Mechanisms of a successful immigration from north-east Asia: population dynamics, life history traits and interspecific interactions in the caprellid amphipod *Caprella mutica* Schurin, 1935 (Crustacea, Amphipoda) in European coastal waters

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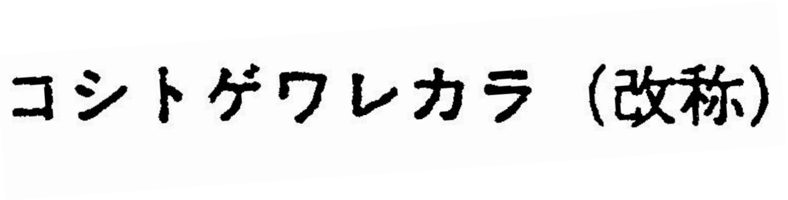

コシトゲワレカラ（改称）

(Caprella mutica)

“Koshitoge-warekara (Jap.): the spine-waist skeleton shrimp”

Silent Samurai

(poet unknown)

silent samurai wind warriors
stand on many mountains
facing the dying sun
slivers of sun skewered
on their swirling swords
their dance at the death of day
silent sentinels
they fight for the spoils of wind
the blood of birds
drips from their blades
as they fill the sky
nowhere for them to go
above or below around or behind
only battle the blades
marvellous and majestic they are
intruders
invaders

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Abstract

The accidental or deliberate introductions of species to areas outside their native ranges often represent irreversible events and can deeply affect native communities. Particularly when spreading and developing spectacular population increases, non-native ('invasive') species may influence local food webs as predators or aggressively compete with other species for limited resources and cause severe ecological and economic damage. To make predictions useful for the management and control of non-native species, it is crucial to understand the nature of successful invaders, the invasion process and the impacts non-native species may have.

In the present work, I applied field and laboratory studies to investigate the underlying mechanisms of the successful establishment of the Japanese Skeleton shrimp *Caprella mutica* Schurin, 1935 (Crustacea, Amphipoda, Caprellidea) introduced to European coastal waters. This was achieved by four different experiments investigating (i) the seasonal population dynamics, abundance and structure of *C. mutica* in the field, (ii) the life history traits of *C. mutica* such as survival, development and reproduction in the laboratory, (iii) the relationships between *C. mutica* and different native predators and (iv) the competitive interactions between *C. mutica* and its native congener, *Caprella linearis* (Linnaeus, 1767).

Seasonal population dynamics

In a detailed investigation the population dynamics of *C. mutica* introduced to two different European areas were studied over a period of 17 months. Monthly sampling structures were deployed at two water depths (surface level and 3-4 m) at each three sites on the west coast of Scotland, U.K. and at the Island of Helgoland, German Bight (North Sea), where *C. mutica* is typically found in fouling communities on artificial substrata. The sites differed in their environmental characteristics and their levels of anthropogenic interference. Seasonal abundance, demographic structure, sex-ratio and size-frequency distributions were analysed.

Temperature was the most consistent factor controlling the population dynamics of *C. mutica* at both study locations. Cycles were in phase with annual seawater temperatures and showed strong increases (> 200,000 ind. m^{-2}) during summer and early autumn.

Population increases were typically accompanied by high percentages of small sized juveniles (up to 80% of the population) reflecting high reproductive activity in female biased populations. During cold seasons population densities declined drastically to only few individuals (Germany) or even to zero (Scotland). Depth did not influence the overall population structure or abundance. Apart from natural stochastic processes in the population of *C. mutica*, the observed low winter and spring densities were most likely on account of limitations in the sampling strategy rather than on the species' ability to persist at low temperatures. Average annual population densities differed significantly between all sites. Different abiotic characteristics jointly affected the population densities of *C. mutica* to different degrees. Two Scottish sites exposed to increased freshwater influxes harboured lower densities than the site without freshwater influx. All sites with increased boating traffic revealed lower population densities than sites with less boating activity. Enhanced food availability at a Scottish salmon fish farm allowed for highest population densities at the Scottish location and largest body sizes. Low intraspecific effects might account for higher densities on isolated and space-limited structures (ropes or nets) than on large connecting surfaces (harbour walls and pontoons).

Life history traits

Over the last 40 years *C. mutica*, indigenous to north-east Asia, has successfully expanded its range into many parts of the world. In the present laboratory-based study, survival, development and reproduction of juvenile and adult individuals of *C. mutica* were investigated. Performances in a wide thermal range between 4 and 26°C were studied to provide a mechanistic interpretation of the seasonal persistence of *C. mutica* in north-western European coastal waters and to assess its range expansion towards high latitudes.

At 4°C, juvenile *C. mutica* reared in the laboratory showed highest survival rates, longest life spans of about four months and longest moulting intervals. Growth, however, was reduced and maturation failed in individuals reared at 4°C. At 10 and 16°C, females matured within two months. Females collected from field populations produced viable broods at experimental temperatures from 4 to 26°C. At 16°C, females showed highest numbers of viable broods with approximately 30 hatchlings in the first reproductive cycle. A maximum number of 85 hatchlings in one clutch was found in the 10°C treatment. The (calculated) thermal tolerance range for reproduction was between > 1.2 and 26.0°C. The results suggest that seasonal temperature ranges of north-western

European waters are optimal for *C. mutica* to persist all year round. High survival rates of winter hatchlings are a prerequisite for rapid population growth in spring and thus, mass occurrences during summer. The physiological ability of *C. mutica* to reproduce along a thermal gradient found at latitudes between 25 to 70°N would allow for a range expansion beyond the latitudes from which it has been reported so far (maximum 62°N). The distribution, however, is restricted to areas, in which temperatures remain between > 4 and 10°C for a minimum of two months (i.e., the maturation time at 10°C) and where periods of temperatures below 4°C do not exceed a duration of 4 months (i.e., the maximum duration of survival without growing mature). In view of globally increasing seawater temperatures, extensions beyond the proposed range may be expected.

Enemy release

In its introduced ranges, the non-native *C. mutica* is found on artificial structures in densities exceeding those of natural bottom-near habitats, where it is typically found in its native range. While enemy release may facilitate invasion success of non-native species, the presence of native enemies, in turn, may determine the abundance and distribution in its new areas. In the marine environment, artificial structures high off bottom-near natural habitats (e.g. harbour constructions, aquaculture facilities or offshore wind parks) may serve as refuges with reduced predatory pressure and available resources, thus opening ‘invasion opportunity windows’ for non-native species.

In the present study, laboratory-based feeding trials revealed that native benthic and nektonic predators (the shore crab *Carcinus maenas* (Linnaeus, 1758) and the goldsinny wrasse *Ctenolabrus rupestris* (Linnaeus, 1758), respectively) selectively fed on large individuals of *C. mutica* rather than on small individuals and consumed more caprellids in bottom near habitats than at surface level. Transcribed to the field, artificial structures, widely isolated from natural bottom-near habitats, may serve as enemy poor refuges supporting dense populations of *C. mutica* while benthic predation pressure restricts mass occurrences and the spread of the non-native species into natural habitats.

Competition

The overall absence of the native European caprellid amphipod *Caprella linearis*, formerly inhabiting artificial structures in areas of human activity in the German Bight (North Sea), is hypothesized to be the result of interspecific competition with the non-native congener *C. mutica*. In the present study, the underlying mechanisms of interspecific competition for space between *C. linearis* and *C. mutica* were studied. Different densities and density combinations were tested in laboratory experiments. Initially low (equivalent to 1,000 ind. m^{-2}) and high (equivalent to 10,000 ind. m^{-2}) numbers of *C. mutica* were each confronted with low and high numbers of *C. linearis* for 24 hours. Displacement, mortality and mutual predation were assessed for both competitors.

In all experimental approaches and density combinations the introduced *C. mutica* remained unaffected by the native *C. linearis*. Likewise, initially low densities of *C. linearis* remained unaffected by competition with *C. mutica*, even if densities of the latter were tenfold higher. Initially high densities of *C. linearis*, by contrast, provoked intraspecific effects, making the native caprellid subject to intense interspecific competition. In encounters with initially high densities of *C. linearis, C. mutica* successfully out-competed *C. linearis* by direct interference irrespective of the initial densities of the invader. Mutual predation was the mechanism of interference competition resulting in enhanced mortality of *C. linearis*. The present results support the assumption that populations of the native *C. linearis* have been displaced from artificial habitats by the non-native *C. mutica*. In contrast, natural benthic habitats may provide sufficient space and suitable substratum to allow for habitat segregation. However, because of the generally patchy and fluctuating occurrence of *C. linearis*, the overall persistence of local populations of the native caprellid in European coastal waters may be endangered by the introduced non-native congener *C. mutica*.

The results from the present work suggest that apart from species-specific traits which enable *C. mutica* to perform superiorly in its introduced ranges (i.e., rapid growth, short maturation time, high reproductive activity and broad tolerance towards environmental conditions), the availability of suitable structures is of paramount importance to the species' invasion succes in European coastal waters. Seasonal temperatures in north-western European waters provide optimal conditions for high reproductive activity and all year round peristence in its new habitats, but only on isolated artificial structures directed away from the seabed, *C. mutica* is able to avoid benthic predation pressure and thus, to develop massive population densities and out-compete its native congener.

Zusammenfassung

Der Eintrag gebietsfremder Arten in Regionen außerhalb ihres natürlichen Verbreitungsgebietes stellt oft ein irreversibles Ereignis dar und kann einen starken und nachhaltigen Einfluss auf bestehende Artengemeinschaften haben. Durch ihre starke Ausbreitungstendenz und die Ausbildung von Massenvorkommen können so genannte „invasive gebietsfremde Arten“ sowohl starke ökologische als auch ökonomische Schäden verursachen. Beispielsweise können sie mit einheimischen Arten in Konkurrenz um Raum und/oder Nahrung treten oder zu erheblichen Störungen etablierter Nahrungsnetze führen. Die Beurteilung der mit dem Eintrag gebietsfremder Arten verbundenen Risiken setzt eine genaue Kenntnis der Biologie und Ökologie dieser Arten sowie der Einwanderungsprozesse und der möglichen Einflüsse erfolgreicher Einwanderer auf einheimische Arten voraus. In kombinierten Freilanduntersuchungen und Laborexperimenten wurden in der vorliegenden Arbeit die Mechanismen der erfolgreichen Einwanderung des in europäische Küstengewässer eingetragenen und dort etablierten nordostasiatischen Gespensterkrebses *Caprella mutica* Schurin, 1935 (Crustacea, Amphipoda, Caprellidea) untersucht. Hierfür wurden (i) die saisonale Populationsdynamik von *C. mutica* im Freiland, (ii) Lebensdaten wie z.B. Überlebensraten, Entwicklung und Reproduktion im Labor, (iii) Beziehungen mit einheimischen Räubern und (iv) Konkurrenzbeziehungen zwischen *C. mutica* und der einheimischen Gespensterkrebsart *Caprella linearis* (Linnaeus, 1767) untersucht.

Saisonale Populationsdynamik

Über einen Zeitraum von 17 Monaten wurde die Populationsdynamik von *C. mutica* an zwei verschiedenen europäischen Standorten untersucht. Dafür wurden monatlich Proben von der Wasseroberfläche und in 3-4 m Tiefe an je drei Probennahmestellen an der Westküste Schottlands (Großbritannien) und der Insel Helgoland (südöstliche Nordsee, Deutschland) genommen, an denen *C. mutica* in der Regel in Aufwuchsgemeinschaften auf künstlichen Substraten zu finden ist. Die jeweiligen Probennahmestellen unterschieden sich in ihrer Umweltbeschaffenheit sowie im Grad anthropogener Störung. Aufgenommen wurden die saisonalen Veränderungen der

Abundanz, der demographischen Struktur, des Geschlechterverhältnisses und der Größenhäufigkeitsverteilung der Tiere.

