters.

Lobster aquaculture is highly capital intensive (D'Abramo and Conklin, 1985). Several programmes aimed at enhancement of European stocks by rearing larvae in the laboratory through their planktonic stages to produce large numbers of small juveniles that were maintained and fed for 3 months or more (Bannister and Addison, 1998; van der Meeren et al., 1998). In previous European release programmes a satisfactory number of cultured lobsters could be recaptured at marketable size (Burton et al., 1994; Cook, 1995; Tveite and Grimsen, 1995; Bannister and Addison, 1998; Moksness et al., 1998; van der Meeren et al., 1998; Agnalt et al., 2004; Manuscript I).

For lobster culture, the use of wild-captured females as a seed supply is critical because these can carry diseases into the brood-stock culture system. However, this risk varies from population to population. Assurance of a continuous and predictable source of egg-bearing female lobsters requires complete control of the reproductive cycle.

Larval lobsters consume easily available food; they take two weeks to complete their three planktonic stages when reared at the optimal temperature of 20 °C (Schmalenbach and Franke, in prep.; Manuscript II). The larvae are generally reared in specific tanks which are designed to maintain a homogeneous spatial distribution of the cannibalistic larvae by means of a spiralling upward flow pattern (Hughes et al., 1974). Larval survival in the rearing tanks is influenced by the density of larvae, food availability, temperature, light regime and water quality (Carlberg and Van Olst, 1976; Fiore, 2005).

Juvenile lobsters can be cultured in containers either individually or in groups. Typically grow-out systems consist of rearing containers for individuals (Conklin and Chang, 1983). In contrast, in communal rearing systems the density of lobster is strongly limited while losses are high due to cannibalism (Van Olst et al., 1975; Sastry and Zeitlin-Halle, 1977). Deleterious behaviour of lobsters could be reduced by removal of chelipeds or dactyls (Aiken and Young-Lai, 1981). Increased growth rates could attain by eyestalk ablation which suppresses the moult-inhibiting hormone (Castell et al., 1986). Nutritional research has focused on the definition of nutrient requirements and the development of a suitable diet for the grow-out phase of lobster. Different natural and artificial diets were used in lobster culture (Conklin et al., 1980; Boghen and Castell, 1981; Beard et al., 1985; Bordner and Conklin, 1981; Waddy, 1988; Floreto et al., 2000; Schmalenbach et al., 2009).

Release sites of hatchery-reared lobsters must provide high quality habitats affording maximum protection and minimal predation pressure (Mills et al., 2008). Loss of lobsters by predation was highest during the first hour after release, when the animals were without shelter (van der Meeren, 2000). However, divers observed that juvenile lobsters were not attacked during their descent from the sea surface to the sea bottom (Howard, 1983). Furthermore, van der Meeren (1993) reported that hatchery-reared juvenile lobsters react adequately to predators and show good burrowing behaviour.

At Helgoland, the main competitor of the lobster for food and shelter is the edible crab, *Cancer pagurus* (Linnaeus, 1758) (Anger and Harms, 1994). Due to the overfishing of cod, the abundance of *C. pagurus* has been significantly increasing over the past decades around the island of Helgoland. Van der Meeren (2000) suggested release sites to be previously examined by recording the local crustacean and fish species as well as the availability of sufficient shelters for lobsters.

Study area

The island of Helgoland is located 45 miles offshore in the southeast part of the North Sea (German Bight, 54°11.3'N, 7°54.0'E, Figure 5), parts of which designated as a nature reserve in 1981.

The intertidal and subtidal area around Helgoland consists of hard-bottom covering about 35 km² at a maximum depth of 24 m and is exposed to tidal currents and strong winds (Hickel, 1972). The hard-bottom community of Helgoland is geographically and ecologically isolated from similar hard-bottom areas and neighbouring populations in Norway and Britain by some hundred miles of sandy or muddy bottoms.

The inflows of fresh water carrying anthropogenic pollution by the rivers Westerschelde; Maas,

Figure 5 Location of the island of Helgoland in the German Bight, North Sea. Picture: Thorsten Meyer, 2006.

Rhine, Weser and Elbe reach Helgoland only in very diluted form. Therefore, the water at Helgoland is relatively little polluted compared to other locations in the German Bight (see Harms, 1993).

At Helgoland, average surface water temperatures have been rising by about 1.5 °C since 1962 (Wiltshire et al., 2008, for the period up to 2005). This ongoing warming trend of the North Sea waters strongly influences the structure and function of marine communities in terms of changes in species distribution and local species composition as well as phenological shifts (Southward et al., 1995, Greve et al., 1996; Beare et al., 2004, Edwards and Richardson, 2004; Franke and Gutow, 2004; Greve et al., 2004; Perry et al., 2005; Reichert and Buchholz, 2006, IPCC, 2007; Manuscript II).

There is an extensive literature on studies of the hard-bottom communities around the island of Helgoland (see Harms, 1993; Franke and Gutow, 2004; Reichert et al., 2008).

Along the German coast, a small lobster population (*Homarus gammarus*) is only present at the rocky basement of the island of Helgoland.

Commercial lobster landings from 1615 to 2008

For over a century, lobster fishing has been important for the island of Helgoland (Ehrenbaum, 1894). The following report on historic lobster landings from 1615 up to 2008 are based on Schnackenberg (1953), Klimpel (1965), Goemann (1990) and Anonymous (1980-2008) (Figure 6, Appendix: Table 1).

At Helgoland, the first record of lobster landing was in 1615 with around 37,000 lobsters per year and in the 1790s with around 40,000 to 50,000 lobsters per year. Since the 1880s, lobster landings have been more or less continually reported and the local fishery consisted of around 45 fishing boats until 1944.

From 1790 to 1906, total landings ranged from 30,000 to 70,000 lobsters per year at a value of 50-90,000 DM (German marks). At that time, landed lobsters weighed around 0.5 kg. During the 19th century, the lobster fishery underwent considerable changes. From 1907 to 1930, the annual landings decreased to 20,000-30,000 lobster per year due to the destruction of important fishing grounds by building harbour areas, by military target practice and exercise. However, a new fishing area called "Steingrund" was discovered in 1910.

Figure 6 Landings of the European lobster (*Homarus gammarus*) around the island of Helgoland during 1883 to 2008 (Klimpel, 1965; Goemann, 1980; Anonymous, 1980-2008).

From 1930 to 1937, catches increased partly due to the lobster fishery starting up in a new area (NNO Helgoland) and landed about 74,000 lobsters per year. Peak landings reached 82,750 lobsters in 1931 and about 87,000 lobsters (41 tons) in 1937.
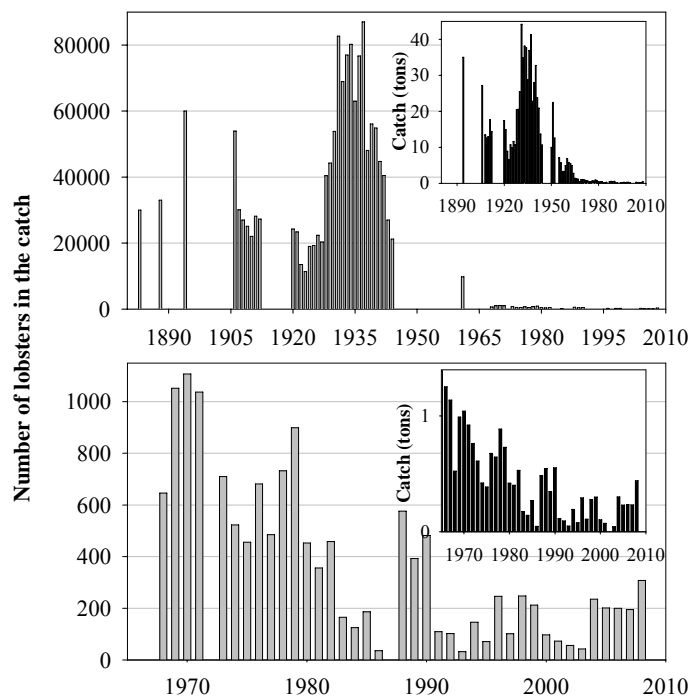
After the last peak in 1937, landings decreased to 21,200 lobsters in 1944 due to military actions. In 1945, the islanders were evacuated to the mainland. During the post-war era (1945-1952), the island was used as training target for bombing pilots. During that period, the fishermen mainly came from Cuxhaven, from Hörnum and Büsum of the State of Schleswig-Holstein to the island of Helgoland and landed about 20 tons lobsters per year with 25-30 fishing boats. During the next decade (1950-1960), the annual catch decreased from 20,000 to 10,000 animals. After that, from 1960 to 1980, lobster catches decreased dramatically to only around 500 lobsters per year. Since the 1980s, landings of lobsters have been fluctuating at a low level of only a few hundred specimens per year. Nowadays, the Helgoland fishery consists of maximal 10 boats and 260 lobster pots. In the seasons 2005 to 2007 about 200 animals (0.23 tons) per year were landed and in the latest season 2008, the local fishermen captured about 308 animals (0.44 tons). The lobsters weighed between 1.5-2 kg per animal and measured a total length of about 35 cm.

Reasons for the decline

The reasons for the dramatic decline of the economically important lobster population may include land reclamation in the 1930s, habitat destruction by bombing the island during and after the Second World War, and the big blasting operation "Big Bang" (6,000 tons munitions) in 1947, as well as extensive fishing pressure after the Second World War as described above.

Since the 1970s the anthropogenic pollution of the North Sea waters have been increasing, resulting from increased oil and gas production, shipping traffic, impact of chemicals and industrial wastes carried along by the rivers Elbe and Rhein (van Bernem and Lübbe, 1997). As a consequence, the pollution was 10 times higher in the North Sea waters than in the open Atlantic Ocean (BLMP, 2000, 2002). In 1996, the total hydrocarbon concentration near Helgoland averaged between 0.84 and 1.5 $\mu g \cdot l^{-1}$ (Meeresumwelt-Datenbank, MUDAB). Studies have shown that crude oil influences the foraging and agonistic behaviour of lobsters at very low concentrations of 6.2-7.7 $\mu g \cdot l^{-1}$ (Walter et al., 2008), and lobsters maintained for three weeks at concentrations of 1.8-2.9 $\mu g \cdot l^{-1}$ responded about 1,000 times less to food stimuli than the edible crab *Cancer pagurus* (Thoma, unpubl.). This confirmed the findings of Atema and Stein (1974) that American lobsters changed their behaviour (e.g. foraging) when they were exposed to low oil concentrations.

Reasons for the missing recovery

Since the 1980s the population of the edible crab *C. pagurus* has increased with decreasing North Sea cod (*Gadus morhua* Linnaeus, 1758) stocks, which have been, since 1990, at levels at which the risk of stock collapse is considered to be high (Cook et al., 1997). The decline of the cod population especially in the North Sea resulted primarily from overfishing (Daan et al., 1994; Hannesson, 2007) and in recent years a temperature rise in the North Sea waters exerted additionally pressure on an already overexploited stock by further reducing recruitment (Drinkwater, 2005). From 1990 to 2005, cod landings decreased to 37 % while landings of *C. pagurus* increased by 25 % (Fishery Statistics, 1980-2005; Anonymous, 1980-2005). The considerable increase in abundance of *C. pagurus* around Helgoland (2007: landing of about 10 tons of crab claws, called "Knieper") could lead to increasing interspecific predation and competition between the crab *C. pagurus* and lobster *H. gammarus* for food and shelter (Anger and Harms, 1994; Mehrtens, 2008).

The Intergovernmental Panel on Climatic Change (IPCC, 2007) predicts a further temperature rise for the North Sea by 1-2 °C until 2100. Therefore, we hypothesize that increasing winter temperatures reduce the embryonic development duration and thus may result in a seasonal forward shift of larval release (Manuscript II). After mild winters larval release might occur at too low temperatures and at a time when larval food abundance is poor, *sensu* Cushing's match-mismatch hypothesis (Cushing, 1975).

With respect to the local fishery, the annual number of lobster landings stagnated, although water pollution decreased over the last decades (BLMP, 2000, 2002) and new lobster management regulations were passed. We suspect that the population size is far below the critical threshold, and that this is the main reason for the population's failure in recovery to dimensions as in the 1930s.

Fishery regulations

The first regulations were introduced by fisheries authorities in 1894, when a minimum size (9 cm carapace length, measured with rostrum) for landed lobsters was defined, and a closed season from July 15 to August 31. The carapace length is measured from the tip of the rostrum to the postero-dorsal margin of the carapace in the midline. The closed season is centred at the time of peak moulting, mating and spawning of females. Until then, the closed season was only a loose agreement among the fishermen (Schnackenbeck, 1953). Legislative regulations for the Helgoland lobster stock were decided by the Ministry of Agriculture, Environment and Rural Areas of the State of Schleswig-Holstein (Ministerium für Landwirtschaft). The rocky basement and shores of the island of Helgoland (5138 ha without Helgoland and dune) were designated as a nature reserve in 1981 (Figure 7).

The local fishermen have a fishing licence for this nature reserve. In 1999, new regulations were passed in accordance with advice by BAH; a raise of the minimum size to 11 cm carapace length (including rostrum) for landed lobsters, a ban on landings of ovigerous females, and a closed season of July 15 to August 31. These regulations require that all berried females are returned to the sea or are turned over to the Marine Biological Station on Helgoland. The Marine Station requires all tagged lobsters from the commercial fishery. Furthermore, a no-catch protection area (~400 ha) was established south of the dune island of Helgoland (Figure 7).
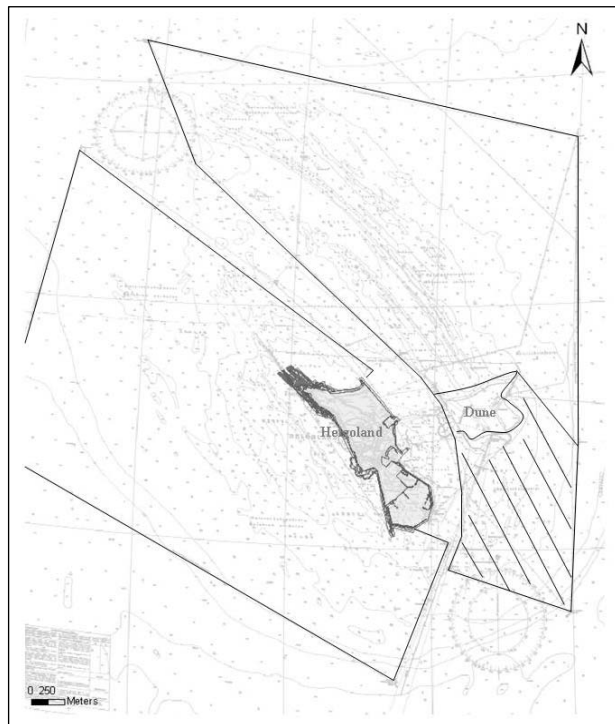

Figure 7 The rocky basement and shores of the island of Helgoland were designated as a nature reserve (5138 ha without island and dune) in 1981. A no-catch protection area (~400 ha, dashed area) was established in 1999. Map: Modified after Bartsch and Tittley, 2004.

Previous studies on the European lobster at Helgoland

Studies on the local lobster population with respect to behaviour, reproduction, growth, genetics, fishery, aquaculture, and population development were published (Ehrenbaum, 1894; Klimpel, 1965; Rickmers, 1980; Goemann, 1990; Anger and Harms, 1994; Harms et al., 1995; Ulrich et al., 2001; Franke and Gutow, 2004; Mehrtens et al., 2005; Walter et al., 2008), or laid down in PhD-theses (Ulrich, 1998; Walter, 2005; Mehrtens, 2008) and Diploma-theses (Finsterle, 1996; Binner, 1999; Thoma, 2006;).

In 1997, a research programme on lobsters was started at the Biological Marine Station at Helgoland in cooperation with the local fishermen and financially supported by the Ministry of Fisheries and Agriculture of the State of Schleswig-Holstein, Germany. The aim of this programme was a quantitative assessment of the present state of the local lobster stock and to develop a basis for a future restocking programme. The basis for a successful restocking is that the lobsters are restricted to the habitat around the island of Helgoland.

A first dissertation in this project reported that the lobster population is genetically isolated from other European stocks and therefore restricted to the rocky subtidal zone of Helgoland (Ulrich et al., 2001). A further dissertation (also financed by grants from the University of Hamburg) reported on impacts of chronic oil pollution on the behaviour and resilience in the lobster (Walter et al., 2008). This study was followed by behavioural studies, biochemical analyses and the start of a mark-recapture programme of hatchery-reared juvenile lobsters (Mehrtens, 2008). It was continued by the present PhD-work.

Outline of the thesis

The main objective of the dissertation was to increase the knowledge on the recruitment processes, to give a quantitative assessment of the status of the local lobster population around the rocky island of Helgoland, to find reasons for the missing recovery of the population from its previous decline and finally to lay a basis for a large restocking programme.

In a first approach, the growth conditions of cultured lobsters released into the field and the local population were considered during a mark-recapture programme. Furthermore, in the second study, the environmental constraints of temperature, current and light on the embryonic and larval development were considered, and thirdly, larval behaviour was examined. Finally rearing conditions for juvenile lobsters were optimized in order to reduce the costs of a future restocking project.

The results of the combined laboratory and field studies are presented and discussed in form of four manuscripts for publication in appropriate scientific journals.

Manuscript I was based on the initial mark-recapture study of Mehrtens (2008) which started in 2000. In this and the subsequent study, substantial numbers of cultured juvenile lobsters were continuously released at yearly intervals at different sites at the rocky basement of Helgoland. From recaptured lobsters data could be obtained on growth rates, onset of maturity size, attainment of legal size, and on whether cultured lobsters settled successfully at or near their release sites. Combined with this approach, the abundance and size composition of the wild lobster was monitored as far as possible to assess the present status of the local stock for the first time and to help define further fishery regulations and management.

In Manuscript II the potential impact of the recent warming trend of North Sea waters on the embryonic and larval development was assessed. The duration of embryonic development and the timing of larval release were determined under different experimental temperature cycles. To quantify the effect of temperature on development and survival through the Zoea stages I-III, lobster larvae were maintained at different temperatures in the laboratory. The hypothesis was tested that continuing warming of the North Sea will affect the recruitment success of the local lobster stock. Warming would mainly result in a decoupling of the seasonal peak appearance of larvae from optimal temperature and food conditions, impairing larval development.

In Manuscript III, due to the unavailability of larvae in the field, a laboratory study was designed to assess the vertical positioning and swimming performance of cultured lobster larvae in an artificial water column. This study was supposed to give an insight into how larvae move in light and currents and help to interpret larval behaviour in selecting an optimal habitat for growth and survival at Helgoland.

Lastly, since the maintenance of lobsters is time and cost intensive, in Manuscript IV the rearing conditions for juvenile lobsters were optimized to reach maximum productivity at lowest cost. The study was aimed to utilize local resources. In this respect, discards of the edible crab fishery at Helgoland provide a suitable and cheap food for the juvenile lobsters. In order to increase the survival rates, the deposits of food remains and other debris in the lobster compartments were reduced by co-culturing juvenile lobsters with live juvenile isopods.

GENERAL MATERIALS AND METHODS

An overview is given on the material and methods applied, including the origin of lobsters, the maintenance of berried females, juvenile lobsters and larvae. Detailed descriptions are given in the manuscripts.

The field and laboratory studies were carried out in the years 2005 to 2008 at the Marine Biological Station at Helgoland, North Sea.

Origin of lobsters

Lobsters were captured by employees of the Marine Biological Station and local fishermen in the rocky subtidal zone at Helgoland (North Sea, 54°11.3'N, 7°54.0'E).

Marine Biological Station

The Marine Station deployed about 11 lobster pots and a few traps by the research cutter "Aade". The station's scientific divers used the dive cutter "Diker", and assisted to capture lobsters and swam transects to determine the density of lobsters (Figure 1; Mansucript I).
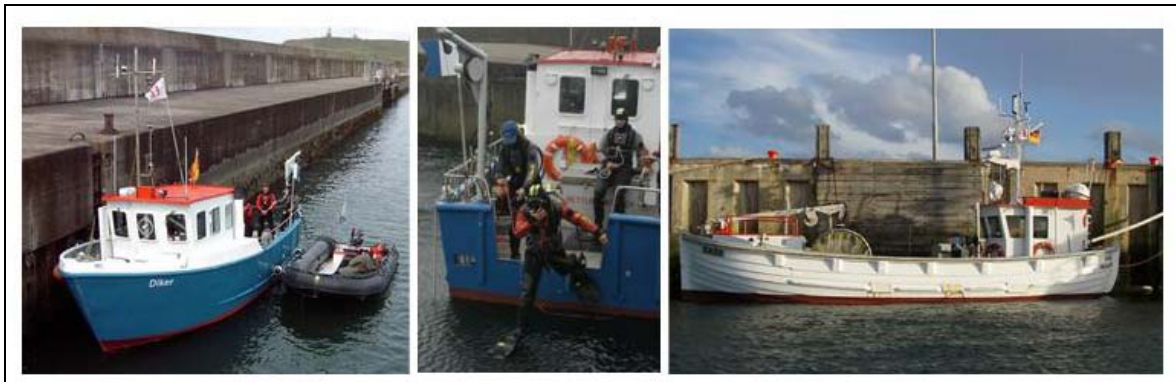

Figure 1 The dive cutter "Diker" and the research vessel "Aade" of the Marine Station.

Local fishermen

The local lobster fishery consists of maximal 10 fishing boats and ~260 lobster pots

(Figure 2). In 2006, a logbook was established by statuary ordinance of the state fisheries authority to report commercial landings of lobsters and crabs. In support of the lobster management by the Marine Biological Station a carbon copy is being supplied containing information on catch date and numbers of specimens. Since 2007, nearly each commercially landed lobster was recorded for marks, catch-location, sex and size. Generally, tagged and berried lobsters were bought by the Marine Station.

Figure 2 Fishing boats of the local fishermen at Helgoland.

Capture equipment and procedures

Three methods were used for catching juvenile and adult lobsters: lobster pots, traps (Figure 3) and hand-catch by divers. The lobsters which escaped the pots were captured with traps. However, divers were able to capture all sizes of lobsters directly from their shelters.

Figure 3 Lobster pot, trap and flag to mark the release position. Picture: Eva Nossek (lobster pot)

The lobster pots consisted of a steel frame (60 x 60 x 40 cm) surrounded by netting (80 mm mesh-size). The round entrance was near the top and hinged by small ropes. There were two openings into the pot (25 x 25 cm), one at each end. They were funnel-shaped,

having the same diameter as the framework-netting at the end. A piece of bait (fish or crab) was placed inside the pot before it was lowered to the sea bottom. A rope attached to each pot had a Styrofoam buoy at the end. Lobster posts were controlled daily.

The traps consisted of six segments with a mesh size of 30 mm. Each segment was 7 m long with openings at each end. These entrances were funnel-shaped and had a mesh size of 20 mm. The traps were not baited.

The divers were equipped with a hand-net. The diver checked crevices and holes for visible claws or antennae. The net was then extended and placed before the entrance and the lobster was carefully chased into the net using a stalk (e.g. *Laminaria* spp.).

Maintenance of lobsters

Females

Berried lobsters were placed individually into tanks (49 x 79 cm, filled to a depth of 20 cm) with running sea water and maintained under the seasonal temperature cycle, at ca. 31 psu salinity, and the natural light-dark cycle (Manuscript IV). They were fed *ad libitum* with a mixture of easily available crustaceans (*Carcinus maenas* Linnaeus, 1758, *Crangon* spp., *Liocarcinus* spp.) and small fish (*Pholis gunellus* Linnaeus, 1758, *Myoxocephalus scorpius* Linnaeus, 1758, *Pleuronectes platessa* Linnaeus, 1758). A specific plankton tank for hatching (Figure 4) or a nylon sieve was placed under each outlet.

Figure 4 Plankton tanks for hatching were placed under each outlet of holding tanks with individual female lobsters.

Larvae

The newly hatched larvae were reared in specific rearing tanks (Hughes et al., 1974) in ambient flowing seawater (Figure 4) or individually transferred to 70 or 80 ml cylindrical bowls and acclimated to the experimental temperature (Manuscripts II, III and IV). The larvae in the specific rearing tanks were fed daily with newly hatched *Artemia franciscana* (Kellogg 1906) nauplii (cysts from Sander's Brine Shrimp Company) and every other day with minced crab *Cancer pagurus* Linnaeus, 1758. The larvae reached the post-larval stage (stage IV) approximately two weeks after hatching.

Juveniles

After moulting to post-larvae, the animals were placed in rectangular frames with separate compartments (9 x 7 cm, height of water level: 7 cm; Figure 5) (Manuscript IV).
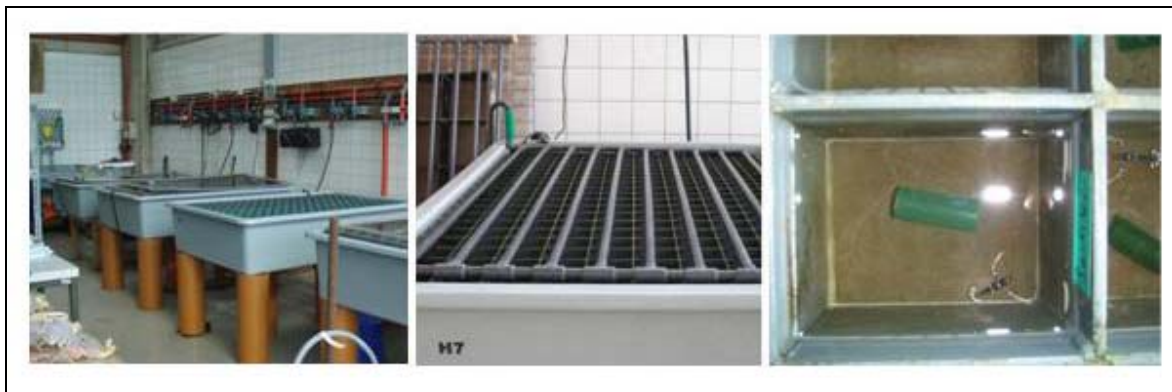

Figure 5 Individual rearing systems for juvenile lobsters (*Homarus gammarus*).

Lobsters larger than 3-4 cm and up to about 8 cm total length were separated in bigger compartments (19 x 10 cm, 19 x 19 cm, height of water level: 10 cm). The bottoms of the compartments were made of nylon gauze (300-μm mesh size). The rectangular frames for 200 lobsters were covered with a light shield. The flow rate of fresh seawater into the culture system was at 4-5 l·min^{-1} supplied to each compartment by sprinklers. The system provided a constant circulation of sea water at a natural seasonal temperature cycle or at a constant temperature, and a natural light-dark cycle. The animals were fed *ad libitum* a mixture of newly hatched *Artemia* sp. nauplii, minced *C. pagurus* and *C. maenas*, and live juvenile isopods *Idotea emarginata* Fabricius, 1793). A short section of a plastic tube provided shelter. The lobsters were controlled for mortality and moults, and the mean temperature (the mid-point between the high and low values for each day) were measured

daily. The cultured lobsters were similar in morphology and colour to the wild stock (see Svåsand, 1993). Juvenile lobsters were released at a total length above 3 cm and the age varied in relation to the rearing temperature between 3 and 12 months (Manuscript I, IV).

LIST OF MANUSCRIPTS

This cumulative thesis is composed in the form of four manuscripts which are submitted (Manuscript I), prepared for submission (Manuscript II), in press (Manuscripts III) and published (Manuscript IV). Four manuscripts are listed with information on the scientific contributions of the different authors.

MANUSCRIPT I: Schmalenbach, I., Janke, M., Buchholz, F., (submitted). Growth, reproduction, movement and abundance of the European lobster, *Homarus gammarus,* at the rocky island of Helgoland, North Sea. Submitted to *Marine Ecology Progress Series*.

All analyses, text writing and graphical presentation were done by Isabel Schmalenbach in cooperation with Prof. Dr. Friedrich Buchholz. Michael Janke assisted all practical parts of the study. Eva Nossek, Jacob Hauschildt and Carsten Dittmayer who served as voluntaries within their "Freiwilliges Ökologisches Jahr" helped to maintain larvae and juvenile lobsters.

MANUSCRIPT II: Schmalenbach, I., Franke, H.-D., (to be submitted). Temperature effects on embryonic and larval development of the European lobster (Homarus gammarus) at Helgoland, North Sea - potential impact of the recent warming trend on lobster recruitment. To be submitted to *Marine Biology*.

Isabel Schmalenbach developed the concept of this study and carried out the analyses advised by Prof. Dr. Friedrich Buchholz. The interpretation of the data, text writing and graphical presentation were done in cooperation with Prof. Dr. Heinz-Dieter Franke.

MANUSCRIPT III: Schmalenbach, I., Buchholz, F., 2009. Vertical positioning and swimming performance of lobster larvae (*Homarus gammarus*) in an artificial water column at Helgoland, North Sea. In press by *Marine Biology Research*.

All analyses, the text writing and the graphical design were performed by Isabel Schmalenbach in cooperation with Prof. Dr. Friedrich Buchholz.

MANUSCRIPT IV: Schmalenbach, I., Buchholz, F., Franke, H.-D., Saborowski, R., 2009. Improvement of rearing conditions for juvenile lobsters (*Homarus gammarus*) by co-culturing with juvenile isopods (*Idotea emarginata*). In press by *Aquaculture* 289, 297-303.

Isabel Schmalenbach developed the concept of this study and conducted the analyses, supervised by Prof. Dr. Buchholz. The interpretation of the data and text writing was done in cooperation with the last author. The manuscript was improved by all co-authors.

MANUSCRIPT I

GROWTH, REPRODUCTION, MOVEMENT AND ABUNDANCE OF THE EUROPEAN LOBSTER, *HOMARUS GAMMARUS*, AT THE ROCKY ISLAND OF HELGOLAND, NORTH SEA

Isabel Schmalenbach, Michael Janke, Friedrich Buchholz

Biologische Anstalt Helgoland, Foundation Alfred Wegener Institute for Polar and Marine Research, 27498 Helgoland, Germany

ABSTRACT

From 2000 to 2008, ca. 9,000 one-year-old hatchery-reared, 560 larger hatchery-reared lobsters and 730 wild captured lobsters were tagged and released at Helgoland, North Sea. To date, the recapture rate of hatchery-reared lobsters varied from 6-21 % for lobsters, which were released in a semi-open area (outer harbour) and 2-7 % for lobsters which were released in the wild.

Since 2005, the growth conditions and movement of hatchery-reared lobsters in the field have been recorded and data on growth, recruitment, size composition and the abundance of the local wild stock are provided.

Hatchery-reared juvenile lobsters released at the rocky shore of Helgoland, survived in substantial numbers to allow up to 6 % to be captured by commercial fishermen. After ≥4 years lobsters matured to the egg carrying stage.

Catch per unit effort showed that the landings of legal sized lobsters varied from 0.010 to 0.017 in the years 2006-2008 at a theoretical population size range of 21000 to 29000 adult lobsters. Minimum landing size (85 mm carapace length) was reached in female and male lobsters after 4 to 5 years.

In conclusion, the local stock stagnates at a low level but fishery regulations possibly prevented a further decline. The population parameters found in conjunction with the special island habitat encourage a large scale lobster restocking programme in view of a better definition of the ecological situation of the Helgoland microcosm as a whole.

Keywords: European lobster, growth, recruitment, movement, population size, Helgoland

INTRODUCTION

Stocks of European lobsters (*Homarus gammarus* Linnaeus, 1758) are the basis of fisheries along the coastline of the northeast Atlantic, i.e. in Scotland, Norway (van der Meeren et al., 1998), England and Wales (Bannister, 1986), France, Ireland (Tully et al., 2006), Sweden, Denmark and Spain (see Dow, 1980) reaching approximately 3,400 metric tons (t) with a value of 45 million Euros in 2006 (Fishery Statistics, 2006).

At the German coast, the subtidal cliffs of the island of Helgoland (North Sea, German Bight) harbour a small population of *H. gammarus* in an area of about 33 km². This population is geographically and ecologically isolated from similar hard-bottom areas and neighbouring populations in Norway and Britain by some hundred miles of predominantly soft bottom (Ulrich et al., 2001).

Until the 1930s, the fishery for lobster used to be an important resource with substantial economic value at Helgoland with catches of up to 80,000 animals (38 t) per year (Klimpel, 1965). Since the 1960s, the population size has declined dramatically and landings of lobster fluctuated at a low level. To date, lobster landings stagnate at about 200-300 lobsters per year (Goemann, 1990; Anonymous, 1980-2008). The reasons for the decline in landings of the Helgoland lobsters are not known in detail, but may include habitat destruction by the bombing of the island during and after the second world-war, extensive fishing pressure in the 1950s and 1960s, and anthropogenic pollution of the North Sea waters by oil spills and industrial wastes which increased strongly in the late 1960s and in the end by competition for food and space of the edible crab *Cancer pagurus* (Klimpel, 1965; Anger and Harms, 1994; Walter et al., 2008). Furthermore, climatic warming affects embryonic development and the timing of the larval phase (Schmalenbach and Franke, in prep.).

At Helgoland, legislative regulations from 1981 and 1999 may have prevented a complete disappearance of the local stock. These regulations include the establishment of a no-catch protection area, an agreement on a minimum landing size of 11 cm carapace length (measured from the tip of the rostrum to the posterior edge of the carapace) for landed lobsters, a ban on landings of berried females, and a closed season of 1.5 month in July-August (Ministerium für Landwirtschaft, 1981, 1999).

However, we suspect that these measures did not suffice to help with the population's recuperation and that it still remains below a critical threshold which is necessary for a recovery at a large scale. As a whole, little is known on the composition and dynamics of the Helgoland population.

In Norway a comparable reduction in lobster landings was noted from about 1,000 t in the 1930s to about 50 t during the last 20 years (Agnalt et al., 1999). Here, a large scale restocking programme was conducted with a release of hatchery-reared lobsters. Similarly, van der Meeren (1998) released a large number of relatively small cultured juveniles which were maintained and fed for >3 months within stock enhancement programmes. Since 1980, substantial numbers of hatchery-reared juvenile lobsters have been released in Norway, France, the United Kingdom, and Ireland (Bannister and Addison, 1998). These previous release programmes on European lobster have shown that a considerable number of hatchery reared lobsters could be recaptured at marketable sizes (Burton et al., 1994; Cook, 1995; Tveite and Grimsen, 1995; Bannister and Addison, 1998; Moksness et al,. 1998, van der Meeren et al., 1998; Agnalt et al., 2004) and provided data on growth, maturity sizes, length frequencies, movement and catch per unit effort of the lobsters in their habitats.

The Ministry of Fisheries and Agriculture of the State of Schleswig-Holstein in Germany supported a mark-recapture programme of hatchery reared juvenile lobsters (*H. gammarus*) at the Marine Biological Station on Helgoland between 2000 and 2008. The programme integrated the cooperation of the local fishermen. Major aims were to assess the status of the local population, find reasons for the missing recovery and to lay the basis for a large scale restocking experiment.

First of all, lobster breeding was optimized and juvenile lobsters were found to be released most economically into the wild after they had reached a total length of 3 to 4 cm, corresponding to approximately one year of maintenance (Schmalenbach et al., 2009).

The objectives of the current study was to rear substantial numbers of juvenile lobsters, to release them to the rocky cliffs of Helgoland, and to describe how lobsters developed and survived in the wild, after which period in the field they reached maturity and market size and if they showed fidelity to their original release site.

The first part of the study summarizes (1) the release and recapture information, describes the (2) growth conditions and (3) movement of recaptured hatchery-reared lobsters. Within a dive census, the density of lobsters was determined in a previous release area of hatchery-reared juvenile lobsters to estimate how well lobsters accepted their original release area.

The second part of the study describes how capture and recapture data can be used to determine (1) growth and (2) size composition, and to estimate (3) the abundance of the local wild stock. The data of commercially landed lobsters in catch per unit effort was examined in parallel based on the logbook records of the local fishermen.

The results of the study provide information about the present status of the local lobster population, may contribute to further fishery regulations and last not least to a possible large scale stock enhancement programme.

MATERIALS AND METHODS

The studies were carried out in the years 2005 to 2008 at the Marine Station at Helgoland in cooperation with the local fishermen. A wild or a cultured lobster was classified by the absence or presence of the first tag (see below). Table 1 summarizes the data of all specimens tested.

Table 1 The number of tested lobsters (*Homarus gammarus*) in the years 2005 to 2008. (Egg-berried females captured in 2008 are not included).

Number tested	2005	2006	2007	2008	Total
Commercial landings measured: -legal size (including marked wild + cultured lobsters)	-	-	114 (9 wild)	194 (9 w. + 3 c.)	308
Field samples: -legal size	94	81	151	182	508
-sub-legal <85 mm carapace length	58	50	29	68	205
Total tested	152	131	294	444	1,021
Wild lobsters (including marked wild lobsters + multiple captures)					
Females non-ovigerous	41 (3+3)	15 (2+0)	35 (1+0)	57 (6+1)	148
Females ovigerous	30 (2+0)	46 (2+0)	37 (2+2)	36 (1+0)	149
Males	22 (5+0)	12 (3+1)	149 (12+2)	234 (14+1)	417
Cultured lobsters (including multiple captures)					
Females non-ovigerous	26 (1)	28 (7)	19 (2)	32	105
Females ovigerous	0	4 (1)	12 (2)	9 (1)	25
Males	33 (1)	26 (4)	42 (5)	76 (13)	177
Total recaptures (including multiple captures)	72 (5)	66 (13)	93 (13)	140 (16)	370
Recaptures per 100 tested	47	50	31	32	36

Rearing, tagging, release and capture procedures of juvenile and adult lobsters

Origin and maintenance of lobsters

Ovigerous female lobsters (*Homarus gammarus*) (mean total length: 31 cm; mean weight: 960 g) were captured by local fishermen at the rocky subtidal zone at Helgoland (North Sea, 54°11.3'N, 7°54.0'E). The animals were placed individually into tanks (49 x 79 cm, filled to a depth of 20 cm) with running sea water (ca. 31 psu) and maintained under the seasonal temperature cycle and the natural light-dark cycle. The adult lobsters were fed a mixture of easily obtainable crustaceans (*Carcinus maenas* Linnaeus, 1758, *Crangon* spp., *Liocarcinus* sp.) and small fish (e.g. *Pholis gunellus* Linnaeus, 1758, *Myoxocephalus scorpius* Linnaeus, 1758, *Pleuronectes platessa* Linnaeus, 1758). A specific plankton tank for hatching or a nylon sieve was placed under each outlet to collect larvae.

The newly hatched larvae were transferred and reared in cylindrical rearing tanks (Hughes et al., 1974) in ambient flowing seawater. The larvae were fed daily with newly hatched *Artemia franciscana* (Kellogg 1906) nauplii (cysts from Sanders Brine Shrimp Company, USA) and every other day with minced crab (whole carcasses of *Cancer pagurus* Linnaeus, 1758). The larvae reached the post-larval stage (Stage IV) approximately 17 days after hatching.

After moulting to post-larvae the animals were placed in rectangular frames with 200 separate compartments (9 x 7 cm, height of water level: 7 cm) (Schmalenbach et al., 2009). About hundred juvenile lobsters larger than 3-4 cm and ~8 cm were separated in bigger compartments (19 x 10 cm, 19 x 19 cm, height of water level: 10 cm), respectively. The bottoms of the frames were made of nylon gauze (300 µm mesh size). The rectangular frames were covered with a light shield. Constant water supply to each compartment was by sprinklers. This system allowed for separation of animals and provided a constant circulation of sea water under the seasonal temperature cycle and/or constant temperature and the natural light-dark cycle. A short section of a plastic tube provided shelter. The animals were fed *ad libitum* a mixture of newly hatched *A. franciscana* nauplii, minced crabs (*C. pagurus*, *C. maenas*) and live juvenile isopods *Idotea emarginata* (Fabricius, 1793). The lobsters were allowed to eat their moults. In terms of morphology, colour, genetic provenance and behaviour, specimens appeared similar to wild lobster (see Svåsand, 1993). Juvenile lobsters with a total length of 3-4 cm and at an age of about 8-12 months were released to the field as described below.

Tagging procedure

All lobsters were tagged with Visible Implant Fluorescent Elastomer (Northwest Marine Technology Inc.). The colour tag is available in four colours (red, orange, yellow and green) that fluoresce under UV Light. Elastomer liquid was injected ventrally along the abdomen into one of the abdominal segments using a syringe with a needle. The volume that could be injected was limited by the size of the animal (Linnane and Mercer, 1998). Holes of about 5 mm diameter were punched in one or more segments of the tail fan for additional individual marking in larger lobsters.

Hatchery-reared juvenile lobsters with a total length of 3-4 cm and at an age of 8-12 months were tagged with one mark of Visible Implant Fluorescent Elastomer. The first marks of colours were positioned according to a code denoting the release-area and cohort of the lobsters.

Larger hatchery-reared (total length = 5-9 cm) and wild captured lobsters were individually tagged with three marks and a hole punched in one or more segments of the tail fan. The individual marks of colours and holes were positioned according to a code denoting the release-area, age, total length (TL: from the tip of the rostrum to the end of the telson), carapace length+R (CL+R: from the tip of the rostrum to the posterior edge of the carapace), carapace length (CL: from the eye socket to the posterior edge of the carapace) and weight of the lobsters. Recaptured cultured lobsters were re-tagged individually.

Release area

Tagged hatchery-reared juvenile lobsters were released at different sites of the rocky basement around the island of Helgoland (Figure 1), where the sea bed comprises a substantial scattering of boulder, and cobble. The two major release sites were further subdivided, namely into (1) the sheltered outer harbour area as a semi-open system (Embankment "Schüttung" and Fog Horn "Nebelhorn") and (2) the field (Institute pier "Hausmole", Pool-Mole "Schwimmbadmole_Landungsbrücken", 6-m-station, North-sheltered site "Weisse Rinne", North-exposed site "vor Nord"). Tagged adult lobsters were mostly released into the specific no-catch protection area called "Danskermannshörn", South of the Dune-island of Helgoland (Ministerium für Landwirtschaft, 1981), and individually at different sites around Helgoland (Outer Harbour; West-side: "Rosengarten" and "Repulse"; East-side: "Hausmole"; North: "Nathurnbrunn" "Wittkliffbrunn", "Weisse Rinne" and "Sellebrunn").
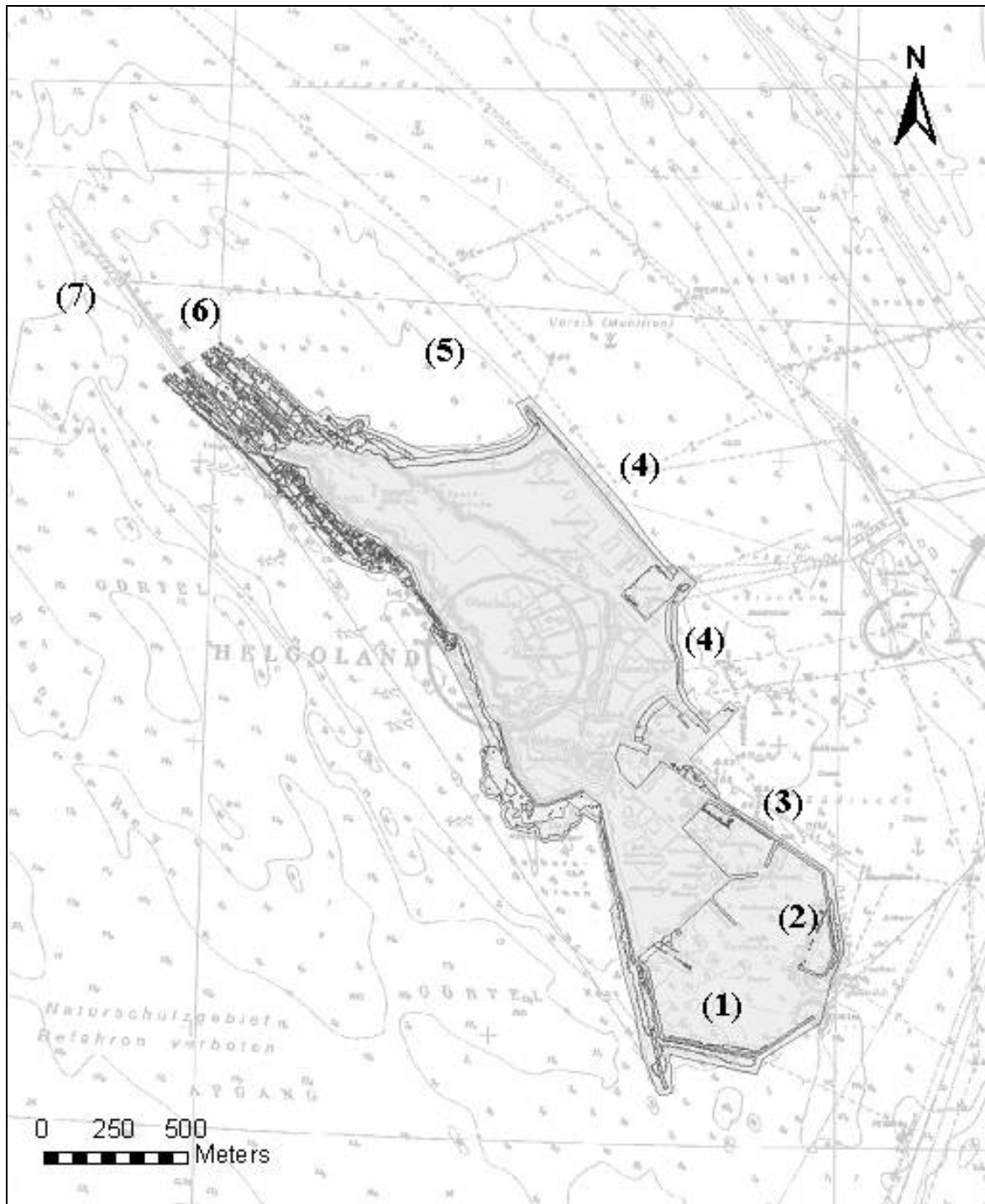
Figure 1 Release-sites of hatchery-reared juvenile lobsters (*Homarus gammarus*) at Helgoland. The sheltered outer harbour area: (1) Embankment "Schüttung" and (2) Fog Horn "Nebelhorn", the field (3) Institute pier "Hausmole", (4) Pool-Mole "Schwimmbadmole_Landungsbrücken", (5) 6-m-station, (6) North-sheltered site "Weisse Rinne", and (6) North-exposed site "vor Nord". Map: Modified after Bartsch and Tittley, 2004.

Hatchery-reared juvenile lobsters released into the sheltered outer harbour were easier to recapture and these data were used to determine growth and age. From previous dive surveys it was known that the outer harbour area corresponded to a semi-natural habitat. The data of recaptured hatchery-reared and wild animals from around the island were used to further determine the size distribution, the mobility on the rocky basement and to calculate the stock-size of the lobster population.

Transport and release procedure

At Helgoland, the distance between the lobster rearing facility to the release sites was only short and thus easier to handle. If the rearing temperature of the lobsters was not the same as the sea temperature they were acclimated to the current sea temperatures for a full week. Hatchery-reared juvenile lobsters were individually placed in separate cylindrical transportation bowls filled to a water level of one centimetre and arrived at the release location less than 1 h by the research cutter "FK Aade". There was no mortality of juveniles during transport. The lobsters were released directly at the sea surface in shallow water (≤10 m) twice a year in late spring and autumn, and at sea temperatures above ~10 °C. The young juvenile lobsters were still shelter-bound (see Mehrtens et al., 2005) and preferred thus to seek shelter in rocky areas, where they can hide in the crevices from predators. Therefore, the lobster loss to predators was highest in the first hours after release, when the lobsters were out of shelter (van der Meeren, 2000). The release during the night reduced loss to visibly orientated fishes. Larger lobsters were transported in buckets without water and were released mostly during day time.

Capture equipment and procedures

In this study three methods were used for catching juvenile and adult lobsters: lobster pots, traps and hand-catch by divers. The lobsters which escaped the pots were captured with traps. However, divers were able to capture all sizes of lobsters directly from their shelters. The lobster pots consisted of a steel frame (60 x 60 x 40 cm) surrounded by netting (80 mm mesh-size). The round entrance was near the top and hinged by small ropes. There were two openings into the pot (25 x 25 cm), one at each end. They were funnel-shaped, having the same diameter as the framework-netting at the end. A piece of bait of fish or crab was placed inside the pot before it was lowered to the sea bottom. A rope attached to each pot had a Styrofoam buoy at the end. Lobster posts were controlled daily.

The traps consisted of six segments wit a mesh size of 30 mm. Each segment was 7 m long with openings at each end. These entrances were funnel-shaped and had a mesh size of 20 mm. The traps were not baited.

The divers were equipped with a hand-net. The diver checked crevices and holes for visible claws or antennae. The net was then extended and placed before the entrance and if the hole had a back entrance as in most cases the lobster was carefully chased into the net using a stalk (e.g. *Laminaria* spp.).

Local fishermen

The local lobster fishery consists of a maximum of 10 open fishing boats and 260 lobster pots. In 2006, it was established by statuary ordinance of the state fisheries authority to report commercial lobster landings in a logbook. In support of the lobster management of the Marine Biological Station a carbon copy is being supplied containing information on catch date and number of lobsters. Additionally, since 2007, marks, catch-location, sex and size have been recorded for almost every landed lobster. Tagged and berried lobsters were bought by the Marine Station.

Marine Biological Station

The Marine Biological Station regularly deployed 11 lobster pots and a few traps by the research cutter "Aade". The station's scientific divers used the dive cutter "Diker", and assisted with the capture of lobsters and swam transects to help to determine the habitat-density of lobsters.

Composition of hatchery-reared lobsters in the field

Recapture rate of hatchery-reared lobsters

In the years 1996 to 2004 about 4,400 one-year-old and 380 larger hatchery-reared lobsters (Ulrich, 1998; Mehrtens, 2008), and from 2005 to 2008 about 4,600 hatchery-reared juvenile lobsters (in total 9,000 one-year-old lobsters) with a total length of 3-4 cm and at an age of 8-12 months, and about 190 larger hatchery-reared (in total 560 larger lobsters) with a total length of 5-9 cm were tagged and released at different sites. From release to recapture, the number of tagged and released lobsters at each release site (as described above), year of release and/or cohort (year-class) is shown in Tables 2 and 3.

All captured lobsters were checked for "Black Spot" shell disease (Ayres and Edwards, 1982) and if they had developed a crusher claw.

We determined the recapture rates of lobsters at a minimum size of ≥58 mm CL (~3 years-old), where an individual was marked at time t and recaptured at $t+1$. The percentage recapture rate RR was estimated by

$$RR = \frac{n_2 \times 100}{n_1},\tag{1}$$

where n_1 is the initial number of tagged specimens at time t_1, and n_2 is the total number of recaptured lobsters at time t_2.

Growth and maturity of hatchery-reared lobsters in the field

The growth of recaptured marked hatchery-reared juveniles (females: n = 130; males: n = 173) was calculated from the weight data, total length, and carapace lengths and cohorts. The sizes were classified with the year-classes (from 2 to 9 years) (see Uglem et al., 2005). Growth factors decreased logarithmically at successive moults and were fitted by a hyperbolic model (Mauchline, 1976). The relation between length increment y and age x of recaptured lobsters was analyzed by the following regression model (with m representing the "slope", and $a = y$ for x approaching ∞):

$$y = \frac{a \times x}{m + x}\tag{2}$$

The size and the age at the onset of functional maturity of recaptured cultured female lobsters were determined, based on the presence of eggs attached to the abdominal pleopods.

Sex and size distribution of hatchery-reared lobsters in the field

The sex and size distribution of all cultured lobsters was examined for the years 2005 to 2008. The male:female ratio was calculated for 2007 and 2008. All lobsters were also inspected for any visible signs of diseases.

Mobility of hatchery-reared lobsters

Two methods were used to determine the movements, and with this the fidelity to the release sites, of hatchery-reared lobsters at the rocky basement of Helgoland.

Firstly, the mark-recapture approach was used: The locations and size compositions of recaptured cultured lobsters (n = 270), which were released as one-year old lobsters, were related to their original release sites and with reference to the larger areas (harbour area or field). The period between the release and recapture of lobsters averaged 4 ± 1 years (range: 1-7 years). The distance between release and recapture location was determined. The size composition was compared between the lobsters which were captured at their original release site and the lobsters which were captured at other sites.

Secondly, the density of lobsters was determined in a previous release area of hatchery-reared juvenile lobsters using scuba-census: A previous release site called North-sheltered "Weisse Rinne", (54°11.5'N, 7°51.8'E) North of Helgoland (Figure 2) was surveyed at water temperatures of 18 °C in summer 2007. Here, in the year 2002, six hundred one-year-old lobsters had been released at an area of 32,500 m² (~2 individuals·100 m^{-2}). The study area was defined by dive transects and was approximately 350 m by 200 m. The depth ranged from 1.5 to 4 m, the topography consisted of rocks and stones (diameter: 5-35 cm), and the substrate of natural shelly sediments (particle size: 1-5 mm) and bare red sandstone. The highest abundance of associated flora was in the brown alga *Laminaria* spp.

For detailed examinations, a scientific diver swam slowly over a straight transect in the direction of the prevailing current and with the help of a compass. The area of transect is given by the length of the transect line multiplied by its width. The width of transect was defined by a board with 0.5 to 1 m width depending on water clarity (visibility), substrate type and diving conditions. The length of transect was established by GPS data at the beginning and end of census. The global positioning system (GPS) was used for marking transect locations with a deviation of ±1 m measured 6 times at a 20 m transect line. The diver swam slowly above the bottom checking each possible burrow for adult *H. gammarus*.
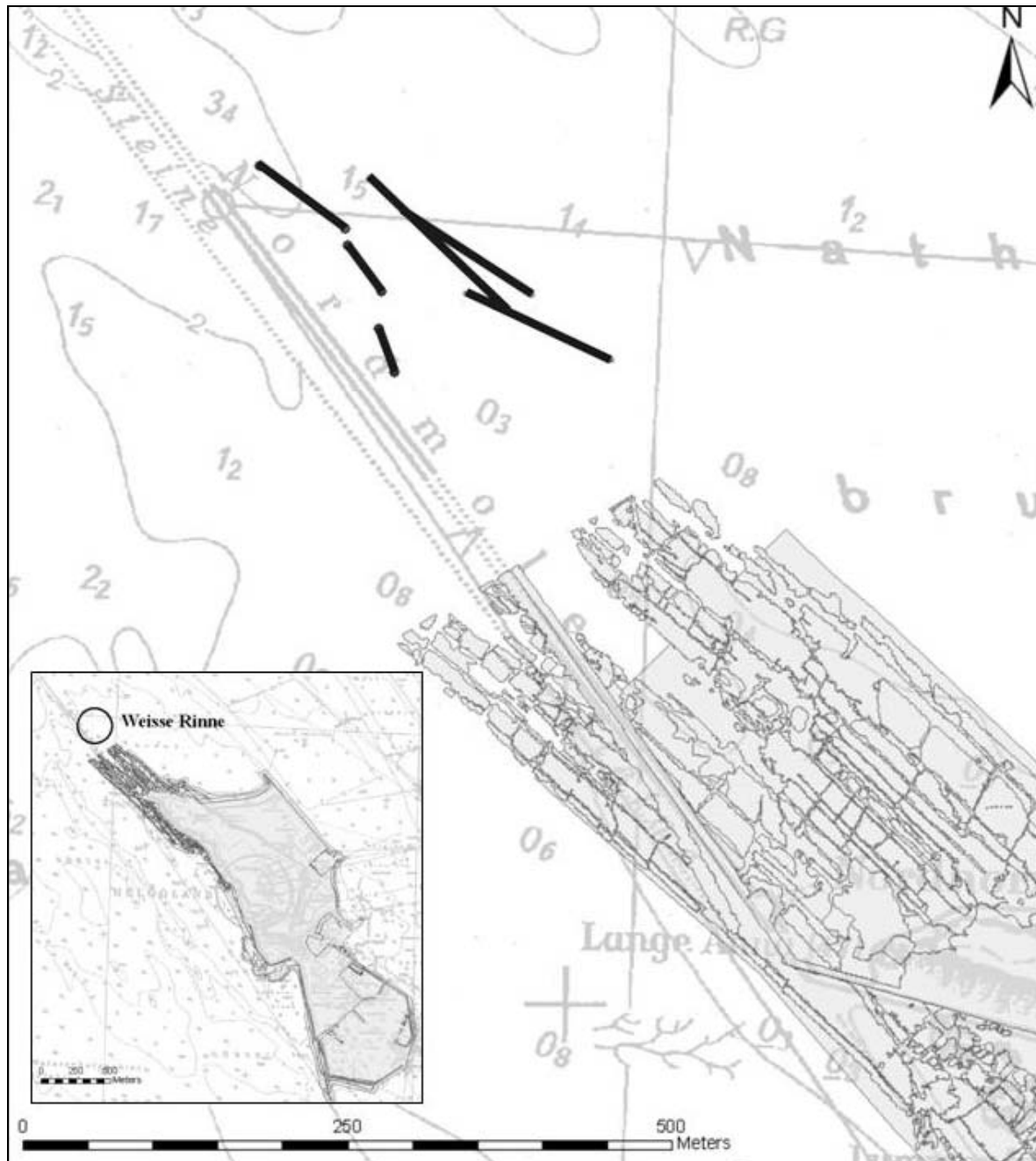
Figure 2 Lines represent the dive transects in the north-sheltered site "Weisse Rinne" at Helgoland. Map: Modified after Bartsch and Tittley, 2004.

Six transects were swum, with a mean transect area of 92 m² and a total area of 550 m² covered where each lobster was counted. The density of lobsters was calculated by the number of lobsters per 100 m². During this study, cultured and wild lobsters could not be distinguished.

Composition of the wild population

Catch per unit effort

In the years 2006 to 2008 data of commercially landed lobsters were obtained through a fishermen logbook programme (Anonymous, 2006-2008). The data set was used to calculate the weekly catch-per-unit-effort (CPUE). A weekly CPUE was found more reliable for assessing the fishery than a daily CPUE since the lobster catchability is highly variable as it depends on a series of environmental, physiological, and behavioural factors (Drinkwater et al., 2006).

Growth conditions of wild lobsters

All captured lobsters were inspected for any visible signs of diseases, particularly for the "Black Spot" shell disease, when measured. Length-weight relationships were determined for all captured lobsters; the weight W and CL (females: $n = 442$; males: $n = 442$) was expressed by the following equation:

$$W = a \times m^{CL}, \tag{3}$$

where a is the intercept with the Y axis and m represents the slope. The data was log-transformed and described by linear regression. The length-weight relationship between cultured and wild lobsters was not statistically compared because the size range and numbers of captured lobsters was significantly different.

Pre-moult and post-moult carapace lengths for tagged lobsters that were known to have moulted only once in the wild between tagging and recapture were measured to determine the percentage of growth increment for lobster in pre-moult. The data were fitted by linear regression for females (n = 11) and males (n = 9) according to Hiatt (1948).

$$Post\text{-}moult\ CL = a + m*Pre\text{-}moult\ CL, \tag{4}$$

where a is the intercept with the Y axis and m is the slope. The number of double moulters (n = 5) was too low for adequate regression analysis.

Sex and size distribution of wild lobsters

The sex and size distribution of all wild captured lobsters were examined for the years 2007 and 2008. The male:female ratio was calculated for 2007 and 2008.

Estimation of population size

In addition to the released hatchery reared lobsters (total: 9,560), in the years 1998 to 2004 about 320 (Ulrich, 1998; Mehrtens, 2008), and from 2005 to 2008 about 400 wild captured lobsters (total: 730) were tagged and released at Helgoland.

The population size was estimated using the data of the mark-recapture studies of 2007 and 2008. The Lincoln-Petersen method was used to estimate the total population size N (Hart and Gorfine, 1997) of lobster at ≥ 58 cm CL for an open system (The data of captured animals from the harbour area were not included).

$$N = \left(\frac{(n_1 + 1) \times (n_2 + 1)}{(m_2 + 1)} \right) - 1$$

$$Var(N) = \left(\frac{(n_1 + 1) \times (n_2 + 1) \times (n_1 - m_2) \times (n_2 - m_2)}{(m_2 + 1)^2 \times (m_2 + 2)} \right),$$

(5)

where n_1 is the initial number of tagged released animals at time t_1, that reached a carapace length of ≥ 58 mm CL at time t_2, (fishing mortality but not natural mortality rates were not included), n_2 is the total number of recaptured lobsters less fishing mortality at time t_2, and m_2 is the number of all recaptured tagged lobsters at time t_2.

The 95 % confidence limits for N are

$$95\%CL = N \pm 1.96\sqrt{V}.$$

(6)

Statistics

Statistical analyses were performed following Sokal and Rohlf (1995). Data are presented as means and standard deviations (SD) of replicates. All data sets were first examined for normal distribution and similarity of variances using the statistical software package GraphPadPrism 3.0 and Sigma Stat 2.03 (SPSS Inc.). To test the differences in catch-per-unit-effort, a one factorial analysis of variance (ANOVA) followed by a Tukey's multi-comparison test at a significance level of $\alpha = 0.05$ was performed. Unpaired t-test was applied to test the differences in growth conditions between females and males. All regressions were given with fitted parameters and coefficients of determination (r^2), analyzed with SigmaPlot 9.0.

RESULTS

Composition of hatchery-reared lobsters in the field

Recapture rate of hatchery-reared lobsters

Recapture data sets of released hatchery-reared juvenile lobsters and wild captured lobsters are summarized in Tables 2, 3 and 4. Recapture rates depended on the release site and year-class. Animals were easier to recapture in the harbour area than around Helgoland because the catch procedures depended on tide and weather conditions. Accordingly, recapture rates of juvenile lobsters in the outer harbour were much higher (6.0-20.8 %) than captures outside (1.5-6.8 %). Furthermore, the recapture rates of larger hatchery-reared lobster were 21 % for the harbour area and 4% for lobsters which were captured in the wild.

The proportion of legal sized hatchery-reared lobsters to all measured lobsters reported by the commercial fishery was 6.2 and 2.5 % in 2007 and 2008.

Table 2 The number *n* of one-year-old hatchery-reared lobsters (*Homarus gammarus*) released and recaptured, in the years 2000 to 2008. From 2000 to 2004 hatchery-reared lobster were tagged and released by Mehrtens (2008).

Cohort	Release year	Release area	*n* released	*N* recaptures + (multiple captures)						Recaptures/
				-2004	2005	2006	2007	2008	Total	100 released
		Harbour								
1999	2000	(1)	669	117 (35)	9	2 (5)	6 (3)	5 (4)	138	20.8
2000	2001	(1)	367	40	6 (2)	3 (7)	8 (3)	3 (2)	60	16.3
2002	2003	(2)	998	0	17	2	18 (1)	23 (5)	60	6.0
2003	2004	(1)	1042	-	4	35	31 (1)	50 (3)	120	11.5
		Field								
2000	2001	(7)	268	0	13	2	1	2	18	6.7
2001	2002	(6)	601	5	3	0	0	1	9	1.5
2001	2002	(3)	427	25	3	1	0	0	29	6.8
2004	2005	(4)	1082	-	0	0	0	17	17	1.6
2005	2006	(4)	1666	-	-	0	0	0		
2006	2007	(5, 6)	1364	-	-	-	0	0		
2007	2008	(5)	510	-	-	-	-	-		
	N total		8994	187 (35)	55 (2)	45 (12)	64 (8)	101 (14)	451	

Abbreviations: The shelter outer harbour area: (1) Embankment "Schüttung" and (2) Fog Horn "Nebelhorn", the field (3) Institute pier "Hausmole", (4) Pool-Mole "Schwimmbadmole_Landungsbrücken", (5) 6-m-station, (6) North-sheltered site "Weisse Rinne", and (7) North-exposed site "vor Nord".

Table 3 The number *n* of older (two and three-years-old) hatchery-reared lobsters (*Homarus gammarus*) released and recaptured, from 1996 to 2008. From 1996 to 2004 hatchery-reared lobster were tagged and released by Ulrich (1998) and Mehrtens (2008).

Release year	Release area	*n* released	*N* recaptures + (multiple captures)						Recaptures/
			-2004	2005	2006	2007	2008	Total	100 released
96-01	(1, 3)	198	38 (5)	0	1	(1)	2	41	20.7
2002	(2)	78	n.s.	0	0	0	0	0	0
2003	(5)	24	n.s.	0	0	0	0	0	0
2004	(5)	78	n.s.	0	0	0	0	0	0
2005	(3, 4)	50	-	2	0	0	0	2	4
2006	(3, 4)	55	-	-	0	0	0	0	0
2007	(4)	35	-	-	-	0	0	0	0
2008	(4)	48	-	-	-	-	0	0	0
N total		*556*	*38 (5)*	*2*	*1*	*(1)*	*2*	*43*	

Abbreviations: n.s. = not specified, (1) Outer Harbour; (2) West-side: "Rosengarten" and "Repulse"; (3) East-side: Institute pier "Hausmole", Pool-Mole "Schwimmbadmole_Landungsbrücken", (4) North: 6-m-station, "Nathurnbrunn", "Weisse Rinne" and "Sellebrunn", (5) no-catch protection area "Danskermannshörn", South of the Dune-island of Helgoland.

Table 4 The number of wild captured lobsters (*Homarus gammarus*) released and recaptured, from 1998 to 2008. From 1998 to 2004 wild captured lobster were tagged and released by Ulrich (1998) and Mehrtens (2008).

Release year	Release area	N released	N recaptures + (multiple captures)						Recaptures/
			-2004	2005	2006	2007	2008	Total	100 released
98-01	(1, 2)	65	6	2	0	3 (1)	5	10	15.4
2002	(1, 2)	20	n.s.	0	0	0	0	0	0
2003	(1, 2)	39	n.s	0	1	1	3	5	12.8
2004	(1, 2)	200	n.s	5	4	6	5	20	10
2005	(1, 2)	82	-	3 (3)	1 (1)	5 (3)	2 (1)	11	13.4
2006	(2)	65	-	-	1	1	0	2	3.1
2007	(2)	87	-	-	-	0	2	2	2.3
2008	(2)	168	-	-	-	_	4 (1)	4	2.4
N total		726	6	10 (3)	7 (1)	16 (4)	21 (2)	*59*	

Abbreviations: n.s. = not specified, (1) the sheltered outer harbour area as a semi-open system and (2) the field.

Table 5 Size of tagged lobsters (*Homarus gammarus*) recaptures by age (mean ± SD) in the years 2005 to 2008.

Age (year)	2	3	4	5	6	7	8	9
All females								
N	1	28	24	34	18	16	8	1
Mass (g)	14	145 ± 64	362 ± 129	441 ± 246	532 ± 129	683 ± 126	836 ± 133	1110
TL (mm)	82	172 ± 27	226 ± 28	245 ± 26	259 ± 20	281 ± 19	303 ± 10	333
CL+R (mm)	37	76 ± 12	100 ± 13	108 ± 12	114 ± 10	124 ± 10	134 ± 5	149
CL (mm)	26	58 ± 9	78 ± 10	84 ± 10	90 ± 9	99 ± 6	107 ± 5	115
Berried females								
N	-	-	2	4	4	8	4	1
Mass (g)	-	-	485 ± 92	690 ± 134	710 ± 80	840 ± 146	990 ± 96	1200
TL (mm)	-	-	244 ± 9	260 ± 16	280 ± 14	293 ± 16	309 ± 8	333
CL+R (mm)	-	-	109 ± 4	113 ± 4	125 ± 5	131 ± 7	136 ± 6	149
CL (mm)	-	-	84 ± 1	91 ± 6	100 ± 5	103 ± 5	108 ± 3	115
Male								
N		29	32	57	31	7	9	8
Mass (g)	-	186 ± 100	435 ± 188	583 ± 237	840 ± 250	1114 ± 307	1396 ± 263	1656 ± 271
TL (mm)	-	183 ± 35	235 ± 33	258 ± 33	288 ± 31	321 ± 20	336 ± 13	345 ± 15
CL+R (mm)	-	82 ± 15	110 ± 21	115 ± 16	130 ± 15	143 ± 9	154 ± 9	158 ± 8
CL (mm)	-	63 ± 12	84 ± 13	91 ± 12	102 ± 11	114 ± 9	122 ± 7	126 ± 7

Abbreviations: N= Number of measured lobsters, CL+R= Carapace length measured with rostrum, CL= carapace length measured without rostrum.

Growth and maturity of hatchery-reared lobsters in the field

There was no evidence of "Black Spot" shell disease and 95 % of lobsters had developed a crusher claw. Lobsters originally released at approx. 12 mm CL were recaptured 2-9 years later at 30-115 mm CL in female (n = 130) and 40-140 mm CL in male (n = 173) lobsters (Table 5; Figure 3). The size at age varied between different cohorts by about 1 growing year (Figure 4). Legal minimum landing size (85 mm CL) was reached in female lobsters after 5 and in male lobsters after 4-5 years.

The relationship between carapace length and age as expressed in non linear regressions is shown in Figure 3, along with the coefficients, r^2 (all > 0.98). The slope of the regression curves is significantly steeper in males than in females (m (female) = 6.69 ± 0.87; m (male) = 8.12 ± 1.13; p < 0.001). The difference in size between both sexes increased at maturity size.
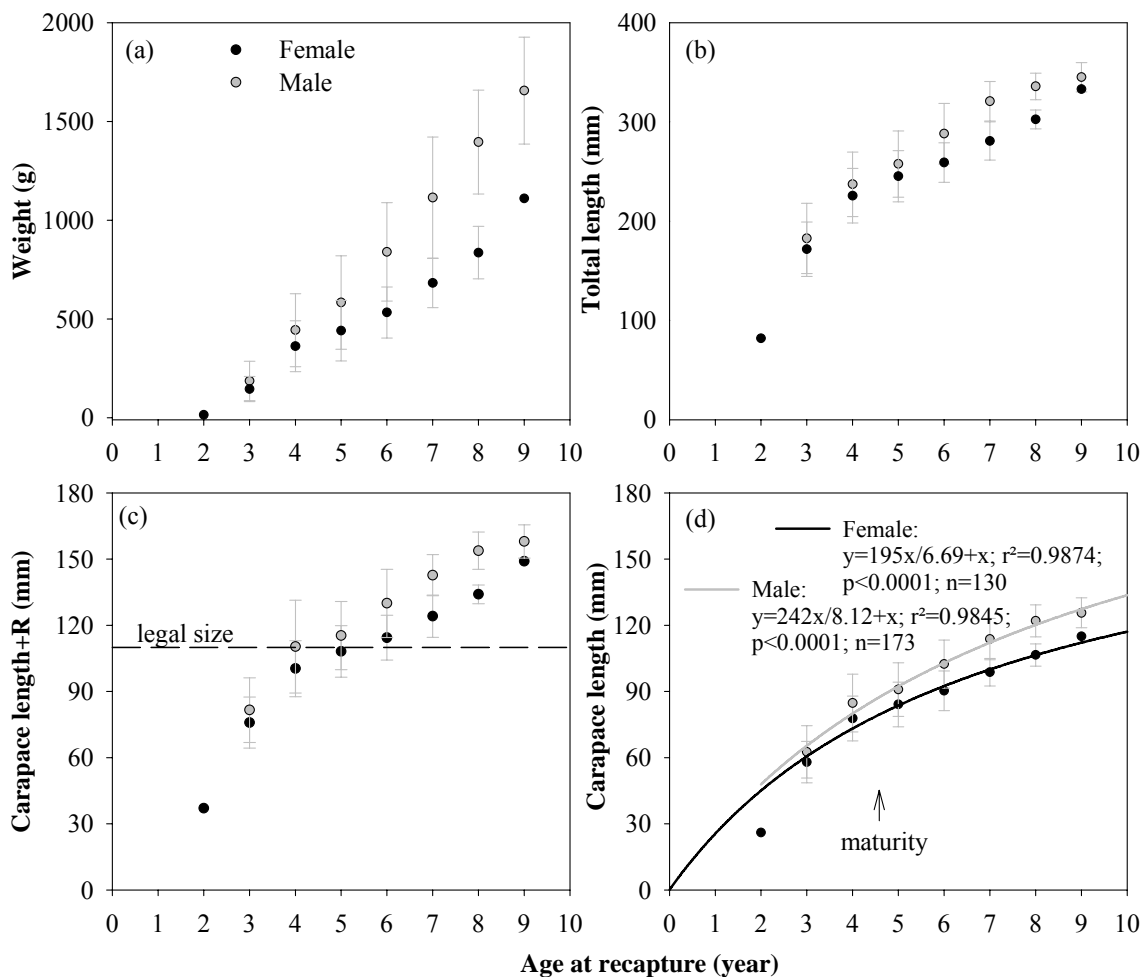
Figure 3 Growth (mean ± SD) of released hatchery-reared juvenile lobsters (*Homarus gammarus*) at Helgoland. (a) Females were weighed without eggs. (d) Growth is expressed as a hyperbolic function.
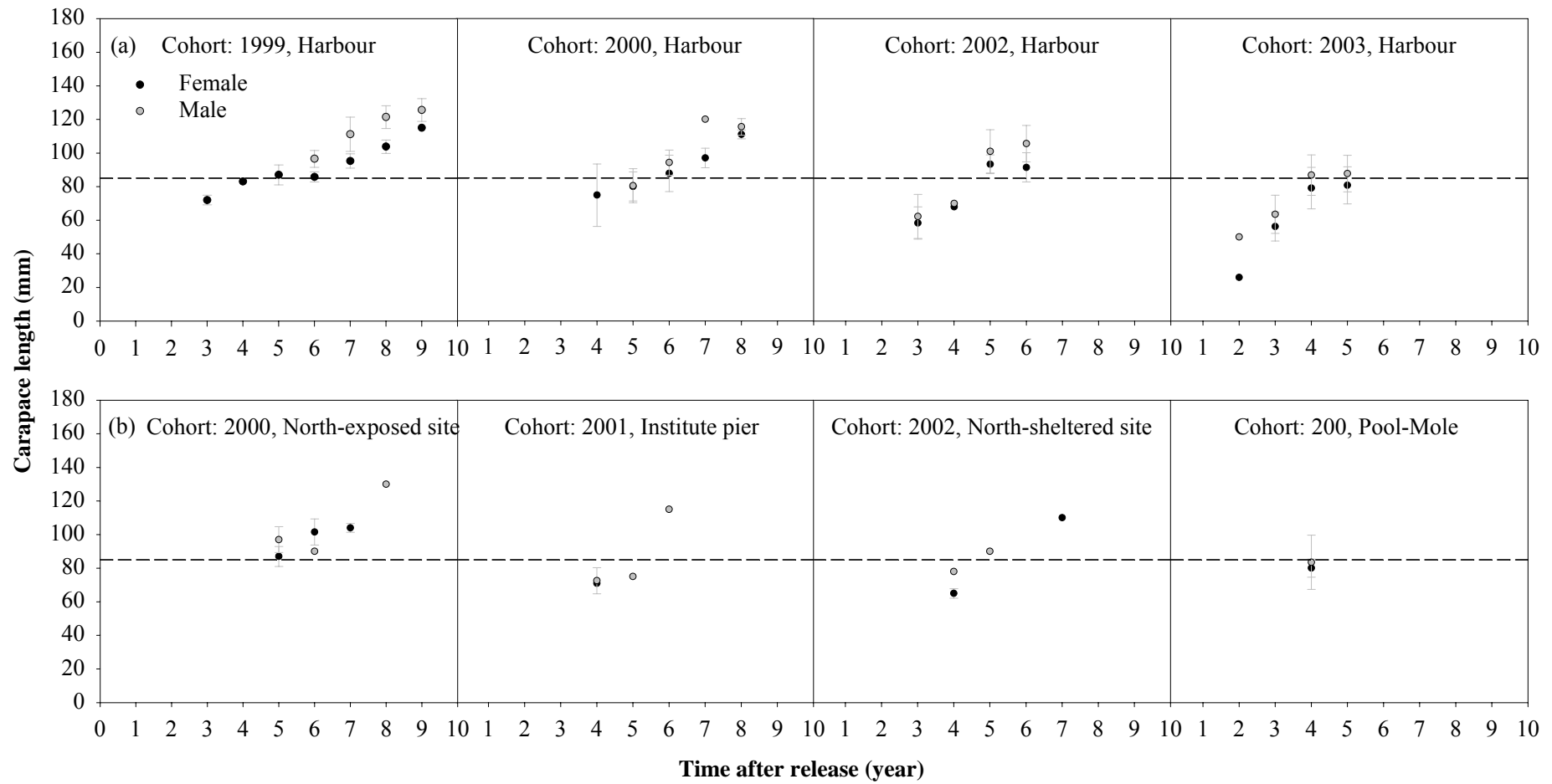
Figure 4 Growth (mean ± SD) of different cohorts of released hatchery-reared juvenile lobsters (*Homarus gammarus*) in (a) the harbour area and (b) the field. Horizontal lines represent legal size for landing lobsters.

In 2005 to 2008, 130 cultured females were recaptured, 23 females of these carried eggs, indicating that hatchery lobsters had successfully mated in the wild. Two female lobsters were berried with ca. 83 mm CL at an age of 4 and 5 years from hatching (Table 5).

Sex and size distribution of hatchery-reared lobsters in the field
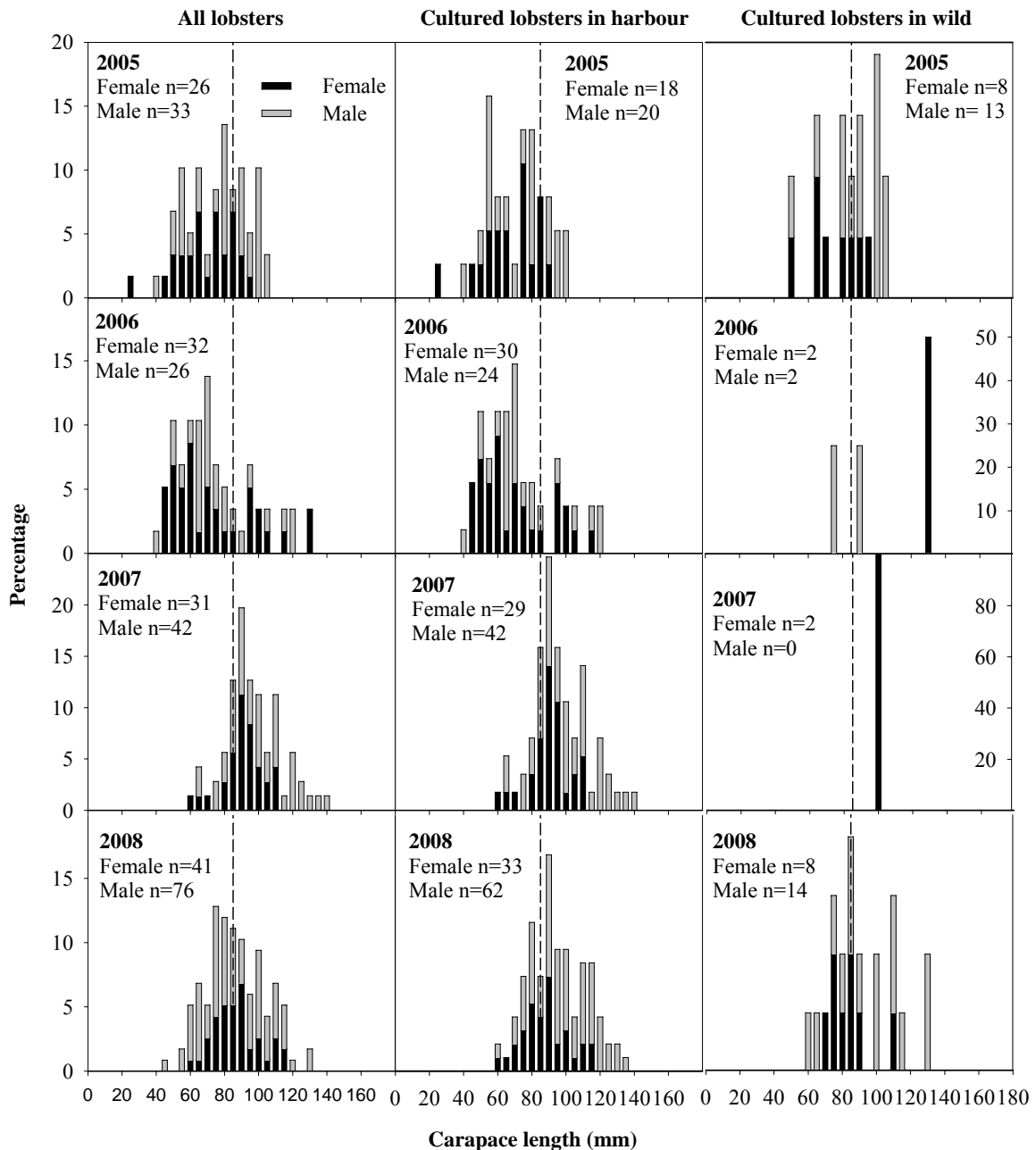
Figure 5 Sex and size distribution of cultured lobsters (*Homarus gammarus*) per 5 mm size group captured in the outer harbour and in the field. Vertical lines represent legal size for landing lobsters.

The sex and size distribution of lobsters in the years 2005 to 2008 is shown in Figure 5. Most of the cultured lobsters were captured in the outer harbour. The last release year of hatchery-reared lobsters into the harbour was in 2004, and the size distribution showed that there was a shift to larger sizes from 2005 to 2008. The male:female ratio varied from 1:0.5 to 1:1.2.

Mobility of hatchery-reared juvenile lobsters

The majority of one-year-old lobsters remained close to their release sites (Figure 1). Of those which were released in the outer harbour 99.6 % (n = 227) were recaptured in that area. Of those which were released in the wild 76.2 % (n = 32) were found within a radius of ≤ 0.5 km of their release site. The other lobsters (n = 11) covered distances between release and recapture locations from 1.0 to 2.5 km (mean: 2 ± 0 km). The overall mean CL of all recaptures until 2008 was 84 ± 20 mm (26-138 mm CL, n = 270). There were no significant differences in sizes when locations were compared (p > 0.8).

Six years after 600 lobsters were released in the area North-sheltered: "Weisse Rinne" in 2002, divers counted 0-3 lobsters 100 m^{-2} (mean: 1.4 ± 1.2 lobsters·100 m^{-2}) along 6 transects (Figure 2).

Composition of the wild population

Commercial landings from 2006 to 2008

Lobster landings of legal sized animals (without berried females) averaged 204 lobsters with 0.011 ± 0.009 CPUE in 2006, 193 lobsters with 0.010 ± 0.007 CPUE in 2007 and 332 lobsters with 0.017 ± 0.011 CPUE in 2008 (Figure 6). Lobster landings in 2008 were significantly (p > 0.01) higher than in 2006 and 2007.

In 2007 and 2008, the proportion of legal sized lobsters (cultured and wild lobsters) in the landings by the commercial fishery was 15 and 7 %, respectively. And the proportion of legal sized female lobsters in the landings reported was 9 % for 2007 and 12 % for 2008.

The catch data of all three years, 2006-2008 (Figure 6) show a regular increase in CPUE in summer and decrease towards autumn and winter. These CPUE data were regressed against the corresponding ambient temperature given a significant positive correlation ($y = -0.001 + 0.001$; $r^2 = 0.80$: $p = 0.0002$; n = 82). The mean sea temperature was in all three season nearly the same and varied between 11.1 to 11.5 °C.
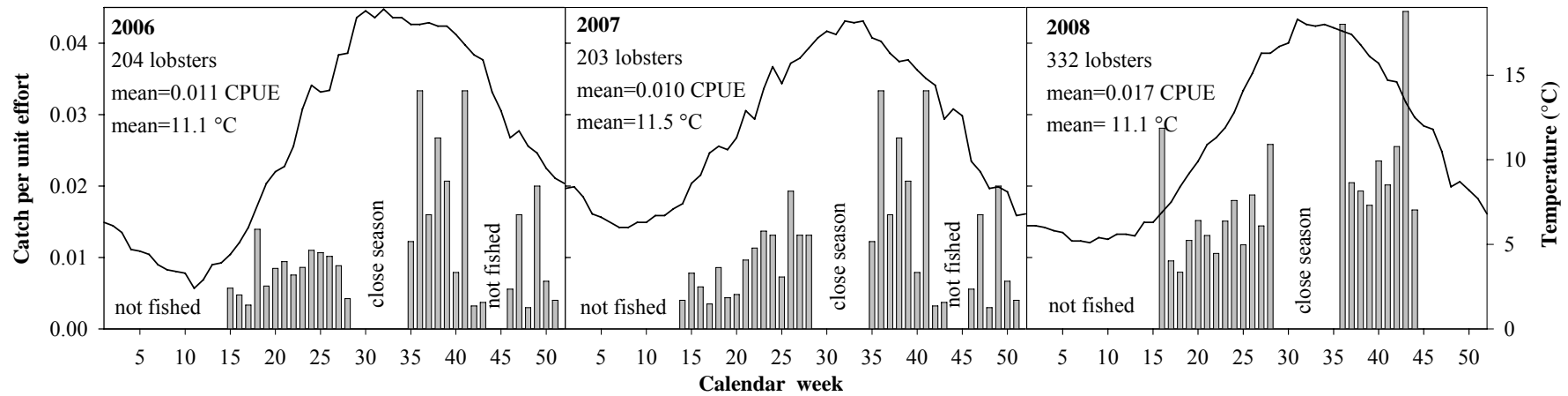
Figure 6 Catch per unit effort (vertical line) per calendar week of legal sized European lobsters (*Homarus gammarus*) in the years 2006, 2007 and 2008 around the island of Helgoland (Anonymous, 2006-2008) and seasonal temperature curves (mean calendar week) at Helgoland waters (Wiltshire et al., 2008). Egg-berried females were not included.