An beiden Standorten wurde die Populationsdynamik von *C. mutica* in erster Linie vom saisonalen Temperaturverlauf bestimmt. Mit ansteigenden Temperaturen im Sommer und Frühherbst stiegen die Populationsdichten auf über 200.000 Ind. m^{-2} an und waren durch hohe Anteile juveniler Tiere bestimmt (bis zu 80% der Population). Die erhöhte reproduktive Aktivität von *C. mutica* in warmen Monaten wurde darüber hinaus durch vornehmlich weiblich dominierte Geschlechterverhältnisse verstärkt. Mit sinkenden Temperaturen nahmen die Populationsdichten am deutschen Standort bis auf einige wenige Individuen pro m^2 ab, während die Populationen in Schottland über die Wintermonate gänzlich verschwanden. Die beprobten Tiefen hatten keinen Einfluss auf die Populationsstruktur oder Abundanz. Abgesehen von natürlichen stochastischen Prozessen innerhalb der Populationen (z.B. altersbedingte natürliche Mortalität) sind die beobachteten niedrigen Populationsdichten während der Wintermonate vermutlich eher auf Limitationen in der Beprobungsstrategie zurückzuführen, als auf eine mögliche geringe Fähigkeit der Tiere Kaltwasserphasen zu überdauern. Die jahresdurchschnittlichen Populationsdichten an den verschiedenen Probennahmestellen beider Standorte schwankten erheblich und wurden durch unterschiedliche Umweltbedingungen verschiedentlich stark beeinflusst. So wurden in Schottland an den beiden Probennahmestellen, die unter starkem Süßwassereinfluss standen, niedrigere Individuendichten gefunden als an der Probennahmestelle, die vergleichsweise wenig ausgesüßt war. Weiterhin waren an den Probennahmestellen, die weniger stark von Booten frequentiert wurden, relativ höhere Dichten zu finden als an den Probennahmestellen, die stark von Booten frequentiert wurden. Die höchsten Populationsdichten und auch die größten Tiere wurden an einer schottischen Lachszucht-Farm gefunden, an der durch ganzjähriges Zufüttern Nahrung im Überfluss verfügbar war. Geringe intraspezifische Effekte (d.h. Dichteeffekte bzw. innerartliche Konkurrenz) mögen mitverantwortlich dafür sein, dass sich auf räumlich begrenzten und weitgehend isolierten Strukturen (z.B. auf Seilen oder Netzen) im Gegensatz zu großflächigen Strukturen (z.B. Hafenwänden oder Pontons) vergleichsweise hohe Populationsdichten ausbilden können.

Lebensdaten

In den letzten 40 Jahren hat sich das Verbreitungsgebiet des ursprünglich in Nordostasien beheimateten Gespensterkrebses *C. mutica* auf viele weltweite Standorte ausgedehnt. Um die erfolgreiche Etablierung von *C. mutica* in nordwest-europäischen Küstengewässern zu erklären und eine mögliche Expansion in höhere Breiten einzuschätzen, wurden in einer Laborstudie die Überlebensraten, die Entwicklung und die Reproduktion juveniler und adulter Individuen entlang eines Temperaturgradienten von 4 bis 26°C untersucht.

Im Labor bei 4°C aufgezogene Jungtiere von *C. mutica* überlebten vier Monate und wiesen damit höhere Überlebensraten, längere Überlebensspannen und längere Häutungsintervalle auf als Artgenossen, die bei höheren Temperaturen aufgezogen wurden. Jedoch war das Wachstum bei 4°C gehemmt und die Tiere wurden nicht geschlechtsreif. Bei 10 und 16°C dagegen erreichten die Weibchen ihre Geschlechtsreife innerhalb von zwei Monaten. Subadulte Weibchen aus dem Freiland reproduzierten sich im Labor erfolgreich bei allen experimentellen Temperaturen (4 - 26°C). Bei 16°C durchliefen die Weibchen die höchste Anzahl an Reproduktionszyklen mit durchschnittlich 30 Jungtieren im ersten Zyklus. Die maximale Anzahl von Jungtieren aus einem einzigen Schlupf betrug 85 bei 10°C. Der (errechnete) Temperaturtoleranzbereich, innerhalb dessen sich *C. mutica* erfolgreich reproduzierte, lag zwischen > 1,2 und 26,0°C. Die Untersuchung zeigte, dass der saisonale Temperaturverlauf nordwest-europäischer Küstengewässer optimale Bedingungen für *C. mutica* bietet, um ganzjährig existieren zu können. Hohe Überlebensraten von im Winter geschlüpften Jungtieren stellen die Grundvoraussetzung für ein schnelles Populationswachstum im Frühling und somit für eine Massenentwicklung im Sommer dar. Auf Grund der Fähigkeit von *C. mutica* entlang eines Temperaturgradienten zu reproduzieren, der typischerweise in Breiten zwischen 25 und 70°N zu finden ist, ist eine nordwärts gerichtete Ausweitung des Verbreitungsgebietes (bisherige maximale nördliche Verbreitung: 62°N) theoretisch nicht auszuschließen. Diese Verbreitung ist jedoch beschränkt auf Gebiete, in denen die Temperatur mindestens zwei Monate lang zwischen > 4 und 10°C liegt (Dauer bis zur Geschlechtsreife bei 10°C) und in denen Kälteperioden < 4°C nicht länger andauern als vier Monate (Überlebensdauer der Tiere ohne Erreichen der Geschlechtsreife). Angesichts der weltweit ansteigenden Temperaturen kann mit Ausdehnungen der Verbreitungsgrenzen über 70°N hinaus gerechnet werden.

Räuber-Beute Beziehungen

In ihrem ursprünglichen Verbreitungsgebiet besiedelt *C. mutica* natürliche bodennahe Habitate in vergleichsweise geringen Dichten. Dagegen ist *C. mutica* in ihren neuen Gebieten in deutlich höheren Abundanzen vornehmlich auf künstlichen Substraten zu finden. Während der Einwanderungsprozess gebietsfremder Arten durch fehlende bestandsregulierende Räuber begünstigt sein kann, kann die Präsenz solcher Räuber einen starken Einfluss auf die Verteilung in einem neuen Habitat nehmen. In marinen Bereichen können künstliche, vom Boden abgewandte Substrate (z.B. Hafenkonstruktionen, Aquakultureinrichtungen oder Offshore-Windkraftanlagen) für gebietsfremde Arten als Refugien mit stark reduziertem Räuberdruck bei gleichzeitig verfügbaren Ressourcen fungieren und so „Gelegenheits-Fenster“ für Invasionen öffnen.

In laborgestützten Fraßversuchen konnte gezeigt werden, dass sowohl einheimische benthische als auch nektonische Räuber (die Strandkrabbe *Carcinus maenas* (Linnaeus, 1758) und der Klippenbarsch *Ctenolabrus rupestris* (Linnaeus, 1758)) selektiv große Individuen von *C. mutica* kleineren vorzogen und dass beide Räuber bodennah mehr Caprellen konsumierten als an der Wasseroberfläche. Auf das Freiland übertragen deuten die Ergebnisse darauf hin, dass künstliche Substrate, die weitgehend vom Boden isoliert sind, Refugien mit reduziertem Räuberdruck darstellen, auf denen sich hohe Populationsdichten entwickeln können. Im Gegensatz dazu scheint in natürlichen bodennahen Habitaten ein erhöhter Räuberdruck sowohl eine verstärkte Ausbreitung als auch eine Massenentwicklung von *C. mutica* zu verhindern.

Konkurrenz

Während die in Europa einheimische *C. linearis* vor dem Eintrag der nordostasiatischen *C. mutica* künstliche Substrate in Gebieten menschlicher Aktivitäten (z.B. bei Helgoland in der südöstlichen Nordsee) besiedelte, ist sie heute kaum mehr in diesen Habitaten zu finden. Es wird angenommen, dass die weitgehende Abwesenheit von *C. linearis* auf künstlichen Substraten auf interspezifische Konkurrenz mit der neu eingewanderten *C. mutica* zurückzuführen ist. In einem Laborexperiment wurden die Mechanismen interspezifischer Konkurrenz um Raum zwischen *C. linearis* und *C. mutica* untersucht. Hierfür wurden beide Arten in verschiedenen Dichten miteinander konfrontiert. Anfänglich niedrige (entspr. 1.000 Ind. m^{-2}) und hohe (entspr. 10.000 Ind. m^{-2}) Dichten von *C. linearis* wurden jeweils mit niedrigen und hohen Dichten von *C. mutica* für 24 h zusammengeführt. Für beide Konkurrenten wurde jeweils die gegenseitige Verdrängung, Mortalität und wechselseitige Prädation aufgenommen.

In allen Versuchsansätzen und Dichtekombinationen blieb *C. mutica* von der einheimischen Gespensterkrebsart *C. linearis* unbeeinflusst. In anfänglich niedrigen Dichten blieb auch *C. linearis* weitgehend von *C. mutica* unbeeinflusst, auch wenn die Dichten des Einwanderers die des Einheimischen um das Zehnfache übertrafen. Im Gegensatz dazu verursachten anfänglich hohe Dichten von *C. linearis* starke intraspezifische Effekte, die eine erhöhte interspezifische Konkurrenz mit *C. mutica* zur Folge hatten. Dabei verdrängte der Einwanderer den einheimischen Gespensterkrebs in direkter Interferenz ungeachtet der Dichten, in denen *C. mutica* zugegen war. Die Experimente zeigten, dass Prädation der zu Grunde liegende Mechanismus der Interferenz durch *C. mutica* war und zu erhöhter Mortalität bei *C. linearis* führte. Die Ergebnisse unterstützen die eingangs geäußerte Vermutung, dass der einheimische Gespensterkrebs *C. linearis* von seinen vormals künstlichen und räumlich begrenzten Habitaten durch die eingewanderte Art *C. mutica* verdrängt wurde. Im Gegensatz zu künstlichen Substraten bieten natürliche benthische Habitate jedoch genügend Raum und geeignetes Substrat für eine mögliche Nischensegregation und damit für eine Koexistenz von *C. linearis* und *C. mutica*. Dennoch muss davon ausgegangen werden, dass die allgemeinen Populationsbestände von *C. linearis* auf Grund ihrer oftmals fleckenhaften Verteilung und stark fluktuierenden Bestandsgrößen in europäischen Küstengewässern in künstlichen und natürlichen Habitaten durch die Präsenz des eingewanderten Gespensterkrebses stark beeinträchtigt werden könnten.

Die vorliegende Arbeit zeigt, dass der Erfolg von *C. mutica* in europäischen Küstengewässern in erster Linie von der Verfügbarkeit geeigneter Besiedlungssubstrate abhängt. Zwar weist *C. mutica* Charakteristika auf, die in vielen erfolgreich eingewanderten Arten zu finden sind, wie z.B. schnelles Wachstum, frühe Geschlechtsreife, hohe Reproduktionsraten und breite Toleranz gegenüber Umweltbedingungen. Jedoch nur auf künstlichen und vom Boden abgewandten Substraten entgeht *C. mutica* der Bestandsregulierung durch einheimische benthische Räuber und ist daher in der Lage hohe Populationsdichten auszubilden und sich erfolgreich gegenüber der einheimischen Gespensterkrebsart *C. linearis* durchzusetzen.