Growth conditions of wild lobsters

About 1 % of lobsters which were captured showed evidence of the "Black Spot" disease. The length-weight relationship of all captured lobsters was determined for 442 females (45-2400 g, 37-156 mm CL) and 498 males (150-5600 g; 58 -190 mm CL). Nonlinear regressions are shown in Figure 7a, along with the coefficients, r^2 (all > 0.99). The slope of the regression curves was significantly steeper in males than in females (m (females) = 1.0239 ± 0.0002; m (males) 1.0234 ± 0.0003; p < 0.001). Furthermore, the slopes of the linear regression of log-transformed data (Figure 7b) showed significant differences between the sexes (m (females) = 2.8578 ± 0.015; m (males) 3.0761 ± 0.018; p < 0.001).

The relationship between pre- and post-moult carapace-length in female and male lobsters was described by linear regression and the equations were y = 13 + 0.9633x (n = 11, r^2 = 0.99) in females and y = 18 + 0.9702x (n = 9, r^2 = 0.99) in males (Figure 8). The slopes of the linear regressions of the two sexes were not significantly different (p = 0.77).

In females between 43 and 110 mm carapace length (77 ± 23 mm CL), average length and weight increments at moult were 10 ± 3 mm (12 ± 5 %) and 170 ± 81 g (34 ± 11 %). In males of 48 and 125 mm CL (83 ± 26 mm CL), increments were 15 ± 5 mm (16 ± 7 %) and 270 ± 164 g ($46 \pm 15\%$). There was a significant difference (p < 0.01) in carapace length increment per moult between both sexes, and there is a negative relationship between percentage increment and original length (linear regression slope: females = - 0.18, males = - 0.20) (Figure 9).
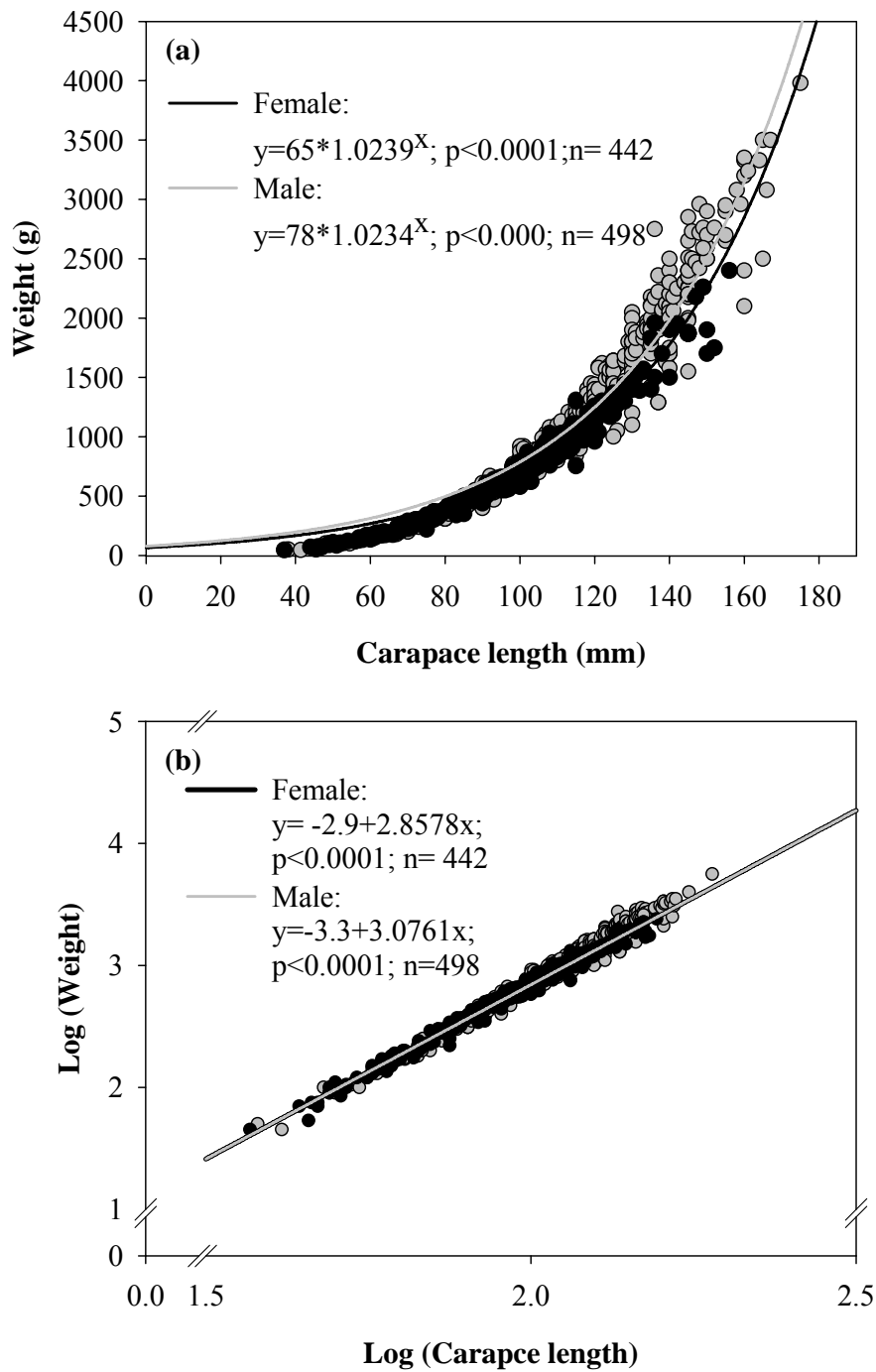
Figure 7 (a) Length-weight relationships of female and male lobsters (*Homarus gammarus*) captured at Helgoland. Females were measured without eggs. (b) Log-transformed data.
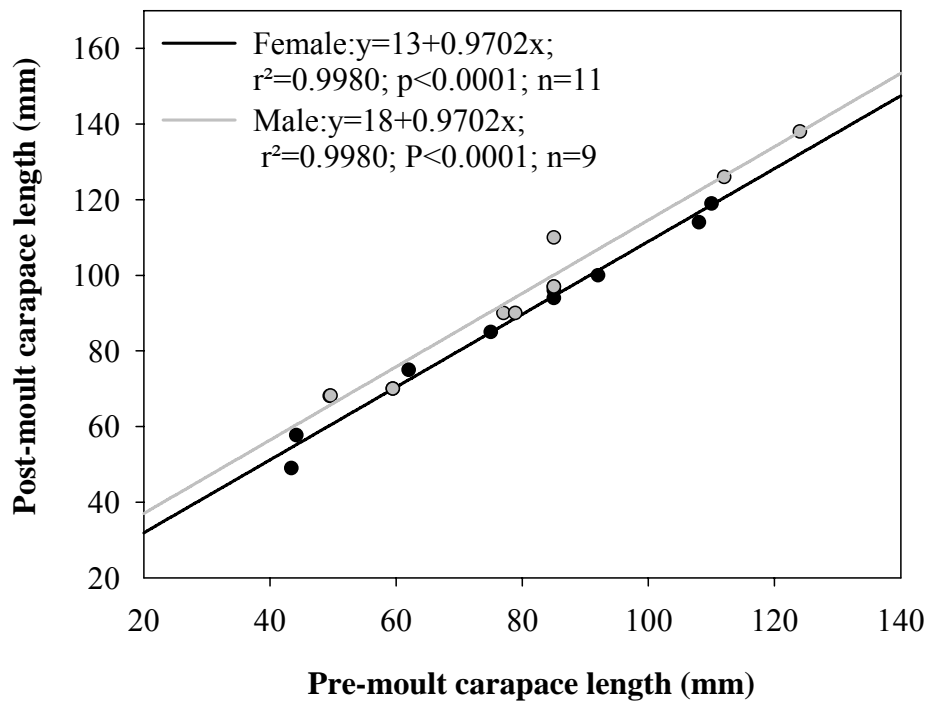
Figure 8 Growth per moult of female and male lobsters (*Homarus gammarus*) in the field.
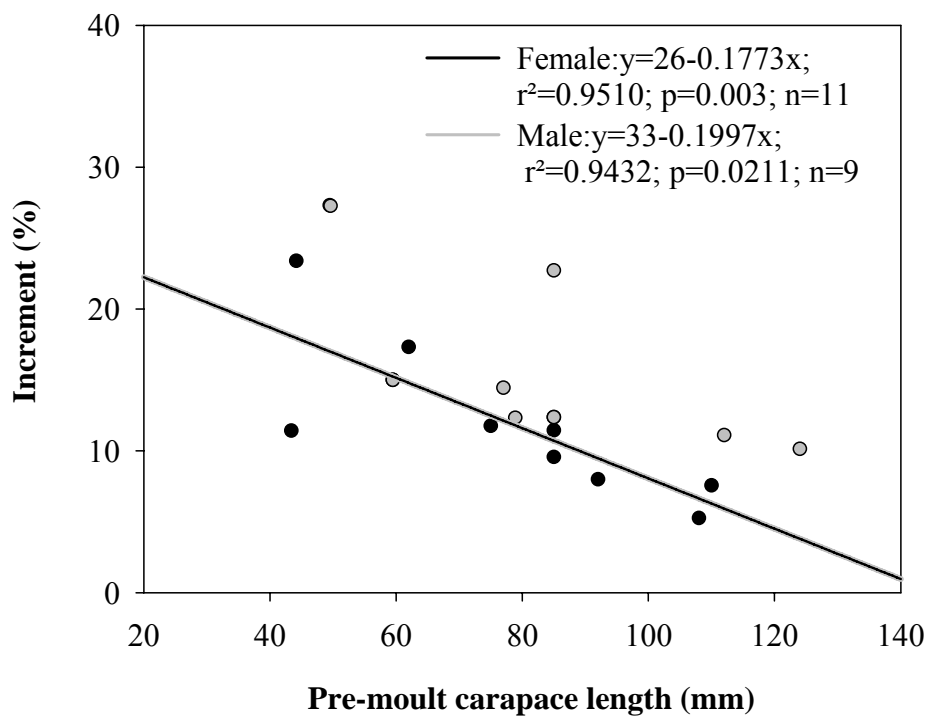

Figure 9 Percentage increment per moult of female and male lobsters (*Homarus gammarus*) in the field.

Sex and size distribution of wild lobsters

The sex and size distribution of 221 wild lobsters caught in 2007 and 327 in 2008 are shown in Figure 10. In 2007 and 2008, the number of males was twice as high than the number of females, the male:female ratio varied from 1:0.5 in 2007 to 1:0.4 in 2008. The size distribution of both wild captured sexes showed no significant difference ($p > 0.05$) between the years 2007 and 2008. The range of the CL was between 37 and 165 mm with a mean of 110 ± 22 mm (114 ± 22 mm CL in 2007 and 110 ± 23 mm CL in 2008) and the total weight of the individual lobsters was between 45 g and 3500 g, with a mean of 1107 ± 670 g (1156 ± 902 g in 2007 and 1099 ± 693 g in 2008).

The mean CL of wild captured females which carried eggs ($n = 149$) ranged from 85 to 140 mm with a mean of 108 ± 11 mm, and of cultured berried females ($n = 25$) ranged from 80 to 130 mm with a mean of 100 ± 12 mm. With increasing maturity size, the percentage number of berried females increased and the numbers of females without eggs decreased. The size-classes with the highest reproductive potential where 75 % of all females were berried ranged from 95 to 115 mm CL. Further 20 % were larger than 115 mm and 5 % were smaller than 95 mm CL.
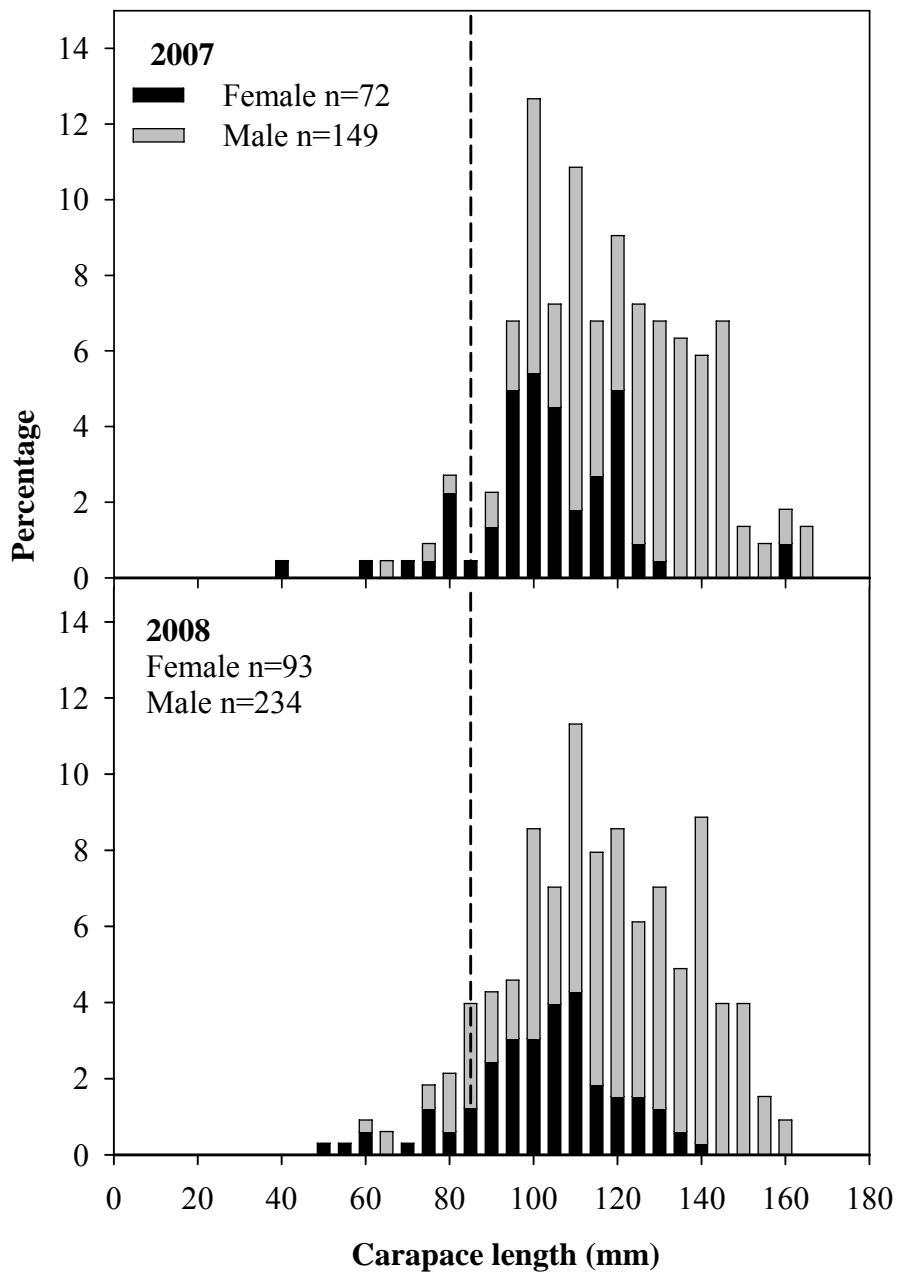
Figure 10 Sex and size distribution of wild captured lobsters (*Homarus gammarus*) per 5 mm size group. Vertical lines represent legal size for landing lobsters.

Estimation of population size

The total population size in the field was calculated according to the Lincoln-Petersen method (Table 6). The data of animals which were captured within the outer harbour area were not used. In 2007 and 2008, the initial number of tagged and released specimens (≥ 58 mm CL) around Helgoland amounted to 3337 and 3403 lobsters. A census of 201 and 328 lobsters checked for tags yielded 31 and 38 tagged lobsters, respectively. Accordingly, the estimated population size varied between 21000 in 2007 and 28000 lobsters in 2008 with a 95 % confidence interval of 6500-8000.

Table 6 Release, recapture and abundance data (mean $\pm$ SD) for lobsters (*Homarus gammarus*) ≥ 58 mm carapace length for the seasons 2007 and 2008 calculated after the Lincoln-Person method.

Capture year	N_1	n_2	m_2	m	$N \pm 95\ \% \ CL$	*Var (N)*
2007	3337	201	31	13	21070 ± 6550	$11*10^6$
2008	3403	328	38	20	28715 ± 8298	$17*10^6$

Abbreviations: n_1 is the initial number of tagged released animals at time t_1, that reached a carapace length of > 58 mm CL at time t_2, n_2 is the total number of recaptured lobsters less fishing mortality at time t_2, m_2 is the number of all recaptured tagged lobsters at time t_2 and m the number of recaptured hatchery-reared lobsters. $N \pm 95\ \%$ confidence level.

DISCUSSION

Growth parameters of female and male lobsters in the field

In the present study, moult increments, growth curves and length-weight relationships showed significant differences in growth between female and male lobsters (Figures 3, 7, 8 and 9). The growth in male lobsters was higher than that in female lobsters which gained less weight per moult than males when sexual maturity approached. The lower growth rates in female lobsters were most probably related to ovary maturation and egg production, which requires more energy than sperm production (Templeman, 1933; Templeman, 1936; Ennis, 1972).

In the wild, length increments per moult in the size class 43-125 mm CL were averaged in females at about 10 mm (12.2 %) and in males at 15 mm (15.6 %). There was a negative relationship between percentage increment and original length, which confirms data in

both *Homarus* species by Ennis (1972), Templeman (1948) and Hepper (1967). This relationship also explained growth data in the preceding study by Mehrtens (2008) who tested lobsters at a smaller size range, between 40-95 mm, and found slightly higher increments per moult of 14.9 % in females and 16.6 % for male lobsters. Similar growth increments with small variation were reported in populations in England with 10.5 % for females and 12.6 % for males (Hepper, 1967), and off Scotland with 12.8 % for females and 15 % for males (Thomas, 1958). Comparable growth increments were also found in the American lobster (*Homarus americanus*, H. Milne Edwards, 1837) with 12-13.9 % for females and 14.6-15.7 % for males by Ennis (1972), Conan et al. (1982), Maynard et al. (1992), and Comeau and Savoie (2001).

In the present study, the minimum size at the onset of functional maturity was 83 mm CL, and corresponded to an age of 4 and 5 years from hatching (Table 7). Similarly, in other European lobster populations the size at maturity varied from 70 to 87 mm CL (Gibson, 1969; Lizárraga-Cubedo et al., 2003; Agnalt et al., 2006; Tully et al., 2006). Simpson (1961) and Little & Watson III (2003) suggested that sexual maturity in both *Homarus* species was attained at smaller sizes in warm- than in cold-water areas, e.g. at the north coast of Wales in the more shallow and warmer waters of Pwllheli, maturity size was smaller (77 mm CL) than in cooler waters of Angelsey (91 mm CL; Simpson, 1961). The size at maturity in the American lobster (*H. americanus*) is similar (Little and Watson III, 2005) with smaller maturity sizes (71 mm CL) in warmer areas than in cooler waters (82 mm CL). However, the mean size of egg bearing decapods can vary under the influence of trophic regime, population density, fishing pressure, or general variability in growth rates (Wenner et al., 1985; Free, 1998).

Table 7 Size compositions of *Homarus gammarus* and *H. americanus* in various regions. The onset of sexual maturity of females was indicated by the presence of external eggs under the abdomen.

Region	CL (mm) range of tested animals	Legal size CL (mm)	Age (year) at legal size	CL (mm) at maturity size	Age (year) at maturity size	References
Homarus gammarus						
Germany (Helgoland)	28 – 120	85	4-5 (♂), 5 (♀)	-	-	Mehrtens (2008)
	26 - 165	85	4-5 (♂), 5 (♀)	83 (♀)	4 – 5 (♀)	This study
England (Bridlington)	55 – 170	85	4	-	4 (♀), 3.5 (♂)	Sheehy et.al. (1999)
	55 – 113	85	4 – 8	-	-	Bannister et al. (1994)
Scotland (Firth of Forth)	62 – 140	85	-	82 (♀)	-	Lizárraga-Cubedo
(Hebrides)	62 – 140	85	-	87 (♀)	-	et al. (2003)
Irland (Wexford,	80 – 140	87	4 – 8	80	-	Tully et al. (2006)
Waterford)	84 – 110	80	-	70-74	-	Gibson (1969)
Norway (Kvitsøy)	35 – 150	88	6	-	-	Uglem et al. (2005)
	75 – 158	88	-	75	-	Agnalt et al. (2006)
Homarus americanus						
USA (southern New England, offshore)	51 – 135	86.4	-	71 – 82	-	Little & Watson III (2005)
(Long Island Sound, Connecticut)	21 - 121	83	-	50 - 60	-	Landers et al. (2001)

Abbreviation: CL= carapace length measured without rostrum.

Growth conditions of hatchery-reared lobsters in the field

From about 9,000 hatchery-reared lobsters which were released in the years 2000 to 2008, 1.5 to 6.8 % of single year-class cultured lobsters were recaptured in the field and 6.0 to 20.8 % were recaptured from the semi-open area of the outer harbour 2 to 9 years after release (Tables 2, 3 and 4). From 2000-2004, first recapture rates were reported by Mehrtens (2008) averaging 3 % in the field and 15 % for the harbour area. The highest return rate of 6.8 % for a single year-class at Helgoland is comparable to the large-scale release programme in south-western Norway, where recapture rates reached 6.2 % (Agnalt et al., 2004). Similarly, the recapture rates of hatchery reared European lobsters in Norway and Great Britain were not higher than 8 % (Burton et al., 1994; Tveite and Grimsen, 1995; Bannister and Addison, 1998; Moksness et al., 1998; van der Meeren et al., 1998; Agnalt et al., 1999).

Agnalt et al. (1999) reported that the recruitment of lobsters increased due to the large-scale release programme at the island of Kvitsøy in south-western Norway which started in 1990. Here, commercial catches consisted to about 50-60 % of cultured lobsters after having released 128,000 cultured juveniles (Agnalt et al., 2004). At Helgoland, the proportion of hatchery-reared lobsters in commercial landings reached 2.5-6.2 % by releasing 1,300 juvenile lobster in 2001 and 2002, which attained legal size in the study years 2007 and 2008. Accordingly, around 10,500 to 26,000 juvenile lobsters must be released at Helgoland to reach a similar proportion of ~ 50 % cultured lobsters in the commercial catches as in Norway. This assessment further indicates that the yield of cultured lobsters in commercial catches was higher than in Norway, probably due to the geographically and ecologically isolated island habitat of Helgoland.

Almost none of the recaptured cultured lobsters had signs of the "Black Spot" disease, which degrades lobster shells, and about 95 % of these lobsters had developed a crusher claw. The development of a crusher claw is important for intra-specific competition for shelter, food, and mates of lobsters, and can serve as an indicator of adequate rearing conditions in juvenile lobsters, because the stimulation of crusher claw growth is timed during the first weeks of life (Wickins, 1986; van der Meeren, 2005). Both observations confirm, that the Helgoland lobster population does not appear to be under too strong an environmental constraint considering physiological and biochemical condition factors previously determined in larvae and juvenile lobster (Mehrtens, 2008).

At Helgoland, the minimum landing size was reached in female and male lobsters after 4 to 5 growing seasons. However, age at legal size varied between different cohorts by about 1 growing year. The previous study on the same population showed the same age at legal size (Mehrtens, 2008). This is in the range of observations on other European lobster populations, e.g. Bannister et al. (1994) reported that lobsters in UK reached legal size (85 mm CL) at a minimum age of 4 years and Uglem (2005) reported that lobsters in Norway need 6 growing seasons to reach a legal size of 88 mm CL. The minimum legal size (85 mm CL) of lobsters at Helgoland corresponded to the onset of functional maturity in females. Accordingly, the minimum legal size should be increased to 90 mm CL to safely assure that female's hatch at least once before taken out of the system (Table 7), and a ban on landings of all females would further enhance lobster recruitment.

Most cultured lobsters (76-99.6 %) were recaptured with a carapace length of 83 ± 20 mm after 3 to 9 years close to their original release sites. The other lobsters were recaptured within a radius of 1-2.5 km of their release sites. This confirms the mark-recapture studies of Bannister et al. (1994) who reported that released lobsters show strong fidelity to their release sites. Karnofsky et al. (1989) and Karavanich and Atema (1998) reported that adult lobster were able to move a few kilometres within their habitat, using larger boulders areas for shelter and feeding displaying normal mating, dominance and territorial behaviour. If lobsters in the present study, moved out of their release area at larger sizes, could not be determined, because the number of larger lobsters, was yet too small. The current study will be continued to examine the mobility of larger cultured lobsters.

The dive census in a previous release area of hatchery-reared lobsters (32,500 m²; i.e. about 2 individual$\cdot$100 m^{-2}) at Helgoland determined a lobster density of 1.5 lobsters$\cdot$100 m^{-2}. In comparison to control dive surveys at Helgoland about 0.5 lobsters$\cdot$100 m^{-2} (in total 620 m²) were observed in areas, where no juvenile lobsters were released (Schmalenbach, unpubl.). Accordingly, the higher abundance of lobsters in the previous release area compared to control areas confirmed that the cultured lobsters settled near the site of release.

In other European habitats, the population densities of *H. gammarus* were not sufficiently defined to calculate the carrying capacity of a habitat at different population sizes. Robinson and Tully (1999) estimated a saturation density of 5 juveniles$\cdot$m^{-2} by a rough

approximation in enclosed and unconfined experimental plots, but suggested that in the wild lobsters are unlikely to reach this density. The growth and survival of juvenile lobsters were influenced by the density of lobsters, number of shelters, predators and food availability (Svåsand et al., 2004). During the 1920s and 1930s a maximum of 80,0000 lobsters were landed at Helgoland (Klimpel, 1965). We estimated that the rocky basement of Helgoland had carried around 1.5 million lobsters with a density of 5 lobsters·100 m^{-2}, at that time, assuming the lobsters were evenly distributed (see also below). Nevertheless, further dive studies should help to assess the carrying capacities of potential release sites around the island of Helgoland.

The lobster population around the island of Helgoland

At Helgoland, the first record of lobster landing stems from 1615, reporting a yield around 37000 lobsters per year and in the 1790s around 40,000-50,000 lobsters per year. Since the 1880s, lobster landings were more or less continually reported (Klimpel, 1965; Goemann, 1990; Anonymous, 1980-2008; local fishermen pers. communication). In the last decade, the estimated annual number of landed lobsters varied between 40-250 lobsters per year. This was the only information on the number of catches that existed until 2006 when a mandatory logbook was established for fishermen to report commercial lobster landings per day and lobster pot. In the years 2006 to 2008, the catch per unit effort (CPUE) varied from between 0.010 and 0.017 CPUE with catches at a low level between 200 and 300 lobsters corresponding to 230 and 440 kg·year^{-1} which is to be considered low (see also below). However, in the season 2008 significantly more lobsters were landed than the two seasons before. However, to assess the present status of the local population more precisely, we need more annual CPUE to estimate if the landings further increase or only fluctuate at a low level according to previous studies of Mehrtens (2008). However, both studies showed that the population did not decrease, at least during the last decade. In comparison to Norway lobster fisheries where the populations have also declined on the long run, the catch of lobsters per pot varied strongly among different locations in 2001; in south-western Norway the catch rate varied between 0.06 and 0.19 CPUE and, in contrast, the data of 0.4 to 0.7 CPUE indicated extremely high abundances of lobsters in north Norway (Nordfolda and Tysford/Stefjord) suggesting also a stable population (Jørstad et al., 2004).

A highly significant dependence of catch rates and ambient seasonal temperature was noted (Figure 6). This dependency may be explained by activity being controlled by temperature: with the seasonal temperature mobility increases and thus exploratory behaviour is enhanced resulting in a higher catchability of the lobster population. Equally, a concomitant decrease is seen with the later year cooling. Corresponding experiments confirmed the activity-temperature relation (Schmalenbach and Buchholz, unpubl.).

The wild population of *H. gammarus* seems to be quite healthy. Only 1 % of wild lobsters captured showed evidence of the "Black Spot" disease.

Generally, males were larger and more frequently captured than females (males: 58-165 mm; females: 37-159 mm CL; both sexes mean: 110 ± 20 mm CL; male:female ratio 1:05) during the seasons 2007 and 2008. The size-classes of berried females ranged from 85 to 135 mm CL and corresponded to 72-93 % of all wild captured female lobsters.

The catchability of lobsters depended on their behavioural interactions, sex and size distribution and that larger lobster are more catchable than smaller sizes, due to their greater mobility or because they inhibit the entry of smaller lobsters to the pots (Miller and Addison, 1995; Addison and Bannister, 1998; Tremblay et al., 2006). In the present study, the size distribution for both sexes showed no significant differences in shift of size. This may imply that the exploitation rates were equal over the two seasons without an obvious trend towards increased proportions in recruit size ranges, and suggested also indirectly that population size had not further decreased.

Within the mark-recapture programme, the total population size of the Helgoland lobster was assessed with the Lincoln-Peterson method and averaged 21000 and 29000 lobsters (≥ 58 mm CL) with a 95 % confidence interval of 6200-8000 for 2007 and 2008, respectively. Similarly, in the preceding study from 2000 to 2004, Mehrtens (2008) estimated a total size of 28000 lobsters falling into the same range. The Lincoln-Petersen estimates of population size are based on a simple ratio and depend on the assumption that the population is closed to immigration or emigration during the sampling period and is considered a rough estimate. Assuming that the lobsters are evenly distributed across the rocky shore of Helgoland, the estimated density would correspond to average of 0.06-0.09 lobsters·100 m^{-2}. This is two orders of magnitude less than the maximum density estimated for Helgoland.

CONCLUSIONS AND PERSPECTIVES

At Helgoland, growth rates throughout the lobster life cycle, as well as size at maturity and legal size were established as components of basic population parameters on a medium time scale for the first time. Accordingly, a baseline was set to follow the development of the Helgoland lobster population in future studies. The initial mark-recapture programme will be continued on the basis of the tagged lobsters which are still out in the field with the institute's logistic support. These data will be integrated into the ongoing long term ecological observation programmes of the benthic and pelagic biotic and abiotic environment at Helgoland (Franke et al., 2004).

The European data basis on lobster has been invaluable to set the Helgoland information into a perspective. Particularly, population data from Norway, the British isles, and Ireland can serve as indications of a healthy Helgoland population, in spite of e.g. a chronical impact of hydrocarbons in the German Bight. However, climatic influence has to be considered: warmer winters lead to earlier release of larvae in spring when it is still too cold for successful development and possible mismatches in the plankton as a food source occur (Schmalenbach and Franke, in prep.). Nevertheless, so far, physiological condition of larvae and juveniles appears favourable (Mehrtens, 2008).

Recent information on larval positioning, (Schmalenbach and Buchholz, in press) and the current population parameters confirm that the Helgoland population may have become sub-critical in size to sustain recruitment on a larger scale. The test of the hypothesis may be possible by following the Norwegian example to establish a restocking programme with a release of >10,000 juveniles p.a. Some pre-requisites are encouraging: the regular growth and recruitment found, no further decrease during the last decades, fidelity to release sites, high carrying capacity of the habitat, no diseases and maintenance procedures optimized (Schmalenbach et al., 2009). These factors may facilitate large scale recruitment and may help to compensate for habitat loss, environmental constraints and interspecific competition of *C. pagurus*. If successful, the re-establishment of a self sustained lobster population can serve as a sign of a healthy environment, at least for the Helgoland microcosm. As a next step the feasibility of a sustainable lobster fishery may be tested. In this context, the ongoing cooperation of Helgoland fishermen is encouraging. In summary, the island habitat is ideally suited to observe and follow a lobster population at close quarters on the one hand but also to use the geographically and ecologically isolated habitat around the island of Helgoland and its distance from similar hard-bottom areas as a

basis to enhance the local lobster population in terms of a large scale restocking programme.

ACKNOWLEDGMENTS

REFERENCES

Addison, J.T., Bannister, R.C.A., 1998. Quantifying potential impacts of behavioural factors on crustacean stock monitoring and assessment: modelling and experimental approaches. In: Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management, 6-10 March1995, Nanaimo, B.C., Edited by G.S. Jamieson and A. Campbell. Canadian Special Publication of Fisheries and Aquatic Sciences 125, 167-177.

Agnalt, A.-L., Kristiansen, T.S., Jørstad, K.E., 2006. Growth, reproductive cycle, and movement of berried European lobsters (*Homarus gammarus*) in a local stock off southwestern Norway. ICES Journal of Marine Science 64, 288-297.

Agnalt, A.-L., van der Meeren, G.I., Jørstad, K.E., Næss, H., Farestveit, E., Nøstvold, E., Svåsand, T., Korsøen, E., Ydstebø, L., 1999. Stock enhancement of European lobster (*Homarus gammarus*); A large-scale experiment off south-western Norway (Kvitsøy). In Stock Enhancement and Sea Ranching. Edited by B. Howell, E. Moksness and T. Svåsand. Oxford, Fishing News Books, Blackwell Science, 401-419.

Agnalt, A.-L., Jørstad, K.E., Kristiansen, T.S., Nøstvold, E., Farestveit, E., Næss, H., Paulsen, O.I., Svåsand, T., 2004. Enhancing the European lobster (*Homarus gammarus*) stock at Kvitsøy Islands: Perspectives on Rebuilding Norwegian stocks. In: Stock enhancement and sea ranching development, pitfalls and opportunities. Edited by K.M. Leber, S. Kitada, H.L. Blankenship and T. Svåsand. Blackwell Publishing Ltd, Oxford, 415-426.

Anger, K., Harms, J., 1994. The Helgoland lobster: a disappearing island population. The lobster newsletter 7, 11–12.

Anonymous, 1980-2008. Die kleine Hochsee- und Küstenfischerei. Jahresbericht des Amtes für ländliche Räume Kiel –Abt. Fischerei, In Das Fischerblatt. Edited by Amt für ländliche Räume Kiel, Ohle Druck.

Ayres, P.A.; Edwards, E., 1982. Notes on the distribution of "Black Spot" shell disease in crustacean fisheries. Chemistry and Ecology. 1, 125-130.

Bannister, R.C.A., 1986. Assessment and population dynamics of commercially exploited shellfish in England and Wales. In: North Pacific Workshop on Stock Assessment and Management of Invertebrates. Edited by G.S. Jamieson and N. Bourne. Canadian Special Publication of Fisheries and Aquatic Science 92, 182-194.

Bannister, R.C.A., Addison, J.T., 1998. Enhancing lobster stocks: A review of recent European methods, results, and future prospects. Bulletin of Marine Science 62, 369-387.

Bannister, R.C.A., Addison, J.T., Lovewell, S.R.J., 1994. Growth, movement, recapture rate and survival of hatchery-reared lobsters (*Homarus gammarus* (Linnaeus, 1758)) released into the wild on the English east coast. Crustaceana 67, 156-172.

Bartsch, I., Tittley, I., 2004. The rocky intertidal biotopes of Helgoland: Present and past. Helgoland Marine Research 58, 289–302.

Burton, C.A., Bannister, R.C.A., Addison, J.T., Cook, W., 1994. Lobster stock enhancement experiments II: Current experiments in the British Isles. ICES Workshop to evaluate the potential for stock enhancement. ICES Mariculture Committee, Charlottenlund, Denmark, 37-40.

Comeau, M., Savoie, F., 2001. Growth increment and molt frequency of the American lobster (*Homarus americanus*) in the southwestern Gulf of St. Lawrence. Journal of Crustacean Biology 21, 923-936.

Conan, G.Y., Robinson, D.G., Maynard, D.R., 1982. Growth at molt of lobsters in two areas of Northumberland Strait, Canada. International Council for the Exploration of the sea Shellfish Committee C.M. 1982/K: 35, 1-10.

Cook, W., 1995. A lobster stock enhancement experiment in Cardigan Bay. Final Report. North Western and North Wales Sea Fisheries Committee, Lancaster, UK. 33 p.

Dow, R.L., 1980. The clawed lobster fisheries. In: The biology and management of lobsters. Volume II Ecology and management. Edited by J.S. Cobb and B.F. Phillips. Academic Press, New York, 265-316.

Drinkwater, K.F., Tremblay, M.J., Comeau, M., 2006. The influence of wind and temperature on the catch rate of the American lobster (*Homarus americanus*) during spring fisheries off eastern Canada. Fisheries Oceanography 15, 150-165.

Ennis, G.P., 1972. Growth per moult of tagged lobsters (*Homarus americanus*) in Bonavista Bay, Newfoundland. Journal of the Fisheries Research Board of Canada 29, 143-148.

Fishery Statistics, 1950-2006. Eurostat database of European Commission. www.epp.eurostat.ec.europa.eu

Franke, H.-D., Buchholz, F., Wiltshire, K.H., 2004. Ecological long-term research at Helgoland (German Bight, North Sea): retrospect and prospect - an introduction, Helgoland Marine Research 58, 223-229.

Free, E.K., 1998. Reproduction in the European Lobster (*Homarus gammaraus* (L.)) Proceedings of the Seminar at Kvitsoey 1995: The European lobster *Homarus gammarus* (L.). Fisken og Havet 13, 4-26.

Goemann, O., 1990. "Echt" Helgoländer Hummer. Kohlrenken Verlag Oldenburg, Oldenburg, 82 pp.

Gibson, F. A., 1969. Age, growth and maturity of Irish lobsters. Irish Fisheries Investigation 85, 37-44.

Hart, A.M., Gorfine, H.K., 1997. Abundance estimation of blacklip abalone (*Haliotis rubra*) II. A comparative evaluation of catch-effort, change-in-ratio, mark-recapture and diver-survey methods. Fisheries Research 29, 171-183.

Hepper, B.T., 1967. On the growth at moulting of lobsters (*Homarus vulgaris*) in Cornwall and Yorkshire. Journal of the Marine Biological Association of the U. K. 47, 629-643.

Hiatt, R.W., 1948. The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. Pacific Science 2, 135-213.

Hughes, J.T., Schleser, R.A., Tchobanoglous, G., 1974. A rearing tank for lobster larvae and other aquatic species. The Progressive Fish-Culturist 36, 129-132.

Jørstad, K. E., Prodöhl, P. A., Agnalt, A.-L, Hughes, M., Apostolidis, A. P., Triantafyllidis, A., Farestveit, E., Kristiansen, T. S., Mercer, J., Svåsand, T., 2004. Sub-arctic Populations of European Lobster, *Homarus gammarus*, in Northern Norway. Environmental Biology of Fishes 69, 223-231.

Karavanich, C., Atema, J., 1998 Individual recognition and memory in lobster dominance. Animal Behaviour 56, 1553-1560.

Karnofsky, E.B., Atema, J., Elgin, R.H., 1989. Field observations of social behaviour, shelter use, and foraging in the lobster, *Homarus americanus*. The Biological Bulletin 176, 239-246.

Klimpel, J., 1965. Die neuzeitliche Entwicklung der Inselgemeinde Helgoland unter besonderer Berücksichtigung des Fremdenverkehrs. Verlagsanstalt Konstanz, Konstanz.

Landers Jr., D.F., Keser, M., Saila, S. B., 2001. Changes in female lobster size at maturity and implications for the lobster resource in Long Island Sound, Connecticut. Marine and Freshwater Research 52, 1283–1290.

Linnane, A., Mercer, J.P., 1998. A comparison of methods for tagging juvenile lobsters (*Homarus gammarus* L.) reared stock enhancement. Aquaculture 163, 195-202.

Little, S.A., Watson III, W.H., 2003. Size at maturity of female American lobsters from an estuarine and coastal population. Journal of Shellfish Research 22, 857-863.

Little S.A., Watson III, W.H., 2005. Differences in the size at maturity of female American lobsters, *Homarus americanus*, captured throughout the range of the offshore fishery. Journal of Crustacean Biology 25, 585-592.

Lizárraga-Cubedo, H.A., Tuck, I., Bailey, N., Pierce, G.J., Kinnear, J.A.M., 2003. Comparisons of size at maturity and fecundity of two Scottish populations of the European lobster, *Homarus gammarus*. Fisheries Research 65, 137-152

Mauchline, J., 1976. The Hiatt growth diagram for crustacean. Marine Biology 35, 79-84

Maynard, D. R., Savoie, F., Landsburg, W., Roach, G., Wade, E., 1992. The Cape Breton experiment on legal minimum lobster size increase: an intermediate report. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 92/64, 1-47.

Mehrtens, F., 2008. Untersuchungen zu den Entwicklungsbedingungen des Europäischen Hummers (*Homarus gammarus*) bei Helgoland in Freiland und Labor. PhD thesis, Universität Hamburg, Germany.

Mehrtens, F., Stolpmann, M., Buchholz, F., Hagen, W., Saborowski, R., 2005. Locomotory activity and exploration behaviour of juvenile European lobsters (*Homarus gammarus*) in the laboratory. Marine and Freshwater Behaviour and Physiolgy 38, 105-116.

Ministerium für Landwirtschaft, Umwelt und ländliche Räume 1981, 1999. Landesverordnung über die Ausübung der Fischerei in den Küstengewässeren (Schleswig-Holsteinische Küstenverordnung – Küfo), Germany.

Moksness, E., Støle, R., van der Meeren, G. 1998. Profitability analysis of sea ranching with Atlantic Salmon (*Salmo salar*), Arctic charr (*Salvelinus alpinus*), and European lobster (*Homarus gammarus*) in Norway. Bulletin of Marine Science 62, 689-699.

Robinson, M., Tully, O., 1999. Mortality and dispersal in a benthic subtidal decapod community and of hatchery reared lobster *Homarus gammarus*. Journal of Shellfish Research 18, 727 p.

Schmalenbach, I., Buchholz, F., in press. Vertical positioning and swimming performance of lobster larvae (*Homarus gammarus*) in an artificial water column at Helgoland, North Sea. Marine Biology Research.

Schmalenbach, I., Buchholz, F., Franke, H.-D., Saborowski, R., 2009. Improvement of rearing conditions for juvenile lobsters (*Homarus gammarus*) by co-culturing with juvenile isopods (*Idotea emarginata)*. Aquaculture 289, 297-303.

Sheehy, M.R.J., Bannister, R.C.A., Wickins, J.F., Shelton, P.M.J., 1999. New perspectives on the growth and longevity of the European lobster (*Homarus gammarus*). Canadian Journal of Fisheries and Aquatic Science 56, 1904 - 1915

Simpson A.C. (1961) A contribution to the bionomics of the lobster (*Homarus vulgaris* Edw.) on the coast of North Wales. Fishery Investigations London, Series 2, 23**,** 1–28.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. The principles and practice of statistics in biological research, 3rd edn. WH Freeman and Co., New York, 887 pp.

Svåsand, T., 1993. Are reared juveniles fit for releases into the wild? ICES C.M 1993/F: 34.

Svåsand, T., 2004. Why juvenile quality and release strategies are important factors for success in stock enhancement and sea ranching, In: Stock Enhancement and Sea Ranching. Developments, pitfalls and opportunities. Edited by K.M. Leber., S. Kitada, H.L. Blankenship and T. Svåsand. Blackwell Publishing Ltd, Oxford, 61-70.

Templeman, W., 1933. Female lobsters handicapped in growth by spawning. Fisheries Research Board of Canada Atlantic Progress Report 6, 5-6.

Templeman, W., 1948. Growth per molt in the American lobster. Bulletin of the Newfoundland Government Laboratory 18, 26-48.

Thomas, H.J., 1958. Observations on the increase in size at moulting in the lobster (*Homarus vulgaris* M. Edw.). Journal of the Marine Biological Association of the U. K. 37, 603-606.

Tremblay, M.J., Smith, S. J.; Robichaud, D. A., Lawton, P., 2006 The catchability of large American lobsters (*Homarus americanus*) from diving and trapping studies off Grand Manan Island, Canadian Maritimes. Canadian Journal of Fisheries and Aquatic Sciences 63, 1925-1933

Tully, O., Bell, M., O'Leary, A., McCarthy, A., O'Donovan, V., Nee, D., 2006. The lobster (*Homarus gammarus* L.) fishery: Analysis of the resource in 2004/2005. Fisheries Resource Series 5.

Tveite, S., Grimsen, S., 1995. Survival of one year old artificially raised lobsters (*Homarus gammarus*) released in southern Norway. ICES. Marine Science Symposia 199, 73-77.

Uglem, I., Belchier, M., Svåsand, T., 2005. Age determination of European lobsters (*Homarus gammarus* L.) by histological quantification of lipofuscin. Journal of Crustacean Biology 25, 95-99.

Ulrich, I., 1998. Populationsgenetische und verhaltensbiologische Untersuchungen am Helgoländer Hummer. Dissertation, Universität Hamburg.

Ulrich, I., Müller, J., Schütt, C., Buchholz, F. 2001. A study of population genetics in the European lobster, *Homarus gammarus* (Decapoda, Nephropidae). Crustaceana 74, 825-837.

van der Meeren, G.I., 2000. Predation on hatchery-reared lobsters *Homarus gammarus* released in the wild. Canadian Journal of Fisheries and Aquatic Sciences 57, 1794-1803.

van der Meeren, G. I., 2005 Potential of ecological studies to improve survival of cultivated and released European lobsters *Homarus gammarus*. New Zealand Journal of Marine and Freshwater Research 39, 399-424.

van der Meeren, G.I., Agnalt, A.L., Jørstad, K.E. 1998. Lobster (*Homarus gammarus*) stock enhancement in Norway, experiences from a large-scale release project from 1990-1997. In: Proceedings of a workshop on lobster stock enhancement held in the Magdalen Islands (Quebec) from October 29 to 31, 1997. Edited by L. Gendron. Canadian Industry Report of Fisheries and Aquatic Sciences 244, 63-68.

Walter, I., Schmidt, M., Buchholz, F., 2008. Der Einfluss von Erdöl auf das Verhalten von Hummern. Effekte auf Nahrungssuche und Aggression. VDM Verlag Dr. Müller Aktiengesellschaft & Co. KG, Saarbruecken.

Wenner, A.M., Page, H.M., Siegel, P.R., 1985. Variation on size at onset of egg production. In: Crustacean Issues 3. Factors in adult growth. Edited by A.M. Wenner. A.A. Balekema, Rotterdam, Boston, 149-165.

Wickins, J.F., 1986. Stimulation of crusher claw development in cultured lobsters, *Homarus gammarus* (L.). Aquaculture and Fisheries Management 17, 267-273.

Wiltshire, K.H., Malzahn, A.M., Wirtz, K., Janisch, S., Mangelsdorf, P., Manly, B.F.J., Boersma, M., 2008. Resilience of North Sea phytoplankton spring blooms dynamics: An analysis of long-term data at Helgoland Roads. Limnology and Oceanography 53, 1294-1302.

MANUSCRIPT II

TEMPERATURE EFFECTS ON EMBRYONIC AND LARVAL DEVELOPMENT OF THE EUROPEAN LOBSTER (*HOMARUS GAMMARUS*) AT HELGOLAND, NORTH SEA - POTENTIAL IMPACT OF THE RECENT WARMING TREND ON LOBSTER RECRUITMENT

Isabel Schmalenbach and Heinz-Dieter Franke

Biologische Anstalt Helgoland, Foundation Alfred Wegener Institute for Polar and Marine Research, 27498 Helgoland, Germany

ABSTRACT

The impact of the warming trend on the endangered population of the European lobster (*Homarus gammarus*) at Helgoland (North Sea, German Bight) was studied in both the field and the laboratory. Embryonic development duration and the date of larval hatching were studied under different seasonal temperature cycles. A temperature cycle with an increased mean temperature (mild winters) accelerated the embryonic development and resulted in a strong seasonal forward shift of larval hatching. There was no successful larval development at temperatures below 14 °C. Larval survival increased from 9 % at 14 °C to 80 % at 22 °C, while larval development duration decreased correspondingly from 26 to 13 days. The optimal temperature range for larval survival was 16-22 °C. 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 North Sea are warming at a rate greater than on the global scale, and therefore responses of marine communities to recent climate change may be expected to be more evident in the North Sea than in many other geographical areas. At Helgoland (North Sea, German Bight) surface water temperature (annual mean) has been rising 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 °C or more over the 21st century (IPCC, 2007).

Associated with rising water temperatures, the structure and function of marine communities are already changing and will even more strongly be affected by climate change in the coming decades (IPCC, 2007). Recent regional changes driven by climate include phenological shifts (e.g. Greve, 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 change in exactly the same way, decoupling of interspecific relationships according to Cushing's match-mismatch hypothesis (Cushing, 1975) may become a frequent phenomenon of grave consequence (e.g. Edwards and Richardson, 2004).

The subtidal cliffs of Helgoland (an area of about 35 km²) harbour a small population of the European lobster (*Homarus gammarus* Linnaeus, 1758) which is geographically (and ecologically) isolated from similar hard-bottom areas and neighbouring populations by some hundred miles of soft bottoms. Up to the 1930s, there was an important lobster fishery at Helgoland, yielding around 38 tons per year (Klimpel, 1965). Since a dramatic decline particularly in the 1960s, landings of lobsters at Helgoland have been fluctuating on an extremely low level of only a few hundred specimens per year (Goemann, 1990; Anonymus, 1980-2008). The reasons for the collapse of the Helgoland stock are not known in detail, but 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 from 1981 and 1999 may have prevented a complete extinction of the local population, but to date did not result in the population's recovery. These regulations include the establishment of a special protection area, an agreement on a minimum size (11 cm

carapace length measured with rostrum) for landed lobsters, a ban on landings of ovigerous females, and a close season of 1.5 month in July-August (Ministerium für Landwirtschaft, 1981, 1999).

The annual reproductive cycle of female lobsters at Helgoland is characterized by late summer mating and spawning, followed by a 9- to 11-months period of embryonic development which spans the winter time and culminates in larval release during a hatching season ranging from late May to August (e.g. Mehrtens, 2008). In both the European (*H. gammarus*) and American lobster (*H. americanus* H. Milne Edwards, 1837) embryonic as well as larval development duration are mainly controlled by temperature (Templeman, 1936a; Perkins, 1972; Branford, 1978; MacKenzie, 1988; Charmantier et al., 1991; Charmantier and Guillaume, 1992; MacDiarmid and Saint-Marie, 2006). On the other hand, Ennis (1973a) and Morgan (1995) reported on an endogenous component in the timing of hatching, with the exact hatching date not be directly coupled to water temperature.

We hypothesise that increased winter temperatures in the German Bight accelerate the embryonic development in the Helgoland lobster population, resulting in a seasonal forward shift of larval release. If so, larvae would run the risk of being released into environmental conditions which are suboptimal (or even detrimental) for their development with respect to temperature (too low) and/or food (too poor), and which thus might reduce the species' recruitment success.

Lobster larvae are extremely rare in plankton hauls at Helgoland (Greve et al., 2004). As suggested by Ennis (1973b) for the European lobster, larvae may be distributed mainly near the bottom and thus are unavailable to plankton nets. Under laboratory conditions, Schmalenbach and Buchholz (in press) observed that newly hatched larvae of *H. gammarus* stayed only for a short time at the surface, and soon started orienting to deeper layers. Consequently, the study of temperature effects on the timing of larval release, larval development duration and larval survival had to rely mainly on appropriately designed laboratory investigations.

In the present paper we examined, for the years 2005 to 2008, whether the timing of larval release in ovigerous females captured in early summer was influenced by the temperature regime which the animals had been exposed to in the field since their spawning in late summer/early autumn the year before. Furthermore, the impact of the predicted future rise

in North Sea water temperature by 2 °C (IPCC, 2007) on embryonic development duration and timing of larval release was analysed in lobsters maintained under laboratory conditions over a one-year-period. Ultimately, lobster larvae were maintained at different temperatures in the laboratory to quantify the effects of temperature on larval development duration and larval survival through the Zoea stages I - III.

MATERIALS AND METHODS

Origin and maintenance of female lobsters

The studies were carried out in the years 2005 to 2008 at the Marine Station on Helgoland. Ovigerous female lobsters (*H. gammarus*) (mean total length: 32 cm; mean weight: 1300 g) were captured by local fishermen from the rocky subtidal at Helgoland (North Sea, 54°11.3'N, 7°54.0'E). The animals were placed individually into tanks (49 x 79 cm, filled to a depth of 20 cm) with running sea water at ca. 31 psu and maintained under the seasonal temperature cycle and the natural LD-cycle. The water temperature was measured daily. The lobsters were fed a mixture of easily obtainable small fish (*Pholis gunellus* Linnaeus, 1758, *Myoxocephalus scorpius* Linnaeus, 1758, *Pleuronectes platessa* Linnaeus, 1758) and crustaceans (*Carcinus maenas* Linnaeus, 1758, *Crangon* spp., *Liocarcinus* spp.).

Study I

Intermoult periods and survival rates of the larval stages (Zoea I, II and III) were determined at different temperatures. Newly hatched larvae (Zoea I) were sampled in the morning, since larvae usually hatch at night. Actively swimming larvae from nine ovigerous females were randomly selected, and individually reared in 80-ml cylindrical plastic bowls. 45 larvae each were raised at 5°, 11°, 12°, 13°, 14°, 15°, 16°, 20°, and 22 °C under otherwise identical conditions (salinity of ca. 31 psu, LD 12:12 h). Every day, food (~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 (postlarval or first juvenile stage). For each larval stage (Zoea I, II, and III) the intermoult period and the survival rate were plotted against culture temperature.

Study II

The second study was conducted to determine a possible relationship between the sea temperature regime which berried females are exposed to following spawning and the timing of larval release in the following year. The experimental animals consisted of female lobsters captured between June 1 and July 9 in 2005 (n = 7), 2006 (n = 20), 2007 (n = 12) and 2008 (n = 23). These females carried fully developed embryos (egg stage 4) which were ready for hatching. Females captured before June were not considered. For each female the beginning and the end of the period of larval release was recorded and a mean seasonal hatch-date and hatch-temperature was calculated.

The sea surface temperature was measured every workday as part of a long-term monitoring programme at 'Helgoland Roads' (PANGAEA, 2004-2008; Wiltshire et al., 2008, for the period up to 2005). In 2005 and 2006, the surface water temperature increased from 2-3 °C in March to about 18-19 °C in August, and decreased thereafter. In February/March 2007 and 2008, however the sea temperature did not drop below 5 °C (Figure 4).

These sea temperature data were used to test for differences between the temperature cycles (August to July, i.e. the typical period from lobster spawning to larval release) of 2004/05, 2005/06, 2006/07, and 2007/08.

Study III

The third study was designed to determine temperature effects on the duration of the embryonic development and on the timing of larval release in females captured soon after spawning and kept in the laboratory until larval hatching in the following year. The females were captured in September/October 2005 (n = 7), 2006 (n = 8), and 2007 (n = 18). Upon capture they carried eggs which had been spawned no more than three weeks before (egg stage 1). The animals were kept under the natural LD-cycle and temperature regime. For each female, hatching dates of their larvae and temperatures at larval hatching were recorded as described above.

During the embryonic development, the culture temperature (measured daily) ranged between 5 and 20 °C in 2005/06 and between 8 and 21 °C in 2006/07 and 2007/08; it was on average 2.6-3.2 °C higher in 2006/07 and 2007/08 than in 2005/06 (Figure 4). This was mainly due to higher water temperatures in the winter. As a result of the construction of the sea water supply system in the Marine Station, water temperatures in the laboratory were

on average 0.8 °C (2005/06), 2.3 °C (2006/07), and 2.2 °C (2007/08) higher than those in the field.

The culture temperature data were used to test for differences between the temperature cycles (September 24 to July 1) of 2005/06, 2006/07, and 2007/08.

Furthermore, the "degree-days" (dd; the sum of daily mean temperatures) were calculated for the period from capture in Sept/Oct to larval hatching in the following year (2006, 2007, 2008). Upon capture of the berried females, however, embryos were already up to about three weeks old (estimated mean: 10 days). Therefore, to get dd-estimates for the complete period of embryonic development, field water temperatures for a 10-day period before capture were added (dd, adj.).

Statistics

Statistical analyses were performed following Sokal and Rohlf (1995). Data are presented as means and standard deviations (SD) of replicates. To test for differences in intermoult periods of larval stages, a two factorial ANOVA with the independent factors temperature 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 analyzed with SigmaPlot 9.0.

A Mann-Whitney t-test (GraphPadPrism 3.0) was applied to test for differences between two temperature cycles, and a one-factorial ANOVA followed by a Kruskal-Wallis's multi-comparison test at a significance level of $\alpha = 0.05$ was performed to test for differences between all temperature cycles.

To test for differences in mean hatch-dates, hatch-temperatures, and durations of embryonic development under different conditions, a one-factorial ANOVA followed by a Tukey's multi-comparison test at a significance level of $\alpha = 0.05$ was performed. Statistical differences (P < 0.05) of data sets in tables and graphs are indicated by different letters. An unpaired t-test (GraphPadPrism 3.0) was applied to compare pairs of means.

RESULTS

Study I

The intermoult periods increased significantly (p < 0.001) with larval stage (Zoea I, II, III) and - in each larval stage – decreased with increasing temperature (Tables 1, 2).

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 ∞):

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

The fitted regression curves and equations are shown in Figure 1, along with the coefficients r² (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).

Table 1 Intermoult periods (days, mean ± SD) of the larval stages (Zoea I, II, and III) and total larval development duration (TLD) of *Homarus gammarus* at different temperatures (°C, mean ± SD).

T (°C)	N	Zoea I	N	Zoea II	N	Zoea III	N	TLD
5.0 ± 0.7		-		-		-		-
10.6 ± 0.2	30	11.4 ± 1.0^a	6	13.7 ± 2.1^a		-		-
11.9 ± 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^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 moulting dates were not exactly known.

Table 2 Results of two-way analysis of variance (ANOVA) on intermoult periods of the larval stages of *Homarus gammarus*. *df* = degrees of freedom, *SS* = sum of squares, *MS* = mean squares, *F* = variance ratio, *p* = probability of rejecting a correct null hypothesis ($p \leq 0.05$).

Source of variation	*Df*	*SS*	*MS*	*F*	*P*
Main effects					
Stage (S)	1	564	564.4	235.7	<0.0001
Temperature (T)	4	1430	357.4	149.3	<0.0001
First-order interactions					
S x T	11	585	53.2	22.2	<0.0001

Homarus gammarus larvae developed successfully to the first juvenile stage (postlarval stage) only when the water temperature was 14 °C or above. At 5 °C Zoea I larvae showed a survival time of 27 ± 11 days (n = 45), but were unable to proceed to the Zoea II stage. 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 1).
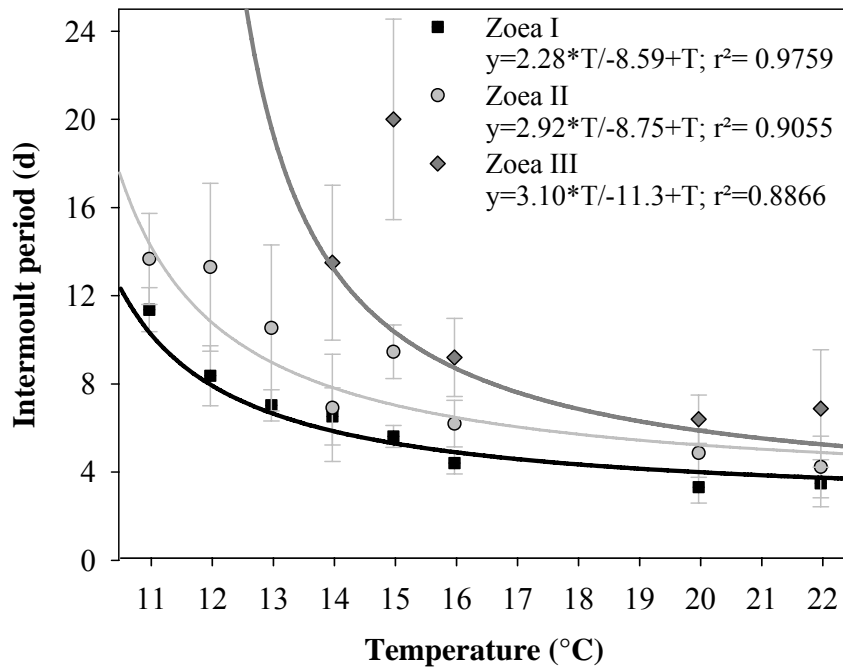
Figure 1 Effect of temperature *T* on intermoult periods (days, mean ± SD) in the larval development of *Homarus gammarus*. Non-linear regression with fitted parameters and coefficients (r²).
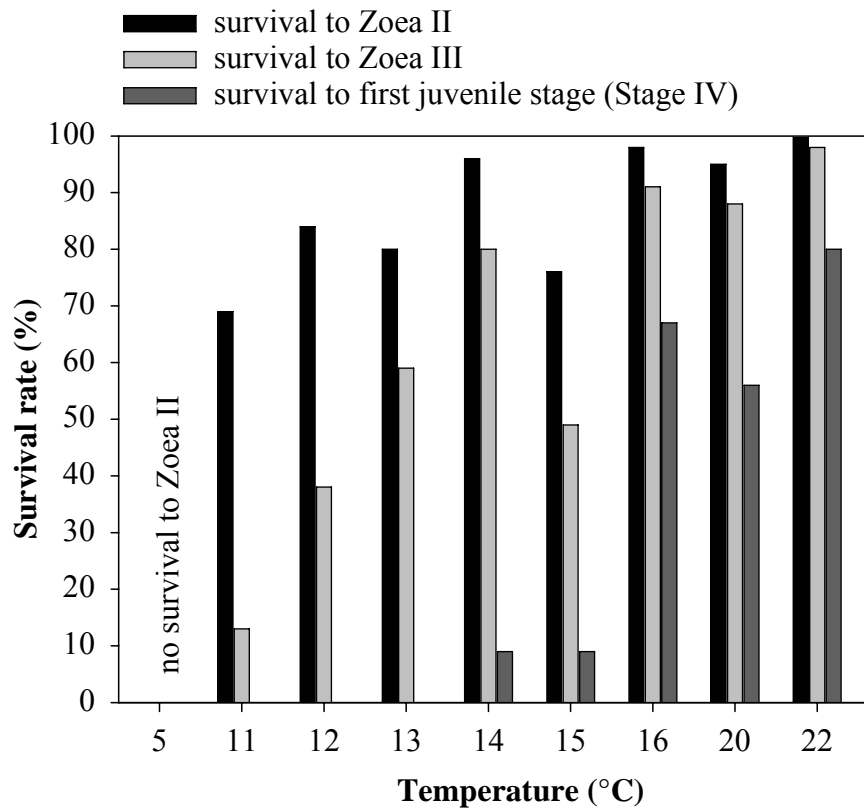

Figure 2 Survival rates (%) for the larval stages of *Homarus gammarus* at different constant temperatures (initial n = 45 individuals per treatment).

The survival rates of larval stages at different temperatures are given in Figure 2. The percentage of larvae which reached the juvenile stage increased significantly from 9 % at 14-15 °C to 80 % at 22 °C.

At all temperatures the percentage of survivors decreased rather steadily over time (Figure 3).
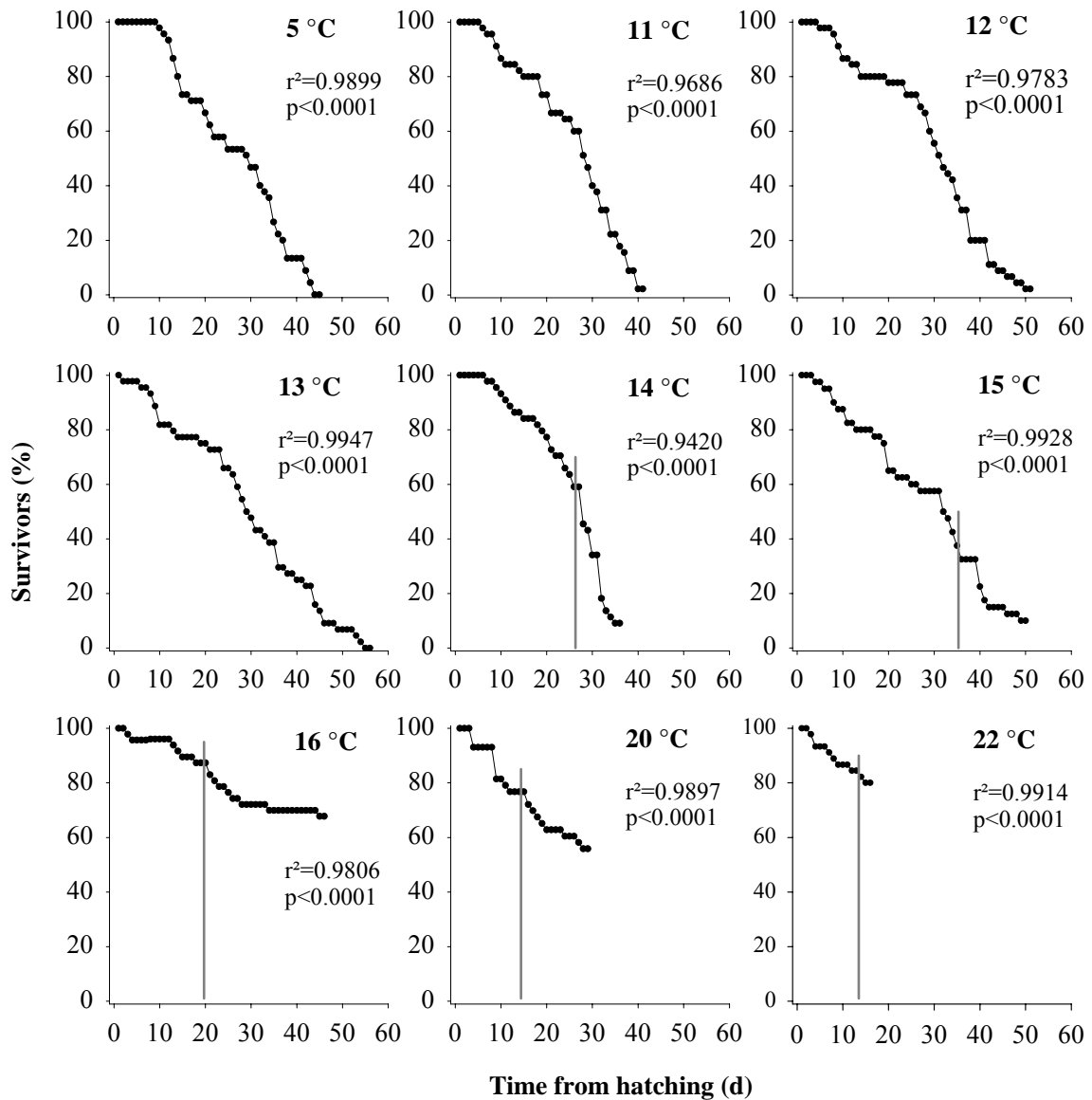

Figure 3 Percentage of surviving lobster larvae over time. A complete larval development (i.e. moulting to the first juvenile stage) occurred only at temperatures of 14 °C and above. Vertical lines represent mean times of moulting to the first juvenile stage.

Study II

During the period August 1, 2006 to July 1, 2007 the mean sea temperature was significantly higher than during all other one-year periods studied (Figure 4, Table 3). The difference ranged between 0.1 °C (2004/05 vs. 2005/06) and 1.7 °C (2004/05 vs. 2006/07). Independent of the period studied, females captured between June 1 and July 15 released their larvae at rather similar dates (usually within 15 days and at night) and at rather similar sea temperatures (Table 3).
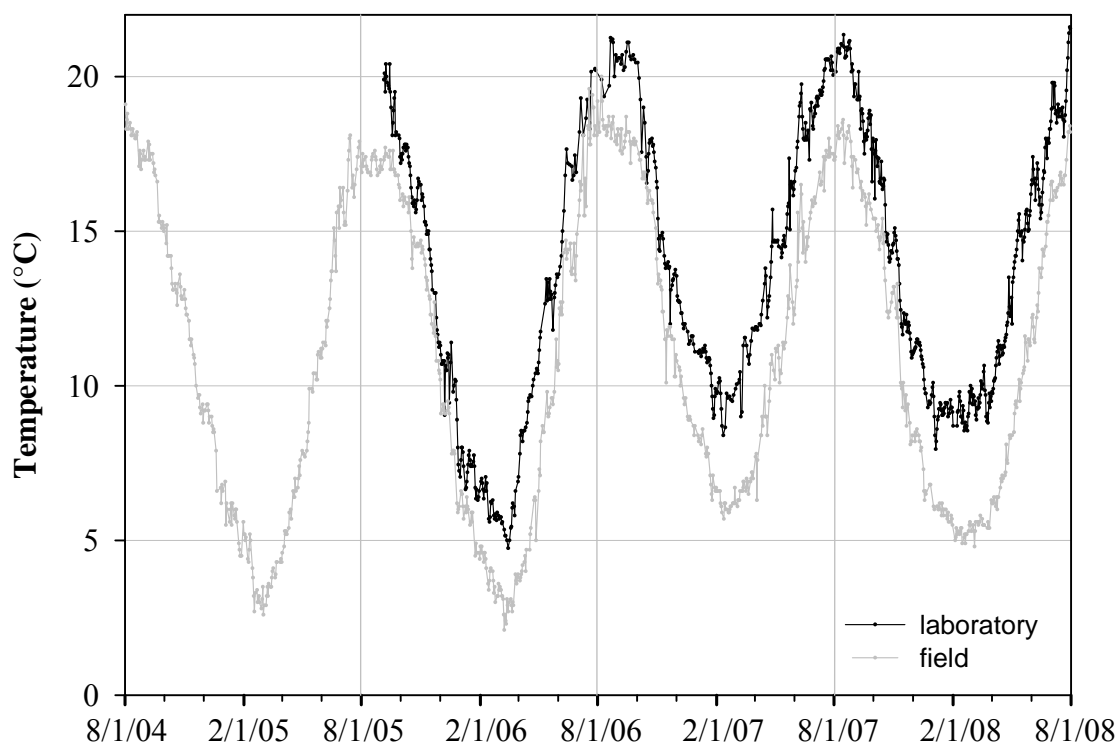

Figure 4 Water temperatures at Helgoland Roads (Wiltshire et al, 2008; PANGAEA, 2004-2008) and in the laboratory of the Marine Station from August 2004 to July 2008.

However, a trend could be recognized suggesting that larvae are released later in the year and at higher water temperatures when the mean water temperature during embryonic development was low. After warmer winters (2006/07 and 2007/08) larval release occurred slightly earlier than after colder winters, but the differences were statistically not significant. The sea temperature at larval release was slightly but significantly higher after the cold winter 2004/05 than after the warmer winters 2006/07 and 2007/08.

Table 3 Results of Study II. A) Mean ($\pm$ SD) sea temperature during four successive 1-year periods from August 1 to July 31; time of larval release (date $\pm$ SD in days) and temperature (mean $\pm$ SD) at larval release; N, number of females observed; one-way ANOVA with paired comparison post hoc tests. Different superscripts denote statistically significant differences at p = 0.05. B) P-values of unpaired *t*-tests comparing single pairs of means.

(A)

Mean sea temperature (°C)			Larval release				
Year	(August 1–July 31)		Year	N	Date ± days		T (°C)
2004/05	10.6	± 5.0 [a]	2005	7	07/13 ± 5 [a]	16.9	± 0.6 [a]
2005/06	10.7	± 5.4 [a]	2006	20	07/10 ± 10 [a]	16.5	± 1.5 [a]
2006/07	12.3	± 4.5 [b]	2007	12	07/04 ± 9 [a]	15.9	± 0.9 [a]
2007/08	11.0	± 4.6 [a]	2008	23	07/07 ± 11 [a]	16.0	± 1.0 [a]

(B)

Year	P Sea Temp.	Year	P Time of larval release	P Temp. at larval release
2004/05 vs 2005/06	0.9365	2005 vs 2006	0.5249	0.4825
2005/06 vs 2006/07	0.0001	2006 vs 2007	0.1128	0.2427
2006/07 vs 2007/08	<0.0001	2007 vs 2008	0.5485	0.7848
2004/05 vs 2006/07	<0.0001	2005 vs 2007	0.0621	0.0171
2004/05 vs 2007/08	0.3424	2005 vs 2008	0.1402	0.0468
2005/06 vs 2007/08	0.3521	2006 vs 2008	0.2347	0.2406

Study III

The temperature regimes which females captured immediately after spawning in late summer/early autumn (September/October) were exposed to in the laboratory until larval hatching, were significantly different among the years 2005/06, 2006/07 and 2007/08 (Table 4). The mean water temperature (from September 24 to July 31) was 11.5 °C (2005/06), 14.6 °C (2006/07) and 13.2 °C (2007/08). Mean dates of larval release, mean temperatures at larval release, und mean durations of embryonic development showed marked changes among years correlated with the temperature regime.

Larval release by single females occurred always within a period of approximately 15 days. The mean date of larval release for the entire experimental population, however,

differed significantly among the years. The mean date showed a significant shift forward (equivalent to an acceleration of the embryonic development) or backward (equivalent to a delay of the embryonic development) depending on the preceding temperature regime. When mean sea temperature was highest (14.6 °C in 2006/07), the mean date of larval release was April 17, the mean water temperature at larval release 13.3 °C, and the mean duration of the embryonic development 205 days. When sea temperature was lowest (11.5 °C in 2005/06), the duration of the embryonic development was significantly lengthened, resulting in a marked delay of larval release by 61 days on average (June 17); correspondingly, the mean water temperature at larval release was significantly higher (16.0 °C). Under the temperature regime of 2007/08 which ranged immediate to those of 2006/07 and 2005/06, the mean date of larval release as well as the mean temperature at larval release und the mean duration of embryonic development ranged correspondingly.

The "degree-days" (dd) for the period of cultivation (sum of daily mean temperatures from the day of capture to the mean day of larval hatching) as well as the adjusted values for the complete embryonic development did not vary significantly among the years (Table 4). The mean dd (adjusted) for the periods of study was 2772 ± 497.

Table 4 Results of Study III. A) Mean (± SD) temperature during three successive culture periods of nearly one year (September 24 to July 31); time of larval release (mean date ± SD in days) and temperature (mean ± SD) at larval release; N, number of females observed; duration (d) and degree-days (dd) for the embryonic development (means ± SD); one-way ANOVA with paired comparison post hoc tests, different superscripts denote statistically significant differences at p = 0.05. B) P-values of unpaired *t*-tests comparing single pairs of means.

(A)

Mean sea temperature (°C)			Larval release					Embryonic development					
Year			Year	N	Date ± days		T (°C)		d (days)		dd		dd (adj)
2005/06	11.5	± 4.4 [a]	2006	7	06/17	± 19 [a]	16.0	± 2.2 [a]	258	± 7 [a]	2759	± 128 [a]	2923 ± 134 [a]
2006/07	14.6	± 3.6 [b]	2007	8	04/17	± 23 [b]	13.3	± 1.3 [b]	205	± 25 [b]	2663	± 351 [a]	2809 ± 358 [a]
2007/08	13.2	± 3.6 [c]	2008	18	05/19	± 25 [c]	14.5	± 2.3 [a, b]	219	± 41 [b]	2537	± 610 [a]	2697 ± 324 [a]

(B)

	P			P	P	P	P	P
Year	Sea temp.		Year	Time of larval release	Temp. at larval release	Embryonic dev. duration	dd	dd (adj.)
2005/06 vs 2006/07	<0.0001		2006 vs 2007	<0.0001	0.0100	0.0001	0.5096	0.4431
2006/07 vs 2007/08	<0.0001		2007 vs 2008	0.0054	0.1599	0.3675	0.5923	0.6418
2005/06 vs 2007/08	<0.0001		2006 vs 2008	0.0106	0.1652	0.0231	0.3563	0.3898

Figure 5 summarizes the results of Studies II and III, giving a graphical representation of the dates of larval release and temperatures at larval release (means ± SD) for the different years of study.
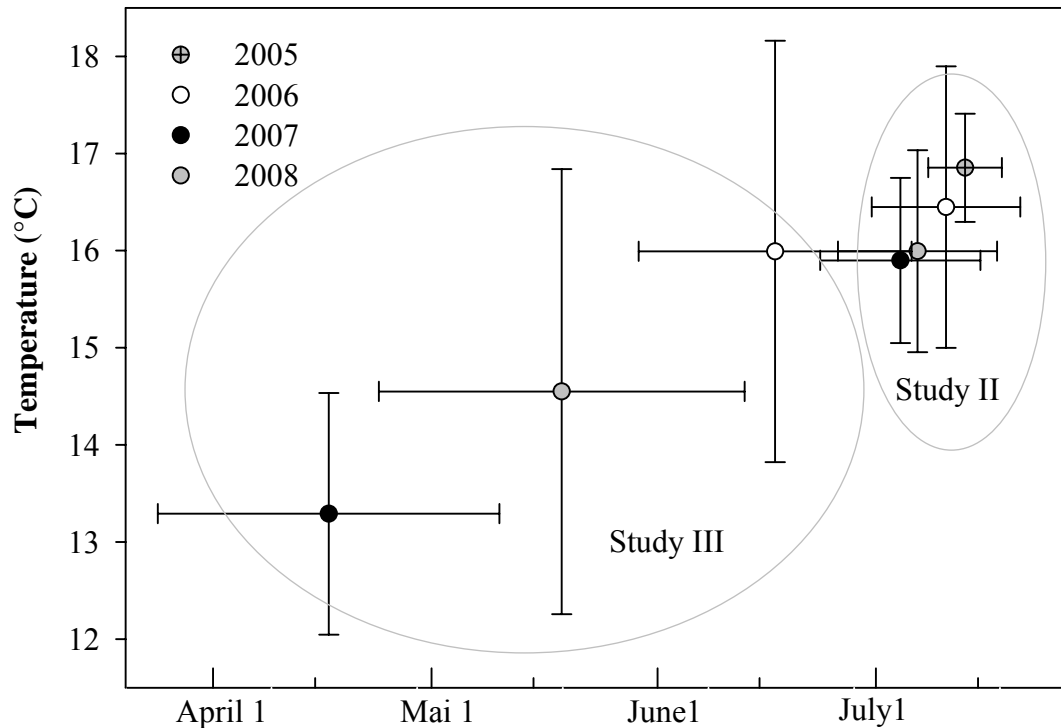

Figure 5 *Homarus gammarus*. Dates of larval release and temperatures at larval release (means ± SD) recorded in Studies II and III in 2005, 2006, 2007 and 2008.

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 would affect recruitment and productivity of commercially important marine species such as cod (e.g. Dippner, 1997; Brander, 2005). For both the European and the American lobster 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 (*Homarus gammarus*) suffers from a dramatic decline about 40 years ago. The recent climate changes, although not responsible for this decline, might impose an additional stress on the recovery of this endangered population. For an adequate assessment of the chances of a restocking programme, it is important to consider effects of climate change on lobster recruitment.

Larval development

The larval development of the European lobster comprises three Zoea stages (I, II, III). Stage IV ("post-larva") is the first juvenile stage. The stages have been illustrated and described e.g. 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 larval development duration. 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 below 11 °C. 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 need higher temperatures for normal development than do less advanced stages. Development to the postlarval stage was only possible at temperatures of 14 °C and above. The percentage of larvae which reached Stage IV increased from 9 % at 14 °C to 67 % at 16 °C while the period of total larval development decreased from 26 days to 14 days. Optimal larval survival occurred within the temperature range of 16 and 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, however, larvae of the American lobster can develop successfully at a temperature as low as 8 °C (Templeman, 1936a). Furthermore, the temperature of optimal larval survival (11 °C) was much lower in the American lobster than in its European relative (Caddy, 1979).

Embryonic development

The embryonic development of the European lobster (the period between spawning in late summer/early autumn and larval release in early summer of the following year) usually spans 10 months or even more. Little is known on how the temperature regime affects the duration of the embryonic development and, thus, the date of larval release. For the American lobster, Perkins (1972) reported that the duration of the embryonic development increased exponentially with temperature.

The years 2004 to 2008 showed clearly different annual temperature regimes (significantly different mean temperatures for the periods from August 1 to July 31; Figure 3), thus allowing for a study on how temperature affects the timing of larval release in the Helgoland lobster.

In Study II, larval hatching was observed in four successive years (2005-2008) in berried females captured between June 1 and July 9. The data collected in this way were probably biased as over the years there might have been a variable percentage of females which were not represented in the data because their larvae had hatched prior to June 1 (see below). As a consequence, larval hatching dates and temperatures at hatching were rather similar over the years of study. There was only a slight trend to larvae being released earlier and at lower ambient water temperature when the mean temperature during the embryonic development was high.

Mean water temperatures at larval release in Study II ranged between 15.9 and 16.9 °C (hatch time: July); i.e. temperature conditions were optimal for larval development, at mean sea temperature (August 1 - July 31) between 10.6 and 12.3 °C. Branford (1978) described that the embryonic development time of European lobster in the North Irish Sea which spawned in August was 11 months at an annual average temperature of 10.4 °C.

A clear relationship between temperature regime during embryonic development, time of larval hatching and temperature at hatching was found in Study III. Soon after spawning in September, females were exposed to laboratory temperatures which changed in keeping with the ambient temperature cycles but were on average about 1.8 °C higher. High mean water temperature during embryonic development correlated with an early date of larval hatching and low temperature at hatching time.

In contrast to the clear differences in embryonic development duration, the "degree-days" for the period of embryonic development were not significantly different over the years of study (2005/06, 2006/07 and 2007/08). The mean dd-value (adjusted) of about 2770 thus represents a rough estimate for predicting the time of larval hatching under a given temperature regime.

Applied to the field situations in 2004/05, 2005/06, 2006/07 and 2007/08 (and taking September 1 as the mean date of spawning), the mean dates of larval hatching would have been: June 27, 2005; June 26, 2006; May 17, 2007; June 21, 2008. For 2005, 2006 and 2008 these dates were only slightly (about 2 weeks) earlier than those given in Study II. In summer 2007, however, after a particularly warm winter, larvae should have hatch much earlier (May 17) than given in Study II (July 4). Apparently, in that summer many females

had released their larvae before June 1, and thus were not represented in the data of Study II.

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 have 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 (Figure 4) can serve as estimates of what lobsters at Helgoland may become confronted with in coming decades. Increased water temperatures 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).

Associated with this shift, problems to lobster recruitment may arise in two different contexts:

1) The increase in water temperature probably will not keep pace with the shift in larval appearance. Larvae will start their development at lower seasonal temperatures and will need some more time to metamorphosis than today. 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 may result in an increased predator-induced mortality as well.

2) The survival of larvae is not only dependent on the ambient 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, the timing of 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. For instance, diatom blooms seem to be relatively stable in time, largely independent of temperature (Edwards et al., 2004; Wiltshire et al., 2008). Considering the strong dependence of the seasonal appearance of lobster larvae on temperature, an increasing decoupling (mismatch) from optimal food conditions may be regarded as a serious problem which lobsters at Helgoland would be confronted with in a warming North Sea.

ACKNOWLEDGMENTS

REFERENCES

Aiken, D.E., Waddy, S.L., 1986. Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective. Canadian Journal of Fisheries and Aquatic Science 43, 2258-2270.

Anonymous, 1980-2007. Die kleine Hochsee- und Küstenfischerei. Jahresbericht des Amtes für ländliche Räume Kiel –Abt. Fischerei, In Das Fischerblatt. Edited by Amt für ländliche Räume Kiel, Ohle Druck.

Anger, K., Harms, J., 1994. The Helgoland lobster: a disappearing island population. The lobster newsletter 7, 11–12.

Beare, D.J., Burns, F., Greig, A., Jones, E.G., Peach, K., Kienzle, M., McKenzie, E., Reid, D.G., 2004. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. Marine Ecology Progress Series 284, 269-278.

Brander, K.M., 2005. Cod recruitment is strongly affected by climate when stock biomass is low. ICES Journal of Marine Science 62, 339-343.

Branford, J.R., 1978. Incubation period for the lobster *Homarus gammarus* at various temperatures. Marine Biology 47, 363-368.

Caddy, J.F., 1979. The influence of variations in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in the southern Gulf of St Lawrence. Rapportes et Proces-Verbaux des Reunions, Conseil International pour l'Exploration de la Mer 175, 204-216.

Charmantier, G., Mounet-Guillaume R., 1992. Temperature-specific rates of embryonic development of the European lobster *Homarus gammarus* (L.). Journal of Experimental Marine Biology and Ecology 1600, 61-66.

Charmantier, G., Charmantier-Daures, M., Aiken, D.E., 1991. Metamorphosis in the lobster *Homarus americanus* (Decapoda): A review. Journal of Crustacean Biology 11, 481-495.

Cushing, D.H., 1975. Marine Ecology and Fisheries. Cambridge University Press.

Dippner, J.W., 1997. Recruitment success of different fish stocks in the North Sea in relation to climate variability. German Journal of Hydrography 49, 277-293.

Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430, 881-884.

Edwards, M., Johns, D.G., Licandro, P., John, A.W.G., Stevens, D.P., 2007. Ecological Status Report: results from the CPR survey 2005/2006. SAHFOS Technical Report 4, 1-8.

Ennis, G.P., 1973a. Endogenous rhythmicity associated with larval hatching in the lobster *Homarus gammarus*. Journal of the Marine Biological Association of the United Kingdom 53, 531-538.

Ennis, G.P., 1973b. Behavioral responses to changes in hydrostatic pressure and light during larval development of the lobster *Homarus gammarus*. Journal of the Fisheries Research Board of Canada 30, 1349-1360.

Ennis, G.P., 1995. Larval and postlarval ecology. In: Biology of the Lobster *Homarus americanus"*. Edited by J.R. Factor. Academic Press, 23-46.

Franke, H.-D., Gutow, L., 2004. Long-term changes in the macrozoobenthos around the rocky island of Helgoland (German Bight, North Sea). Helgoland Marine Research 58, 303-310.