Chapter I

General Introduction

Introduction

Introductions of species to areas outside their native ranges (‘non-native species’) are continuously increasing on a global scale (Carlton, 1996; McKinney and Lockwood, 1999; Callaway and Maron, 2006). In the marine environment, different anthropogenic vectors such as the world-wide transportation of organisms (and their associated fauna and flora) for commercial or scientific reasons, may contribute to range expansions of numerous species (Carlton, 2001). The transit of organisms in ballast waters and sediments of ocean-going ships or in fouling communities on boat hulls significantly intensifies the dispersal of numerous species (Carlton, 1985). Carlton and Geller (1993) coined this phenomenon as ‘ecological roulette’. In their studies on plankton samples, the authors found that ballast waters on Japanese ships calling port in Coos Bay, Oregon (USA), contained more than 350 different taxa, any one of which might be successful in becoming established. Technical improvements in the ship building industry may lead to shortened journeys, which increases survival probabilities of displaced organisms during transit. Constructions of canals, rivers and lakes as well as harbours at river mouths allow for the introduction of estuarine and other species tolerant towards brackish water (Van der Velde et al., 1998). The global increase in temperature is predicted to result in reductions of the Arctic ice-sheets during summer (Minchin, 2007; Bates et al., 2008). As a consequence seasonal shipping traffic may lead to intensified ballast water exchanges between the North Pacific and Atlantic oceans, increasing the probability of species’ introductions via this corridor (Kerr, 2002a; Minchin 2007).

In recent years, the accidental or deliberate introduction of non-native marine species beyond their indigenous ranges has received major attention because of detrimental effects on native communities, threat of biological diversity and economic damage (Carlton and Geller, 1993; Kolar and Lodge, 2001; Barnes, 2002; Schrader, 2002; Occhipinti-Ambrogi and Savini, 2003). Non-native species may compete with native species for resources such as space and/or food, unbalance local food webs as predators or dominant consumers, and appear as parasites or vectors for diseases or cause severe ecological and economic damage by massive spreading (Bax et al., 2003). Accidental escapes or deliberate introductions of non-native aquaculture species into the wild often result in displacement or extinction of native species and strong ecosystem alteration is the consequence (Meinesz et al., 1993; Naylor et al., 2001). The deliberate introduction of the Nile perch *Lates niloticus* into Lake Victoria (East Africa) for fisheries' purposes in the early 1960s led to the extinction of approximately 65% of the endemic cichlid fishes (more than 200 species) (Kitchell et al., 1997). To date, this is considered the most catastrophic extinction event caused by a non-native vertebrate species (Goldschmidt et al., 1993). Another example is the European zebra mussel *Dreissena polymorpha* which was introduced to the Great Lakes of North America via ballast water discharge in the mid 1980s (Griffiths et al., 1991). *Dreissena polymorpha* is a suspension feeder and was found capable of removing large amounts of suspended matter (Holland, 1993). This led to altered transparency and plankton abundance in its introduced areas, thereby severely changing the aquatic food web and the entire local ecosystem (Holland, 1993). Mussel densities have reached 700,000 ind. m^{-2} and large numbers of specimens clog water intake pipes and water filtration and power generating plants; rough damage and associated control estimates amount to more than 100 million US $ per year (Roberts, 1990). Pimentel et al. (2001) have estimated the environmental damage and economic losses caused by non-native species to cost the USA more than 137 billion US $ per year.

In contrast to the above, numerous introductions of non-native species to areas outside their native ranges remain unconcerning as their invasive potential is restricted (defined here as the potential to undergo exponential population growth and becoming etsablished, to rapidly expand and to be an agent of change threatening native biological diversity; Occhipinti-Ambrogi and Galil, 2004). Often, the integration into native ecosystems is the consequence. In the North Sea at least 80 non-native species are listed and their presence seems to contribute to a general increase in biodiversity rather than threatening it (Reise et al., 1998). In the long run, however, this might turn to a large-scale homogenisation of formerly diverse ecosystems, leading to a loss of biodiversity on a global scale (Nehring and Leuchs, 1999; Stachowicz et al., 1999).

The arrival of a non-native species in a new habitat and its initial introduction depend on a variety of factors including dispersal mechanism, environmental conditions in the new region (e.g. temperature or salinity) and the physiological tolerance of the non-native (Carlton, 1996; Vermeij, 1996; Bax et al., 2003).

In contrast, the successful establishment and integration into native ecosystems are long-term events and depend on the non-native's ability to sustain itself successfully through reproduction and/or recruitment and to persist in interspecific interactions with native species (Vermeij, 1996; Holway and Suarez, 1999; Sakai et al., 2001). In fact, according to Williamson and Fitter (1996a) only 0.1% of all plant species that are introduced by humans become established outside their native ranges.

Elton (1958), in his seminal volume 'The ecology of invasions by animals and plants' addresses two major concepts which are fundamental for research in invasion ecology: the characteristics of invading species (invasiveness) and the invasibility of habitats, i.e. the susceptibility of ecosystems towards invasions. Invasiveness asks for specific traits characterising an invasive species and making it more successful than other species (Alpert et al., 2000). Some of the most common characteristics found in different successful marine invaders (Lodge, 1993; Williamson and Fitter, 1996b; Ricciardi and Rasmussen, 1998; Van der Velde et al., 1998; Alpert et al., 2000; Heger and Trepl, 2003; Füreder and Pöckl, 2007) are summarized in Table I-1.

Tab. I-1: Summarized characteristics and life history traits found in successful marine invasive species.

Characteristics
• short life span
• rapid growth
• early maturation
• short generation time
• high fecundity
• wide environmental tolerance
• wide genetic variability and phylogenetic plasticity
• gregarious behaviour
• opportunistic feeding (particularly omnivorous suspension feeding)
• large body size
• rapid dispersal
• ability to repopulate defaunated habitats, following population crashes caused by extreme disturbances
• association with human activities (e.g., aquaculture or harbour facilities, shipping and recreational boating)

The success of non-native species is often explained by the lack of native competitors and/or predators, allowing for mass occurrences and uncontrolled population growth (Van der Velde et al., 1998). For example, the North American ctenophore *Mnemiopsis leidyi* was introduced into the Black Azov Seas in the late 1980s (Travis 1993). On account of missing natural antagonists or predators, the populations grew rapidly while exploiting the native fish stocks by feeding particularly on fish larvae. It has further been suggested that high competitive ability of non-native species is a key factor promoting successful invasions (Crawley, 1990; Vilà and Weiner, 2004). Numerous reports from non-native species found competitive superiority and even the displacement or extinction of native species to have significantly contributed to invasion success (Dick, 1996; Dick et al., 1999; Morrison, 2000; Füreder and Pöckl, 2007). For example, the non-native Atlantic mud snail *Ilyanassa obsoleta* competitively excluded the native Pacific mud snail *Cerithidea californica* from preferred habitats in San Francisco Bay.

However, the native did not go extinct as it was able to seek refuge in habitats, which were beyond the physiological tolerance of the invader (Race, 1982). Recent studies have further suggested that propagule pressure in populations of introduced species is positively correlated with invasion success (Lockwood et al., 2005; Ruiz et al., 2000; Kolar and Lodge, 2001). For example, Grevstad (1999) found that the invasion success of two European chrysomelid beetles introduced to North America was positively correlated with the number of individuals released to the new habitats. Furthermore, non-native species appear to be successful especially in regions with environmental conditions similar to where they originate (Van der Velde et al., 1998).

The scientific approach of understanding ‘invasiveness’ aims to derive general patterns applicable to potential invaders and thus, to predict their dispersal and distribution (MacIsaac et al., 2001). Numerous introductions of non-native species to new habitats remain undiscovered because of poor performance and/or competitive exclusion or predation by native species. Sometimes non-natives take advantage of free resources and harmlessly integrate into native communities, potentially even facilitating native species. For example, the American slipper limpet *Crepidula fornicata*, accidentally introduced to Europe with American oysters, was found impeding efficient feeding in the native blue mussel *Mytilus edulis* by its epizootic behaviour (Thieltges et al., 2006). However, rather than suffocating it, it provided protection against starfish commonly predating on *M. edulis*.

Despite this, prominent examples of successful invasions causing devastating damages have proven the contrary (Nichols et al., 1990; Parker et al., 1999; Simberloff and Schmitz, 1999; Mack et al., 2000). Consequently, a major attempt in terms of natural conservation management is to prevent detrimental invasions, irreversible loss of biodiversity, ecological and economic threats and costly restorations (Alpert et al., 2000). While the concepts of invasiveness (and invasibility) often met theoretical or empirical evidence, the numbers of exceptions from these patterns are high and often generalizations have not been tested statistically (Lodge, 1993). Hence, attempts to categorize certain life history traits of non-native species as characteristically invasive turned out to be inconsistent and not generally applicable (Sher and Hyatt, 1999).

Traits that might be advantageous to a certain species invading one habitat may be useless when invading another. Some traits may be more pronounced in certain invaders than in others or even may be absent. For example, while the giant hogweed *Heracleum* *mantegazzianum* exhibits broad environmental tolerances towards humidity, the Himalayan balsam *Impatiens glandulifera* does not, as it is unable to cope with drought (Heger and Trepl, 2003). Yet, both species are common invasive plants in central Europe. In addition, introductions occur in habitats that differ widely in native species composition and richness, environmental conditions and geography. Not all invaders are capable of exploiting all habitats and not all habitats are equally vulnerable to invasion (Sher and Hyatt, 1999; MacIsaac et al., 2001). In Belgium, for example, the goldfish *Carassius auratus* was observed to reproduce in private garden ponds but not in open public waters (Copp et al., 2007). In England, by contrast, the species rapidly populates open still waters (Copp et al., 2005) where it is known to undermine the genetic integrity of native Crucian carp *Carassius carassius* (Hänfling et al., 2005).

Species that are abundant and widely distributed in their introduced ranges may have undergone a serious of failed introductions before becoming successfully established. For example, the European red deer *Cervus elaphus* was introduced to New Zealand and its spreading had become a serious economic problem. This, however, happened only after 31 previous introductions had failed (Clarke, 1971).

According to the above, detailed case-by-case studies of non-native species introduced to new habitats providing information on life history traits, population biology and relative performance to native species are essential. Only in this way, the underlying mechanisms of successful invasions can be defined and potential impacts and further range expansion of the species' under study can be assessed.

The study object *Caprella mutica* Schurin, 1935

Caprella mutica Schurin, 1935, is a marine amphipod crustacean. It belongs to the suborder Caprellidea, which represents the smallest taxon (22 species) within the amphipod fauna of North West Europe (Hayward and Ryland, 2006). Strongly diverged from the typical gammarid amphipod morphology, caprellids are recognized by their long cylindrical bodies and reduction in number and type of appendages. Because of their slender and stick insect-like appearance they are commonly referred to as ‘skeleton’ or ‘ghost shrimp’.

In caprellid amphipods, the body consists of seven body segments (pereonites I-VII) and a strongly reduced eighth abdominal segment (Fig. I-1a and b) (Arimoto, 1976; Larsen, 1998; Hayward and Ryland, 2006). The head is immovably fused with the first pereonite and carries two pairs of antennae and the first pair of gnathopods (claw-like appendages). While the first two body segments are comparably short in females, they are strongly elongated in males. Further, in males, the second gnathopods insert at the posterior end of the second pereonite whereas it is the anterior end in females (Fig. I-1a and b). The second gnathopods are generally larger in males than in females and are probably used in combats with conspecifics males or when striking prey rather than for clinging to substrata (pers. obs.). In *C. mutica*, the first two pereonites as well as the second gnathopods are covered in dense setation (Fig. I-1b). Club-shaped gills are found on the third and fourth pereonites. The fifth, sixth and seventh pereonite each carry a pair of pereopods used for attachment to suitable substratum (Caine, 1979). In contrast to numerous other caprellids, the dorsal and lateral surfaces of the third (second in females) to seventh pereonites in *C. mutica* are heavily armoured with spiny projections. Males are typically larger than females and may reach body lengths of up to 50 mm (Nishimura, 1995). Generally however, males are about 25 - 30 mm and females about 15 - 20 mm in length. Yet, in comparison to other caprellids (e.g., *Pariambus typicus*, *Phtisica marina* or *Caprella linearis*) *C. mutica* is clearly among the larger species (Hayward and Ryland, 2006). Ovigerous females are easily distinguished by their brood pouch, which is formed by two pairs of lamellae (oostegites) inserting on the third and fourth pereonites (Fig. I-1a).