Franke, H.D., Gutow, L., Janke, M., 1999. The recent arrival of the oceanic isopod *Idotea metallica* Bosc off Helgoland (German, North Sea): an indication of a warming trend in the North Sea? Helgoland Marine Research 52, 347-357.

Goemann, O., 1990. "Echt" Helgoländer Hummer. Kohlrenken Verlag Oldenburg, Oldenburg, 82 pp.

Greve, W., Reiners, F., Nast, J., 1996. Biocoenotic changes of the zooplankton in the German Bight: the possible effects of eutrophication and climate. ICES Journal of Marine Science 53, 951-956.

Greve, W., Reiners, F., Nast, J., Hoffmann, S., 2004. Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. Helgoland Marine Research 58, 274-288.

Greve, W., Reiners, F., Nast, J., Hoffmann, N. 2006. Zooplankton Helgoland-Reede, Jahresübersicht. MURSYS Meeresumwelt-Reportsystem Information aus Nord- und Ostsee.

Harms, J., Schilling, U., Goemann, O., 1995. Der "Helgoländer Hummer". Natur und Museum 125, 33-40.

Havinga, B., 1929. Krebse und Weichtiere. Handbuch der Seefischerei Nordeuropas, Bd. III. Schweizbart`sche Verlagsbuchhandlung, Stuttgart, 145 pp.

IPCC, 2007. Climate Change 2007: Mitigation. Contribution of Working Group III to the fourth Assessment Report of the Intergovernmental Panel on Climate Change. Edited by Metz, O.R. Davidson, P.R. Bosch, R. Dave and L.A. Meyers. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA., 851 pp.

Klimpel, J., 1965. Die neuzeitliche Entwicklung der Inselgemeinde Helgoland unter besonderer Berücksichtigung des Fremdenverkehrs. Verlagsanstalt Konstanz, Konstanz.

MacDiarmid, A.B., Saint-Marie, B., 2006. Reproduction. In: Lobsters Biology, Management, Aquaculture and Fisheries. Edited by B.F. Phillips. Blackwell Publishing, Oxford, 45-68.

MacKenzie, B.R., 1988. Assessment of temperature effects on interrelationship between stage durations, mortality, and growth in laboratory-reared *Homarus americanus* Milne Edwards larvae. Journal of Experimental Marine Biology and Ecology 116, 87-98.

Mehrtens, F., 2008. Untersuchungen zu den Entwicklungsbedingungen des Europäischen Hummers (*Homarus gammarus*) bei Helgoland in Freiland und Labor. PhD thesis, Universität Hamburg, Germany.

Ministerium für Landwirtschaft, Umwelt und ländliche Räume 1981, 1999, 2005. Landesverordnung über die Ausübung der Fischerei in den Küstengewässeren (Schleswig-Holsteinische Küstenverordnung – Küfo), Germany.

Morgan, S.G., 1995. The timing of larval release. In*:* Ecology of Marine Invertebrate Larvae. Edited by L. McEdward. CRC Press, Boca Raton, 175-191.

Nichols, J.H., Lawton, P., 1978. The occurrence of the larval stages of the lobster *Homarus gammarus*, (Linnaeus, 1758) off the northeast coast of England in 1976. Journal du Conseil - Conseil International pour l'Exploration de la Mer 38, 234-243.

PANGAEA (Publishing Network for Geoscientific & Environmental Data): Public library for dissemination of data and metadata via portal networks using georeferenced data related to basic research on earth & environment. 2004-2008. Operated by AWI and MARUM, Germany. www.pangaea.de.

Perkins, H.C., 1972. Developmental rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne-Edwards). Fishery Bulletin 70, 95-99.

Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. Science 308, 1912-1915.

Schmalenbach, I., Buchholz, F., in press. Vertical positioning and swimming performance of lobster larvae (*Homarus gammarus*) in an artificial water column at Helgoland, North Sea. Marine Biology Research.

Sheehy, M.R.J., Bannister, R.C.A., 2002. Year-class detection reveals climatic modulation of settlement strength in the European lobster, *Homarus gammarus.* Canadian Journal of Fisheries and Aquatic Science 59, 1132-1143.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. The principles and practice of statistics in biological research, 3rd edn. WH Freeman and Co., New York, 887 pp.

Southward, A.J., Hawkins, S.J., Burrows, M.T., 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. Journal of Thermal Biology 20, 127-155.

Templeman, W., 1936. The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). Journal of Biology Board of Canada 2, 485-497.

van der Meeren, G.I., Tveite, S., 1998. Fishery and management of the lobster (*Homarus gammarus*) in Norway. In: The European lobster *Homarus gammarus* (L.): Proceedings from the Seminar at Kvitsøy 1995. Edited by G.I. van der Meeren and O. Soldal. Fisken og havet 1998, 13, 72-76.

Walter, I., Schmidt, M., Buchholz, F., 2008. Der Einfluss von Erdöl auf das Verhalten von Hummern. Effekte auf Nahrungssuche und Aggression. VDM Verlag Dr. Müller Aktiengesellschaft & Co. KG, Saarbruecken.

Wiltshire, K.H., Malzahn, A.M., Wirtz, K., Janisch, S., Mangelsdorf, P., Manly, B.F.J., Boersma, M., 2008. Resilience of North Sea phytoplankton spring blooms dynamics: An analysis of long-term data at Helgoland Roads. Limnology and Oceanography 53, 1294-1302.

MANUSCRIPT III

VERTICAL POSITIONING AND SWIMMING PERFORMANCE OF LOBSTER LARVAE (*HOMARUS GAMMARUS*) IN AN ARTIFICIAL WATER COLUMN AT HELGOLAND, NORTH SEA

Isabel Schmalenbach and Friedrich Buchholz

Biologische Anstalt Helgoland, Foundation Alfred Wegener Institute for Polar and Marine Research, 27498 Helgoland, Germany

ABSTRACT

The vertical distribution and swimming ability of the three larval stages (Zoea I, II, and III) of *Homarus gammarus* were determined in laboratory experiments. In an artificial water column, newly hatched larvae were positively phototactic to white light at intensities near 0.6 μmol·m^{-2}·s^{-1}. The positive phototactic behaviour decreased with increasing larval age and stage. Accordingly, older larvae were mostly distributed away from the light source in deeper layers and near the bottom. The measured vertical swimming speed of newly hatched larvae was 4.6 ± 0.5 cm·s^{-1}. Lobster larvae were positively rheotactic and thus able to swim against the current direction. The horizontal swimming ability of the larvae increased with stage from 0.7 ± 1.0 cm·s^{-1} (Zoea I) to about 1.5 ± 0.9 cm·s^{-1} (Zoea II) and 2.2 ± 0.7 cm·s^{-1} (Zoea III). Implications for the persistence of the small, isolated lobster population around the island of Helgoland are discussed.

Keywords: Homarus gammarus, Larvae, North Sea, Phototaxis, Rheotaxis

INTRODUCTION

Stocks of European lobsters (*Homarus gammarus* Linnaeus, 1758) are the basis for important fisheries in Scotland, Norway (van der Meeren and Tveite, 1998), England and Wales (Bannister, 1986), France, Ireland (Browne et al., 2001; Tully et al., 2006), Sweden, Denmark and Spain (see Dow, 1980). Within the past 70 years, total annual European landings have varied between 1,700 and 3,500 tons (Fishery Statistics, 1950-2006). Along the German coast, the European lobster is restricted to the rocky subtidal zone of the island of Helgoland (German Bight, North Sea). Here, the local lobster fishery was important during the 1920s and 1930s and yielded around 38 tons per annum, until in the 1960s a severe decline in population size occurred (Klimpel, 1965; Goemann, 1990). To date, the lobster stock has not recovered and annual landings remain very low but constant at about 200 lobsters per year (Anonymous, 1980-2007). The reasons for the collapse of the Helgoland stock are not known in detail, but may include habitat destruction by the bombing of the island during and after the second world-war, extensive fishing pressure in the 1950s and 1960s, and anthropogenic pollution of the North Sea waters by oil spills, chemicals and industrial wastes which increased strongly in the late 1960s (Klimpel, 1965; Anger and Harms, 1994; Harms et al., 1995; Walter et al., 2008). Legislative regulations from 1981 and 1999 may have prevented a complete extinction of the local population at Helgoland, but until today did not substantially support the population's recovery (Ministerium für Landwirtschaft, 1981, 1999).

The subtidal cliffs of Helgoland at an area of about 33 km² are located 45 miles offshore in the German Bight, and the maximum depth of the Helgoland hard-bottom area reaches 24 m. The local lobster population is geographically and ecologically isolated from similar hard-bottom areas and from neighbouring populations in Norway and Britain by some hundred miles of sandy or muddy bottoms (Ulrich et al., 2001). The island is exposed to strong tidal currents and wind impact which lead to variations in water level and current speeds (Hickel, 1972).

The missing recovery of the Helgoland lobster population may have been caused by the size of the population having become sub-critical and thus leading to continuous larval recruitment failure having been caused by the drift of larvae away from the favourable rocky habitat of Helgoland by the local currents to such an extent that a larger stock could not be sustained any more.

Various larval recruitment mechanisms have been documented for decapod crustacean larvae (Johnson, 1960; Makarov, 1969; Sandifer, 1973) being dependent on factors as water depth, temperature - including climatic change, currents, immigration of ecological competitors and fishing pressure (Ennis, 1983; Harding et al., 1983). Ennis (1983) described three possible conditions for larval settlement: First "larvae maintain their position near parental grounds during larval development", second "larvae relocate parental grounds when ready to settle", and third "larvae are carried passively by currents and their presence near suitable bottom when settling is fortuitous".

In view of these explanations the continuing recruitment failure in the Helgoland lobster population may be demonstrated by very low numbers of larvae found in the field. In vertical plankton hauls of the Helgoland-Road time-series on meso- and macro-zooplankton (Greve et al., 2004) lobster larvae were always very rare, e.g. in 2005 only three Zoeae of stage I were caught. This probably reflected the decline of the lobster stock and the ensuing low density of ovigerous females at the rocky bottom of Helgoland.

Field studies about the temporal and spatial distribution of lobster larvae of *H. americanus* (H. Milne Edwards, 1837) are numerous (e.g. Templeman, 1937; Harding et al., 1987) whereas only few studies on larvae of *H. gammarus* exist (Nichols and Lawton, 1978; Tully and Ó Céidigh, 1987). Larvae of *H. americanus* of all stages were found in large numbers in the plankton (Templeman, 1937, Scarratt, 1964). In contrast, larvae of *H. gammarus* are generally rare in the plankton, and most commonly the first and the fourth larval stages were found (Dun and Shelton, 1983; Minchin, 1984). Nichols (1984) mostly found the first larval stage of *H. gammarus* at the sea surface and Ennis (1973) suggested that older larvae may disperse near the bottom and thus may be unavailable to plankton nets. However, Nichols (1984) confirmed that before 1976 only few larvae were recorded in the coastal waters of Europe generally, but being attributable to methodological inadequacies and the lack of knowledge about the occurrence and behaviour of larvae.

The larval development of the European lobster comprises three Zoea stages and one post-larval stage which were morphologically described by Nichols and Lawton (1978). The locomotion ability of larvae changes during their larval development (Ennis, 1995) and the major swimming appendages of the pelagic larvae are the exopodite branches of the third maxillipeds, the chelipeds and the four pairs of pereipods (Neil et al., 1976). By beating of the exopodites, the larvae carry forward, backwards or upwards; when their motion ceases, however, the larvae sink towards the bottom (Hadley, 1908).

The distribution of larvae is controlled by environmental factors such as currents systems, pressure, the light-dark regime, temperature, predators, and food abundance; and by behavioural components such as swimming ability and the active orientation to these environmental cues (Ennis, 1983; Hudon and Fradette, 1993). Light is known to be important in the depth regulation of crustacean larvae (Forward, 1989). In 2008, in Helgoland waters, only few larvae of stage I were found at the sea surface at night by light-catch (Schmalenbach, pers. observation). In previous experiments, larvae oriented through perception of hydrostatic pressure and showed specific phototactic (Ennis, 1973) and rheotactic behaviour (Ennis, 1986). Hadley (1908) described phototactic responses of larvae of *H. americanus* and found that larvae changed their phototactic behaviour both within and between each stage. Mileikovsky (1973) summarized the larval swimming speed of bottom invertebrates with different methods employed. Generally, the pronounced swimming ability in larvae plays an important role to maintain position in currents (Mileijovsky, 1973; Ennis, 1986).

Due to the unavailability of larvae in the field, a laboratory study was designed to give insight how lobster larvae move in light fields and in currents to help to interpret larval behaviour in selection for an optimal habitat for survival and growth in a restricted area like around the island of Helgoland. Accordingly, we observed the response to light and currents of each Zoea stage (Zoea I, II, and III) to determine (1) the vertical distribution of larvae at different light-dark regimes, (2) their sinking rate, (3) their vertical swimming speed, and (4) their horizontal swimming ability to persist against currents. The data and results of our study on the behaviour of larvae in relation to the specific geographical region can be applied further in models forecasting the recruitment mechanisms of a local lobster population here and in general in order to assess conditions and chances for successful recruitment. On these grounds further management procedures may be decided on to establish and conserve sustainability in lobster fishery.

MATERIALS AND METHODS

Origin of larvae and maintenance

The study was carried out during summer 2007 at the Marine Station on Helgoland. Berried female lobsters (*Homarus gammarus*) (mean total length: 32 cm, mean weight: 1115 g) were captured by local fishermen from the rocky subtidal zone at Helgoland (North Sea, 54°11.3'N, 7°54.0'E). The animals were placed individually into tanks (49 x 79 cm, filled to a depth of 20 cm) with running sea water and maintained at ambient water temperature, at ca. 31 psu salinity, and under a natural light-dark cycle. The adult females were fed with a mixture of easily available crustaceans (*Carcinus maenas* Linnaeus, 1758, *Crangon* spp., *Liocarcinus* spp.) and small fish (*Myoxocephalus scorpius* Linnaeus, 1758, *Pholis gunellus* Linnaeus, 1758, *Pleuronectes platessa* Linnaeus, 1758). Actively swimming larvae were collected in the morning after hatching from tanks with ovigerous females, individually transferred to 70 ml cylindrical glass bowls and acclimated to the experimental temperature. The larvae were maintained at a constant water temperature of 18 °C, ca. 31 psu salinity, and under an artificial 12:12 h light-dark cycle. Water and food (30 freshly hatched *Artemia* sp. nauplii per lobster, cysts from Sander's Brine Shrimp Company) were changed daily.

Phototaxis and vertical distribution

The first series of experiments was performed with differently old Zoea I, II, and III larvae, i.e. Zoea I: freshly hatched, one day, two days and three days after hatching; Zoea II and III: freshly moulted, one day, two days and three days after moulting. The larvae were examined with respect to their behavioural responses to different types of illumination.

The experiments were conducted in four circularly arranged, transparent perspex-cylinders (height: 100 cm, diameter: 20 cm), filled with sea water of 18 °C. A light bulb was positioned alternatively above the top or beneath the bottom of this group of cylinders. The light intensity was set so that it corresponded to the mean photon flux density in Helgoland waters (in July: 143 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 2 m depth, Lüning and Dring (1979)). Light intensity was 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the lit end (measured directly in front of the light source) of the water columns, and 0.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 1 m distance from the source of light (white incandescent light of 380-750 nm, measured with a Quantum irradiance meter: Quantum-Sensor LI-190SA, Licor Data Logger LI-1400). No other light sources were allowed to interfere. The larvae were fed one hour before the experiments started. All experiments

were conducted at the same time of day (start at 9 a.m., i.e. 3 h after change from "night-time" to "day-time").

For each run of experiment the four cylinders were equipped each with four larvae of the same age (in total 16 larvae). More than four larvae per column complicated the determination of the larval position in the column and would have increased loss by cannibalism. Four larvae per column was the optimum density found to prevent any interaction.

After transfer into the cylinders, the larvae were allowed to acclimate for 20 min at darkness. Then the light was positioned on the top of the cylinders and turned on. Thirty minutes later, the vertical distribution of the larvae within the water columns was determined in steps of 10 cm: 0-10 cm, 10-20 cm etc., and the light was turned off. After 30 min of darkness, the pattern of vertical distribution was determined again under red light. Red light did not disturb lobsters in their behaviour (Foxon, 1934; Weiss et al., 2006). Thereafter the light was placed beneath the cylinders and turned on for another 30 min. A subsequent determination of the vertical larval distribution terminated the experimental run. The larvae were used for one run only. The larval behaviour was considered as positive phototaxis if larvae moved actively towards the light stimulus, and as negative phototaxis if larvae moved away from the source of light.

Sinking rate

The second series of experiments was performed with all three larval stages (Zoea I, II, and III) to determine the sinking rate of dead larvae. To kill the larvae, specimens were placed carefully with tweezers into an Eppendorf cap filled with 200 µl seawater, and were shock-frozen at - 80 °C for a few minutes. After animals were dead, they were defrosted carefully at the experimental temperature of 18 °C. Thereby, the larvae were kept intact and the process did not change body fluid osmolality. Subsequently, the sinking rate was directly tested by placing an individual dead larva (n = 10) at the water surface of the experimental cylinder, as described above for live specimens. The time was measured for the individual larva to sink the 100 cm water column to the bottom of the cylinder.

Vertical swimming speed

The third series of experiments was performed with newly hatched Zoea I larvae only. It was conducted to determine the vertical swimming speed in response to white light in a cylinder, as described above. In preliminary studies the swimming speed of larvae was also tested in an experimental cylinder according to Jacoby (1982). The vertical swimming speed could not be determined for Zoeae II and III, because larvae of these stages did not swim directly towards the light source and the method was thus abandoned.

An individual larva (n = 10) was placed into the cylinder at a water temperature of 18 °C. The bottom of the cylinder was lit and the time was measured for the individual larva to swim the 100 cm straight without stopping or turning. The swimming speed of newly hatched larvae was calculated as the difference between the swimming speed measured and the sinking rate in cm·s^{-1}.

Rheotaxis and horizontal swimming ability

The fourth series of experiments was performed with all three larval stages (Zoea I, II, and III). It was conducted to determine the larval responses to current stimulation. Previous studies served as comparison to optimize procedures (Ennis, 1986; Shirley and Shirley, 1988).

Larvae of stage I (n = 32), II (n = 35) and III (n = 40) of different female lobsters were used and raised as described above. The rheotactic responses and the swimming ability of individual larvae were observed in a horizontal flow channel (length = 52 cm, width = 5.5 cm, water level = 14 cm) at a water temperature of 18 °C. The material of the channel wall consisted of black PVC. A funnel-shaped construction was at one end of the flow channel in order to concentrate the incoming current evenly into the channel. A pump maintained a closed circuit at 3.2 ± 0.3 cm·s^{-1}. The flow channel was not covered to allow observation. The set-up was illuminated by a bulb with diffuse white light. The light source was positioned 1 m above the experimental channel and the light intensity was 50 μmol·m^{-2}·s^{-1} (white incandescent light of 380-750 nm, measured with a Quantum irradiance meter: Quantum-Sensor LI-190SA, Licor Data Logger LI-1400). The surface flow velocity in the channel was determined using polystyrene balls. The horizontal swimming ability of the larvae and their positioning in the flow channel (near the surface or near the bottom) were determined for all individual larvae by observation from above.

A single larva was positioned at the beginning of the flow channel. The time taken by the larva to pass through the channel was measured. Rheotaxis was positive if the larvae were

oriented in the direction of the current flow. The horizontal swimming ability was calculated as the difference between the water current and the drift velocity of the larvae measured.

Statistics

Statistical analyses were performed according to Sokal and Rohlf (1995). Data were presented as the mean and standard deviation (SD) of replicates. The tests were performed with the computer programs SigmaStat 2.03 (SPSS) and Statistica 7.1 (StatSoft). The data were tested for normal distribution with the Kolmogorov-Smirnov test. If normal distribution failed, a Mann-Whitney t-test was applied. The vertical distributions of the larvae were subjected to a four factorial analysis of variance (ANOVA) and the sinking rate and vertical swimming speed were subjected to a one-way analysis of variance (ANOVA) followed by a Tukey's multi-comparison test at a significance level of $\alpha = 0.05$. The positioning of larvae in the flow channel was analysed by linear regression given with fitted parameters and coefficients (r^2). Statistical differences ($p < 0.05$) of data sets in tables were indicated by different letters.

RESULTS

Phototaxis and vertical distribution

Preliminary experiments had shown that the larval distributions were neither influenced by red light nor of the position of the light source (i.e. light from the top and then light from the bottom and the other way around). At the beginning of each experimental run and after their adaptation in the dark phase, the larvae were distributed just the same as after the experimental run in the darkness, i.e. their initial start position corresponded to their position in darkness depicted in Figures 1, 2, and 3, middle column of diagrams, respectively. When the light was turned on, larvae always responded by swimming actively. The larvae reacted directly to the change of the experimental light regime and the adaptation time of 30 minutes stabilized the distribution.

The four factorial analysis of variance with the independent factors light, water layer, larval age and larval stage showed significant effects (p = 0.012) on vertical distribution (Table 1). The multi-comparison test showed the following results:

Table 1 The vertical distribution of lobster larvae (Zoea I, II, and III) of *Homarus gammarus* was observed in a water column (0-100 cm) under three different types of illumination (light from the top of the cylinder, in the darkness, light from the bottom). Four replicate experiments were run with four larvae each. *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					
Stage (*S*)	2	6.1	3.0	0.024	*0.9767*
Light/Dark (*LD*)	2	0.9	0.4	0.003	*0.9966*
Ages (*A*)	3	1.3	0.4	0.003	*0.9997*
Water layers (*W*)	9	40,7326.8	45,258.5	351.886	*<0.0001*
First-order interactions					
LD x S	4	4.3	1.1	0.008	*0.9999*
A x LD	6	2.6	0.4	0.003	*1.0000*
A x S	6	7.8	1.3	0.010	*1.0000*
S x W	18	10,002.6	555.7	4.321	*<0.0001*
LD x W	18	102,117.2	5,673.2	44.109	*<0.0001*
A x W	27	10,549.9	390.7	3.038	*<0.0001*
Second-order interactions					
A x LD x S	12	23.4	2.0	0.015	*1.0000*
LD x S x W	36	21,393.2	594.3	4.620	*<0.0001*
A x LD x W	54	14,303.0	264.9	2.059	*<0.0001*
A x S x W	54	16,407.1	303.8	2.362	*<0.0001*
Third-order interactions					
A x LD x S x W	108	18,822.0	174.3	1.355	*0.0120*

Zoea I (Figure 1)

Light from top: The newly hatched larvae were significantly (p < 0.0001) more often distributed in the uppermost 10 cm of the water column (90-100 cm) (62 ± 32 %) than below (0-90 cm). The older the larvae, the more larvae were found in the lower parts of the cylinder (p < 0.05). Darkness: Newly hatched larvae were evenly distributed in the upper half of the cylinder (p = 0.0749). However, older larvae were more often found in the lower parts of the cylinder (p < 0.0001) and more than half of the larvae (50-63 %) were distributed near the bottom. Light from bottom: Almost all larvae (95 ± 3 %) stayed near the bottom (p < 0.0001).
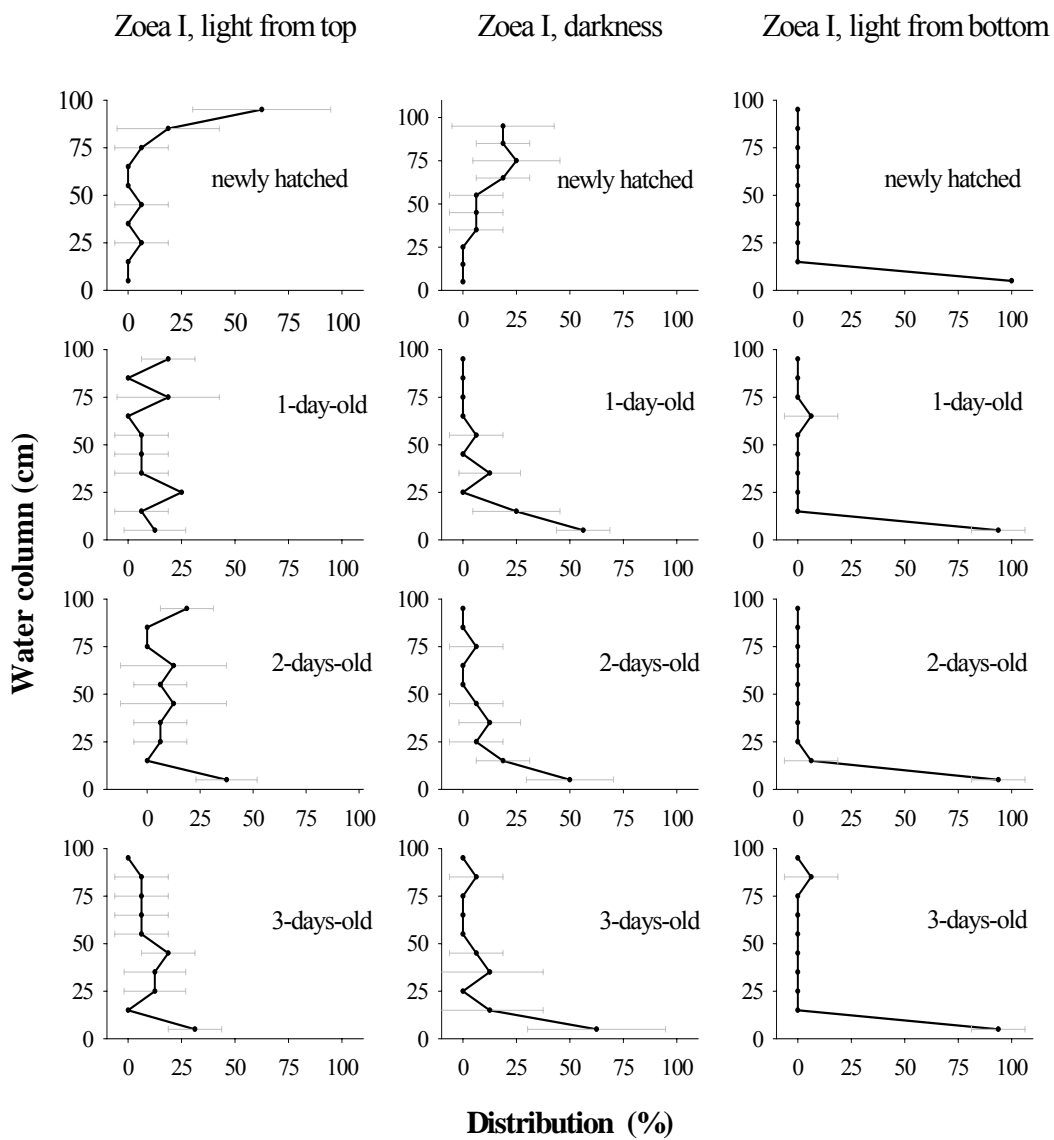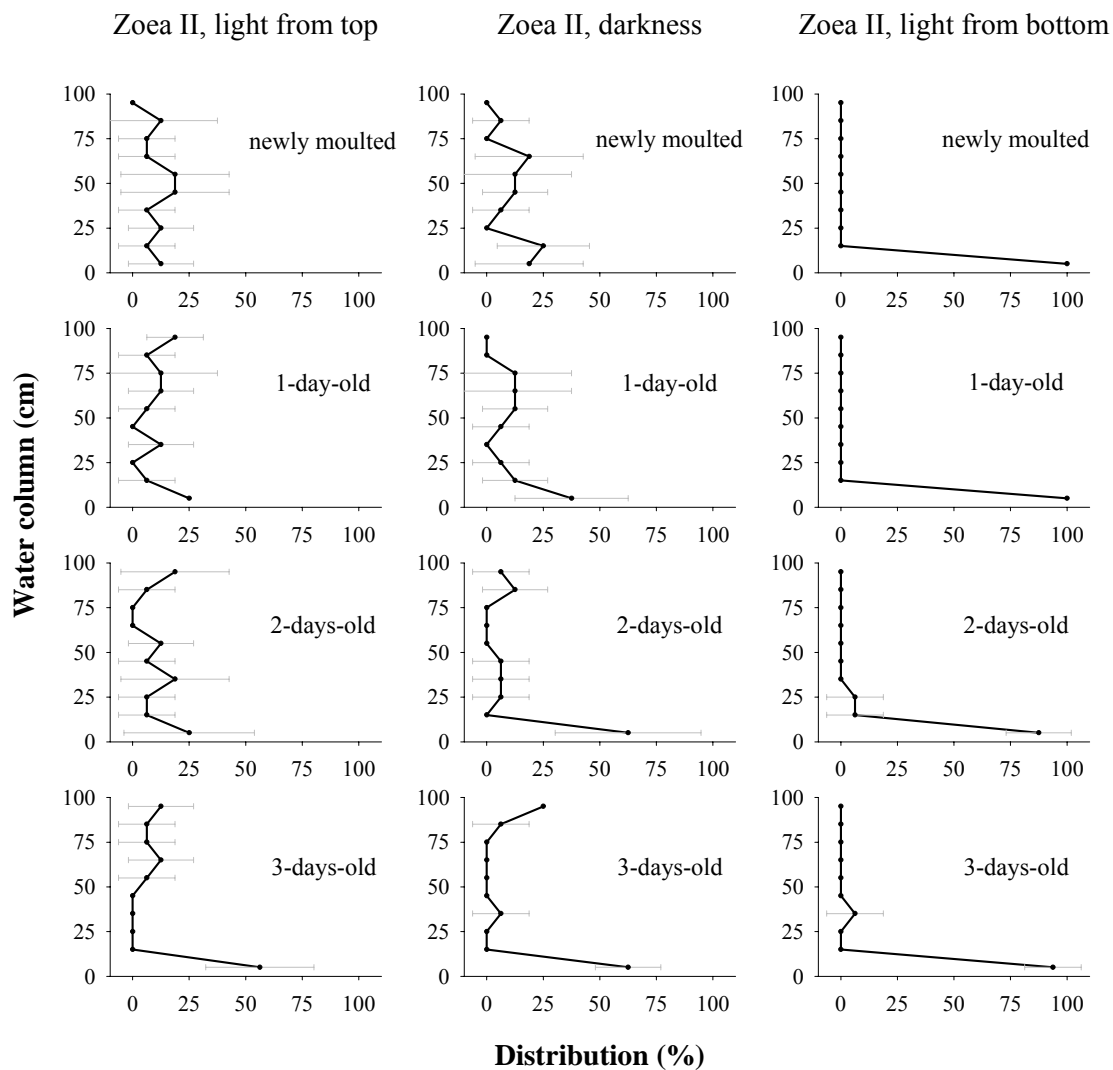

Figure 1 Vertical distribution (%, mean ± SD) of Zoea-I larvae (*Homarus gammarus*) of different age in a water column (height: 100 cm, diameter: 20 cm) at different types of illumination (light from the top, darkness, light from the bottom).

Zoea II (Figure 2)

Light from top: Newly moulted as well as one- and two-days-old Zoea II stages were evenly distributed in the water column. However, half of the three-days-old larvae (50 ± 27 %) were distributed near the bottom ($p < 0.0001$). Darkness: Newly moulted and one-day-old larvae were evenly distributed in the water column ($p > 0.05$). However, more than half of the two- and three-days-old larvae (63 ± 23 %) were situated near the bottom ($p < 0.0001$). Light from bottom: Independent of age, almost all larvae (94 ± 6%) were distributed near the bottom ($p < 0.0001$).
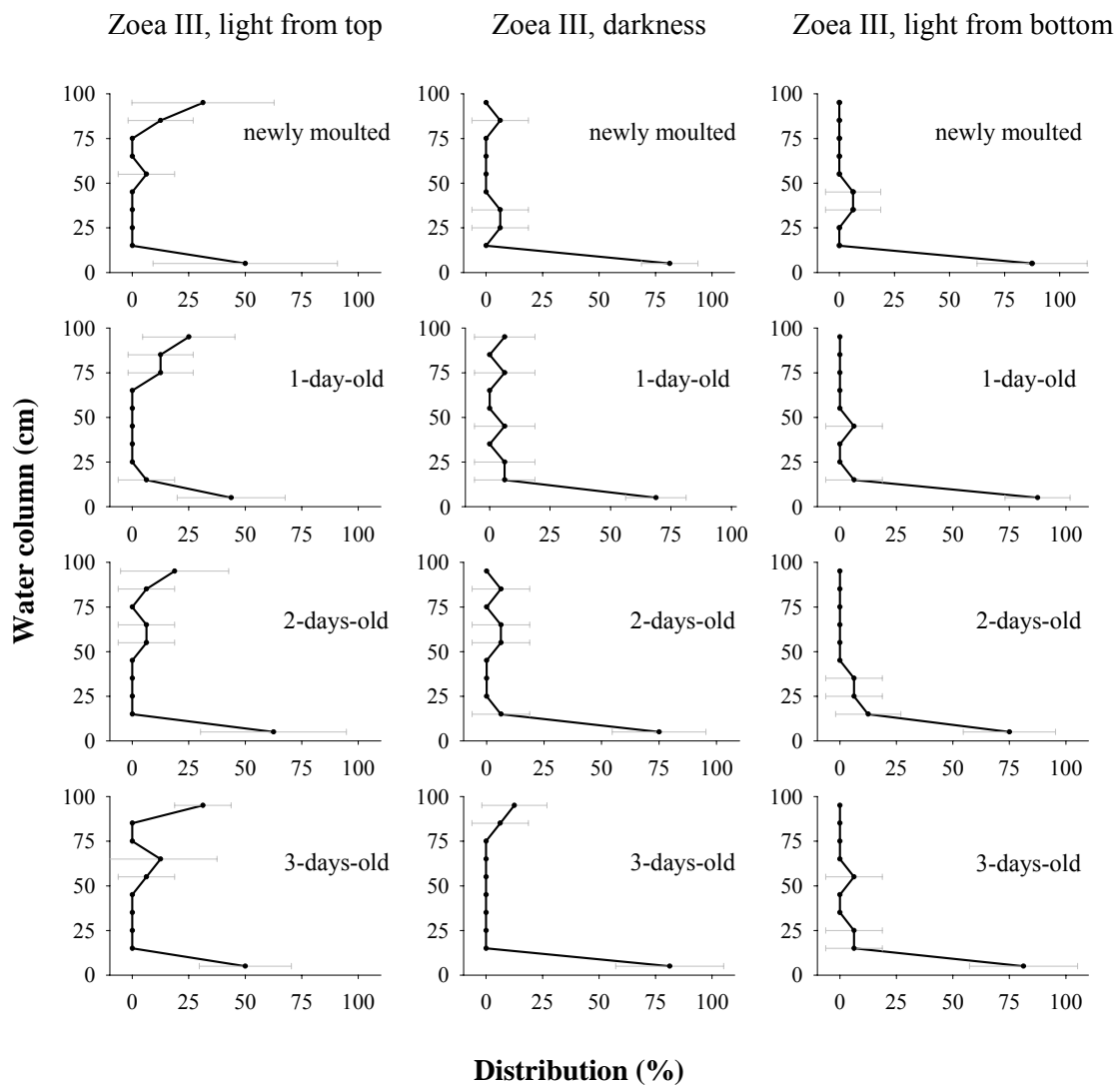

Figure 2 Vertical distribution (%, mean ± SD) of Zoea-II larvae (*Homarus gammarus*) of different age in a water column (height: 100 cm, diameter: 20 cm) at three different types of illumination (light from the top, darkness, light from the bottom).

Zoea III (Figure 3)

In this stage, the distribution pattern was independent of larval age (newly moulted, one-, two- and three-days-old Zoea III). Light from top: A quarter of the larvae (27 ± 21 %) were always distributed in the uppermost layer (90-100 cm) of the cylinder, and about half the larvae (52 ± 28 %) stayed near the bottom ($p < 0.0001$). Darkness: Almost all larvae (84 ± 16 %) were distributed near the bottom ($p < 0.0001$). Light from bottom: Almost all larvae (82 ± 18 %) were found near the bottom ($p < 0.0001$).

Figure 3 Vertical distribution (%, mean ± SD) of Zoea-III larvae (*Homarus gammarus*) of different age in a water column (height: 100 cm, diameter: 20 cm) at three different types of illumination (light from the top, darkness, light from the bottom).

Sinking rate

The sinking rate of Zoea stage I (1.7 ± 0.1 cm·s^{-1}) was significantly different (ANOVA, $p < 0.001$) from those of Zoea II and III (2.2 ± 0.1 cm·s^{-1} and 2.3 ± 0.2 cm·s^{-1}) and there was no difference between stage II and III larvae.

Vertical swimming speed

Newly hatched larvae (Zoea I) swam directly downwards along the 100 cm to the light source with a measured velocity of 4.6 ± 0.5 cm·s^{-1}. The sinking rates of Zoea stage I were deducted from the vertical swimming speed measured and the swimming velocities of the larvae were averaged at 2.9 ± 0.5 cm·s^{-1}.

Rheotaxis and horizontal swimming ability

All larvae attempted to swim against the flow and none could maintain its position against the current (3.2 ± 0.3 cm·s^{-1}). However, the larvae turned immediately frontally to the oncoming current. The horizontal swimming ability of all larvae increased with stage from 0.7 ± 1.0 cm·s^{-1} (Zoea I) to about 1.5 ± 0.9 cm·s^{-1} (Zoea II) and 2.2 ± 0.7 cm·s^{-1} (Zoea III) (Table 2). The difference between all larval stages (Zoea I, II, and III) was statistically significant ($p < 0.001$).

Table 2 The drift velocity (cm·s^{-1}, mean $\pm$ SD) of drift bodies and of the larvae stages (Zoea I, II, and III) of *Homarus gammarus* were measured in a horizontal flow channel. The horizontal swimming abilities were calculated as the difference of current velocity and drift velocity of larvae.

	N	Drift velocity (cm·s^{-1})	Swimming ability (cm·s^{-1})
drift body	16	3.2 ± 0.3 [a]	
Zoea I	32	2.5 ± 1.0 [b]	0.7 ± 1.0 [a]
Zoea II	35	1.7 ± 0.9 [c]	1.5 ± 0.9 [b]
Zoea III	40	1.0 ± 0.8 [d]	2.2 ± 0.7 [c]

Different superscripts denote statistically significant differences (one-way ANOVA and paired comparisons post hoc test ($p = 0.05$)). N = Number of measured lobsters.

In the water channel, only newly hatched larvae swam mainly near the surface. The percentage of larvae swimming near the bottom increased with stage (linear regression: $r^2 = 0.0259$, $p = 0.0259$) (Figure 4). Larvae of stage I stayed at 7 % near the bottom, those of stages II and III at 40 % and 78 %, respectively.
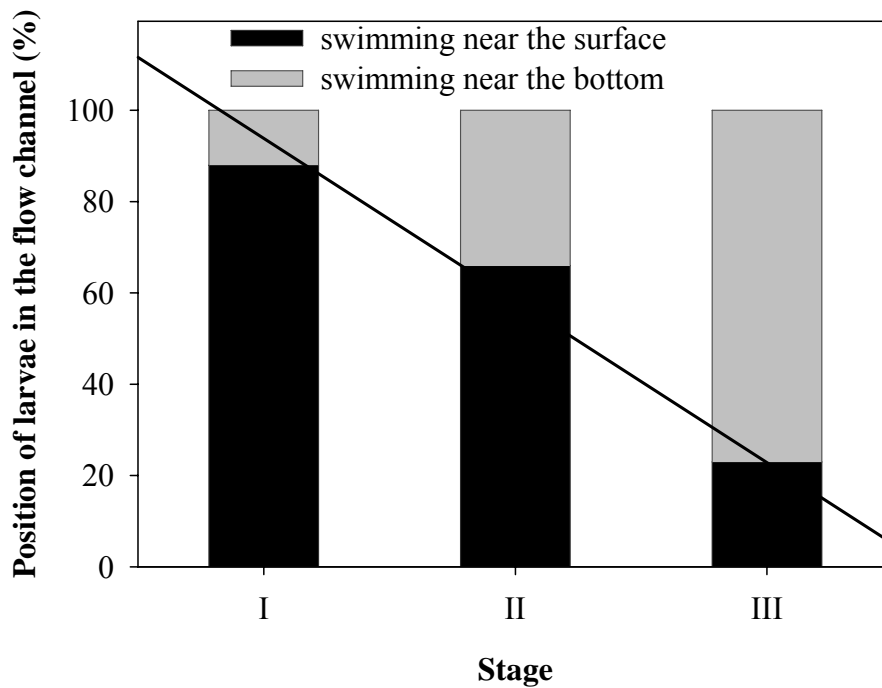

Figure 4 Percentage position of larvae (swimming near the surface or the bottom) (Zoea I, II, and III) of *Homarus gammarus* during passage through a flow channel. Fitted line of linear regression: $y = -35.5x + 129$, $r^2 = 0.9983$, $p = 0.0259$.

DISCUSSION

Phototaxis and vertical distribution

In the present study, newly hatched lobster larvae showed a marked positive phototaxis, starting already at the lowest light intensity of 0.6 μmol·m^{-2}·s^{-1}. The experimental light intensities were within the range measured in Helgoland waters (in July: 143 μmol·m^{-2}·s^{-1} at 2 m depth and decreases to 0.7 μmol·m^{-2}·s^{-1} at 15 m depth (Lüning and Dring, 1979)). Furthermore, the visual pigment absorption maxima of 27 species of benthic crustaceans from semi-terrestrial, estuarine and coastal areas have values ranging from 483 to 516 nm (Forward et al., 1988). Previous studies have shown that crustacean larvae of *Rhithropanopeus harrisii* (Gould, 1841) responded positively to light intensities between 0.0006 and 1 W m^{-2}, measured at 500 nm (i.e. 0.003 to 4 μmol·m^{-2}·s^{-1}) (Forward, 1974). We used light at abroad range of 380-750 nm wavelengths. Accordingly, the experimental light must have been well discernible by the lobster larvae.

Under laboratory conditions newly hatched larvae always stayed at the surface and swam directly towards any light source in accordance with observations of Neil et al. (1976), Dunn and Shelton (1983) and Watt and Arthur (1996) who reported that larvae after hatching always swim towards the sea surface. In our experiments the newly hatched lobster larvae reacted immediately to light - irrespective of the direction - even if it came from the bottom and responded with a downward vertical swimming speed of about 4-5 cm·s^{-1} (including the sinking rate of 1.7 cm·s^{-1}). The same positive phototatic reaction was observed in the first larval stage of the American lobster, *Homarus americanus* (Hadley, 1908). Furthermore, other crustacean larvae respond equally in their first Zoea stage, e.g. *Cancer pagurus* (Linnaeus, 1758)*, Carcinus maenas, Macropipus* spp. (Sulkin, 1984), and the first larval stage of *Galathea strigosa* (Linnaeus, 1761) and *Galathea dispersa* (Bate, 1859) reached maximum swimming speeds of approximately 2 cm·s^{-1} (Foxon, 1934).