Like all peracarid crustaceans, caprellids lack larval stages and brood their young until they emerge from the brood pouches as small replicates of the adult individuals (this work, Chapter III). Ashton (2006) counted a maximum number of 363 hatchlings per clutch from a single female reflecting the species high fecundity.

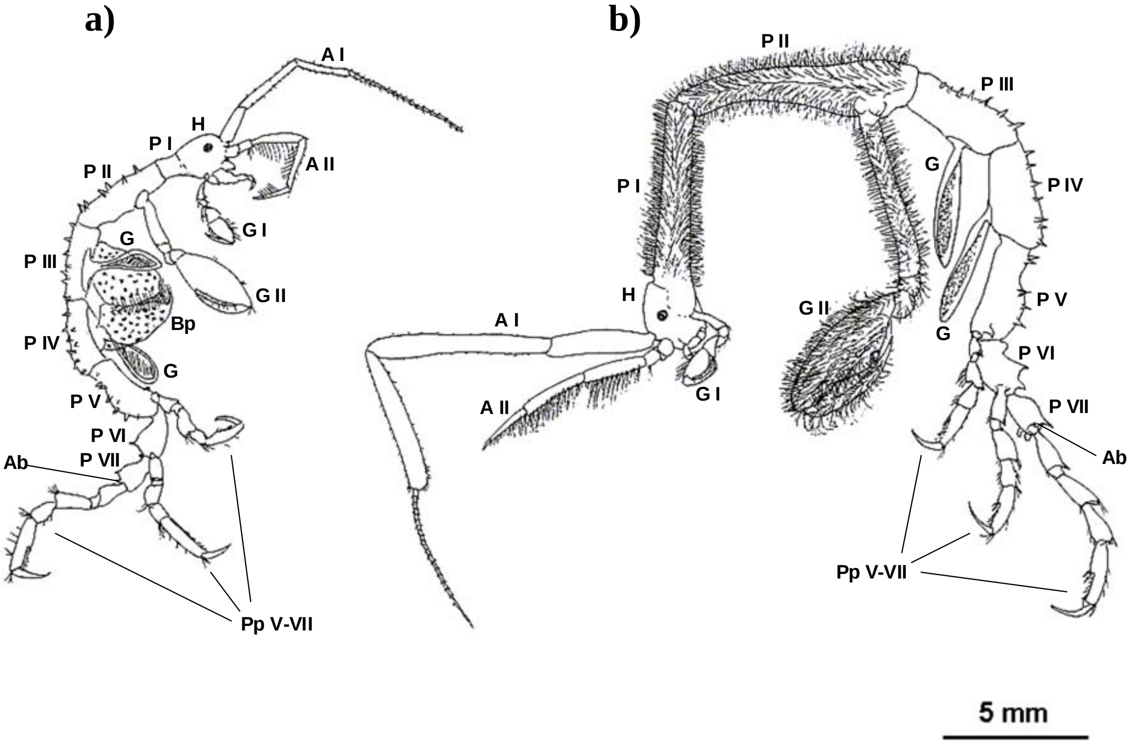

Fig. I-1: Schematic overview of a) female and b) male *Caprella mutica*. A I and II = antennae I and II, H = head, P I-VII = pereonites I-VII, Ab = abdomen, Pp V-VII = pereopods V-VII, Bp = brood pouch, G = gills, G I and II = gnathopods I and II (modified after Platvoet et al., 1995).

Caprella mutica is indigenous to north-east Asia and was first described by Schurin (1935) from Peter the Great Bay, Vladivostok. It is distributed along the Russian coasts of the Sea of Japan and the Japanese archipelago (Arimoto, 1976; Fedotov, 1991; Vassilenko, 2006) (Fig. I-2). In its native range *C. mutica* is typically reported from sheltered bays in the littoral zone to about 13 m in depth where it inhabits different macroalgae such as *Neorhodomela larix*, *Polysiphonia morrowii*, *Sargassum miyabei*, *S. Pallidum*, *Cystoseira crassipes*, *Laminaria japonica*, *Dichloria viridis* and others (Vassilenko, 2006). Maximum densities in natural habitats average around 2,600 ind. m^{-2} in summer periods (Vassilenko, 2006).

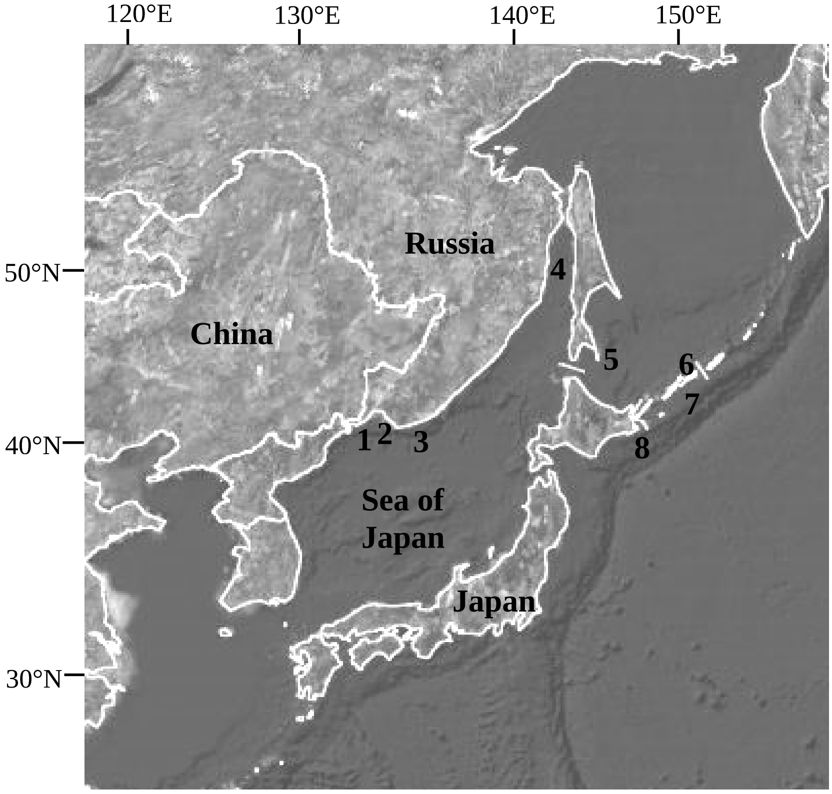

Fig. I-2: Native range of *Caprella mutica* with locations around the Sea of Japan (1-8). 1) Possjet Bay, Russia (Fedotov, 1991); 2) Peter the Great Bay, Russia (Schurin, 1935); 3) Olarovsky Cape, Russia (Vassilenko, 2006); 4) Signalny Cape, Russia (Vassilenko, 2006); 5) Sea of Okhotsk, Sakhalin Island (Vassilenko, 2006); 6) Kunashir (Vassilenko, 2006); 7) Shikotan, Japan (Vassilenko, 2006); and 8) Akkeshi Bay, Japan (Arimoto, 1976).

During the past 40 years, *C. mutica* has become successfully established in 31 locations outside its native range (Ashton, 2006; Ashton et al., 2007a, 2008a). Distributed by several introductions from multiple sources since the 1970s (Ashton et al., 2008b), *C. mutica* spread to the Pacific and Atlantic coasts of the United States (Carlton, 1979; Marelli, 1981; Cohen and Carlton, 1995; Cohen et al., 1998, 2002; MIT Sea Grant, 2003; USGS, 2005), Alaska (Ashton et al., 2008a) and Canada (B. Sainte-Marie, pers. com.). In the mid 1990s first European populations of *C. mutica* were found in The Netherlands (Platvoet et al., 1995). In the following years, occurrences from Norway, Belgium, Ireland and Scotland were reported (Heilscher, 2000; ICES, 2003; Tierney et al., 2004; Willis et al., 2004). In the early 2000s, large populations of *C. mutica*, were reported from the islands of Sylt and Helgoland, German Bight (North Sea) for the first time (Buschbaum and Gutow, 2005). However, careful re-inspection and identification of alcohol samples from earlier years and anecdotal evidence on size and abundance untypical for the native congeneric species, *Caprella linearis* (Linnaeus, 1767), suggests the introduction of *C. mutica* to date back to the mid 1990s. The so far only record from the southern hemisphere is from Timaru, New Zealand, where *C. mutica* was found in 2004 (Ashton et al., 2007a).

Caprellids typically inhabit the littoral zone of coastal waters, but have been reported to depths of 4,790 m (McCain & Steinberg 1970). They often represent dominant members in epibenthic communities, inhabiting macroalgae, hydroids, ascidians, anthozoans, bryozoans, sponges and sea grasses, to which they are well adapted to cling to with their hind appendages (McCain, 1968; Takeuchi and Hirano, 1992; Guerra-García, 2001; González et al., 2008). For example, in its native range, *Caprella cristibrachium* Mayer, 1903 was recorded at a maximum density of 95,000 ind. m^{-2} (Vassilenko, 1991). Caprellids are important trophic links in food webs and prey for numerous predatory fishes and invertebrates in coastal water systems (Caine, 1987, 1989, 1991; Holbrook and Schmitt, 1992; Kvenseth et al., 2003). Caprellids show a variety of different feeding mechanisms such as browsing, filter-feeding, predation, scavenging and scraping, reflecting broad diets and omnivorous feeding (Caine, 1974, 1977, Guerra-García et al. 2001, Sano et al., 2003). Filter feeding, in which food particles are captured with rapid down-thrusts of the antennae, was suggested to be of importance in caprellids with setose antennae such as those found in *C. mutica* (Nauwelaerts et al., 2007; Michel et al., 2007).

In its introduced ranges, *C. mutica* is typically found clinging to different hydrozoans, bryozoans, ascidians and/or macroalgae fouling on artificial substrata (e.g., buoys, pontoons, ropes and boat hulls) in areas of human activity such as harbours, aquaculture facilities or offshore wind farms (Ashton, 2006; Schrey, 2006; Schneider, 2007; Dong Energy et al., 2006; Page et al., 2006; Buschbaum and Gutow, 2005). Depending on their algal or faunal hosts or their pelagic dietary requirements, *C. mutica* camouflages in different colourations and shades of brown, orange, red, purple and turquoise (pers. obs.). Densities of European populations can exceed several 100,000 ind. m^{-2} during summer months (Ashton, 2006). Threat display and combat between conspecifics of both sexes is common (pers. obs.), suggesting high aggressive behaviour and competitive superiority towards other species.

The successful distribution of *C. mutica* is most likely the consequence of increased global and local shipping traffic (transit in ballast water or on fouled boat hulls) as well as of co-transports along with introduced aquaculture organisms such as the Pacific Oyster *Crassostrea gigas,* native to the Sea of Japan (Takeuchi and Sawamoto, 1998; Cohen and Carlton, 1995; Gollasch, 2002; Tierney et al. 2004; Ashton et al., 2006b). Thiel et al. (2003) suggested that artificial (buoys, ropes, litter) and natural (macroalgae) floating materials may facilitate the dispersal of different caprellid species. In fact, *C. mutica* has been reported from floating macroalgae off the west coast of Scotland (Ashton, 2006). *Caprella mutica* is an opportunistic feeder (Sano et al., 2003; Cook et al., 2006a) and exhibits wide environmental tolerance (Ashton et al., 2007b; Shucksmith, 2007). In his studies on invasibility and the role of biodiversity in determining community susceptibility to invasion, Shucksmith (2007) found *C. mutica* to be competitively superior over the native caprellids *C. linearis* and *Pseudoprotella phasma*.

Thesis outline

Previous studies have highlighted the successful establishment of *C. mutica* in European coastal waters (Ashton, 2006; Schrey, 2006; Ashton et al., 2007a; Cook et al., 2007a, 2007b; Schneider, 2007; Shucksmith, 2007). These studies have shown high population densities, high fecundity, environmental tolerance and rapid dispersal as well as high competitive superiority to have significantly contributed to the successful invasion.

In the present study, I performed combined experimental field surveys and laboratory investigations in order to evaluate the underlying mechanisms responsible for the mass occurrences of *C. mutica* in European habitats, its high fecundity and its ability to persist in interspecific interactions. The aim of the present study was to contribute to the knowledge of invasiveness and to give a mechanistic explanation for the success of *C. mutica* in European coastal waters.

The main questions of the present study were:

- (i) How are the seasonal population dynamics and population structures of *C. mutica* at two different locations in Europe affected by environmental conditions and anthropogenic activities?
- (ii) How does temperature affect survival, development, growth and reproduction in *C. mutica* and determine range expansion?
- (iii) Are populations of *C. mutica* in their European habitats controlled by native predators?
- (iv) What are the mechanisms of the competitive superiority of *C. mutica* over native resident species?

The questions were addressed through a series of field and laboratory experiments mainly conducted at the Biologische Anstalt Helgoland (BAH), Marine Station of the Alfred Wegener Institute for Polar and Marine Research (AWI) on the island of Helgoland, German Bight, North Sea. For comparative and additional studies, research was carried out on the west coast of Scotland at the Scottish Association for Marine Science (SAMS), Dunstaffnage Marine Laboratory, Oban, Argyll. The experiments are presented in separate chapters outlined below.

Chapter II:

Seasonal population dynamics of the non-native *Caprella mutica* Schurin, 1935 (Crustacea, Amphipoda) at different areas in European coastal waters

In this field study I present a 17 month investigation on the population dynamics of *C. mutica* at two different European locations. It was tested, whether differences in the environmental conditions or habitat settings and the anthropogenic activities at the sites under study influenced the population dynamics, abundance and structure of *C. mutica*.

Chapter III:

Life history traits of *Caprella mutica* Schurin, 1935 (Crustacea, Amphipoda) - implications for invasion success and range expansion

Life history responses of *C. mutica* along a thermal gradient are widely unknown. In this laboratory work I studied survival, development and reproduction of juvenile and adult individuals of *C. mutica* at annual sea water temperature ranges typical for European coastal areas. Distributional limitations to high latitudes were estimated according to the physiological abilities for reproduction found in *C. mutica*.

Chapter IV:

Testing the enemy release hypothesis - consequences for habitat specific distribution in the non-native amphipod *Caprella mutica* Schurin, 1935

No dedicated studies have been conducted in testing whether the successful establishment of *C. mutica* in its introduced ranges can be explained by the release from specialist predators. In laboratory-based feeding trials I studied the selective feeding behaviour of native benthic and nektonic predators on *C. mutica*.

Chapter V:

Mechanisms of density dependent interference competition by the non-native *Caprella mutica* Schurin, 1935 (Crustacea: Amphipoda) on its European native congener *C. linearis* (Linnaeus, 1767)

The underlying mechanisms of the competitive superiority of *C. mutica* in relation to ecologically similar species have rarely been studied. In the present laboratory experiment I investigated the effective mechanisms of interspecific interaction between *C. mutica* and its native congener *C. linearis* when competing for space at different density combinations.

In the final Chapter VI the results from the four studies are synthesized. The findings are viewed in the context of the major questions set out above and the mechanisms responsible for the successful establishment of *C. mutica* in European coastal waters are discussed.

Chapter II

Seasonal population dynamics of the non-native *Caprella mutica* Schurin, 1935 (Crustacea, Amphipoda) in European coastal waters

Introduction

In view of globally increasing numbers of species' invasions in marine environments (Carlton, 1987; Lodge, 1993; Reise et al., 1998; Ruiz et al., 2000; Kolar and Lodge, 2001), numerous attempts have been made to identify key factors which determine invasion success and may help to predict future invasions (Williamson and Fitter, 1996a, 1996b; Heger and Trepl, 2003; Townsend Peterson, 2003). For example, Ricciardi and Rasmussen (1998) identified particular characteristics in the life history of non-native species, such as high reproductive capacity and wide environmental tolerance as general attributes of successful invaders, often resulting in high population densities in the species' new areas.

The successful colonization process and the establishment of non-native species is, however, highly unpredictable and may differ strongly from one area to another (Von Holle and Simberloff, 2005). Invasion success and the potential impacts of an introduced species depend on the non-native's ability to cope with the local abiotic conditions (e.g. temperature or salinity), to withstand disturbance (exposure to physical forces) and to persist in interactions with other species (Von Holle and Simberloff, 2005).

Phillips and Shine (2006) found that the phylogeographical structure of non-native species may be low at first introduction. Structural variation among populations was, therefore, attributed to environmental effects causing phenotypic plasticity or rapid adaptation in the invader (Sakai et al. 2001). Accordingly, Shea and Chesson (2002) suggested that successful invasion depends on variable characteristics of the invader, the invaded communities, resources and natural enemies functioning jointly on a spatial and temporal scale and thus, leading to variable 'niche opportunities' for introduced species.

During the past four decades, the caprellid amphipod *Caprella mutica* Schurin, 1935, indigenous to sub-boreal waters of north-east Asia (Sea of Japan), has successfully invaded numerous locations world wide (Ashton et al., 2007a). Established and thriving populations are found typically on artificial substrata such as submerged parts of pontoons or boat hulls, ropes, buoys or nets. First records of European populations are from the Netherlands and date back to the mid 1990s (Platvoet et al., 1995). At the west coast of Scotland and the islands of Helgoland and Sylt, German Bight (North Sea) *C. mutica* was identified in 2004 (Willis et al., 2004; Buschbaum and Gutow, 2005) and has successfully established at these sites (Ashton, 2006; Schrey, 2006; Schneider, 2007).

In its native range, the seasonal population dynamics of *C. mutica* was studied during the 1980s by Fedotov (1991) in subtidal macrophyte beds at Posyet Bay (Sea of Japan). Lowest abundances of about 25 ind. m^{-2} were found in spring and increased with increasing water temperature to about 1,200 ind. m^{-2} during summer. At Bolshoi Pelis Island, near Vladivostok, Fedotov (1987 cited in Vassilenko, 2006) observed maximum abundances of *C. mutica* inhabiting different macroalgal species of approximately 2,600 ind. m^{-2}.

The only study on seasonal population dynamics of *C. mutica* outside its native range is from the west coast of Scotland (Ashton, 2006). In an 18-month field study, the author investigated population abundance and structure, sex ratio, fecundity and size-frequency distribution of *C. mutica* on artificial structures at four sites with varying levels of anthropogenic disturbance. Similar to its native range, abundances fluctuated along with annual seawater temperatures. Average annual densities were about ten times higher in the new range with maximum densities of > 300,000 ind. m^{-2} in summer. While *C. mutica* typically inhabits natural benthic habitats in its native range, introduced populations on artificial structures outnumber their native conspecifics from natural habitats more than hundredfold.

Knowledge on the population dynamics of a non-native species in different invaded environments or habitats is crucial to the understanding of patterns and underlying mechanisms of invasion success (Schoener and Spiller, 1995; Phillips and Shine, 2006). Due to environmental and biotic differences among sites, variation in invasion success is probably the rule rather than the exception (Ruiz et al., 2000). Hence, the question is how much variation exists in space and time and which factors determine this variation. Comparative quantitative studies on the establishment of a non-native species at different locations may help to elucidate potential factors and mechanisms responsible for variation. For example, Grosholz and Ruiz (1996) compared ecological characteristics of three spatially independent invasions of the European green crab

Carcinus maenas (Linnaeus, 1758). Variable habitat usage and body size of the crabs influenced invasion success, whereas diet preferences and ecological impacts were similar if not consistent characteristics at all three study sites.

While different environmental and anthropogenic characteristics affecting population abundances may be used as measures to explain invasion success, detailed information on population dynamics may also serve as an excellent basis for addressing other questions concerning specific life history traits of the non-native and interactions with other species (competitive or predatory relationships) (Parker et al., 2003; Phillips and Shine, 2006).

Complementing the investigations of Ashton (2006), the present study compares the seasonal dynamics of successfully established populations of *C. mutica* on the west coast of Scotland with those from the island of Helgoland in the German Bight, North Sea. The aim of the study was to investigate, whether differences in the environmental conditions or habitat settings at the sites under study influenced:

(i) the seasonal abundance and distribution,
(ii) the population structure,
(iii) the sex ratio, and
(iv) the size-frequency distribution,

of *C. mutica* and, thus, its invasion success.

Material and Methods

In the present study I collected monthly samples of *C. mutica* over a 17 month period to investigate the seasonal population dynamics, structures and abundances. For this purpose, settlement structures were attached to ropes and deployed at three different sites at each two European locations.

Study locations and experimental set up

From November 2005 to February 2007 monthly samples were taken from each three sites on the west coast of Scotland (U.K.) near Oban in the Firth of Lorne (Dunnstaffnage Bay; 56°27.06'N/ 5°26.37'W) and on the island of Helgoland (German Bight, North Sea; 54°10.57'N/ 07°53.01'E) (Fig. II-1).

The Firth of Lorne is a large sea loch of approximately 60 km in length and an average of 8 km in width (Cook et al., 2006b). It stretches southward from a narrow mouth (180 m) at Loch Linnhe to a wide opening (25 km) into the Atlantic Ocean (Pearson, 1970). Surface waters around the study sites experience regular freshwater run-offs of 80 x 10^7 m^3 d^{-1} from Loch Lhinne in the north and Loch Etive in the east (Barnes and Goodley, 1958). Vertical mixing in the winter months (January to April; Pearson, 1970) enhances surface nutrient levels and leads to maximum phytoplankton production in May (Grantham, 1981).

The island of Helgoland represents a geographically isolated rocky locality within the sandy and muddy bottoms of the German Bight (south-eastern North Sea) about 60 km of the German mainland coast (Franke and Gutow, 2004). The rocky intertidal and subtidal covers an area of about 35 km². Currents around Helgoland are influenced by northern and western Atlantic water inflows and freshwater run-offs from the large rivers along the Dutch and German coasts (Muus and Nielsen, 1999; Reid et al., 2003). Because of the large distance between Helgoland and the mainland, however, freshwater influxes do not affect offshore salinities (Gilbricht, 1994). Salinities are between 30 and 35 psu (Berberich, 1989) and have, in fact, increased over the past 40 years (Wiltshire and Manly, 2004). Due to average depths of about 8 m in the direct vicinity the island of Helgoland, water masses are generally well mixed (Wiltshire and Manly, 2004).