In the field, Dunn and Shelton (1983) and Nichols (1984) found newly hatched larvae of the European lobster always at the surface. In the present study, we found a marked positive response to light only in newly hatched Zoea I larvae, which swam straight towards the light source whether this was placed on the top or at the bottom. With progressing larval age and stage this positive response to light rapidly disappeared, and the larvae were oriented predominantly to the deeper layers irrespective of the type of

illumination (light from the top, light from the bottom, darkness). Additionally, the low sinking rate of Zoea I facilitates their positive phototactic behaviour before they tend to swim to the deeper layers in the later stages. Moreover, Hadley (1908) found that phototactic responses of larvae of *Homarus americanus* changed both within and between each stage. He reported that larvae in early second- and third-stages are negatively phototactic, but again respond positively to light shortly (~ one day) before moulting. A shift from positive to negative phototaxis may explain behavioural changes in many pelagic larvae (Forward, 1974; Shirley and Shirley, 1988), but apparently this does not apply to the larvae of *Homarus gammarus*. With decreasing positive response to light, larvae accumulated near the bottom even if the light came from just this direction. Ennis (1973) reported that the depth regulation of the first three Zoea stages responded to water pressure changes and that overhead light reduced the reaction time at low water pressure, i.e. at shallow depths.

From an ecological point of view, the positive response to light of the first larval stage may be a means to promote animal dispersal at the rocky bottom around the island of Helgoland, and the early and abrupt change in larval behaviour reduces the threat of drifting away from this suited environment.

Current and swimming ability

Our experiments showed that with successive larval stages the ability of larvae increased to swim in the current, resulting from an increase in horizontal swimming ability from 0.7 cm·s^{-1} (Zoae I) to 1.5 cm·s^{-1} (Zoea II) and ultimately to 2.2 cm·s^{-1} (Zoea III). This is the same order of magnitude as in other decapod crustacean larvae which show swimming speeds ranging from 0.1 to 3.3 cm·s^{-1}. Equally, the locomotion varies with the age of the larva (see Chia et al., 1984). In our experiment the percentage of larvae swimming near the bottom increased with stage during the drift through the current channel. This change of locomotion abilities during larval development of lobster larvae facilitates the active movement in currents, i.e. positive rheotactic behaviour, and may help to prevent larvae to be swept downstream by the current in the later stages. However, Ennis (1986) observed that larvae of *H. americanus* can hold their position only for few minutes in a current of 2 cm·s^{-1} and the response is relatively weak to swim against the current but increases in Stage IV.

Larval recruitment around the island of Helgoland

The habitat of the Helgoland lobster population is limited at only about 33 km² and is isolated from other hard-bottom areas, so that the exchange with neighbouring populations is low (Ulrich et al., 2001). Nevertheless, the Helgoland habitat is exposed to strong tidal currents with a velocity of up to 102 cm·s^{-1} (2 nm·h^{-1}). The tides shift the water mass during a half tide at about 5-10 nm in a tidal ellipse around the island and the resulting residual current is low with a mean of 10 cm·s^{-1} (0.2 nm·h^{-1}) (Hickel, 1972).

Despite of the inherent difficulties associated with any transfer of behavioural data from the laboratory to the field, the present results may give an idea how the life history of *H. gammarus* allows for the existence of a self-sustaining lobster stock at Helgoland. During the early phase of the Zoea I stage, a strong positive phototaxis results in a preference of the larvae for the uppermost water layers. Here, the risk of being swept away is highest. In summer, the development of Zoea I larvae takes about 4 days (Schmalenbach and Franke, in prep.), roughly corresponding to the critical drift phase. However, the water masses circle the island several times (Hickel, 1972) and therefore the probability may be high that the larvae remain above the rocky base of the island of Helgoland. At a small scale, a current induced change of local habitat is facilitated which may be seen as an ecological advantage. However, the older larvae tend to hold their position near the bottom where current speeds are considerably lower and may thus be able to remain in the favoured habitat. In contrast, Scarratt (1964) suggested that surface drift carries the larvae of *H. americanus* from parent stock to possible areas of settlement. This may be seen as an advantage in a more homogeneous environment.

Generally, recruitment of the lobster population is dependent on stock-size, density of ovigerous females, survival and development time of larvae, and fishery mortality. At Helgoland, legislative regulations may have prevented a complete extinction of the local population. These regulations include the establishment of a special protection area, an agreement on a minimum size (11 cm carapace length, including rostrum) for landed lobsters, a ban on landings of ovigerous females, and a closed season of 1.5 month in July-August (Ministerium für Landwirtschaft, 1981, 1999). We suspect though that these measures did not result in the population's recovery and that it still remains below a critical threshold which is necessary for the population to recover at a large scale.

The knowledge about the positioning of larvae around the island of Helgoland helps to understand the life-history of the Helgoland lobster population and may be helpful in assessing the development of a future stock enhancement programme. Harding et al. (2005) used field observations of the lobster larval distribution in the Gulf of Maine for modelling larval drift to estimate probable source areas for settling of stage IV post-larvae. Furthermore, there are different lobster larval transport models which combine oceanographic processes and behavioural traits (Katz et al., 1994; Incze and Naimie, 2000; Annis et al., 2007). The life history data gained will be used to parameterize and optimize a set of models. These can be used to assess the status and to forecast the recruitment and development of the local lobster population allowing further managerial measures in order to establish a sustainable fishery at Helgoland and other areas of lobster occurrence.

ACKNOWLEDGEMENTS

REFERENCES

Anger, K., Harms, J., 1994. The Helgoland lobster: a disappearing island population. The lobster newsletter 7, 11–12.

Annis, E.R., Incze, L.S., Wolff, N., Steneck, R.S., 2007. Estimates of in situ larval development time for the lobster, *Homarus americanus*. Journal of Crustacean biology 27, 454-462.

Anonymous, 1980-2007. Die kleine Hochsee- und Küstenfischerei. Jahresbericht des Amtes für ländliche Räume Kiel –Abt. Fischerei, In Das Fischerblatt. Edited by Amt für ländliche Räume Kiel, Ohle Druck.

Bannister, R.C.A., 1986. Assessment and population dynamics of commercially exploited shellfish in England and Wales. In: North Pacific Workshop on Stock Assessment and Management of Invertebrates. Edited by G.S. Jamieson and N. Bourne. Canadian Special Publication of Fisheries and Aquatic Science 92, 182-194.

Browne, R.M., Mercer, J.P., Duncan, M.J., 2001. An historical overview of the Republic of Ireland's lobster (*Homarus gammarus* Linnaeus) fishery, with reference to European and North American (*Homarus americanus* Milne Edwards) lobster landings. Hydrobiologia 465, 49-62.

Chia, F.-S., Buckland-Nicks, J., Young, C.M., 1984. Locomotion of marine invertebrate larvae: a review. Canadian Journal of Zoology 62, 1205-1222.

Dow, R.L., 1980. The clawed lobster fisheries. In: The biology and management of lobsters. Volume II Ecology and management. Edited by J.S. Cobb and B.F. Phillips. Academic Press, New York, 265-316.

Dunn, J., Shelton, R.G.J., 1983. Observations on lobster, *Homarus gammarus* (L.), larvae held in a Loch Ewe enclosure. ICES CM 1983/L, 30, 1-6.

Ennis, G.P., 1973. Endogenous rhythmicity associated with larval hatching in the lobster *Homarus gammarus*. Journal of the Marine Biological Association of the United Kingdom 53, 531-538.

Ennis, G.P., 1983. The effect of wind direction on the abundance and distribution of decapod crustacean larvae in a Newfoundland nearshore area. Canadian Technical Report of Fisheries and Aquatic Sciences 1138, 19 pp.

Ennis, G.P., 1986. Swimming ability of larval American lobsters, *Homarus americanus*, in flowing water. Canadian Journal of Fisheries and Aquatic Sciences 43, 2177-2183.

Ennis, G.P., 1995. Larval and postlarval ecology. In: Biology of the Lobster *Homarus americanus"*. Edited by J.R. Factor. Academic Press, 23-46.

Fishery Statistics, 1950-2006. Eurostat database of European Commission. www.epp.eurostat.ec.europa.eu

Forward, R.B. Jr., 1989. Depth regulation of larval marine decapod crustaceans: test of a hypothesis. Marine Biology 102, 195-201.

Forward, R.B. Jr., Cronin, T.W., Douglass, J.K., 1988. The visual pigments of crabs. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 162, 479-490.

Foxon, G.E.H., 1934. Notes on the swimming methods and habits of certain crustacean larvae. Journal of the Marine Biological Association of the UK 19, 829-849.

Goemann, O., 1990. "Echt" Helgoländer Hummer. Kohlrenken Verlag Oldenburg, Oldenburg, 82 pp.

Greve, W., Reiners, F., Nast, J., Hoffmann, S., 2004. Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. Helgoland Marine Research 58, 274-288.

Hadley, P.B., 1908. The behaviour of the larval and adolescent stages of the American lobster (*Homarus americanus*). Journal of Comparative Neurology 18, 199-303.

Harding, G.C., Drinkwater, K.F., Vass, W.P., 1983. Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Dulf of Maine: a new synthesis. Canadian Journal of Fisheries and Aquatic Science 40, 168-184.

Harding, G.C., Pringle, J.D., Vass, W.P., Pearre, Jr. S., Smith, S.J., 1987. Vertical distribution and daily movements of larval lobsters *Homarus americanus* over Browns Bank, Nova Scotia. Marine Ecology Progress Series 41, 29-41.

Harding, G.C., Drinkwater, K.F., Hannah, C.G., Pringle, J.D., Prena, J., Loder, J.W., Pearre, J.R. S., Vass, W.P., 2005. Larval lobster (*Homarus americanus*) distribution and drift in the vicinity of the Gulf of Maine offshore banks and their probable origins. Fisheries Oceanography 14, 112-137.

Harms, J., Schilling, U., Goemann, O., 1995. Der "Helgoländer Hummer". Natur und Museum 125, 33-40.

Hickel, W., 1972. Kurzzeitige Veränderungen hydrographischer Faktoren und der Sestonkomponenten in driftenden Wassermassen in der Helgoländer Bucht. Helgoländer Wissenschaftliche Meeresuntersuchungen 23, 383-392.

Hudon, C., Fradette, P., 1993. Wind-induced advection of larval decapods into Baie de Laisance (Îles de la Madeleine, Québec). Canadian Journal of Fisheries and Aquatic Sciences 50, 1422-1434.

Incze, L.S., Naimie, C.E., 2000. Modelling the transport of lobster (*Homarus americanus*) larvae and postlarvae in the Gulf of Maine. Fisheries Oceanography 9, 99-113.

Jacoby, C.A., 1982. Behavioural responses of the larvae of *Cancer magister* Dana (1852) to light, pressure, and gravity. Marine Behaviour and Physiology 8, 267-283.

Johnson, M.W., 1960. On the dispersal of lobster larvae into the East Pacific barrier (Decapoda, Palinuridea). Fishery Bulletin 72, 639-647.

Katz, C.H., Cobb, J.S., Spaulding, M., 1994. Larval behavior, hydrodynamic transport, and potential offshore-to-inshore recruitment in the American lobster *Homarus americanus*. Marine Ecology Progress Series 103, 265-273.

Klimpel, J., 1965. Die neuzeitliche Entwicklung der Inselgemeinde Helgoland unter besonderer Berücksichtigung des Fremdenverkehrs. Verlagsanstalt Konstanz, Konstanz.

Lüning, K., Dring, M.J., 1979. Continuous underwater light measurement near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. Helgoländer Wissenschaftliche Meeresuntersuchungen 32, 403-424.

Makarov, RR., 1969. Transport and distribution of decapod larvae in the plankton of the western Kamchatka shelf. Oceanology 9, 251-259.

Mileikovsky, S.A., 1973. Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. Marine Biology 23, 11-17.

Minchin, D., 1984. Larvae of the lobster *Homarus gammarus* (L.) from the plankton of Lough Hyne (Ine), Co. Cork. Irish Naturalists' Journal 21, 334-336.

Ministerium für Landwirtschaft, Umwelt und ländliche Räume 1981, 1999. Landesverordnung über die Ausübung der Fischerei in den Küstengewässeren (Schleswig-Holsteinische Küstenverordnung – Küfo), Germany.

Neil, D.M., MacMillan, D.L., Robertson, R.M., Laverack, M.S., 1976. The structure and function of thoracic exopodites in the larvae of the lobster *Homarus gammarus* (L.).

Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences 274, 53-68.

Nichols, J.H., 1984. The occurrence of lobster larvae (*Homarus gammarus* L.) in Galway Bay. Irish Naturalists' Journal 21, 275-278.

Nichols, J.H., Lawton, P., 1978. The occurrence of the larval stages of the lobster *Homarus gammarus*, (Linnaeus, 1758) off the northeast coast of England in 1976. Journal du Conseil - Conseil International pour l'Exploration de la Mer 38, 234-243.

Sandifer, P.A., 1973. Distribution and abundance of decapod crustacean larvae in the York River Estuary and adjacent lower Cheaspeake Bay Virginia, 1968-1969. Cheaspeake Science 14, 235-257.

Scarratt, D.J., 1964. Abundance and distribution of lobster larvae (*Homarus americanus*) in Northumberland Strait. Journal of the Fisheries Research Board of Canada 21, 661-680.

Shirley, S.M., Shirley, T.C., 1988. Behavior of red king crab larvae: phototaxis, geotaxis and rheotaxis. Marine Behaviour and Physiology 13, 369-388.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. The principles and practice of statistics in biological research, 3rd edn. WH Freeman and Co., New York, 887 pp.

Sulkin, S.D., 1984. Behavioral basis of depth regulation in the larvae of branchyuran crabs. Marine Ecology Progress Series 15, 181-205.

Templeman, W., 1937. Habits and distribution of larval lobsters (*Homarus americanus*). Journal of the Biological Board of Canada 3, 343-347.

Tully, O., Ó Céidigh, P., 1987. The seasonal and diel distribution of lobster larvae (*Homarus gammarus* (Linnaeus)) in the neuston of Galway Bay. Journal du Conseil - Conseil International pour l'Exploration de la Mer 44, 5-9.

Tully, O., Bell, M., O'Leary, A., McCarthy, A., O'Donovan, V., Nee, D., 2006. The lobster (*Homarus gammarus* L.) fishery: Analysis of the resource in 2004/2005. Fisheries Resource Series 5.

Ulrich, I., Müller, J., Schütt, C., Buchholz, F. 2001. A study of population genetics in the European lobster, *Homarus gammarus* (Decapoda, Nephropidae). Crustaceana 74, 825-837.

van der Meeren, G.I., Tveite, S., 1998. Fishery and management of the lobster (*Homarus gammarus*) in Norway. In: The European lobster *Homarus gammarus* (L.): Proceedings from the Seminar at Kvitsøy 1995. Edited by G.I. van der Meeren and O. Soldal. Fisken og havet 1998, 13, 72-76.

Walter, I., Schmidt, M., Buchholz, F., 2008. Der Einfluss von Erdöl auf das Verhalten von Hummern. Effekte auf Nahrungssuche und Aggression. VDM Verlag Dr. Müller Aktiengesellschaft & Co. KG, Saarbruecken.

Watt, L., Arthur, G., 1996. The improvement of the Shetland lobster fishery through stock enhancement-1. North Atlantic Fisheries College. Fisheries development note 2, 4 pp.

Weiss, H.M., Lozano-Alvarez, E., Briones-Fourzan, P., Negrete-Soto, F., 2006. Using red light with fixed-site video cameras to study the behavior of the spiny lobster, *Panulirus argus*, and associated animals at night and inside their shelters. Marine Technology Society Journal 40, 86-95.

MANUSCRIPT IV

IMPROVEMENT OF REARING CONDITIONS FOR JUVENILE LOBSTERS (*HOMARUS GAMMARUS*) BY CO-CULTURING WITH JUVENILE ISOPODS (*IDOTEA EMARGINATA*)

Isabel Schmalenbach, Friedrich Buchholz, Heinz-Dieter Franke, Reinhard Saborowski

Biologische Anstalt Helgoland, Foundation Alfred Wegener Institute for Polar and Marine Research, 27498 Helgoland, Germany

ABSTRACT

Growth conditions of the juvenile lobsters, *Homarus gammarus*, were optimized in view of a restocking project of the lobster population at Helgoland (German Bight, North Sea) aimed to produce more than ten thousand juvenile lobsters per year. Growth and survival rates of juvenile lobsters depend on diet, temperature and water quality. In the present study, diet at optimum temperature was considered, but special emphasis was placed on the optimization of cleaning and feeding methods from both an economical and ecological point of view. Six dietary treatments of juvenile lobsters (each n = 99) were tested in individual compartments in a semi-closed re-circulation system at around 20 °C. Lobsters were fed with combinations of two diets, newly hatched Artemia sp. nauplii and minced crabs Cancer pagurus (whole carcasses), every two or four days until a carapace length of 10 mm was reached. During the experiment (max. 105 d), juvenile isopods, *Idotea emarginata*, were constantly present in the lobster boxes. More frequent feeding significantly growth rates of the juvenile lobsters while different feeding combinations had no effect. The highest growth rate (0.091 ± 0.02 mm·CL·day^{-1}) was at a feeding frequency of every two days for each diet. At this rate the carapace length of 10 mm was reached in 68-71 days. The survival rate of the juvenile lobsters ranged from 90-97 %. The diet consisting of *C. pagurus* was most cost-efficient and was obtained as discards from the crab fishery at Helgoland. The co-culture of juvenile lobsters with juvenile isopods *I. emarginata* as "cleaning organisms" was ideally suited for the rearing of lobsters and reduced the maintenance time by 50 %. The isopods also served as supplementary diet.

Keywords: Co-culture; *Homarus gammarus*; *Idotea emarginata*; Rearing conditions; Diet; Growth; Survival.

INTRODUCTION

European lobsters (*Homarus gammarus* Linnaeus, 1758) form valuable fisheries along the coastline of the northeast Atlantic. In 2006, the annual European landings from the major lobster exporting countries, i.e. UK, Norway, Greece, Ireland and France reached approximately 3,400 metric tons (t) with a value of 45 million Euros (Fishery Statistics, 1999-2006). Along the German coast, a sustainable lobster population is only present at the rocky subtidal of the island of Helgoland (North Sea, German Bight), where the lobster fishery was important during the 1920s and 1930s with catches of up to 80,000 animals (38 t) per year (Klimpel, 1965). Since the 1960s, the catch rates decreased drastically and reached a minimum of a few hundred lobsters per year in the 1980s (Goemann, 1990; Anonymous, 1980-2008). The reasons for the collapse of the Helgoland lobster population may include the destruction of the habitat by the bombing of the island during and after the second world-war, extensive fishing pressure in the 1950s and 1960s, pollution of the North Sea waters by oil spills, chemicals, and industrial wastes, and interspecific competition for food and shelter with the crabs, *Cancer pagurus* (Linnaeus, 1758) (Klimpel, 1965; Anger and Harms, 1994; Harms et al., 1995).

In order to provide specimens for biological research, a lobster rearing facility was established in 1997 at the Marine Station at Helgoland. Berried females were provided by local fishermen and kept in aquaria until the larvae hatched. The larvae were raised to post-larvae and juveniles. Based on the experience in lobster rearing, a restocking programme was initiated to enhance the natural lobster population around Helgoland with laboratory raised juveniles. Within a 5-year programme it is anticipated to raise and release more than ten thousand juveniles per year. The local rearing capacities have to be extended accordingly.

Since the maintenance of lobsters is time and cost intensive, the present work was aimed to optimize the breeding conditions for juveniles to reach maximum productivity at lowest cost. A principal goal of our study was to utilize local resources. In this respect discards of the crab fishery around the island of Helgoland provide a suitable and cheap food for the juvenile lobsters. Preliminary feeding trials with minced crab meat showed good acceptance and satisfactory growth rates. However, remains of the crab meat frequently blocked the water circulation system and drastically increased the effort for cleaning and maintenance of the rearing facilities and sometimes caused complete loss of the lobster

stock. Despite the initial failure, crab meat from *C. pagurus* seems to be a suitable, abundant, and inexpensive feed for lobsters at Helgoland. Therefore, we focussed our attempts on improving the rearing systems and rearing conditions to minimise the adverse effects when feeding minced crab meat. In order to increase the survival rates we tried to reduce food waste and other debris by co-culturing juvenile lobsters with live juvenile isopods, *Idotea emarginata* (Fabricius, 1793). These isopods are known as debris feeders and thus appeared useful to keep the rearing system clean and thus to maintain water quality.

MATERIALS AND METHODS

The experiments were carried out in summer 2006 at the Marine Station at Helgoland. The feeding experiments were run at 20.5 ± 0.6 °C (at ca. 33 psu) and maintained under the natural light/dark-cycle.

Origin of animals

The post-larval lobsters used in the experiments were raised in the laboratory as reported by Ulrich (1998). The larvae were a mix from the eggs of eight different ovigerous females. The females were captured by local fishermen from the rocky subtidal at Helgoland (North Sea, 54°11.3'N, 7°54.0'E). The newly hatched larvae were reared in specific semi-flow through tanks (Hughes et al., 1974) in ambient seawater (17-19 °C). The larvae were fed daily with newly hatched *Artemia* sp. nauplii and every other day with minced crabs (whole carcasses of *Cancer pagurus*). The larvae reached the post-larval stage (stage IV) approximately 17 days after hatching. After moulting to post-larvae the specimens were separated in 40 ml glass containers. Every day, the water was exchanged and the post-larvae were fed with newly hatched *Artemia* sp. nauplii. After five days, the carapace of the post-larval lobsters hardened and the initial weights and the carapace lengths (CL-R = without rostrum) were determined.

The culture system

The semi-closed recirculation system was developed and built in the Marine Station of Helgoland (Figure 1). It consisted of three tanks (34 x 95 x 150 cm). In each tank a rectangular polyvinylchloride frame (140 x 90 x 9 cm) was adjusted which was partitioned in 198 single compartments (9 x 7 cm, height of water level: 7 cm). The bottom of the frame was made of nylon gauze (300 μm mesh size). The rectangular frames were covered with sprinklers and a light shield. The flow rate of fresh seawater into the semi-closed recirculation system was at 4-5 l·min^{-1}. This system allowed for separation of animals and provided a constant circulation of sea water. The water quality was not monitored within the compartments but within the seawater supply system of the institute. The flow rate through each cubicle allowed for complete water exchange every 15 min. Therefore, the juveniles received the best possible water quality close to natural conditions. The juvenile lobsters were maintained at $20.5 \pm 0.6\,°C$. Each post-larva was placed in a separate compartment. A short plastic tube (1.5 x 3.5 cm) provided shelter.
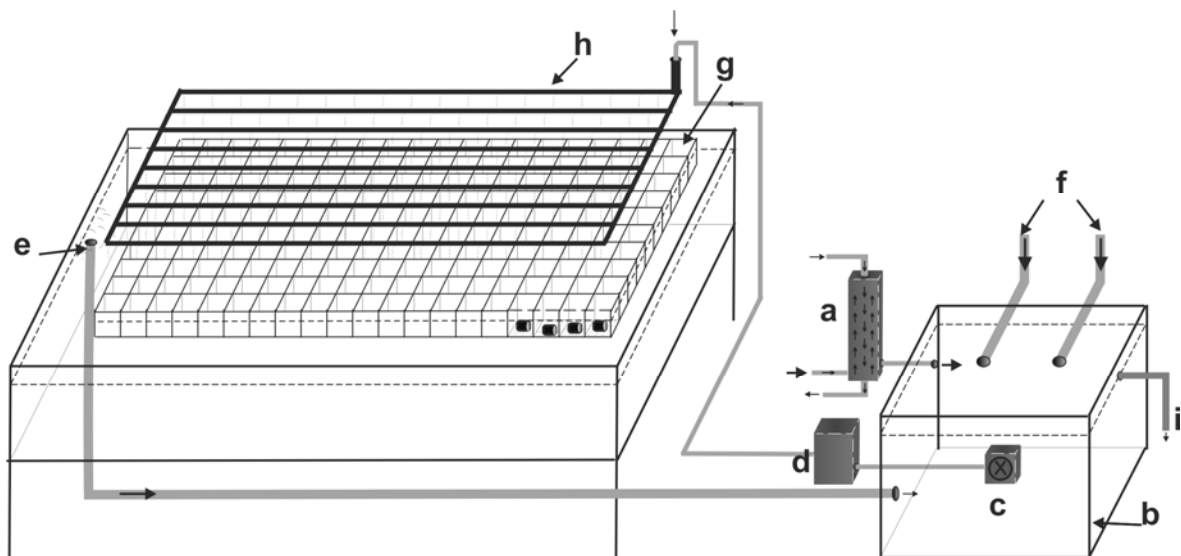

Figure 1 Semi-closed recirculation system used for the culture of juvenile lobsters. The figure shows only one of three culture systems which were run in parallel. Key: (a) continuous flow heater of fresh sea water (gravel filter), flow rate 4.8 l·min^{-1}, sea water at 20 °C and 33 psu; (b) tank reservoir, volume 170 l; (c) centrifugal pump, capacity 1900 l·h^{-1}; flow rate 8.8 l·min^{-1} (d) wadding filter, volume 18 l; (e) overflow, (f) overflow of two additional culture systems; (g) PVC-frame (140 x 90 x 90 cm) with 198 compartments (9 x 7 x 9 cm, volume 440 ml, gauze 300 μm mesh size) and shelters (approx. 1.5 x 3.5 cm); (h) sprinkling; (i) discharge.

The diets

The principal diets offered to the post-larvae were live *Artemia* sp. nauplii and minced crab. Juvenile isopods, *Idotea emarginata*, were supplemented. They served as an additional food source and kept the rearing system clear of accumulated debris. Newly hatched *Artemia* sp. nauplii from cysts (Sanders Brine Shrimp Company, USA) were reared in a temperature controlled room (25 °C). *C. pagurus* (discards of the crab-fisheries on Helgoland) were provided by local fishermen. The whole crabs, including shells, muscle tissue, and internal organs, were minced, divided in portions and stored deep frozen. The live juvenile isopods *I. emarginata* (3-4 mm total length) were taken from mass cultures which are established since several years at the Marine Station at Helgoland (Franke and Janke, 1998).

The gross composition (CHN) of the diets was analysed with a CHN Analyser (Fision EA 1108). Samples of the diets were lyophylised for 48 h. Subsamples were weighed on a microbalance (Mettler UMT2, precision: ± 0.1 µg) and used for CHN analysis. Acetanilide (HEKAtech, 141 d) was used as a standard. The carbon content was used to calculate the energy content of the samples according to Salonen et al. (1976).

The experimental design

The growth and the survival of juvenile lobsters were studied under six dietary treatments. In each treatment 99 juvenile lobsters (initial mean weight of 38.5 ± 16.8 mg and carapace length (CL-R) of 4.0 ± 0.4 mm) were fed with combinations of the diets described above. Three groups were fed every two days while the other three groups were fed every four days. The lobsters received food *ad libitum* (ca. 200-300 *Artemia* sp., 300-400 mg minced crabs, and ca. 20-30 juvenile isopods). Additionally, the lobsters were allowed to eat their moults.

The lobsters were examined daily for mortality and moults. Dead animals were removed from the culture system but were not replaced by new lobsters. When lobsters moulted their new carapace length was not measured until seven days after their moult to avoid injuries of the soft bodies. The carapace lengths and weights were not measured in all experimental animals but 20 individuals of each treatment were randomly selected to be measured after their next moult.

The experiment continued until the animals reached a size of 10 mm carapace length. Specific growth rates and moult increments were used to evaluate growth. The specific growth rate was calculated from the weight data and the carapace length after each post-

moult stage from the beginning to the end of the experiment according to Hopkins (1992). The specific growth rate (*SGR*, % per day) in post moult wet weight and in carapace length (CL-R) is described as

$$SGR = (\ln \mathit{final\ weight, length} - \ln \mathit{initial\ weight, length}) \times \frac{100}{\mathit{number\ of\ days}}. \quad (1)$$

The cleaning effect of isopods

The accumulation of feeding remains, debris, and faeces in the lobster compartments was investigated in a separate experiment. Three treatments with 10 replicates each were run in the culture system described above. In treatment 1 each of the lobster compartments was stocked with one juvenile lobster of 3 cm total length (10 mm CL-R) and 20-30 juvenile isopods (3-4 mm total length). In treatment 2 only juvenile lobsters was placed in the compartments while in treatment 3 only 20-30 juvenile isopods were used. The animals of all treatments were fed every other day with about 340 mg of minced crabs. Every day the numbers of juvenile isopods in the compartments were controlled and if necessary restocked. The experiment was terminated after 20 days. The accumulated remains of food and debris in the compartments were aspirated and collected on cellulose nitrate filters, 12 µm pore size. The filters were dried for 48 h at 60 °C and then weighed on a microbalance.

Statistics

All data sets, presented as mean ± standard deviation (SD), were first examined for normal distribution and similarity of variances using the statistical software package, Statistica 7.1 (StatSoft). The data were subjected to a one-way or two-way ANOVA. Multiple comparisons of data sets were performed with a Tukey's post-hoc test at a significance level of $\alpha = 0.05$ (Sokal and Rohlf, 1995). The size increments were plotted and linear and curvilinear regressions were applied to calculate the growth rate and the time when the juvenile lobsters reached a carapace length of 10 mm.

The time course of the specific growth rates (SGR) in %·day^{-1} was best described by the equation

$$SGR = a \exp (-0.5 (\ln (x/x0)/b)2), \quad (2)$$

where a, b, and x0 are the coefficient of variation, and x are the days from stage IV. Data obtained within intervals of ten days were averaged and statistically analysed.

Survival analyses were carried out after Kaplan and Meier (1958). The Kaplan-Meier estimator of Ŝ is given by

$$\hat{S}(t) = \prod_{t_i \leq t} (1 - \frac{d_i}{n_i}),$$

(3)

where n_i is the number of the risk set at t, and d_i the number of observed events at t_i, i = 1, 2, …, N.

RESULTS

Diet

The gross compositions and energy contents of the three diets (*Artemia* sp. nauplii, minced crabs (whole carcasses of *C. pagurus*) and juvenile *I. emarginata*) were significantly different (p < 0.001, Table 1). *Artemia* sp. nauplii showed the highest carbon and nitrogen contents and, thus, the highest energy content of 454 J·mg⁻¹ AFDW. All parameters were significantly higher than in *C. pagurus* and *I. emarginata*.

Table 1 Gross compositions (carbon, hydrogen, nitrogen) and energy contents (mean ± SD) of diets (*Artemia* sp. nauplii, minced crabs (*Cancer pagurus*) and juvenile *Idotea emarginata*).

Diet	*Artemia* sp.	*C. pagurus*	*I. emarginata*
N	25	24	25
C (%)	47.5 ± 0.5 [a]	40.5 ± 1.7 [b]	29.8 ± 1.1 [c]
H (%)	6.9 ± 0.1 [a]	6.1 ± 0.3 [b]	4.1 ± 0.2 [c]
N (%)	9.7 ± 0.5 [a]	7.9 ± 0.4 [b]	5.2 ± 0.3 [c]
C:N – Ratio	4.9 ± 0.1 [a]	5.1 ± 0.1 [b]	5.7 ± 0.1 [c]
J·mg⁻¹·AFDW	454 ± 10 [a]	330 ± 26 [b]	179 ± 13 [c]

Different superscripts denote statistically significant differences (one-way ANOVA and paired comparisons post hoc test (p = 0.05)). N = Number of lobsters, AFDW = Ash-free dry weight.

Table 2 Survival and growth rates (mean ± SD) of juvenile lobsters (*Homarus gammarus*) kept at 20.5 ± 0.6 °C. Growth rates were calculated after each moult from the beginning to the end of the experiment. Initial mean weight was 38.5 ± 16.8 mg and initial carapace length (CL-R) 4.0 ± 0.4 mm. Juvenile lobsters were fed every two or every four days with two main diets (*Artemia* sp. nauplii and minced crabs (*C. pagurus*) and every day with *I. emarginata*. Key: AI = *Artemia* sp. nauplii and *I. emarginata*; CI: *C. pagurus* and *I. emarginata*; ACI = *Artemia* sp. nauplii, *C. pagurus* and *I. emarginata*

Treatment	Survival (%)	n	Growth CL-R (mm·day^{-1})	Growth Weight (mg·day^{-1})	SGR_CL-R (%·day^{-1})	SGR_Weight (%·day^{-1})
2 AI	96	95	0.088 ± 0.024[a]	5.93 ± 2.28[a]	1.47 ± 0.42[a]	4.04 ± 1.05[a]
2 ACI	90	91	0.091 ± 0.020[a]	6.65 ± 2.40[a]	1.51 ± 0.31[a]	4.25 ± 0.84[a]
2 CI	92	99	0.087 ± 0.022[a]	6.17 ± 2.50[a]	1.44 ± 0.34[a]	4.00 ± 1.03[a]
4 AI	97	110	0.071 ± 0.014[b]	4.98 ± 1.30[b]	1.17 ± 0.30[b]	3.25 ± 0.79[b]
4 ACI	93	126	0.069 ± 0.022[b]	4.67 ± 1.79[b]	1.17 ± 0.41[b]	3.20 ± 1.08[b]
4 CI	95	108	0.073 ± 0.025[b]	5.00 ± 1.97[b]	1.22 ± 0.46[b]	3.40 ± 1.17[b]

Different superscripts denote statistically significant differences (one-way ANOVA and paired comparisons post hoc test ($p = 0.05$)). n = Number of measured lobsters, CL-R = Carapace length without rostrum, SGR = Specific growth rate (SGR = ((ln post-moult weight, length - ln initial weight, length) * 100/experimental time)).

Growth and survival

The growth rates of all juvenile lobsters ranged from 0.069 to 0.091 mm·day^{-1}·CL-R^{-1} or 4.67 to 6.65 mg·day^{-1}. This corresponds to a specific length increase of 1.17 to 1.51 %·day^{-1}·and a weight increase of 3.20 to 4.25 %·day^{-1}. The diets given had no significant effect on the growth rates of the lobsters. However, the feeding frequency significantly influenced growth rates (Tables 2 and 3). The growth rates of lobsters which were fed every four days were approximately 20 % lower than those of lobsters fed every two days.

Table 3 The specific growth rates of length (A) and specific growth rates of weight (B) of juvenile lobsters (*Homarus gammarus*) were determined on FF = Feeding frequency in day and diet. Six dietary treatments with each 99 replicate experiments were run. Key: *df* = degrees of freedom, *SS* = sum of squares, *MS* = mean squares, *F* = variance ratio, *p* = probability of rejecting a correct null hypothesis (p $\leq$ 0.05).

(A) length-SRG					
Analysis of variance					
Source of variation	*Df*	*SS*	*MS*	*F*	*p*
Main effects					
FF	1	15.87	15.869	104.73	*<0.0001*
Diet	2	0.08	0.039	0.26	*0.7749*
First-order interactions					
FF x Diet	2	0.45	0.223	1.47	*0.2308*
(B) weight-SRG					
Main effects					
FF	1	120.36	120.36	110.18	*<0.0001*
Diet	2	0.45	0.22	0.20	*0.8159*
First-order interactions					
FF x Diet	2	6.23	3.12	2.86	*0.0584*

The feeding experiment was terminated when the lobsters reached a carapace length of 10 mm (Figures 2 and 3). The lobsters which were fed every two days reached 10 mm carapace length after 68 to 71 days. Those lobsters which were fed every four days reached the same length after 89 to 95 days. The linear regressions and equations are shown in

Figure 2, along with the coefficients of determination, r^2 (all ≥ 0.98). The slopes of these regressions were significantly higher for lobsters which were fed every two days than for lobsters which were fed every four days (ANOVA, $p < 0.001$). At the end of the experiment the average live body weight of all six dietary treatments was 524 ± 83 mg.
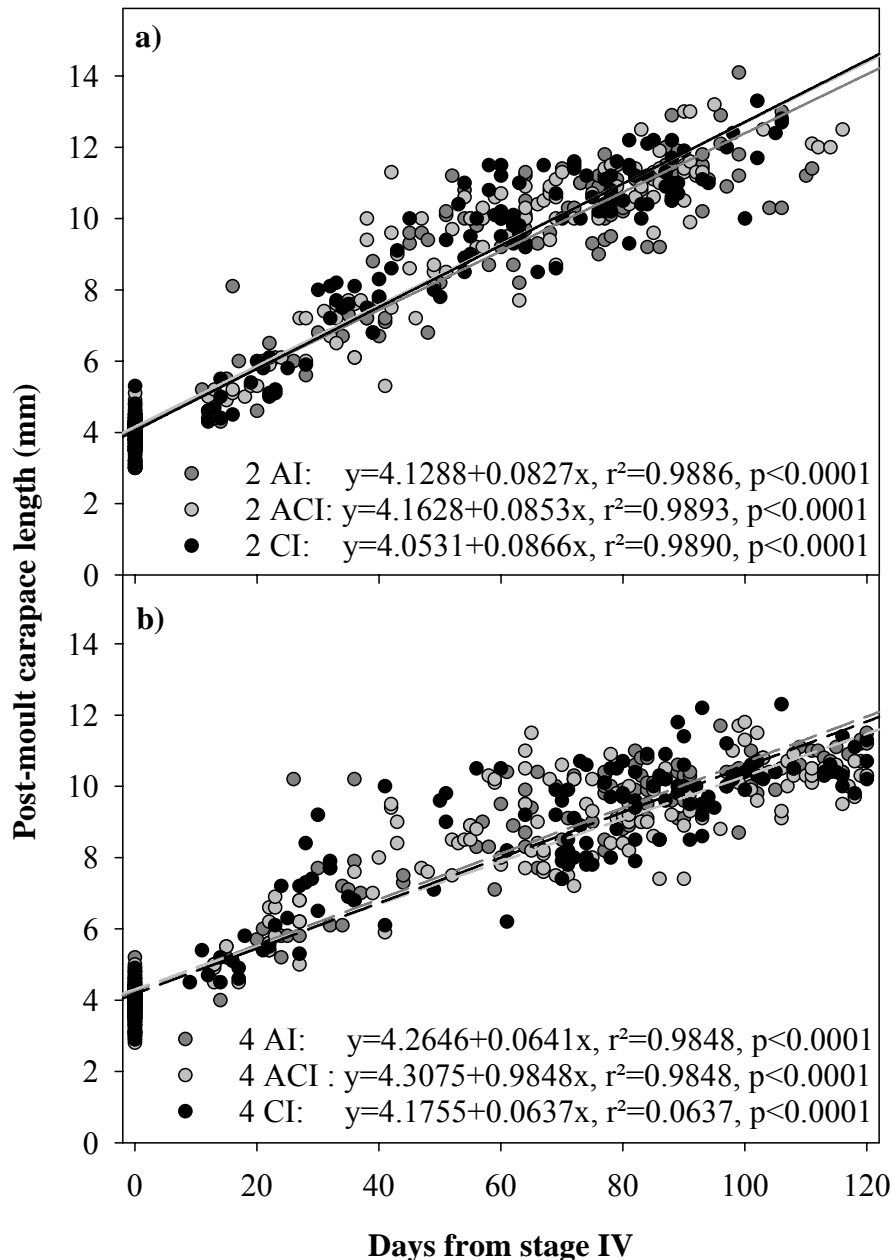

Figure 2 Growth over time of juvenile lobsters (*Homarus gammarus*). The lobsters were kept at 20 °C and were fed with two main diets (*Artemia* sp. nauplii and/or minced crab carcasses (*C. pagurus*), separately and in combination) (a) every two or (b) every four days and were fed with live juvenile *I. emarginata* every day. Key: AI = *Artemia* sp. nauplii and *I. emarginata*; CI = *C. pagurus* and *I. emarginata*; ACI = *Artemia* sp. nauplii, *C. pagurus* and *I. emarginata*.
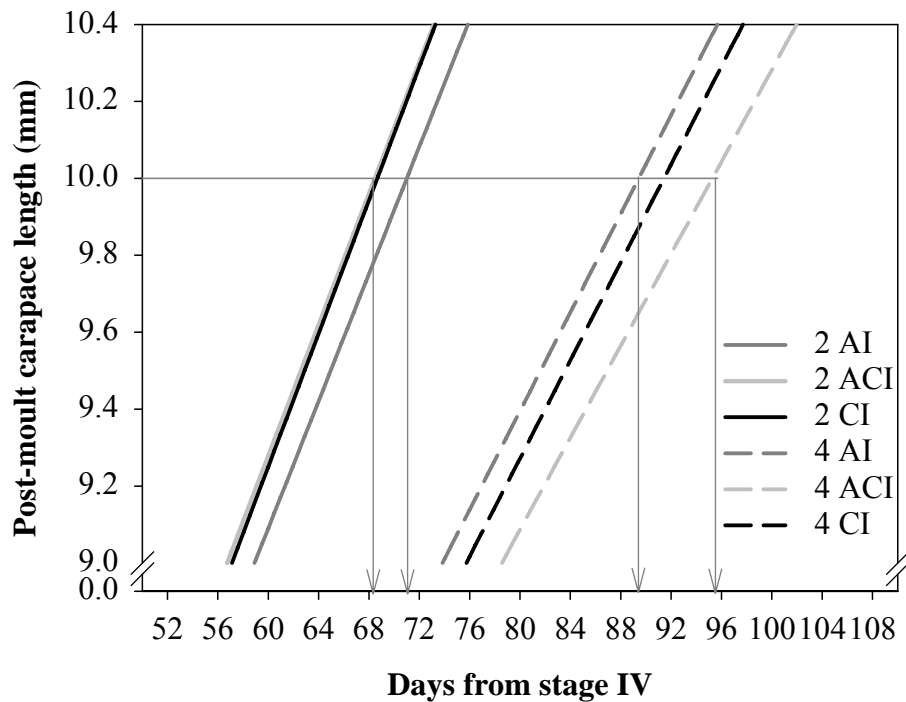
Figure 3 Growth over time of juvenile lobsters (*Homarus gammarus*). Juvenile lobsters were kept at 20 °C and were fed with two main diets (*Artemia* sp. nauplii and/or minced crabs (*C. pagurus*), separately and in combination) every two or every four days and were fed with live juvenile *I. emarginata* every day. Key: AI = *Artemia* sp. nauplii and *I. emarginata*; CI = *C. pagurus* and *I. emarginata*; ACI = *Artemia* sp. nauplii, *C. pagurus* and *I. emarginata*. For the juvenile lobsters, the experiment was ended when a carapace size of 10 mm was reached. The horizontal reference lines designate the end size of the lobsters at 10 mm carapace length.
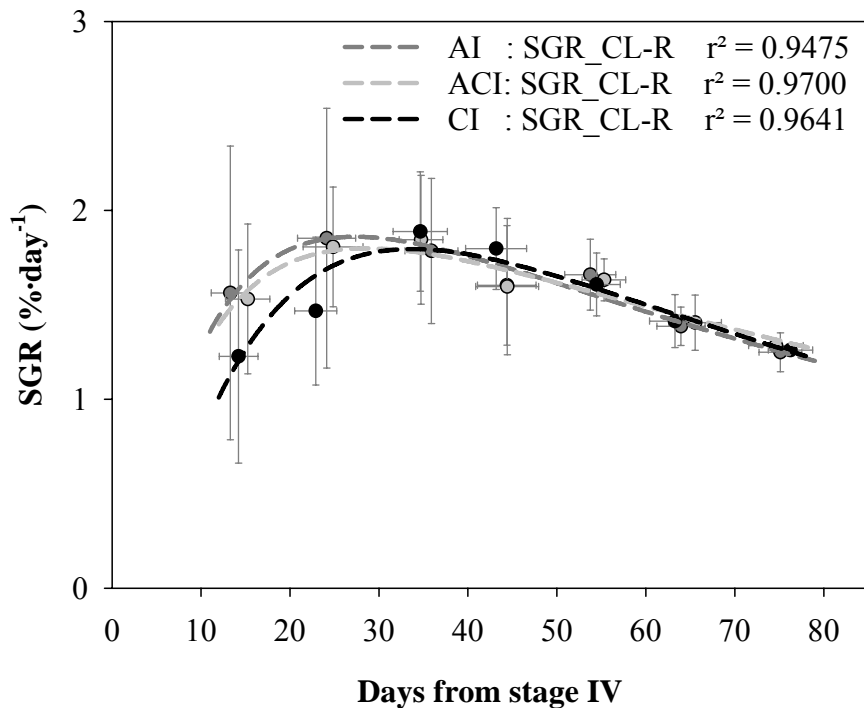
Figure 4 Specific growth rates (SGR_CL-R, mean ± SD) of juvenile lobsters (*Homarus gammarus*) which were kept at 20 °C and were fed with two main diets (*Artemia* sp. nauplii and/or minced crabs (*C. pagurus*)) every two days and were fed with live juvenile *I. emarginata* every day. Key: CL-R = Carapace length without rostrum, AI = *Artemia* sp. nauplii and *I. emarginata*; CI = *C. pagurus* and *I. emarginata*; ACI = *Artemia* sp. nauplii, *C. pagurus* and *I. emarginata*. Data obtained within intervals of ten days were averaged and statistically analysed. Nonlinear regressions showed the development of the growth rates during the experiment.