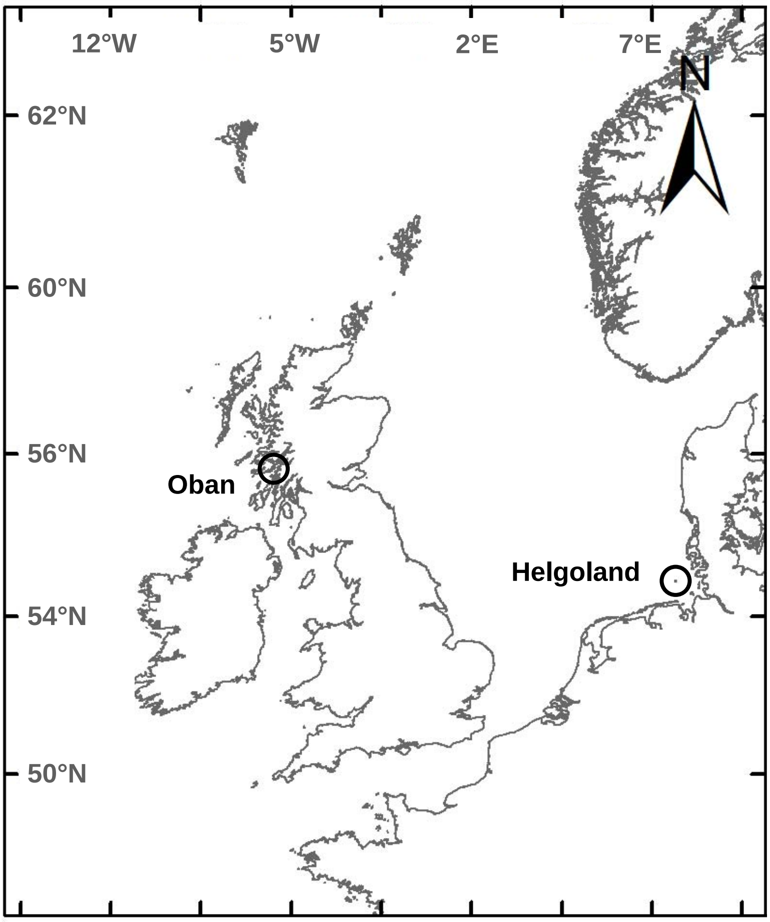

Fig. II-1: Geographic positions of the study locations at Helgoland (Germany) and Oban (U.K.) in north-west Europe.

At each location three study sites were chosen with different artificial substrata and environmental characteristics (Fig. II-2a and b, Tab. II-1). Around Oban following sites were chosen: (i) a fish farm cage, (ii) 10 berths of a local marina, and (iii) an isolated moored pontoon (Fig. II-2a, Tab. II-1).

Dunstaffnage fish farm (site hereafter referred to as: Oban fish farm), a mariculture raising Atlantic salmon *Salmo salar*, is located outside Dunstaffnage Bay in the Firth of Lorne approximately 500 m from shore at a depth of 30-45 m (Fig. II-2a). Between 8 and 163 T of feed are fed monthly (Ashton, 2006) causing enhanced food supply in surrounding waters and sediments. The cage (type: ‘polar circle’) was approximately 15 m in diameter with two plastic ring buoys (diameter: 30 cm) supporting a free hanging net of approximately 20 m depth. Tidal fluxes and surface currents may be characterised as moderate to very strong with maximum speeds of 21.0 cm s^{-1} measured over a 29 day period (Cook et al., 2006b). While boats may pass though the Firth of Lorne rather regularly, only working boats and tenders dock temporarily at the fish farm cages.

The other two sites were located in Dunstaffnage Bay, which covers an area of about 1.0 km² (Fig. II-2a, Tab. II-1). It is referred to as a sheltered and shallow bay (depth about 5 m) (Ashton, 2006). However, it experiences very strong currents, particularly during spring tides, and fresh water run-offs from Loch Etive (Cook, pers. com.), which may be intensified by a channel system created by a small island located at the entrance of the bay. In addition, northern and northwestern winds can cause strong turbidity and mixing of water bodies (Cook, pers. com.). Dunstaffnage Marina (site hereafter referred to as: Oban marina), a recreational boating marina (about 100 solid berths permanently fixed to the seabed and 30 moorings) is located in the outer area of Dunstaffnage Bay, and has an open design, i.e. it is not enclosed by harbour walls. This site provides berthing for numerous regional and international visitors. The isolated pontoon (about 2 x 6 m; site hereafter referred to as: Oban pontoon), owned by the Scottish Association for Marine Science (SAMS) and used irregularly for experimental work, is moored in the inner area of Dunstaffnage Bay.

At Helgoland, the following sites were chosen: (i) a harbour wall in the northeast harbour of Helgoland, (ii) a moored pontoon in the south harbour of Helgoland, and (iii) an offside area in the south harbour of Helgoland (Fig. II-2b, Tab. II-1).

The northeast harbour of Helgoland (site hereafter referred to as: Helgoland marina) covers an area of about 0.02 km² and provides about 60 berths for local yachts and on exception also for visitors (Fig. II-2b, Tab. II-1). Helgoland marina is enclosed by surrounding break walls with regularly placed ladders which were used for the deployment of the sampling structures (see below). The marina has an average depth of about 5-6 m at mid tide and can be accessed by boat only through a narrow opening entrance.

The south harbour is larger than the northeast harbour and consists of an inner and outer basin with a total area of about 0.3 km² (Fig. II-2b). The inner area provides berthing for more than 150 local and international yachts, research vessels, international fishing boats and daily commuting ferries. At the entrance to the inner basin of the south harbour, a pontoon (site hereafter referred to as: Helgoland pontoon) with a length of about 4 x 13 m, is moored to the harbour wall all year round and only accessed by boats of the Waterways and Shipping Office authorities. The outer basin of the south harbour is relatively larger than the inner area. There are no berths in the outer area and mooring is scarce. An off-side area was chosen as isolated site (hereafter referred to as: Helgoland south harbour) and buoys were anchored for attachment purposes. In this off-side area, experimental structures are regularly deployed by staff of the Marine Biological Station (BAH) and therefore only accessed by research vessels.

Similar to the northeast harbour, the south harbour is surrounded by break walls and can be accessed only through a narrow entrance (Fig. II-2b). The average depth at mid tide is about

5-6 m. Both harbours are characterized as sheltered habitats experiencing low turbidity (Schultze et al., 1990; Chrapkowski-Llinares, 2005). Strong winds and storms, however, may cause enhanced turbidity and mixing of the water column leading to high amounts of suspended matter within the harbours.

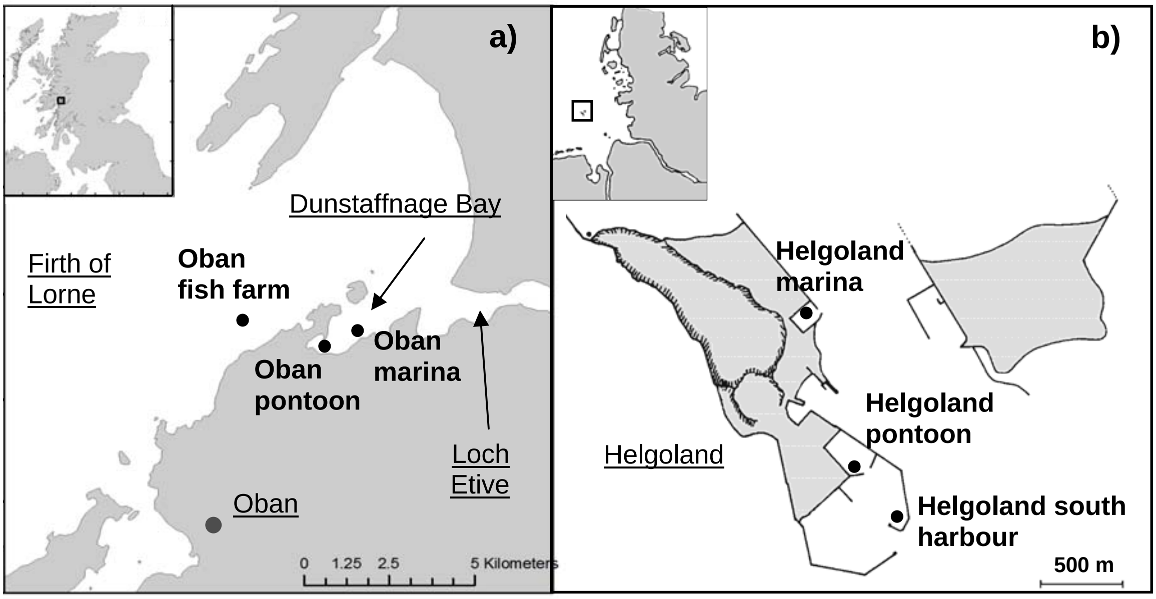

Fig. II-2: Positions of the study sites at a) the Firth of Lorne and Dunstaffnage Bay (Oban location), and b) the island of Helgoland (map of Scottish sites by A. Davis; map of Helgoland modified after Benoit, 1998).

Tab. II-1: Overview of the anthropogenic and environmental characteristics of the three study sites from Oban, Scotland and Helgoland, Germany.

	Oban, Scotland			**Helgoland, Germany**		
Site characteristics	**Oban fish farm**	**Oban marina**	**Oban pontoon**	**Helgoland pontoon**	**Helgoland marina**	**Helgoland south harbour**
Exposure	naturally exposed (open Sea loch)	naturally sheltered (bay), wide access	naturally sheltered (bay), wide access	sheltered (enclosed harbour design) narrow access	sheltered (enclosed harbour design) narrow access	sheltered (enclosed harbour design) narrow access
Currents	strong currents	strong currents, high turbidity	strong currents, high turbidity	circulations in the bay, low turbidity	circulations in the bay, low turbidity	circulations in the bay, low turbidity
Frequency of boats at sites	low to regular (temporary docking)	high (boats passing and mooring)	rare (short term docking)	regular to high	regular to high (boats passing and mooring)	rare (short term docking)
Food availability	enhanced	natural	natural	natural	natural	natural
Available settlement space on surrounding artificial structures	restriced space of solid structures (ring buoys), large surfaces of filamentous structures (nets)	large surfaces of solid structures (berths and harbour walls), restricted surfaces of filamentous structures (mooring ropes)	restricted space of solid structures (submerged area of pontoon), resticed space of filamentous structures (ropes)	restricted space of solid structures (submerged area of pontoon), but large surfaces from nearby harbour walls, resticed space of filamentous structures (ropes)	large surfaces of solid structures (berths and harbour walls), restricted surfaces of filamentous structures (mooring ropes)	space is only provided by the sampling structures (mesh: 20 x 30 cm) attached to anchored ropes
Architecture of settlement structures on site	isolated (fish farm cage)	connected (to harbour constructions)	isolated pontoon	connected (to harbour constructions)	connected (to harbour constructions)	isolated
Depth (at mid tide level)	30-45 m	5-6 m	5-6 m	5-6 m	5-6 m	5-6 m

In order to test for differences between depths, two settlement structures each (plastic meshes, Helgoland: 30 x 20 cm, Oban: 25 x 10 cm, mesh size 5 mm; Clean-ups, EGL Homecare) were attached to ropes, one about 20 cm below the water surface level (hereafter: surface) and one at 3-4 m depth (hereafter: bottom). At each study site ten ropes were deployed and either tied to locally fixed structures (i.e., marina berths, pontoons, ladders, or the fish farm cage) or to buoys anchored for this experiment (i.e. at Helgoland south harbour). Deployment at each site warranted constant submergence of sampling structures with tidal change.

At each site the ropes were initially deployed in two steps. Firstly, a group of five ropes was deployed. The second group was deployed four weeks later. The meshes (5 x ‘surface’ and 5 x ‘bottom’) of each group were alternately sampled in monthly intervals. The meshes were replaced on each sampling date, allowing each mesh to be exposed for a period of eight weeks (Fig. II-3). Due to adverse weather conditions in autumn and winter 15 ropes (three sets of samples) were lost from the Oban fish farm.

Seawater temperatures were measured at Helgoland at each sampling date. Three replicated measurements were taken each time at 1 m depth using a digital temperature meter (Cond 330i; accuracy ≤ 0.1 K ± 1 digit, WTW GmbH, Weilheim, Germany).

At the Scottish location temperature was logged using electronic dataloggers (TinyTag monitors, resolution: 0.1°C, recording at 12 min intervals; Gemini Data Loggers, U.K.) deployed in the vicinity of Oban marina from November 2005 - June 2006 as part of a separate study and at Dunstaffnage fish farm cages from June 2006 - February 2007 as part of the present study. Monthly averages were computed from measurements taken at 12:00 h a.m. of each sampling day and the day before and after sampling (N = 3).

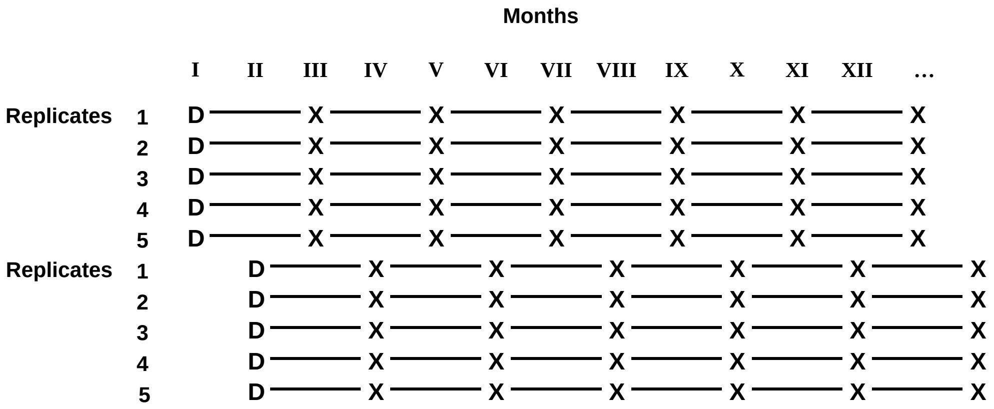

Fig. II-3: Schematic overview of the experimental sampling design for one site. ‘D’ indicates initial deployment of meshes; ‘X’ indicates alternating sampling dates and exchanges of meshes.

Laboratory processing

The collected meshes were placed in separate labelled containers and either frozen or fixed in 4% buffered formalin until further processing. Rinsed and/or thawed samples were repeatedly passed through a 100 µm sieve to retain mobile organisms. Individuals of *C. mutica* were sorted out and fixed in 85% ethanol (ethanol was infused with 4% propylene glycol to prevent the animals from desiccation in case of alcohol evaporation). Leftover individuals of *C. mutica* on the mesh were picked off using forceps and preserved as well. Finally, the mesh was rinsed repeatedly into a sorting tub in order to collect the smallest specimens and juvenile individuals which may have been overlooked. The water was then strained again and the organisms preserved.

The total number of individuals was counted from each sample and standardised to m^2. Individuals from samples with low or moderate abundances were counted in total. Depending on visual estimation of the densities, sub-samples were taken from samples with high abundances, applying the Huntsman Marine Laboratory (HML) beaker technique (Van Guelpen et al., 1982). Sub-samples amounted to 25% of the original sample or at least 100 remaining individuals in the sub-sampled fraction are recommended (Van Guelpen et al., 1982; Barbour and Gerritsen, 1996). In preliminary approaches, however, fractions of 12.5% of the respective original sample were taken. On average, these sub-samples consisted of 233.5 ± 138.5 individuals and were therefore still way above the aimed-for 100 individuals. Subsequently, 12.5% fractions were used instead of 25% fractions. The sub-sampling procedure consisted of a serial dilution of the original samples with tap water starting from a fixed volume of 400 ml. While constantly stirring, equal amounts were alternately poured into each of two beakers until the sample was completely split in half. This procedure was run three times in total, randomly choosing one of the two halves for further splitting, until aliquots of 12.5% of the original sample were produced in three dilution steps. According to Van Guelpen et al. (1982) stratification occurring while stirring and pouring could be neglected because any layer will tend to be split without prejudice and will be distributed evenly among two halves.

Numbers of adult males, females and subadult or juvenile individuals of *C. mutica* were determined for each sample. Allocation of individuals to one of the sex/age groups was determined according to size and/or visible signs of maturity or prematurity, respectively (Tab. II-2). Body length was measured from the head (base of antennae) to the distal end of the abdomen to the nearest 0.1 mm using computer based imaging software 'analySIS', Version 3.2 (Soft Imaging System GmbH, Münster) connected to a dissection microscope. Ovigerous females were not distinguished from non-ovigerous females because freezing of the samples or storage in formalin dispersed the oostegites and clutches were typically lost. The remaining numbers of eggs or embryos in the brood pouches were, therefore, not representative for assessing fecundity.

Tab. II-2: Characteristics used to assign individual specimens of *Caprella mutica* to different sex/age groups.

Allocation to groups	Characteristics
Adult males	Insertion of gnathopods II clearly positioned on posterior end of pereonite II and/or strong setation on pereonites I and II and gnathopods II
Adult females	Insertion of gnathopods II on anterior end of pereonite II and brood pouch fully developed; eggs present or absent from brood pouch
Subadults/ Juveniles	Insertion of gnathopods II ranging from middle to anterior end of pereonite II and/or brood pouch underdeveloped

Statistical analysis

Annual temperature variation in Oban and Helgoland was analysed by a two-way repeated measures ANOVA (STATISTICA 7.0). Effects of fixed factors ‘location’ and ‘months’ were tested. Temperature data (N = 3) were previously fourth-root transformed to meet the assumptions of normality (Kolmogorov-Smirnov test, P > 0.05) and homogeneity of variance (Bartlett’s test, P > 0.05).

Differences in annual population structure and densities were tested by three-factorial PERMANOVAs (permutation-based multivariate analysis of variance; Anderson, 2005) with 4999 permutations. PERMANOVA is a multivariate procedure that tests the simultaneous response of one or more variables to one or more factors as commonly used in ANOVA designs. It is based on any distance measure using permutation methods (Anderson, 2005). Bray-Curtis dissimilarity was chosen as distance measure, as it can be applied to qualitatively different types of data and it is not affected by joint absences, which are commonly found in ecological data sets (Day et al., 1971; Field et al., 1982).

The abundances of males, females and juveniles served as response variables to test for differences in population structure. For the analysis, monthly samples (N = 5) were pooled for seasons: winter (December - February), spring (March - May), summer (June - August) and autumn (September - November) (Garcia and Mantelatto, 2001; Ashton, 2006). The effects of the fixed factors ‘site’ (three levels: each three study sites), ‘season’ (four levels: winter, spring, summer and autumn) and ‘orientation’ (surface and bottom) on abundance and population structure were tested. To prevent from confounding effects due to differences at the two study locations, separate analyses were run for Oban and Helgoland sites.

Although being a non-parametrical analysis *sensu lato*, data were previously fourth-root transformed to improve homogeneity of variances as PERMANOVA is sensitive to differences in variability among groups (Anderson, 2005). Significant pair-wise *a posteriori* comparisons with multivariate *t*-statistics based on distance measure chosen for the analysis (included in the programme; Anderson, 2005) were followed by Kruskal-Wallis or Mann Whitney-U tests to compare for differences in individual variables.

Size records of *C. mutica* were assigned to 2 mm size classes (0.0 - 2.0 mm, 2.1 - 4.0 mm, 4.1 - 6.0 mm and so forth; Flores and Paula, 2002; Ashton, 2006) and size-frequency distributions were determined from seasonally grouped data sets for each site and location. Measurements from the surface and bottom populations were pooled as differences between males, females and juveniles from bottom and surface populations varied only between 0.7 to 1.3 mm and were considered negligible for this purpose. Seasonal changes at sites were described by comparing the median sizes of individual groups by Kruskal-Wallis or Mann Whitney-U tests.

Results

Temperature

At Oban, the lowest temperature of 7.4°C was found in March 2006 and the highest of 14.3°C in October 2006. Water temperatures at Helgoland ranged from 3.5°C in March 2006 to 20.2°C in July 2006. Statistical analysis showed clear differences between sites and months (P for both factors < 0.01). Throughout the study period, the temperature varied stronger at Helgoland than at Oban (interaction of site and month, P < 0.01; Fig. II-4).

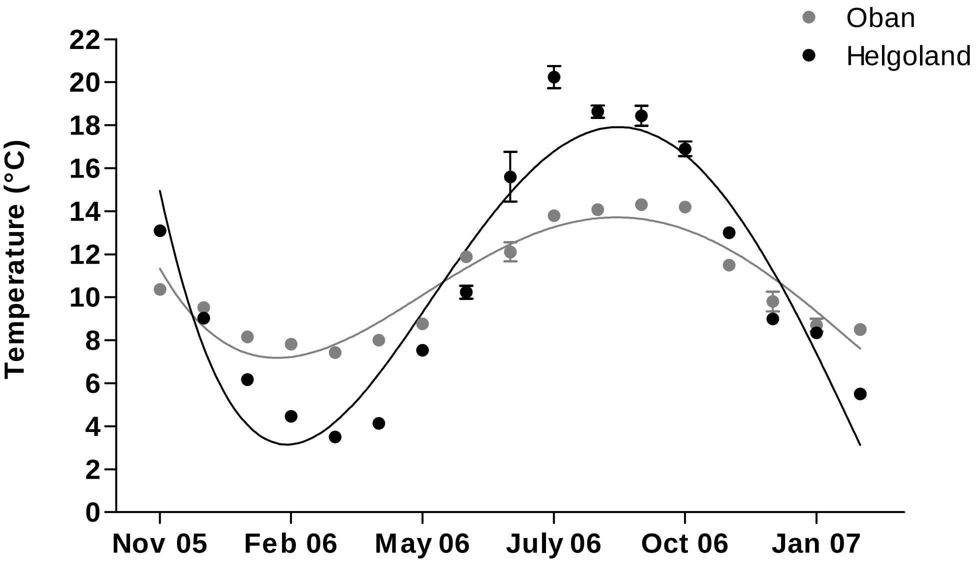

Fig. II-4: Water temperatures at Oban and Helgoland for the 17 month study period (mean ± SD; N = 3). Curves are fourth order polynomials depicting course of temperature over time.

Population dynamics, structure and abundance

At both study locations populations of *C. mutica* showed strong seasonal density fluctuations throughout the study period (Fig. II-5, Appendix Tab. II-4 and II-5). At Oban sites, population densities varied between zero and a maximum total density recorded from a single mesh at Oban fish farm of 99,840 ind. m^{-2} in August 2006. At Helgoland sites specimens were found throughout the year. Maximum densities of 205,790 ind. m^{-2} found on a single mesh were recorded in September 2006 at Helgoland south harbour.

The analyses for both locations revealed that populations differed typically in overall abundances but not in the population structure (i.e. proportions of males, females and juveniles, respectively) (Fig. II-6 and II-7). The population structure of *C. mutica* varied seasonally. Throughout summer, autumn and winter juvenile individuals dominated the populations at both locations (between 70 and 80% of the populations). At this time, males' shares of the populations were typically lower than females' shares (Fig. II-6 and II-7, Appendix Tab. II-4 and II-5). During spring juveniles' shares decreased to 45-50% while adult shares increased. At this time, males were more abundant than females. This was, however, only be observed at Helgoland sites, as *C. mutica* was absent from Oban sites during spring.

Due to the structural consistency between populations from different locations, the results from the analyses will refer solely to total population abundances.