The specific growth rates (SGR_CL-R) varied significantly (p < 0.05) during the experiment (Figure 4). At the beginning the growth rates increased. They reached their maximum of 1.9 % per day at 35 days in the group which was fed with minced crabs (2CI). The other treatments (2AI and 2ACI) showed a maximum of 1.8 %·day^{-1} at 25 days. Thereafter, the growth rates continuously decreased towards 1.3 %·day^{-1} after 75 days of experiment.
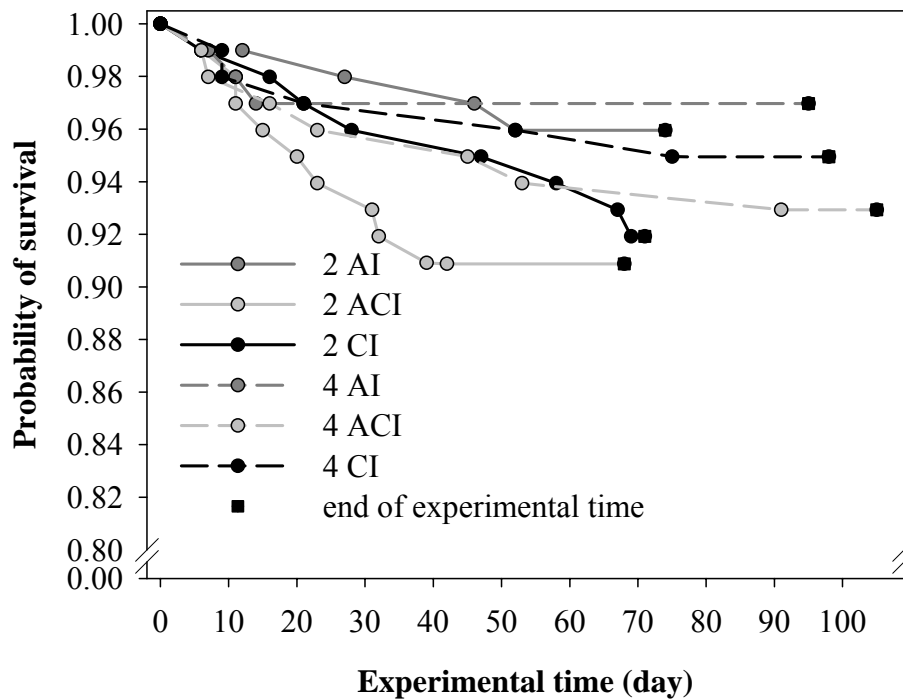
Figure 5 Kaplan-Meier survival curve of juvenile lobsters (*Homarus gammarus*) were kept at 20 °C and were fed with two main diets (*Artemia* sp. nauplii and/or minced crabs (*C. pagurus*), separately and in combination) every two or every four days and were fed with live juvenile *I. emarginata* every day. Key: AI = *Artemia* sp. nauplii and *I. emarginata*; CI = *C. pagurus* and *I. emarginata*; ACI = *Artemia* sp. nauplii, *C. pagurus* and *I. emarginata.* For the lobsters, the experiment was ended when a carapace length of 10 mm was reached.

The survival rates of juvenile lobsters ranged from 90 to 97 %. The Kaplan-Meier survival curves are shown in Figure 5. The experimental treatments had an effect on the mortality. Juveniles fed every four days showed better survival than those fed every two days. Lobsters fed the main diet of *Artemia* sp. nauplii showed the highest survival rates. The earliest mortality in the dietary treatments occurred after 6 days.

Cleaning effect of isopods

The amount of debris in the lobster compartments differed significantly between the three treatments (ANOVA, $p < 0.0001$, Figure 6). The food remains in the lobster boxes amounted to 0.79 ± 0.25 mg·day^{-1} in treatment 1 (only lobsters), and 0.44 ± 0.17 mg·day^{-1} in treatment 2 (only isopods). In the boxes of treatment 3 (lobsters and isopods), the amount of the debris was 0.33 ± 0.16 mg·day^{-1}. The treatments which included isopods showed significantly lower amounts of debris than the treatment with lobsters only. The water in the compartments without juvenile isopods flow over because the fine nylon gauze of the compartments was blocked.
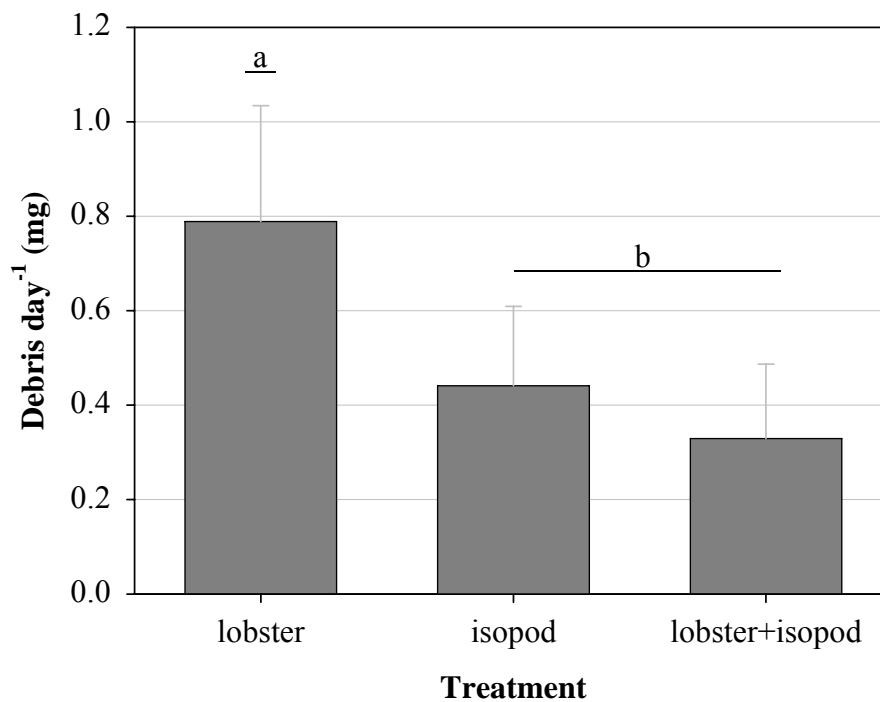

Figure 6 Debris accumulates per day (mean ± SD) in lobster compartments (n = 10). The animals of all treatments were fed every other day with minced crabs (*C. pagurus*). Different superscripts denote statistically significant differences (one-way ANOVA and paired comparisons post hoc test (p = 0.05)).

DISCUSSION

The major challenges in rearing juvenile lobsters (*H. gammarus*) are the supply with clean seawater, feeding with high quality but reasonable food, and the prevention of cannibalisms. These aspects require expensive or technically ambitious solutions and may entail high staff costs. We established a cost-efficient rearing and feeding method for easiest handling and maintenance but highest possible productivity of juvenile lobsters.

Separation of animals

Clawed lobsters are agonistic and cannibalistic when kept at high densities. Therefore, mass cultures often suffer from high mortality (Van Olst et al., 1975; Sastry and Zeitlin-Hale, 1977; Aiken and Waddy, 1995; Jørstad et al., 2001). In contrast, individually reared juveniles showed higher survival rates (Beard et al., 1985; Aiken and Waddy, 1988; Waddy, 1988) but they may exhibit lower growth rates due to space limitation. Aiken and Waddy (1978) showed that the growth of lobsters strongly depends on container size. An area of approximately 75 cm² is required to allow for unrestricted growth of juvenile lobsters up to 3 cm total length. To grow up to the double size, a total length of 6 cm, juvenile lobsters need a four times larger area. In our rearing system the area for each juvenile lobster amounted to 63 cm^2. This area is sufficient to maintain juvenile lobsters to up to 10 mm carapace length which corresponds with a total length of 3 cm. After reaching this length the juvenile lobsters were released into the wild. The system allows for the rearing of 140 juvenile lobsters per square meter at high survival rates of more than 90 %. Accordingly, this system provides a suitable trade-off between demand of space, the final size of the juveniles, and the duration of intensive maintenance period.

Diet

The best diet for optimum growth, survival, and normal coloration is natural food such as fresh and fresh-frozen marine molluscs, crustacean and macroalgae (Waddy, 1988). We chose in our experiment three food types: newly hatched *Artemia* sp. nauplii, minced *C. pagurus* and live juvenile isopods, *I. emarginata*. Except *Artemia* sp., the crab *C. pagurus* and the isopod *I. emarginata* occur in the same habitat as the lobsters and, thus, form a potential natural prey.

Newly hatched *Artemia* nauplii provide all nutrients required by juvenile lobsters for growth and health (Shleser and Gallagher, 1974). Moreover, no accumulation of debris occurred and, therefore, *Artemia* sp. nauplii do not excessively deteriorate water quality.

However, since feeding with *Artemia* sp. nauplii is costly and work intensive it is not suitable as the exclusive diet.

The best protein sources for crustaceans are from other crustaceans (Boghen and Castell, 1981). Discards of the Edible crab *C. pagurus* can be cheaply obtained from local fishermen. Lobsters which were fed in a preliminary experiment with minced crab carcasses showed high growth rates. However, a disadvantage of this diet is the lack of natural pigments which results in poorly pigmented lobsters. Therefore, *C. pagurus* is not suitable as exclusive diet but must be given in combination with diets that contain pigments. Moreover, minced crab meat blocked the fine nylon gauze which formed the bottom of the maintenance compartments and, thus, impaired water exchange and water quality.

Live isopods, e.g. *I. emarginata,* are easily produced in mass culture (Franke and Janke, 1998). Preliminary feeding attempts showed good acceptance by juvenile lobsters and satisfactory growth rates. The presence of live isopods encouraged the predatory behaviour and increased the feeding activity of the lobsters. The juvenile isopods were available for the juvenile lobsters at any time and provided pigments for full coloration of the lobsters.

A preliminary experiment showed that feeding with either *Artemia* sp. nauplii, or *C. pagurus* or live juvenile isopods alone resulted in poorer growth than feeding a combined diet. Similar results were reported by Beard et al. (1985) and Waddy (1988). In their experiments, too, the combination of different natural food, i.e. a mixed diet, gave better growth and survival rates. Lobsters which were fed with artificial diets had lower growth rates (0.05 mm·day^{-1}; Conklin et al., 1980; D'Abramo and Conklin, 1985) than with natural foods (0.1 mm·day^{-1}; Waddy, 1988). In comparison to natural mixed diets, artificial feeds must be supplemented with balanced nutrients which make them expensive.

Growth and survival

Juvenile lobsters grow best at 20 °C (Beard et al., 1985; Waddy, 1988; Wray, 2005; Schmalenbach, unpubl.). This corresponds to about the highest summer water temperature around Helgoland. Rearing at 20 °C and feeding every two days a combination of natural diets resulted in highest growth rates of almost 0.1 mm CL-R per day. The juvenile lobsters reached a carapace length of 10 mm after 69 days of post-larval development with a survival rate of 90-96 % at a feeding frequency of every two days. Similar growth rates

of juvenile lobsters were reported by Waddy (1988) and Kristiansen et al. (2004). The juvenile lobsters in our experiment which were fed every four days needed an additional two to three weeks to reach 10 mm carapace length at a survival rate of 93-97 %. This might suggest that the highest feeding frequency of every two days would result in the highest growth rates with adequate survival rates. Other studies have shown that there are already significant differences in growth between feeding every two days and every three days (Richards and Wickins, 1979). Feeding less frequently helps to reduce the accumulation of debris and to maintain good water quality and higher survival rates. Indeed, our rearing experiments showed not only good growth rates, but also high yield of juvenile lobsters at survival rates of 90 to 97 %.

Co-culture with isopods

The well-being, health, and the survival of juvenile lobsters strongly depend on clean water. However, accumulation of food remains, excrements, or other waste products significantly impairs water quality. Accordingly, a major burden in our lobster rearing facility was the frequent manual cleaning of each of the single compartments. Manual cleaning is time and personnel-intensive and, therefore, expensive. The addition of live juvenile isopods into the single compartments of the juvenile lobsters significantly improved the rearing conditions. The isopods consumed remaining food and, thus, prevented the gauze which formed the bottom of the compartments from becoming blocked. This, in turn, ensured a constant water flow through each of the compartments and, thus, guaranteed best water quality for the juvenile lobsters. The juvenile isopods, moreover, provided a permanently available prey for the lobsters and could stimulate their foraging behaviour. Studies about the spiny lobster *Jasus edwardsii* have shown that a daytime-dependent feeding rhythms by the presence or absence of predators influenced the growth and trained patterns of foraging and emergence (Oliver et al., 2006). A preliminary experiment showed that feeding with either *Artemia* sp. nauplii, or minced crabs or live juvenile isopods alone and in combination resulted in different shell pigmentations. Feeding with isopods improved the pigmentation of the lobsters. Watt and Arthur (1996) added into the lobster box a few mussel spat for the proper development of their crusher claws. In the present study, substrates were avoided because it would cause further cleaning efforts. The live isopods encouraged the lobsters to actively hunt for prey. This, again, appears to be favourable for the proper development of their crusher claws (e.g. Wickins, 1986).

Another advantage of the co-culture of lobsters and isopods is that the lobsters can feed on the isopods when desired. Lobsters are active during the night (Mehrtens et al., 2005) but in the rearing facilities the food is usually offered during the daytime at working hours. Foraging and feeding during the night may increase the assimilation efficiency because it better matches with the natural diurnal activity rhythms of the lobsters. Foraging in darkness influences the growth rate of juvenile lobsters. Bordner and Conklin (1981) observed that juvenile lobster grew significantly faster when kept in dimmed light or long periods of darkness. Therefore, we covered the basins with a dark Perspex lid.

CONCLUSIONS

An extensive restocking programme for the endangered Helgoland lobster population requires laboratory rearing and subsequent release of large numbers of juveniles lobsters. For the implementation of such a programme we developed a rearing method with is optimized from both economic and ecological viewpoints.

Minced crab meat from discards of the Helgoland crab fisheries proved to be a suitable and inexpensive food for juvenile lobsters but it blocked the rearing system and impaired water circulation. The co-culture of juvenile lobsters with juvenile isopods provided significant advantages in terms of feeding as well as cleaning of the rearing facilities. The maintenance of a conventional culture system for 600 juveniles, including feed preparation, feeding, and cleaning, takes about 14 man hours per week. The use of isopods as cleaning organisms and supplementary diet reduced the maintenance time by 50 % to seven man hours per week. The isopods served as a permanently available food for the juvenile lobsters, and simultaneously, the isopods fed on food remains and reduced the amount of debris which, in turn, ensured a continuous water flow through the maintenance compartments.

ACKNOWLEDGEMENTS

REFERENCES

Aiken, D.E., Waddy, S.L., 1978. Space, density and growth of the lobster (*Homarus americanus*). Proceedings of the World Mariculture Society 9, 461-467.

Aiken, D.E., Waddy, S.L., 1988. Strategies for maximizing growth of communally reared juvenile American lobsters. World Aquaculture 19, 61-63.

Aiken, D.E., Waddy, S.L., 1995. Aquaculture. In: Biology of the Lobster *Homarus americanus*. Edited by J.R. Factor. Academic Press, 153-175.

Anger, K., Harms, J., 1994. The Helgoland lobster: a disappearing island population. The lobster newsletter 7, 11–12.

Anonymous, 1980-2008. Die kleine Hochsee- und Küstenfischerei. Jahresbericht des Amtes für ländliche Räume Kiel −Abt. Fischerei, In Das Fischerblatt. Edited by Amt für ländliche Räume Kiel, Ohle Druck.

Beard, T.W., Richards, P.R., Wickins, J.F., 1985. The techniques and practicability of year-round production of lobsters, *Homarus gammarus* (L.), in laboratory recirculation systems. Ministry of Agriculture, Fisheries and Food Directorate of Fisheries Research, Lowestoft, Fisheries Research Technical Report 79, 22 pp.

Boghen, A.D., Castell, J.D., 1981. Nutritional value of different dietary proteins to juvenile lobsters, *Homarus americanus*. Aquaculture 22, 343-351.

Bordner, C.E., Conklin D.E., 1981. Food consumption and growth of juvenile lobsters. Aquaculture 24, 285-300.

Conklin, D.E., D'Abramo, L.R., Bordner, C.E., Baum, N.A., 1980. A successful purified diet for the culture of juvenile lobsters: the effect of lecithin. Aquaculture 21, 243-249.

D'Abramo, L.R., Conklin, D.E., 1985. Lobster aquaculture. In: Crustacean and mollusk aquaculture in the United States. Edited by J.V Huner and E.E. Brown. AVI Publishing Company, Inc. Westport, Connecticut, 159-201.

Fishery Statistics, 1950-2006. Eurostat database of European Commission. www.epp.eurostat.ec.europa.eu

Franke, H.-D., Janke, M., 1998. Mechanisms and consequences of intra- and interspecific interference competition in *Idotea baltica* (Pallas) and *Idotea emarginata* (Fabricius) (Crustacea: Isopoda): A laboratory study of possible proximate causes of habitat segregation. Journal of Experimental Marine Biology and Ecology 227, 1-21.

Goemann, O., 1990. "Echt" Helgoländer Hummer. Kohlrenken Verlag Oldenburg, Oldenburg, 82 pp.

Harms, J., Schilling, U., Goemann, O., 1995. Der "Helgoländer Hummer". Natur und Museum 125, 33-40.

Hopkins, K.D., 1992. Reporting fish growth: A review of the basics. Journal of the World Aquaculture Society 23, 173-179.

Hughes, J.T., Schleser, R.A., Tchobanoglous, G., 1974. A rearing tank for lobster larvae and other aquatic species. The Progressive Fish-Culturist 36, 129-132.

Kaplan, E.L., Meier, P., 1958. Non parametric estimation from incomplete observations. Journal of the American Statistical Association 53, 457-481.

Klimpel, J., 1965. Die neuzeitliche Entwicklung der Inselgemeinde Helgoland unter besonderer Berücksichtigung des Fremdenverkehrs. Verlagsanstalt Konstanz, Konstanz.

Kristiansen, T.S., Drengstieg, A., Bergheim, A., Drengstieg, T., Kollsgård, I., Svendsen, R., Nøstvold, E., Farestveid, E., Aardal, L., 2004. Development of methods for intensive farming of European lobster in recirculated seawater. Results from experiments conducted at Kvitsøy lobster hatchery from 2000 to 2004. Fisken og havet 6, 52 pp.

Mehrtens, F., Stolpmann, M., Buchholz, F., Hagen, W., Saborowski, R., 2005. Locomotory activity and exploration behaviour of juvenile European lobsters (*Homarus gammarus*) in the laboratory. Marine and Freshwater Behaviour and Physiolgy 38, 105-116.

Oliver, M.D., MacDiarmid, A.B., Stewart, R.A., Gardner, C., 2006. Spiny lobster population enhancement: moderation of emergence behaviour of juvenile *Jasus edwardsii* reared in captivity. New Zealand Journal of Marine and Freshwater Research 40, 605-613.

Richards, P.R., Wickins, J.F., 1979. Lobster culture research. Ministry of Agriculture, Fisheries and Food Directorate of Fisheries Research, Lowestoft, Laboratory Leaflet 47.

Salonen, K., Sarvala J., Hakala, I., Viljanen M.-L., 1976. The relation of energy and organic carbon in aquatic invertebrates. Limnology and Oceanography 21, 724-730.

Sastry, A.N., Zeitlin-Hale, L., 1977. Survival of communally reared larval and juvenile lobsters, *Homarus americanus*. Marine Biology 39, 297-203.

Shleser, R., Gallagher, M., 1974. Formulations of rations for the American lobster, *Homarus americanus*. Proceedings of the World Mariculture Society 5, 157-164.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. The principles and practice of statistics in biological research, 3rd edn. WH Freeman and Co., New York, 887 pp.

Ulrich, I., 1998. Populationsgenetische und verhaltensbiologische Untersuchungen am Helgoländer Hummer. Dissertation, Universität Hamburg.

Van Olst, J.C., Carlberg, J.M., Ford, R.F., 1975. Effects of substrate type and other factors on the growth, survival, and cannibalism of juvenile *Homarus americanus* in mass rearing systems. Proceedings of the World Mariculture Society 6, 261-274.

Waddy, S.L., 1988. Farming the homarid lobsters: State of the art. World Aquaculture 19, 63-71.

Watt, L., Arthur, G., 1996. The improvement of the Shetland lobster fishery through stock enhancement-1. North Atlantic Fisheries College. Fisheries development note 2, 4 pp.

Wickins, J.F., 1986. Stimulation of crusher claw development in cultured lobsters, *Homarus gammarus* (L.). Aquaculture and Fisheries Management 17, 267-273.

Wray, T., 2005. Molluscs, lobster & crab. Fish Farming International 32.

GENERAL DISCUSSION AND CONCLUSIONS

The present studies on conditions for growth, reproduction and recruitment in the European lobster (*Homarus gammarus* Linnaeus, 1758) at Helgoland have been performed to assess the status of the local lobster population in view of environmental constraints particularly temperature effects on life history traits and behavior. The recent small size of the local population is the result of a dramatic decline some decades ago, from which the population has not recovered yet. As to that, the current studies serve as a pilot project for restocking and to decide if a successful settlement of hatchery-reared juvenile lobsters at Helgoland is feasible. In this context, the maintenance procedures and lobster production were optimized using local resources, and the environmental conditions for releasing lobsters were discussed.

The status of the Helgoland lobster population

The development and survival of embryos, larvae, juvenile and adult lobsters depend on various environmental conditions (temperature - including climate change; light regime; currents; shelters, predation and food availability; carrying capacity), behavioural and physiological components (mating and territorial behaviour; moulting activity, density-dependent growth; swimming ability of larvae) and finally fishery pressure (Ennis, 1983; Harding et al., 1983; Svåsand et al., 2004; Hudon and Fradette, 1993).

The *development of the embryos and larvae* are strongly influenced by temperature (Templeman, 1936a; Perkins, 1972; Branford, 1978; MacKenzie, 1988; Charmantier et al. 1991; Charmantier and Guillaume, 1992; MacDiarmid and Saint-Marie, 2006). The effect of temperature on the embryonic and larval development was examined in order to assess (1) if lobster larvae can successfully develop at Helgoland under the conditions of the recent warming trend of the North Sea, and (2) how lobsters at Helgoland might respond when becoming confronted in coming decades with an ongoing warming trend (Manuscript II).

Although the recent warming is not directly responsible for the decline of the lobster population, it might exert an additional stress on a potential recovery of the population.

The present study confirmed a strong effect of temperature on the timing and duration of larval development and survival. Development to the post-larval stage (IV-stage) was only

possible at temperatures above 14 °C, and optimal larval survival occurred within the temperature range of 16 and 22 °C. In contrast, larvae of the American lobster (*Homarus americanus*) developed successfully to the juvenile stage at much lower temperatures than larvae of the European lobster (Caddy, 1979; MacKenzie, 1988).

During the tri-annual study at Helgoland, the mean annual temperature was different by maximal 1.7 °C. This allowed for a study on how these temperature differenced affected the embryonic development duration and the timing of larval release. Firstly, the larval hatching dates and hatching temperatures were rather similar over the years of study at ambient temperatures (in July at 15.9-16.9 °C). Secondly, females kept under laboratory conditions with an annual average temperature difference of maximum 3.1 °C released larvae at very different dates and temperatures (from April to June at 13.3-16 °C), while the sum of daily temperature values over the period of embryonic ("degree days") was rather similar at about 2770. In conclusion, increased water temperatures related to climatic warming of the North Sea resulted in a forward shift in the annual peak abundance of larvae. If the recent warming trend would continue, larvae would run the risk of being released at environmental conditions which were suboptimal for their development and survival. This relates to the critical temperature of 14 °C below which development is not possible, and/or on the trophic conditions. Such an effect may cause a serious problem for a successful recruitment of the local stock.

A further problem for a high recruitment success is that larvae could drift away from their suited habitat, because the island of Helgoland is exposed to strong tidal currents (Hickel, 1972). Furthermore, the habitat is isolated from similar hard-bottom areas and neighbouring populations by some hundred miles of soft bottom which represent an ecological barrier.

The recruitment mechanism of larvae was considered in a laboratory study (Manuscript III; Schmalenbach and Buchholz, in press) to determine the vertical positioning and swimming performance of lobster larvae (Zoea I, II, and III) in response to light and current, and to interpret how lobster larvae move in the field and select their habitat.

Newly hatched larvae (Zoea I stage) swam directly towards any light source and showed a marked positive phototaxis, as was similarly described by Neil et al. (1976), Dunn and Shelton (1983) and Watt and Arthur (1996) for lobster populations in Scotland. This critical drift stage takes about 4 days in summer. Hickel (1972) reported that the water mass circles around Helgoland several times in a tidal ellipse, which leads to the

assumption that the larvae could remain within their habitat. During the following stages, the positive response to light rapidly decreased and larvae tended to hold their position near the bottom. Furthermore, the ability to swim against currents increased. This specific larval recruitment mechanism avoids an uncontrolled drift and facilitates larvae to remain at the suitable substratum for further development.

The further *growth conditions of juvenile lobsters* in the field were examined by releasing about ten thousand hatchery-reared lobsters between 2000 and 2008 at Helgoland (Manuscript I). The high recapture rate of cultured lobsters (6.8 %) at Helgoland is comparable to the large-scale release programme in south-western Norway (6.2 %), where the recruitment of lobsters increased (Agnalt et al., 2004) Furthermore, previous studies of Burton et al. (1994), Tveite and Grimsen (1995), Bannister and Addison (1998), Moksness et al. (1998), van der Meeren et al. (1998) and Agnalt et al. (1999) have shown similar return rates of hatchery reared European lobsters. The recaptured lobsters indicated good development and growth conditions and did not show any evidence of shell disease. They matured to the egg carrying stage at an age of 4 years and at a carapace length (CL) of 83 mm similar to other European lobster populations (Gibson, 1969; Lizárraga-Cubedo et al., 2003; Agnalt et al., 2006; Tully et al., 2006), and the first released cohort grew to a maximum size of 115 mm CL for females and of 138 mm CL for males after 9 growing seasons. The mark-recapture and dive studies have shown that the cultured lobster successfully settled in their release site, and thus, remained around the island of Helgoland which confirms Bannister et al. (1994) who also reported that released lobsters kept closely to their releases sites.

The *growth parameters of the adult female and male lobsters* such as moult increments, length-weight relationships, size at maturity and legal size (85 mm CL) was comparable to other European lobster populations (Manuscript I). Females grew at lower rates than males (length increments: 12.2 % in females, 15.6 % in males) but showed similar growth increments with small variation in England, Scotland and Wales (length increments: 10.5-12.8 % in females, 12.6-15 % in males; Thomas, 1958; Hepper, 1967, 1970), and in *H. americanus* (length increments: 12-13.9 % in females and 14.6-15.7 % in males; Ennis, 1972; Conan et al., 1982; Maynard et al., 1992; Comeau and Savoie, 2001). The lower growth rates for female lobsters are most probably related to egg production, which requires more energy than sperm production (Templeman, 1933; Templeman, 1936b;

Ennis, 1972; Aiken and Waddy, 1980; Estrella and McKiernan, 1989). Furthermore, ambient temperature affects lobster growth: Functional maturity was attained at smaller sizes in warm- (77 mm CL) than in cold-water areas (82 mm CL) (Simpson, 1961; Little and Watson III, 2005). At Helgoland, the minimum size at the onset of functional maturity was at 83 mm CL, and corresponded to an age of 4 to 5 years from hatching, again similar to other European lobster populations (Gibson, 1969; Lizárraga-Cubedo et al., 2003; Agnalt et al., 2006; Tully et al., 2006).

The Ministry of Fisheries and Aquaculture of the State of Schleswig-Holstein established a logbook in 2006 to report *commercial lobster landings* (Manuscript I). Using this data source, catch per unit effort was determined for the following years. The analysis showed that in 2008 significantly more lobsters per unit effort (0.017 CPUE) were landed than in 2006 and 2007 (~0.01 CPUE). However, the overall catch fell into the low range of 200-300 legal-sized lobsters caught annually during the last decades. Further data are needed to verify any trend. The sampling programme at Helgoland will be continued.

The size distribution of all landed lobsters in 2007 and 2008 suggested that the exploitation rates were equal over the two seasons without an obvious trend towards increased proportions in recruit size ranges, and implied indirectly that population size had not further decreased. In accordance with the previous study of Mehrtens (2008), the population size has possibly become is too small for successful recruitment and thus the local stock is currently below the critical threshold allowing for recovery to its former dimension.

The population size was estimated to values between 21,000 and 29,000 lobsters ($\geq$ 58 mm CL). Assuming the lobsters are evenly distributed across the subtidal cliffs (an area of 33 km²) of Helgoland, the population density would amount to about 0.08 lobsters·100 m^{-2}. In contrast, density calculations for the 1920s and 1930s suggested about 1.5 million lobsters with a density of 5 lobsters·100 m^{-2} living on the cliffs of Helgoland. This indicates that the carrying capacity of the habitat for the lobster is not exploited presently and that there is a high potential for much larger population.

Maintenance and releasing conditions of cultured lobster

New findings are presented on the current status, the development and recruitment processes of the European lobster population at Helgoland, with further indications that cultured lobsters have good growth conditions from juvenile to adult lobsters in the wild. For example, the recruitment of lobsters in Norway increased due to a large scale restocking programme (Agnalt et al., 1999). Accordingly, a large-scale programme at Helgoland could be effective. This would include the optimization of rearing conditions allowing for a cost-efficient and ecologically sustainable production of large numbers of juvenile lobsters to be released into the field (Manuscript IV; Schmalenbach et al., 2009).

A principal goals in optimizing *rearing conditions for juvenile lobsters* were (1) to utilize local resources, (2) to reduce maintenance costs; (3) to prevent cannibalisms, while (4) using high quality but reasonable food to reach maximum productivity (5).

In this context, discards of the local crab (*Cancer pagurus*) fisheries provide a suitable and cheap diet for juvenile lobsters. This food showed good acceptance and allowed for high growth rates in preliminary experiments; however, the mortality of lobsters increased, because remains of the crab meat frequently blocked the water exchange in the rearing facilities. Co-culturing juvenile lobsters with live juvenile isopods (*Idotea emarginata*) reduced the deposits of food remains and other debris in the rearing tanks so that water quality and survival rates of lobsters were maintained. Furthermore, the manual *cleaning* of the single compartments was less time consuming by ca. 50 %.

In the culture system, juvenile lobsters were reared in single compartments because clawed lobsters are agonistic and cannibalistic when kept at high densities and in mass cultures (Van Olst et al., 1975; Sastry and Zeitlin-Hale, 1977; Beard et al., 1985; Aiken and Waddy, 1988; Waddy, 1988; Aiken and Waddy, 1995; Jørstad et al., 2001). Unrestricted growth was achieved up to a release size of 3 cm total length (i.e. 10 mm carapace length) (see also Aiken and Waddy, 1978).

Boghen and Castell (1981), Beard et al. (1985), Waddy (1988), Kristiansen et al. (2004) and Wray (2005) reported that the best diet for optimum growth, survival rates and normal coloration of lobsters was achieved by a mixed natural diet, which included protein sources from other crustaceans. In the present study, lobsters reached good growth rates and showed optimal development when feeding a combination of three diets at 20 °C: Newly hatched *Artemia* sp. nauplii provided all nutrients for growth and health (Shleser and Gallagher, 1974) and did not excessively deteriorate water quality. However, *Artemia* sp.

are costly and therefore not suitable as exclusive food. Minced crabs of *C. pagurus,* which can be cheaply obtained from the local fisheries provided a suitable protein source, but lacked pigments. Juveniles fed on co-cultured live isopods (*I. emarginata*), which are produced in mass cultures (Franke and Janke, 1998) showed good growth rates and dark shell pigmentation. Figure 1 shows the shell colouration of few months old lobsters, which were fed with different diets in preliminary experiments. The darker the colour of the young lobsters the better they are adapted to their environment.
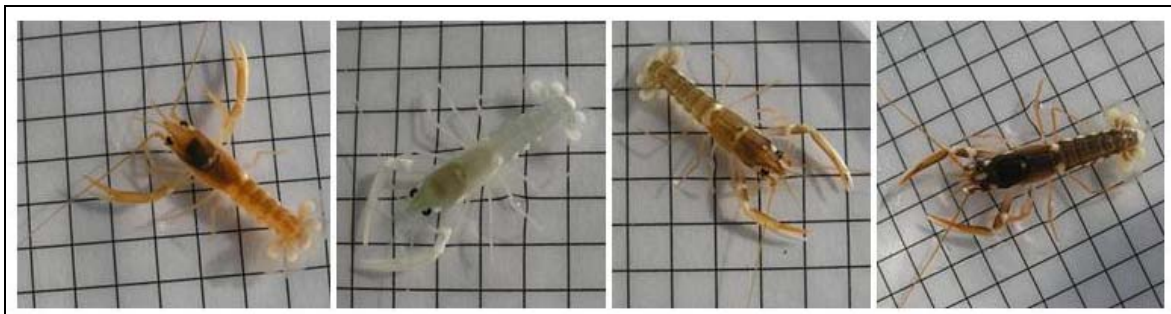

Figure 1 Different diets produced differences in shell colouration of two-months old lobsters. Lobsters were fed with *Artemia* sp. nauplii, minced crab (*Cancer pagurus*), live juvenile isopods (*Idotea emarginata*) and a combination of the mentioned diets (from left to right; scale: 0.5 cm).

Using these diets, juvenile lobsters reached good growth rates (0.1 mm day^{-1}), similar to data provided by Waddy (1988), and higher rates than reported for lobsters fed with artificial diets (0.05 mm day^{-1}; Conklin et al., 1980; D'Abramo and Conklin, 1985). Additionally, they showed survival rates of more than 90 %.

Temperature is the most important factor when considering the appropriate period of rearing lobsters and *releasing* them into the wild. Van der Meeren (2000) suggested that juvenile lobster should be released in winter when predators are less abundant than in summer. However, we think that the release temperature should consider the activity of lobsters, allowing them to find suited shelters quickly. We found that the release temperature should be above 12 °C which is the case at Helgoland from May to October. Thus two release periods per year for laboratory-reared juvenile lobsters can be defined: Animals reared over winter can be released in spring, while those reared over summer in autumn (Schmalenbach and Buchholz, unpubl.). Prior to release, juveniles were acclimated to the sea temperature to avoid stress. Additionally, release was at night and at suited weather, in accordance with the animals' nocturnal activity and in order to minimise loss to

sight-orientated fishes such as the shorthorn sculpin (*Myoxocephalus scorpius*), and the rock cook wrasse (*Centrolabrus exoletus*)

Furthermore, release sites should provide high quality habitats affording maximum protection, low predation pressure and low interspecific competition for food and shelter. At Helgoland, the edible crab *C. pagurus* is the most abundant crab and a potential competitor for food and shelter (Anger and Harms, 1994). Predation by fishes and crustaceans are mainly relevant in the first hours after release. The released juvenile lobsters are shelter-bound, they prefer rocky sites, where they can hide from predators in crevices (Van der Meeren, 2000), where they spend most of the time in the first years (Karnofosky et al., 1989). According to van der Meeren (1993), the release sites should be examined previously with respect to the abundance of predators and competitors as well as the presence of sufficient shelters to reduce losses after release.

Considering the improve knowledge of the habitat of the local lobster population, of optimal rearing conditions, release time and release temperature, as well as considering the successful measures to reduce costs of an intensive production of hatchery-reared juvenile lobsters, a future lobster stock enhancement programme at Helgoland appears feasible.

Perspectives

Based on the current observations and data, future studies on the Helgoland lobster population should focus on the following approaches:

Recruitment process of larvae

- In relation to the warming trend of the North Sea waters, the timing of larval release should be further observed to predict the recruitment success of the lobster stock.
- The larval development should be examined under the aspect of a further temperature rise in relation to earlier seasonal hatch time to observe if larvae are able to develop successfully when released at too low spring temperatures.
- The present data and results on the behaviour of larvae should be applied in forecasting and recruitment models to assess conditions for successful recruitment of the local lobster population.

Monitoring and fishery management plan

- Within a monitoring programme in cooperation with local fishermen, quantitative fishery and dive programmes should assess the recruitment dynamics of lobster. Detailed studies should consider carrying capacities of release sites, density dependent growth and reproduction as well as survival at different life history stages.

- A further concept for fishery regulation and management should be developed, e.g. a ban on landings of all females and an increase of the minimum legal landing size.

Stock enhancement

- Within a large-scale restocking programme more than ten thousand juveniles per year should be raised and released. The extensive enhancement programme should then help the endangered Helgoland lobster population to increase above the critical level.

- To this aim, maintenance time and costs of the culture system should be further minimised e.g. by an automatic feeding system. Optimum water circulation of the culture system should be ensured by installing a tidal system.

Two further studies on lobster life history in relation to a restocking programme were not included to the dissertation and may be used as reference for further investigations:

-The effect of temperature on the catch-rate of landed lobsters and on the moulting and locomotory activities of juvenile lobsters was examined to determine the optimum release temperature.

-Dive census was used to define optimum release sites for hatchery-reared lobsters with low interspecific predation and competition by the edible crab *C. pagurus* for food and shelter.

REFERENCES

Agnalt, A.-L., Kristiansen, T.S., Jørstad, K.E., 2006. Growth, reproductive cycle, and movement of berried European lobsters (*Homarus gammarus*) in a local stock off southwestern Norway. ICES Journal of Marine Science 64, 288-297.

Agnalt, A.-L., Jørstad, K.E., Kristiansen, T.S., Nøstvold, E., Farestveit, E., Næss, H., Paulsen, O.I., Svåsand, T., 2004. Enhancing the European lobster (*Homarus gammarus*) stock at Kvitsøy Islands: Perspectives on Rebuilding Norvegian stocks. In: Stock enhancement and sea ranching development, pitfalls and opportunities. Edited by K.M. Leber, S. Kitada, H.L. Blankenship and T. Svåsand. Blackwell Publishing Ltd, Oxford, 415-426.

Agnalt, A.-L., van der Meeren, G.I., Jørstad, K.E., Næss, H., Farestveit, E., Nøstvold, E., Svåsand, T., Korsøen, E., Ydstebø, L., 1999. Stock enhancement of European lobster (*Homarus gammarus*); A large-scale experiment off south-western Norway (Kvitsøy). In Stock Enhancement and Sea Ranching. Edited by B. Howell, E. Moksness and T. Svåsand. Oxford, Fishing News Books, Blackwell Science, 401-419.

Aiken, D.E., Young-Lai, W.W., 1981. Dactylotomy, chelotomy and dactylostasis: Methods for enhancing survival and growth of small lobsters (*Homarus americanus*) in communal conditions. Aquaculture 22, 45-52.

Aiken, D.E., Waddy, S.L., 1978. Space, density and growth of the lobster (*Homarus americanus*). Proceedings of the World Mariculture Society 9, 461-467.

Aiken, D.E., Waddy, S.L., 1980. Reproductive biology. In: The biology and management of lobsters. Volume I Physiology and Behaviour. Edited by J.S. Cobb and B.F. Phillips. Academic Press, New York, 215-276.

Aiken, D.E., Waddy, S.L., 1988. Strategies for maximizing growth of communally reared juvenile American lobsters. World Aquaculture 19, 61-63.

Aiken, D.E., Waddy, S.L., 1995. Aquaculture. In: Biology of the Lobster *Homarus americanus*. Edited by J.R. Factor. Academic Press, 153-175.

Anger, K., Harms, J., 1994. The Helgoland lobster: a disappearing island population. The lobster newsletter 7, 11–12.

Anonymous, 1980-2008. Die kleine Hochsee- und Küstenfischerei. Jahresbericht des Amtes für ländliche Räume Kiel –Abt. Fischerei, In Das Fischerblatt. Edited by Amt für ländliche Räume Kiel, Ohle Druck.

Atema, J., Stein, L.S., 1974. Effects of crude oil on the feeding behaviour of the lobster *Homarus americanus*. Environmental Pollution 6, 77-86.

Atema, J., Voigt, R., 1995. Behavior and sensory biology. In: Biology of the Lobster *Homarus americanus*. Edited by J.R. Factor. Academic Press, 313-348.

Atema, J., Jacobson, E., Karnofsky, E., Oleszko-Szuts, S., Stein, L., 1979. Pair formation in the lobster, Homarus americanus: Behavioral development, pheromones and mating. Marine Behaviour and Physiology 6, 277-296.

Bannister, R.C.A., 1986. Assessment and population dynamics of commercially exploited shellfish in England and Wales. In: North Pacific Workshop on Stock Assessment and Management of Invertebrates. Edited by G.S. Jamieson and N. Bourne. Canadian Special Publication of Fisheries and Aquatic Science 92, 182-194.

Bannister, R.C.A., Addison, J.T., 1998. Enhancing lobster stocks: A review of recent European methods, results, and future prospects. Bulletin of Marine Science 62, 369-387.

Bannister, R.C.A., Addison, J.T., Lovewell, S.R.J., 1994. Growth, movement, recapture rate and survival of hatchery-reared lobsters (*Homarus gammarus* (Linnaeus, 1758)) released into the wild on the English east coast. Crustaceana 67, 156-172.

Bartsch, I., Tittley, I., 2004. The rocky intertidal biotopes of Helgoland: Present and past. Helgoland Marine Research 58, 289–302.

Beare, D.J., Burns, F., Greig, A., Jones, E.G., Peach, K., Kienzle, M., McKenzie, E., Reid, D.G., 2004. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. Marine Ecology Progress Series 284, 269-278.

Beard, T.W., Richards, P.R., Wickins, J.F., 1985. The techniques and practicability of year-round production of lobsters, *Homarus gammarus* (L.), in laboratory recirculation systems. Ministry of Agriculture, Fisheries and Food Directorate of Fisheries Research, Lowestoft, Fisheries Research Technical Report 79, 22 pp.

Bennet, D.B., 1980. Perspectives on European lobster management. In: The biology and management of lobsters. Volume II Ecology and management. Edited by J.S. Cobb and B.F. Phillips. Academic Press, New York, 317-331.

Binner, M., 1999. Experimentelle Untersuchungen zu Habitatwahl und Raum-Konhurrenzverhalten bei *Homarus gammarus* (L.) und *Cancer pagurus* (L.). Diplomarbeit, Freie Universität Berlin.

BLMP, 2000. Meeresumwelt 1994-96. 2, 40 pp.

BLMP, 2002. Meeresumwelt 1997-98. 66 pp.

Boghen, A.D., Castell, J.D., 1981. Nutritional value of different dietary proteins to juvenile lobsters, *Homarus americanus*. Aquaculture 22, 343-351.

Bordner, C.E., Conklin D.E., 1981. Food consumption and growth of juvenile lobsters. Aquaculture 24, 285-300.

Branford, J.R., 1978. Incubation period for the lobster *Homarus gammarus* at various temperatures. Marine Biology 47, 363-368.

Browne, R.M., Mercer, J.P., Duncan, M.J., 2001. An historical overview of the Republic of Ireland's lobster (*Homarus gammarus* Linnaeus) fishery, with reference to European and North American (*Homarus americanus* Milne Edwards) lobster landings. Hydrobiologia 465, 49-62.

Burton, C.A., Bannister, R.C.A., Addison, J.T., Cook, W., 1994. Lobster stock enhancement experiments II: Current experiments in the British Isles. ICES Workshop to evaluate the potential for stock enhancement. ICES Mariculture Committee, Charlottenlund, Denmark, 37-40.

Caddy, J.F., 1979. The influence of variations in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in the southern Gulf of St Lawrence. Rapportes et Proces-Verbaux des Reunions, Conseil International pour l'Exploration de la Mer 175, 204-216.

Carlberg, J.M., Van Olst, J.C., 1976. Brine Shrimp (*Artemia salina*) consumption by the larval stages of the American lobster (*Homarus americanus*) in relation to food density and water temperature. Proceedings of the World Mariculture Society 7, 379-389.

Castell, J.D., Mauviot, J.C., Covey, J.F., 1986. The use of eyestalk ablation in nutrition studies with American lobsters (*Homarus americanus*). Proceedings of the World Mariculture Society 7, 431-443.

Charmantier, G., Mounet-Guillaume R., 1992. Temperature-specific rates of embryonic development of the European lobster *Homarus gammarus* (L.). Journal of Experimental Marine Biology and Ecology 1600, 61-66.

Charmantier, G., Charmantier-Daures, M., Aiken, D.E., 1991. Metamorphosis in the lobster *Homarus americanus* (Decapoda): A review. Journal of Crustacean Biology 11, 481-495.

Cobb, J.S., Castro, K.M., 2006. *Homarus* species. In: Lobsters: Biology, management, aquaculture and fisheries. Edited by B. Phillips. Blackwell Publishing Ltd, Oxford, 310-339.

Cobb, J.S., Phillips, B.F., 1980. The biology and management of lobsters. Volume I Physiology and behaviour. Academic Press, Inc. (London) Ltd., 463 pp.

Cobb, J.S., Wahle, R.A., 1994. Early life history and recruitment processes of clawed lobsters. Crustaceana 67, 1-25.

Comeau, M., Savoie, F., 2001. Growth increment and molt frequency of the American lobster (*Homarus americanus*) in the southwestern Gulf of St. Lawrence. Journal of Crustacean Biology 21, 923-936.

Comeau, M., Savoi, F., 2002. Maturity and reproductive cycle of the female American lobster, *Homarus americanus*, in the southern Gulf of St. Lawrence, Canada. Journal of Crustacean Biology 22, 762-774.

Conan, G.Y., Robinson, D.G., Maynard, D.R., 1982. Growth at molt of lobsters in two areas of Northumberland Strait, Canada. International Council for the Exploration of the sea Shellfish Committee C.M. 1982/K: 35, 1-10.

Conklin, D.E., Chang, E.S., 1983. Grow-out techniques for the American lobster, *Homarus americanus*. In: Handbook of Mariculture 1: Crustacean Aquaculture. Edited by J.P. McVey. CRC Press Boca Raton, Florida, 277-286.

Conklin, D.E., D'Abramo, L.R., Bordner, C.E., Baum, N.A., 1980. A successful purified diet for the culture of juvenile lobsters: the effect of lecithin. Aquaculture 21, 243-249.

Cook, W., 1995. A lobster stock enhancement experiment in Cardigan Bay. Final Report. North Western and North Wales Sea Fisheries Committee, Lancaster, UK. 33 p.

Cook, R.M., Sinclair, A., Stefansson, G., 1997. Potential collapse of North Sea cod stocks. Nature 385, 521-522.

Cushing, D.H., 1975. Marine Ecology and Fisheries. Cambridge University Press.

Daan, N., Heessen, H.J.L., Pope, J.G., 1994. Changes in the North Sea cod stock during the twentieth century. ICES. Marine Science Symposia 198, 229-243.

D'Abramo, L.R., Conklin, D.E., 1985. Lobster aquaculture. In: Crustacean and mollusk aquaculture in the United States. Edited by J.V Huner and E.E. Brown. AVI Publishing Company, Inc. Westport, Connecticut, 159-201.

Dunn, J., Shelton, R.G.J., 1983. Observations on lobster, *Homarus gammarus* (L.), larvae held in a Loch Ewe enclosure. ICES CM 1983/L, 30, 1-6.

Dow, R.L., 1980. The clawed lobster fisheries. In: The biology and management of lobsters. Volume II Ecology and management. Edited by J.S. Cobb and B.F. Phillips. Academic Press, New York, 265-316.

Drinkwater, K.F., 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. . ICES Journal of Marine Science 62, 1327-1337.

Dybern, B.I., 1973. Lobster burrows in Swedish waters. Helgoländer wissenschaftliche Meeresuntersuchungen 24, 401-414.

Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430, 881-884.

Ehrenbaum, E., 1894. Der Helgoländer Hummer, ein Gegenstand der deutschen Fischerei. Wissenschaftliche Meeresuntersuchungen NF 1, 278-300.

Ennis, G.P., 1972. Growth per moult of tagged lobsters (*Homarus americanus*) in Bonavista Bay, Newfoundland. Journal of the Fisheries Research Board of Canada 29, 143-148.

Ennis, G.P., 1973. Endogenous rhythmicity associated with larval hatching in the lobster *Homarus gammarus*. Journal of the Marine Biological Association of the United Kingdom 53, 531-538.

Ennis, G.P., 1983. The effect of wind direction on the abundance and distribution of decapod crustacean larvae in a Newfoundland nearshore area. Canadian Technical Report of Fisheries and Aquatic Sciences 1138, 19 pp.

Ennis, G.P., 1995. Larval and postlarval ecology. In: Biology of the Lobster *Homarus americanus"*. Edited by J.R. Factor. Academic Press, 23-46.

Estrella, B.T., McKiernan, D.J., 1989. Catch-per-unit-effort and biological parameters from the Massachusetts coastal lobster (*Homarus americanus*) resource: description and trends. United States Department of Commerce, NOAA Technical Report NMFS SSRF 81, 1-21.

Finsterle, K., 1996. Experimentelle Untersuchungen zu Aufzucht und Verhalten juveniler Hummer, *Homarus gammarus*. Diplomarbeit, Carl von Ossietzky Universität Oldenburg.

Fiore, D.R. Tlusty, M.F., 2005. Use of commercial *Artemia* replacement diets in culturing larval American lobsters (*Homarus americanus*). Aquaculture 243, 291-303.

Fishery Statistics, 1950-2007. Eurostat database of European Commission. www.epp.eurostat.ec.europa.eu

Floreto, E. A. T., Bayer, R.C., Brown, P.B., 2000. The effects of soybean-based diets, with and without amino acid supplementation, on growth and biochemical composition of juvenile American lobster, *Homarus americanus*. Aquaculture 189, 211–235.

Franke, H.-D., Gutow, L., 2004. Long-term changes in the macrozoobenthos around the rocky island of Helgoland (German Bight, North Sea). Helgoland Marine Research 58, 303-310.

Franke, H.-D., Janke, M., 1998. Mechanisms and consequences of intra- and interspecific interference competition in *Idotea baltica* (Pallas) and *Idotea emarginata* (Fabricius) (Crustacea: Isopoda): A laboratory study of possible proximate causes of habitat segregation. Journal of Experimental Marine Biology and Ecology 227, 1-21.

Gendron, L., Sainte-Marie, B., 2006. Growth of juvenile lobster *Homarus americanus* off the Magdalen Islands (Quebec, Canada) and projection of instar and age at commercial size. Marine Ecology Progress Series 326, 221-233.

Gibson, F.A., 1969. Age, growth and maturity of Irish lobsters. Irish Fisheries Investigation 85, 37-44.

Goemann, O., 1990. "Echt" Helgoländer Hummer. Kohlrenken Verlag Oldenburg, Oldenburg, 82 pp.

Greve, W., Reiners, F., Nast, J., 1996. Biocoenotic changes of the zooplankton in the German Bight: the possible effects of eutrophication and climate. ICES Journal of Marine Science 53, 951-956.

Greve, W., Reiners, F., Nast, J., Hoffmann, S., 2004. Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. Helgoland Marine Research 58, 274-288.

Hannesson, R., 2007. Geographical distribution of fish catches and temperature variations in the northeast Atlantic since 1945. Marine Policy 31, 32-39.

Harding, G.C., Drinkwater, K.F., Vass, W.P., 1983. Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Dulf of Maine: a new synthesis. Canadian Journal of Fisheries and Aquatic Science 40, 168-184.

Harms, J., 1993. Check list of species (algae, invertebrates and vertebrates) found in the vicinity of the island of Helgoland (North Sea, German Bight) - a review of recent records. Helgoland Marine Research 47, 1-34.

Harms, J., Schilling, U., Goemann, O., 1995. Der "Helgoländer Hummer". Natur und Museum 125, 33-40.

Hedgecock, D., Nelson, K., Simons, J., Schleser, R., 1977. Genetic similarity of American and European species of the lobster *Homarus*. The Biological Bulletin 152, 41-50.

Hepper, B.T., 1967. On the growth at moulting of lobsters (*Homarus vulgaris*) in Cornwall and Yorkshire. Journal of the Marine Biological Association of the U. K. 47, 629-643.

Hepper, B.T., 1970. The growth at moulting of lobsters (*Homarus vulgaris*) Milne-Edwards, in the Menai Straits, North Wales ICES Shellfish and Benthos Committee 1970/K 10, 6 pp.

Hickel, W., 1972. Kurzzeitige Veränderungen hydrographischer Faktoren und der Sestonkomponenten in driftenden Wassermassen in der Helgoländer Bucht. Helgoländer Wissenschaftliche Meeresuntersuchungen 23, 383-392.

Holthuis, L.B., 1974. The lobsters of the superfamily Nephropidea of the Atlantic Ocean (Crustacean: Decapoda). Bulletin of Marine Science 24, 723-884.

Howard, A.E., 1983. The behaviour of hatchery-reared juvenile lobsters (*Homarus gammarus*), released and observed by divers. ICES CM 1983/K:3.

Hudon, C., Fradette, P., 1993. Wind-induced advection of larval decapods into Baie de Laisance (Îles de la Madeleine, Québec). Canadian Journal of Fisheries and Aquatic Sciences 50, 1422-1434.

Hughes, J.T., Schleser, R.A., Tchobanoglous, G., 1974. A rearing tank for lobster larvae and other aquatic species. The Progressive Fish-Culturist 36, 129-132.

IPCC, 2007. Climate Change 2007: Mitigation. Contribution of Working Group III to the fourth Assessment Report of the Intergovernmental Panel on Climate Change. Edited by Metz, O.R. Davidson, P.R. Bosch, R. Dave and L.A. Meyers. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA., 851 pp.

Jørstad, K.E., Farestveit, E., 1999. Population genetic structure of lobster (*Homarus gammarus*) in Norway, and implications for enhancement and sea ranching operation. Aquaculture 173, 445-455.

Jørstad, K.E, Agnalt, A.-L., Kristiansen, T.S., Nøstvold, E., 2001. High survival and growth of European lobster juveniles (*Homarus gammarus*) reared communally on natural-bottom substrate. Marine and Freshwater Research 52, 1431-1438.

Karnofsky, E.B., Atema, J., Elgin, R.H., 1989. Field observations of social behaviour, shelter use, and foraging in the lobster, *Homarus americanus*. The Biological Bulletin 176, 239-246.

Klimpel, J., 1965. Die neuzeitliche Entwicklung der Inselgemeinde Helgoland unter besonderer Berücksichtigung des Fremdenverkehrs. Verlagsanstalt Konstanz, Konstanz.

Kristiansen, T.S., Drengstieg, A., Bergheim, A., Drengstieg, T., Kollsgård, I., Svendsen, R., Nøstvold, E., Farestveid, E., Aardal, L., 2004. Development of methods for intensive farming of European lobster in recirculated seawater. Results from experiments conducted at Kvitsøy lobster hatchery from 2000 to 2004. Fisken og havet 6, 52 pp.

Lawton, P., Lavalli, K.L., 1995. Postlarval, juvenile, aldolescent, and adult ecology. In: Biology of the Lobster *Homarus americanus*. Edited by J.R. Factor. Academic Press, 47-91.

Little S.A., Watson III, W.H., 2005. Differences in the size at maturity of female American lobsters, *Homarus americanus*, captured throughout the range of the offshore fishery. Journal of Crustacean Biology 25, 585-592.

Lizárraga-Cubedo, H.A., Tuck, I., Bailey, N., Pierce, G.J., Kinnear, J.A.M., 2003. Comparisons of size at maturity and fecundity of two Scottish populations of the European lobster, *Homarus gammarus.* Fisheries Research 65, 137-152

MacDiarmid, A.B., Saint-Marie, B., 2006. Reproduction. In: Lobsters Biology, Management, Aquaculture and Fisheries. Edited by B.F. Phillips. Blackwell Publishing, Oxford, 45-68.

MacKenzie, B.R., 1988. Assessment of temperature effects on interrelationship between stage durations, mortality, and growth in laboratory-reared *Homarus americanus* Milne Edwards larvae. Journal of Experimental Marine Biology and Ecology 116, 87-98.

Maynard, D. R., Savoie, F., Landsburg, W., Roach, G., Wade, E., 1992. The Cape Breton experiment on legal minimum lobster size increase: an intermediate report. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 92/64, 1-47.

Meeresumwelt-Datenbank (MUDAB). Zentrale Datenbank des Bund/Länder-Messprogramms für die Meeresumwelt von Nord- und Ostsee. www.bsh.de.

Mehrtens, F., 2008. Untersuchungen zu den Entwicklungsbedingungen des Europäischen Hummers (*Homarus gammarus*) bei Helgoland in Freiland und Labor. PhD thesis, Universität Hamburg, Germany.

Mehrtens, F., Stolpmann, M., Buchholz, F., Hagen, W., Saborowski, R., 2005. Locomotory activity and exploration behaviour of juvenile European lobsters (*Homarus gammarus*) in the laboratory. Marine and Freshwater Behaviour and Physiology 38, 105-116.

Mills, D.J., Johnson, C.R., Gardner, C., 2008. Bias in lobster tethering experiments conducted for selecting low-predation release sites. Marine Ecology Progress Series 364, 1-13.

Ministerium für Landwirtschaft, Umwelt und ländliche Räume 1981, 1999, 2005. Landesverordnung über die Ausübung der Fischerei in den Küstengewässeren (Schleswig-Holsteinische Küstenverordnung – Küfo), Germany.

Moksness, E., Støle, R., van der Meeren, G., 1998. Profitability analysis of sea ranching with Atlantic Salmon (*Salmo salar*), Arctic charr (*Salvelinus alpinus*), and European lobster (*Homarus gammarus*) in Norway. Bulletin of Marine Science 62, 689-699.

Morgan, S.G., 1995. The timing of larval release. In*:* Ecology of Marine Invertebrate Larvae. Edited by L. McEdward. CRC Press, Boca Raton, 175-191.

Neil, D.M., MacMillan, D.L., Robertson, R.M., Laverack, M.S., 1976. The structure and function of thoracic exopodites in the larvae of the lobster *Homarus gammarus* (L.). Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences 274, 53-68.

Nichols, J.H., Lawton, P., 1978. The occurrence of the larval stages of the lobster *Homarus gammarus*, (Linnaeus, 1758) off the northeast coast of England in 1976. Journal du Conseil - Conseil International pour l'Exploration de la Mer 38, 234-243.

Nicosia, F., Lavalli, K., 1999. Homarid lobster hatcheries: Their history and role in research, management, and aquaculture. Marine Fisheries Review 61, 1-57.

Perkins, H.C., 1972. Developmental rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne-Edwards). Fishery Bulletin 70, 95-99.

Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. Science 308, 1912-1915.

Reichert, K., Buchholz, F., 2006. Changes in the macro-zoobenthos of the intertidal zone at Helgoland (German Bight, North Sea): A survey of 1984 repeated in 2002, Helgoland Marine Research, 60, 213-223.

Reichert, K., Buchholz, F., Gimenez, L. 2008. Community composition of the rocky intertidal at Helgoland (German Bight, North Sea), Helgoland Marine Research, 62, 357-366.

Rickmers, H.P., 1980. Helgoland Naturdenkmal der Nordsee - Deutsche Schicksalsinsel. Carl W. Dingwort Verlag.

Sastry, A.N., Zeitlin-Hale, L., 1977. Survival of communally reared larval and juvenile lobsters, *Homarus americanus*. Marine Biology 39, 297-203.

Schmalenbach, I., Buchholz, F., in press. Vertical positioning and swimming performance of lobster larvae (*Homarus gammarus*) in an artificial water column at Helgoland, North Sea. Marine Biology Research.

Schmalenbach, I., Franke, H.-D., in prep. Temperature effects on embryonic and larval development of the European lobster (*Homarus gammarus*) at Helgoland, North Sea - potential impact of the recent warming trend on lobster recruitment.

Schmalenbach, I., Buchholz, F., Franke, H.-D., Saborowski, R., 2009. Improvement of rearing conditions for juvenile lobsters (*Homarus gammarus*) by co-culturing with juvenile isopods (*Idotea emarginata).* Aquaculture 289, 297-303.

Schnackenberg, W., 1953. Die Deutsche Seefischerei in Nordsee und Nordmeer, Kröger, Hamburg-Blankenese, Germany.

Shleser, R., Gallagher, M., 1974. Formulations of rations for the American lobster, *Homarus americanus*. Proceedings of the World Mariculture Society 5, 157-164.

Simpson A.C., 1961. A contribution to the bionomics of the lobster (*Homarus vulgaris* Edw.) on the coast of North Wales. Fishery Investigations London, Series 2, 23**,** 1–28.

Southward, A.J., Hawkins, S.J., Burrows, M.T., 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. Journal of Thermal Biology 20, 127-155.

Svåsand, T., 1993. Are reared juveniles fit for releases into the wild? ICES C.M 1993/F: 34.

Svåsand, T., 2004. Why juvenile quality and release strategies are important factors for success in stock enhancement and sea ranching, In: Stock Enhancement and Sea Ranching. Developments, pitfalls and opportunities. Edited by K.M. Leber., S. Kitada, H.L. Blankenship and T. Svåsand. Blackwell Publishing Ltd, Oxford, 61-70.

Templeman, W., 1933. Female lobsters handicapped in growth by spawning. Fisheries Research Board of Canada Atlantic Progress Report 6, 5-6.

Templeman, W., 1936a. The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). Journal of Biology Board of Canada 2, 485-497.

Templeman, W., 1936b. Local differences in the life history of the lobster (*Homarus americanus*) on the coast of the Maritime Provinces of Canada. Journal of the Biological Board of Canada 2, 41-88.

Thoma, B., 2006. Auswirkungen einer Belastung mit Erdölkohlenwasserstoffen auf die Chemorezeption und das Verhalten von juvenilen Taschenkrebsen (*Cancer pagurus*, L.) und (*Homarus gammarus*, L.). Diplomarbeit, IfM Kiel.

Thomas, H.J., 1958. Observations on the increase in size at moulting in the lobster (*Homarus vulgaris* M. Edw.). Journal of the Marine Biological Association of the U. K. 37, 603-606.

Tully, O., Bell, M., O'Leary, A., McCarthy, A., O'Donovan, V., Nee, D., 2006. The lobster (*Homarus gammarus* L.) fishery: Analysis of the resource in 2004/2005. Fisheries Resource Series 5.

Tveite, S., Grimsen, S., 1995. Survival of one year old artificially raised lobsters (*Homarus gammarus*) released in southern Norway. ICES. Marine Science Symposia 199, 73-77.

Ulrich, I., 1998. Populationsgenetische und verhaltensbiologische Untersuchungen am Helgoländer Hummer. Dissertation, Universität Hamburg.

Ulrich, I., Müller, J., Schütt, C., Buchholz, F. 2001. A study of population genetics in the European lobster, *Homarus gammarus* (Decapoda, Nephropidae). Crustaceana 74, 825-837.

van Bernem, K.H., Lübbe. T., 1997. Öl im Meer, Katastrophen und langfristige Belastungen. Wissenschaftliche Buchgesellschaft, Darmstadt, Germany.

van der Meeren, G.I., 1993. Initial response to physical and biological conditions in naive juvenile lobsters *Homarus gammarus* L. Marine and Freshwater Behaviour and Physiolgy 24, 79-92.

van der Meeren, G.I., 2000. Predation on hatchery-reared lobsters *Homarus gammarus* released in the wild. Canadian Journal of Fisheries and Aquatic Sciences 57, 1794-1803.

van der Meeren, G.I., Tveite, S., 1998. Fishery and management of the lobster (*Homarus gammarus*) in Norway. In: The European lobster *Homarus gammarus* (L.): Proceedings from the Seminar at Kvitsøy 1995. Edited by G.I. van der Meeren and O. Soldal. Fisken og havet 1998, 13, 72-76.

van der Meeren, G.I., Agnalt, A.L., Jørstad, K.E. 1998. Lobster (*Homarus gammarus*) stock enhancement in Norway, experiences from a large-scale release project from 1990-1997. In: Proceedings of a workshop on lobster stock enhancement held in the Magdalen Islands (Quebec) from October 29 to 31, 1997. Edited by L. Gendron. Canadian Industry Report of Fisheries and Aquatic Sciences 244, 63-68.

Van Olst, J.C., Carlberg, J.M., Ford, R.F., 1975. Effects of substrate type and other factors on the growth, survival, and cannibalism of juvenile *Homarus americanus* in mass rearing systems. Proceedings of the World Mariculture Society 6, 261-274.

Waddy, S.L., 1988. Farming the homarid lobsters: State of the art. World Aquaculture 19, 63-71.

Walter I., 2005. Experimentelle Untersuchungen zum Einfluss von Erdölkohlenwasserstoffen auf Nahrungssuche und Aggressionsverhalten des Europäischen Hummers *Homarus gammarus* (L.). PhD thesis, Universität Hamburg, Germany.

Walter, I., Schmidt, M., Buchholz, F., 2008. Der Einfluss von Erdöl auf das Verhalten von Hummern. Effekte auf Nahrungssuche und Aggression. VDM Verlag Dr. Müller Aktiengesellschaft & Co. KG, Saarbruecken.

Watt, L., Arthur, G., 1996. The improvement of the Shetland lobster fishery through stock enhancement-1. North Atlantic Fisheries College. Fisheries development note 2, 4 pp.

Wickens, J.F., Lee, D.O'C, 2002. Crustacean Farming. Ranching and Culture, Blackwell Science Ltd. London.

Williams, A.B., 1988. Lobster of the world – an illustrated guide. Osprey Books, Huntington, New York.

Wiltshire, K.H., Malzahn, A.M., Wirtz, K., Janisch, S., Mangelsdorf, P., Manly, B.F.J., Boersma, M., 2008. Resilience of North Sea phytoplankton spring blooms dynamics: An analysis of long-term data at Helgoland Roads. Limnology and Oceanography 53, 1294-1302.

Wray, T., 2005. Molluscs, lobster & crab. Fish Farming International 32.

SUMMARY

Growth conditions, reproduction and recruitment processes of the endangered lobster population (*Homarus gammarus*) at Helgoland were examined from 2005 to 2008 to assess the present status and the reasons for the missing recovery of the local stock, and to lay a basis for a future large-scale stock enhancement.

Firstly, the growth conditions for the local population and for released cultured lobsters were examined within a mark-recapture programme. Furthermore, the impact of temperature on the embryonic and larval development as well as the influence of light and currents on the behaviour of larvae were studied. Finally, rearing conditions for juvenile lobsters were improved in order to facilitate a future restocking programme.

The first study (Manuscript I) continued the mark-recapture study initiated by Mehrtens (2008). Since 2006, logbook data from the commercial fishery have been included to this study. Additionally, since 2007 individual data of commercial landed lobsters were recorded. The growth parameters such as the size of females at the onset of functional maturity (85 mm CL) were similar to those reported for other European populations. The population size was estimated at about 25,000 lobsters, similar to previous studies. This corresponds to only about 2 % of its former size (1.5 million lobsters; about 5 lobsters·100 m^{-2}) in the 1930s. In 2008, significantly more lobsters were landed than in the two seasons before. Nevertheless, landings remained at the same low level of 200-300 lobsters per year during the last decade. Apparently, the population size has decreased below a critical level, where reproduction does not suffice to allow for a recovery of the population on its own.

As the carrying capacity of the Helgoland area for lobsters apparently is not limiting presently, it may be expected that released specimens will have a good chance of survival so that their development under natural conditions can be studied. Juvenile lobsters (n = 9,560) released into the outer harbour area and into the field outside the harbour were recaptured at high rates of 20.8 % and 6.7 %, respectively. The return rate of lobsters was comparable to those reported in studies from other countries. Furthermore, cultured lobsters showed strong fidelity to their release sites (> 76 %). This was confirmed by dive census, which recorded higher abundance of lobsters in a previous release area (1.4 lobsters·100 m^{-2}) compared to control areas (0.5 lobsters·100 m^{-2}). Cultured lobsters which were recaptured after 3 to 9 years indicated favourable conditions for lobster

development in the field. The animals attained minimum legal size for commercial use (MLS = 85 mm CL) after 4-5 growing seasons and the proportion of hatchery-reared lobsters in commercial landings reached 6 %.

Furthermore, the proportion of mature females in the commercial catches was about 10 %. The minimum legal size of lobsters should ensure that only specimens are put on the market which have already reproduced. According to the results of the present study, the minimum legal size should be increased for females in general, or else the catch of females should be completely banned. Such measures should help to increase the reproduction potential of the population. Furthermore, the local stock should be enhanced with cultured lobsters, according to measures undertaken in Norway which have shown that the release of laboratory-reared lobsters can actually lead to a sustained increase in population density.

In the second study (Manuscript II) temperature constrains were considered which play an important role in the control of reproduction processes. The effect of temperature on the embryonic and larval development was examined to answer the questions (1) if lobster larvae can still successfully develop at Helgoland in view of potential constraints by the recent warming of the North Sea, and (2) how lobster development might be impacted by an ongoing warming trend. The study showed that larvae developed successfully at temperatures above 14 °C and that the recent warming of the North Sea does not significantly affect the timing of larval hatching in the field. However, an ongoing warming trend with warmer winter periods probably would accelerate the embryonic development to such an extent, that larvae were released earlier in the season at suboptimal environmental conditions for their development. Larval release at too low temperatures and/or too poor food abundance and quality might hamper considerably a successful recruitment of the local lobster population in the future.

The third study (Manuscript III) considered the specific condition connected with the geographical and ecological isolation of the Helgoland lobster population. In this respect, a further problem for recruitment success is that larvae could be swept away from their suited environment. Accordingly, the impact of the light regime and currents on the swimming performance of larvae (Zoea I, II, III) was examined under laboratory conditions to define recruitment mechanisms. Newly hatched larvae showed a marked positive phototaxis and swam directly towards any light source, i.e. in the field probably towards the sea surface. Accordingly, this phase is critical for larval drift. However, water

masses at Helgoland circulate the island with the tides several times, thus probably keeping larvae within the rocky habitat during their short pelagic phase. During the next stages, positive phototaxis decreased so that larvae tended to hold their position near the bottom, and furthermore their ability to swim against currents increased (rheotaxis). This specific larval behaviour helps to avoid uncontrolled drift and to stay near the suitable substrate.

In the final study (Manuscript IV), rearing conditions for juvenile lobsters were optimized. A method allowing for the production of large numbers of juveniles at reasonable costs is a prerequisite for a large-scale restocking programme. These improvements were considered under both ecological and economical aspects. As clawed lobsters are cannibalistic, they were reared in single compartments to increase their survival rate. A sustainable local resource, the carcasses of edible crabs (*Cancer pagurus*), obtained as discard from local fishermen, proved to be suited and valuable diet for lobsters. Furthermore, live juvenile isopods (*Idotea emarginata*), which can be easily produced in mass cultures, were used as supplementary diet and "cleaning organisms" for the lobster boxes. The costs for water supply and energy can be reduced by using recirculation systems and warmer sea temperatures in summer. Under these improved rearing conditions, juvenile lobsters reached a total length of 3 cm (minimum release size) within about 3 months at a survival rate of more than 90 %. Under conventional rearing conditions, this size is not reached until after one year. Accordingly, the improvements allow the production and release of lobsters twice a year.

The field and laboratory studies have shown that the environmental conditions at Helgoland are still favourable to the development of lobsters from the egg to the adult phase. However, to ensure the persistence of the local population, the density of which probably has declined below a critical density, further fishery regulations and stock enhancement programmes should be established accompanied by scientific support and suited management procedures.

ZUSAMMENFASSUNG

Es wurden die Wachstumsbedingungen sowie die Reproduktions- und Rekrutierungsprozesse der stark dezimierten Helgoländer Population des Europäischen Hummers (*Homarus gammarus*) untersucht (2005-2008). Der derzeitige Zustand und die Ursachen der trotz langjähriger Schutzmaßnahmen ausbleibenden Erholung der Population sollten quantitativ abgeschätzt werden. Die Abschätzungen könnten sodann als Basis für eine große Wiederaufstockungsmaßnahme der Population mit Zuchthummern dienen.

Zunächst wurden in Felduntersuchungen die Wachstumsbedingungen der lokalen Population und ausgewilderter Zuchthummern anhand eines Markierungs-Wiederfang-Programms erfasst. Weiterhin wurde der Einfluss der Wassertemperatur auf die Embryonal- und Larvalentwicklung untersucht, außerdem wie Licht und Strömungen das Verhalten von Larven beeinflussen. Parallel dazu wurden die Aufzuchtbedingungen für juvenile Hummer im Hinblick auf eine mögliche Aufstockung der Population optimiert.

Der erste Teil dieser Arbeit (Manuskript I) schließt an das Markierungs-Wiederfang-Programm (2000-2004) von Mehrtens (2008) an. Über die bisherigen Auswertungen hinaus wurden seit 2006 die Logbucheinträge aus der lokalen Fischerei einbezogen und seit 2007 auch die kommerziell angelandeten Hummer miterfasst bzw. vermessen. Die Wachstumsraten sowie die Größe der Weibchen beim Erreichen der Geschlechtsreife (85 mm Carapaxlänge) waren mit entsprechenden Werten anderer Europäischer Populationen vergleichbar. Die Größe des derzeitigen Bestandes beläuft sich auf etwa 25.000 Tiere. Sie deckt sich mit dem in früheren Studien ermittelten Werte, entspricht aber nur etwa 2 % des früheren Bestandes in den 1930iger Jahren von 1.5 Millionen Tieren (etwa 5 Tieren·100 m^{-2}). Die erhobenen Logbuchdaten erfassten 2008 signifikant höhere Fangraten als in den beiden Jahren zuvor. Jedoch stagnierte der Jahresfang bei 200-300 Tieren während der letzten Dekaden. Die Populationsgröße scheint unter eine kritische Grenze geraten zu sein, die es den Tieren stark erschwert oder unmöglich macht, aus eigener Kraft eine wesentliche Erholung des Bestandes herbeizuführen.

Die Tragfähigkeit des Habitats ist vermutlich nicht limitierend, sollte also ein erfolgreiches Aussetzen von juvenilen Zuchthummern erlauben, deren Entwicklung sodann unter natürlichen Bedingungen untersucht werden kann. Im Hafenbereich und auf dem Felssockel Helgolands ausgesetzte juvenile Zuchttiere (n = 9.560) wurden dementsprechend zu 20,8 % bzw. zu 6,7 % wieder gefangen. Die Höhe der

Wiederfangraten aus dem Feld war mit denen in anderen Ländern vergleichbar. Außerdem waren die Tiere ihrem Aussetzgebiet sehr standorttreu (> 76 %). Dies zeigten auch Tauchstudien, die eine höhere Dichte von adulten Hummern in einem früheren Aussetzgebiet (1,4 Tiere·100 m^{-2}) als in Kontrollgebieten (0,5 Tiere·100 m^{-2}) erfassten. Der Zustand der 3 bis 9 Jahre alten wiedergefangenen Zuchttiere zeigte gute Entwicklungsbedingungen im Freiland an. Die Tiere erreichten nach 4-5 Jahren die Mindestfanggröße von 85 mm Carapaxlänge und waren bereits bis zu 6 % im kommerziellen Fang enthalten. Weiterhin bestanden 10 % des Fanges aus reproduktionsfähigen Weibchen. Dabei zeigte sich, dass das derzeitige Mindestfangmaß nicht garantieren kann, dass nur Tiere in den Handel kommen, die sich bereits reproduziert haben. Daher sollten im weiteren Fischerei-Managementplan möglichst die Mindestfanglängen erhöht bzw. alle Weibchen und nicht nur die eiertragenden unter Schutz gestellt werden, um somit das Reproduktionspotenzial des Bestandes zu erhöhen. Zusätzlich könnte versucht werden, den Bestand mit Zuchthummern aufzustocken, in Anlehnung an Studien in Norwegen, die gezeigt haben, dass ein solches Vorgehen die Populationsdichte im Freiland erhöhen kann.

In der zweiten Studie (Manuskript II) wurde besonderes Augenmerk auf den Faktor Temperatur gelegt, da dieser besonders für die zeitliche Steuerung der Reproduktionsabläufe eine entscheidende Rolle spielt. Der Einfluss der Temperatur auf die Embryonal- und Larvalentwicklung wurde untersucht, ausgehend von der Fragestellung (1) ob sich die Larven in Bezug auf die derzeitige Nordseeerwärmung noch erfolgreich entwickeln können und (2) wie sich eine weitere Erwärmung auf die Entwicklung der Hummer bei Helgoland auswirken könnte. Die Studie zeigte, dass sich die Larven erst über 14 °C erfolgreich entwickeln und dass die derzeitige Erwärmung wohl noch keinen negativen Einfluss auf die Larvalentwicklung ausübt. Eine weitere Erwärmung und als Folge davon wärmere Winter könnten die Embryonalentwicklung aber derart verkürzen, dass die Larven deutlich früher im Jahresverlauf bei dann noch suboptimalen Bedingungen hinsichtlich der Wassertemperatur und des Nahrungsangebots schlüpfen. Dies würde den Rekrutierungserfolg der Hummer vermutlich deutlich reduzieren.

Im dritten Teil der Arbeit (Manuskript III) wurde die besondere geographisch und ökologisch isolierte Lage der Insel Helgoland verglichen mit ähnlichen Lebensräumen des Hummers in Betracht gezogen, da eine Verdriftung der Larven aus dem Gebiet den

Rekrutierungserfolg beeinflussen kann. Dazu wurde der Einfluss von Licht und Strömung auf das Schwimmverhalten der Larven (Zoea I, II, III) im Labor untersucht, um den Rekrutierungsmechanismus zu definieren. Frisch geschlüpfte Larven sind positiv phototaktisch. In dieser Phase ist die Gefahr der Verdriftung besonders groß. Da die Wassermassen aber nicht bei jeder Tide vollständig ausgetauscht werden, führt dies zu der Annahme, dass die Larven nicht aus in ihrem Habitat entfernt werden. In der weiteren Larvalentwicklung nimmt die positive Phototaxis ab und die Larven sind mehr und mehr in Bodennähe verteilt. Zusätzlich nimmt die morphologisch bedingte Fähigkeit zu, sich in der Strömung aktiver zu bewegen (Rheotaxis). Dieses spezielle Verhalten zeigt, dass die Larven einer Verdriftung entgegen wirken und somit in ihrem Habitat verbleiben können.

Im Hinblick auf eine möglichst große Wiederaufstockungsmaßnahme wurden in der abschließenden Studie (Manuskript IV) die Zuchtbedingungen optimiert, um bei vertretbarem finanziellen Aufwand Besatztiere in einem solchen Umfang produzieren zu können, wie es für eine deutliche und dann stabile Erhöhung der Dichte der Helgoländer Hummerpopulation im Freiland notwendig ist. Da Hummer kannibalisch sind, ist eine kostenintensive Einzelhälterung notwendig, um eine hohe Überlebensrate zu erreichen. Alle Bestrebungen zur ökologischen und ökonomischen Optimierung müssen von diesem Tatbestand ausgehen. Eine optimale und hochwertige Futterversorgung lieferten die Körper der Taschenkrebse (*Cancer pagurus*), die aus der lokalen Fischerei als Fischereiabfall (Discard) zur Verfügung stehen, da traditionell nur die Scheren der Krabben als Nahrungsmittel in den Handel gebracht werden. Auf diese Weise könnten lokale Ressourcen effektiv und nachhaltig genutzt werden. Zusätzlich dienten juvenile Asseln (*Idotea emarginata*) aus eigener Massenzucht als Zusatzfutter. Diese Futtertiere ermöglichen die schützende Pigmentierung des Hummerpanzers und dienten gleichzeitig als "Reinigungsorganismus" in den Hälterungsboxen. Im Sommer ermöglicht es die lokale Seewassertemperatur, die Heizkosten für die Zucht zu senken. Weiterhin werden die Kosten für Wasseraufbereitung und Temperierung durch den Betrieb von Keislaufanlagen gering gehalten. Unter diesen Zuchtbedingungen erreichen die Tiere spätestens nach 3 Monaten eine Aussetzgröße von 3 cm Gesamtlänge bei einer Überlebensrate von über 90 %. Diese Größe würden sie unter einem natürlichem Jahresgang und herkömmlichen Bedingungen erst nach einem Jahr erlangen. Dementsprechend würden die optimierten Aufzuchtbedingungen zu Wachstumsraten führen, die es ermöglichen zweimal im Jahr eine Gruppe von Tieren zur Aussetzgröße heranzuziehen und ins Freiland zu entlassen.

Die Feld- und Laborstudien zeigten, dass der Helgoländer Felssockel generell gute Entwicklungsbedingungen für den Hummer vom Ei bis zur adulten Phase bietet. Um jedoch den Bestand der Population, deren Dichte offensichtlich eine kritische Größe unterschritten hat, gewährleisten zu können, sollten weitere Schon- und Aufstockungsmaßnahmen, begleitet von wissenschaftlichen Untersuchungen durchgeführt werden.

APPENDIX

Table 1 Lobster landings (1615-2008) of the European lobster (*H. gammarus*) around the island of Helgoland (Klimpel, 1965, Goemann, 1980, Anonymous, 1980-2008, * local fishermen, pers. communication).

Year	Number of lobsters	Catch (tons)	Year	Number of lobsters	Catch (tons)
~1615	37000	-	1932	68950	34.93
~1790	40-50000	-	1933	77011	38.11
1883	30000	-	1934	80238	37.62
1888	33000	-	1935	63047	28.84
~1894	60-70000	35.0	1936	76717	36.88
1906	54000	27.2	1937	87014	41.33
1907	30082		1938	48096	22.77
1908	27000	13.43	1939	56119	28.00
1909	25068	12.58	1940	54878	32.75
1910	22048	13.03	1941	44733	23.76
1911	28173	17.63	1942	40466	20.85
1912	27300	14.36	1943	26989	13.67
1920	24248	17.42	1944	21212	10.65
1921	23363	14.87	1950	-	~10.00
1922	13498	8.91	1951	-	22.46
1923	11357	6.49	1952	-	12.54
1924	18970	10.69	1955	-	7.12
1925	19285	9.93	1956	-	5.67
1926	22405	11.65	1957	-	3.30
1927	20350	10.67	1958	-	3.31
1928	40448	20.47	1959	-	4.90
1929	44260	20.56	1960	-	6.88
1930	53866	25.38	1961	9763	5.82
1931	82751	44.20	1962	-	5.46

Table 1 (*Continued*)

Year	Number of lobsters	Catch (tons)	Year	Number of lobsters	Catch (tons)
1963	-	4.88	1986	36	0.05
1964	-	2.78	1987	-	0.48
1965	-	1.39	1988	576	0.55
1966	-	1.25	1989	393	0.35
1967	-	1.14	1990	482	0.55
1968	646	0.52	1991	109	0.11
1969	1052	0.99	1992	102	0.09
1970	1037	1.04	1993	32	0.05
1971	1037	0.92	1994	146	0.19
1972	-	0.76	1995	71	0.08
1973	710	0.61	1996	246	0.29
1974	523	0.42	1997	101	0.11
1975	456	0.39	1998	248	0.28
1976	681	0.68	1999	212	0.30
1977	485	0.65	2000	97	0.10
1978	732	0.89	2001	73	0.07
1979	899	0.73	2002	56*	-
1980	453	0.42	2003	43	0.04
1981	356	0.40	2004	235*	-
1982	458	0.53	2005	201	0.23
1983	165	0.18	2006	201	0.23
1984	125	0.14	2007	193	0.23
1985	186	0.27	2008	308	0.44

DANKSAGUNG

Weiterhin möchte ich danken Reinhold Müller, Katharina Reichert und Uwe Nettelmann dafür dass ihr da wart.

Zu guter Letzt möchte ich meinen Eltern und meiner Schwester danken, die immer für mich da waren, wenn ich sie gebraucht habe.