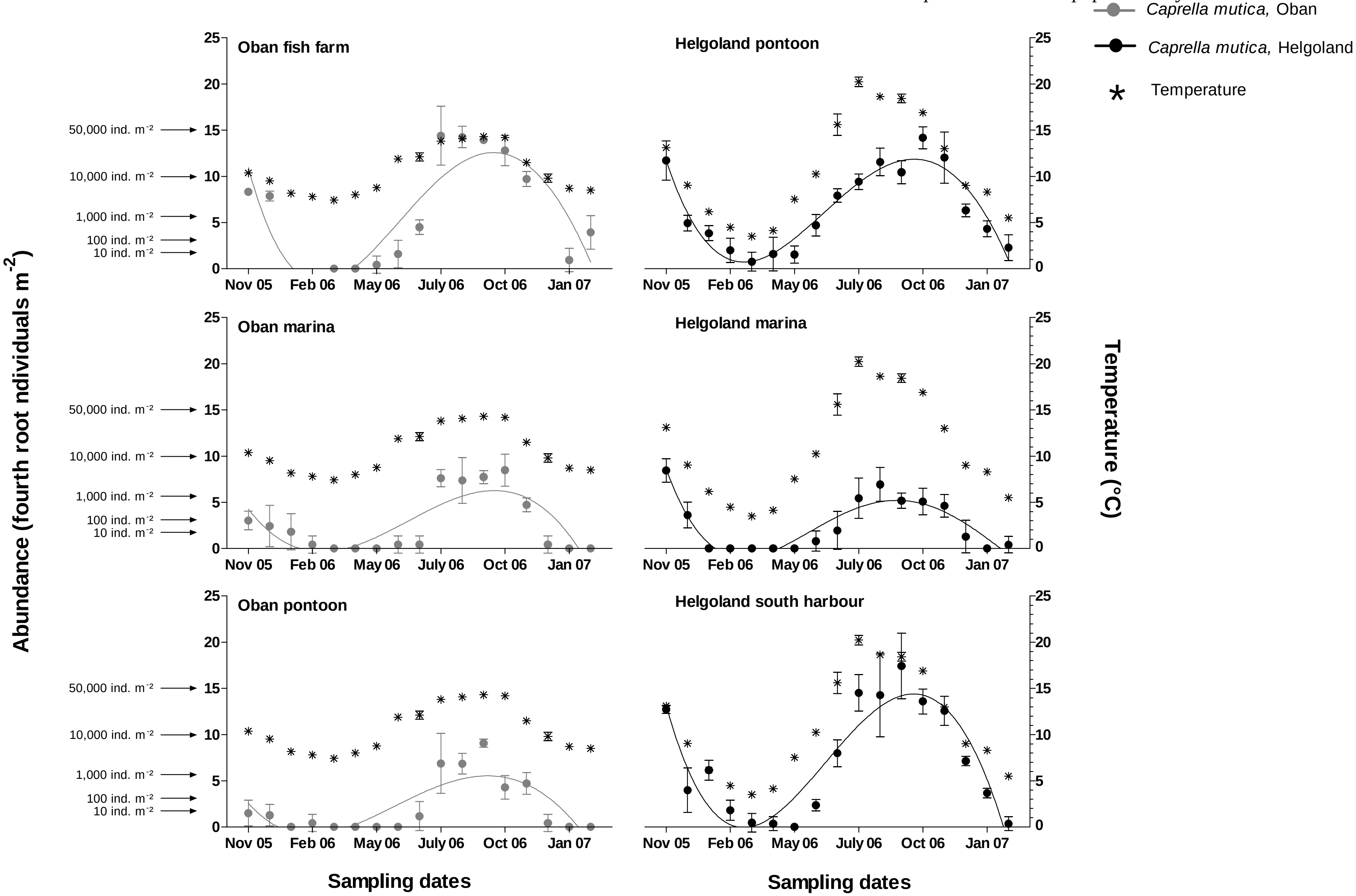

Fig. II-5: Total abundance (averaged for surface and bottom populations) of *Caprella mutica* during the 17 months study period at three Scottish sites Oban fish farm, Oban marina and Oban pontoon (left column of graphs) and three German sites Helgoland pontoon, Helgoland marina and Helgoland south harbour (right column of graphs). Symbols represent average fourth root ind. m^{-2} (± SD; N = 5). Curves are fourth order polynomials depicting population progression over time.

a) Oban

At Oban, the factors site and season significantly affected the population abundances of *C. mutica* (P each < 0.01; Fig. II-6, Tab. II-3, Appendix Tab. II-4).

Highest densities were found at Oban fish farm with an annual average of 11,300 ind. m^{-2} ($P < 0.05$). Both Oban marina and Oban pontoon harboured similarly low annual average densities of 1,200 and 1,000 ind. m^{-2}, respectively ($P > 0.05$).

The results found highest annual average densities during summer (about 9,200 ind. m^{-2}) and autumn (about 8,300 ind. m^{-2}). During winter, abundances decreased to approximately 500 ind. m^{-2} and lowest numbers were found during spring (about 0.4 ind. m^{-2}). During the entire spring period only a single female was found on one mesh at Oban fish farm in May 2006.

The significant interaction between site and season ($P < 0.01$; Tab. II-3) showed that the above described pattern of highest abundances at Oban fish farm and lower abundances at Oban marina and Oban pontoon was particularly clear during summer, autumn and winter. During the entire spring period, however, only a single female individual was found at Oban fish farm, while there were no individuals found at the other two Scottish sites. Yet, the analysis revealed highly significant differences between the Oban fish farm and both Oban marina and Oban pontoon and did not compute for differences between the latter two. Although the analysis does not explicitly assume homogeneity of variance within each group, PERMANOVA will be sensitive to data sets consisting entirely of zeros when compared, as there will be no variance at all (Anderson, 2005). In this specific case, the post-hoc results from the significant interaction between site and season must be interpreted ecologically rather than statistically. According to the consistently very low number of individuals found at the Oban sites during spring, no striking differences between the sites are assumed.

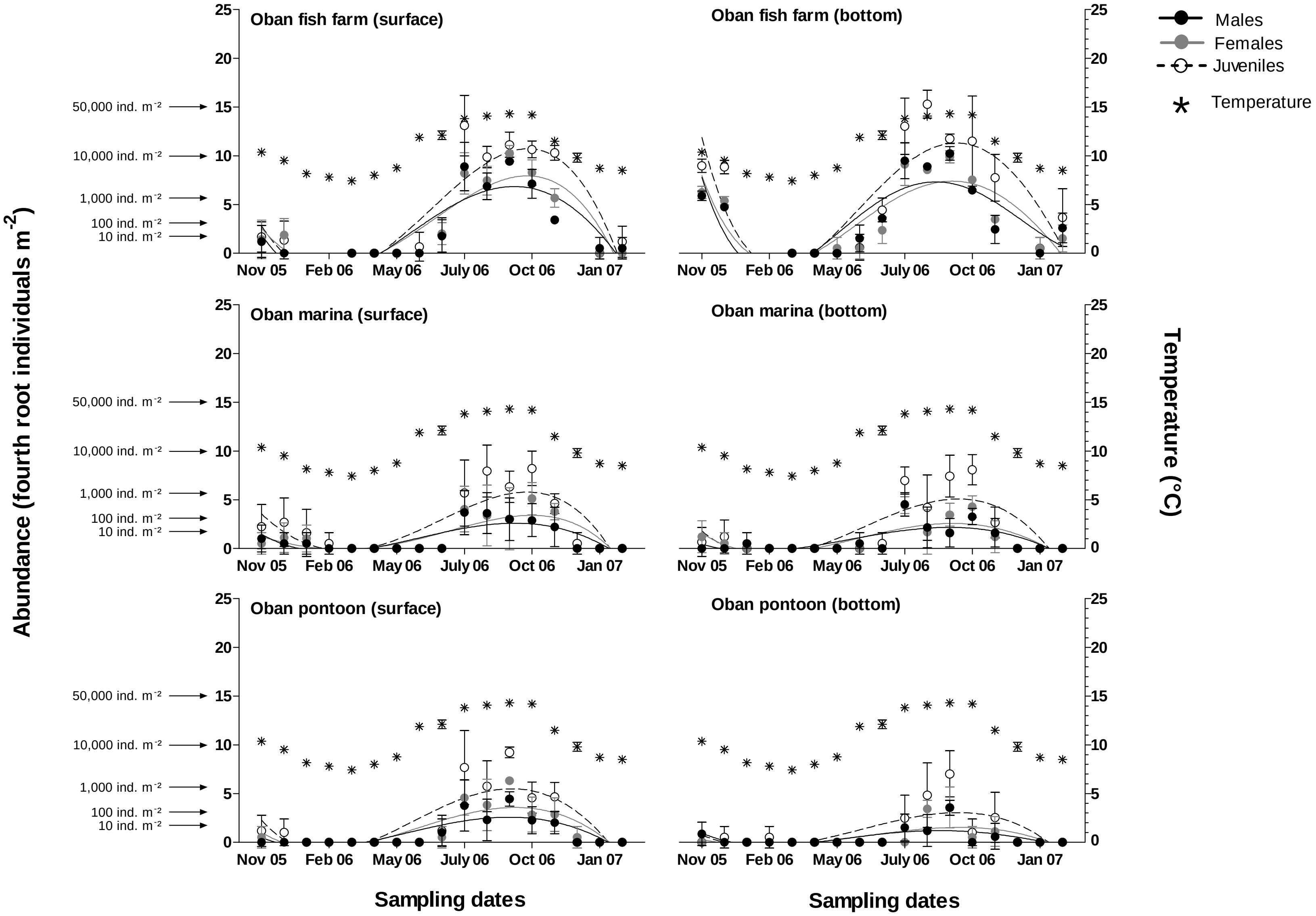

Fig. II-6: Seasonal abundance of male, female and juvenile *Caprella mutica* during the 17 months study period at three Scottish sites Oban fish farm, Oban marina and Oban pontoon. Abundances from surface populations (left column of graphs) and bottom populations (right column of graphs) are presented. Symbols represent average fourth root ind. m^{-2} (± SD; N = 5). Curves are fourth order polynomials depicting population progression over time.

b) Helgoland

At Helgoland the factors site, season and orientation significantly affected the population abundance of *C. mutica* (P for all factors < 0.05; Fig. II-7, Tab. II-3, Appendix Tab. II-5).

Pooled to sites, the results revealed highest average densities at Helgoland south harbour with an annual average of about 22,000 ind. m^{-2}, followed by Helgoland pontoon with about 9,200 ind. m^{-2}. This difference, however, was statistically not significant (P > 0.05). In contrast, significantly lower densities were found at Helgoland marina with an annual average of about 900 ind. m^{-2} (P for each comparison < 0.05).

When pooled to seasons, the results found highest average densities during autumn (about 25,700 ind. m^{-2}) followed by summer (about 17,000 ind. m^{-2}). During winter, abundances decreased to approximately 500 ind. m^{-2} and lowest numbers were found during spring (about 70 ind. m^{-2}). At all seasons the population abundances were significantly different from each other (P for all comparisons < 0.05).

The significant interaction between site and season (P < 0.01; Tab. II-3) confirmed that equally high densities at Helgoland south harbour and Helgoland pontoon and lower densities at Helgoland marina were consistent throughout winter and spring. During summer and autumn, however, the differences between Helgoland south harbour and Helgoland pontoon became significant. Highest abundances were found at Helgoland south harbour.

The analysis of the factor orientation revealed significantly larger surface populations than bottom populations (P < 0.01). This however, was only due to vertical differences at Helgoland pontoon (interaction between site and orientation, P < 0.01). Moreover, the significant interaction confirmed that the different pattern of high abundances at Helgoland south harbour and Helgoland pontoon and low abundances at Helgoland marina were particularly true for bottom populations (P < 0.05). In contrast, in the surface populations, all three sites revealed similar densities (P > 0.05).

The significant interaction of all three factors highlights how differences between surface and bottom densities fluctuate with site and season (P < 0.01; Fig. II-7, Tab. II-3, Appendix Tab. II-5).

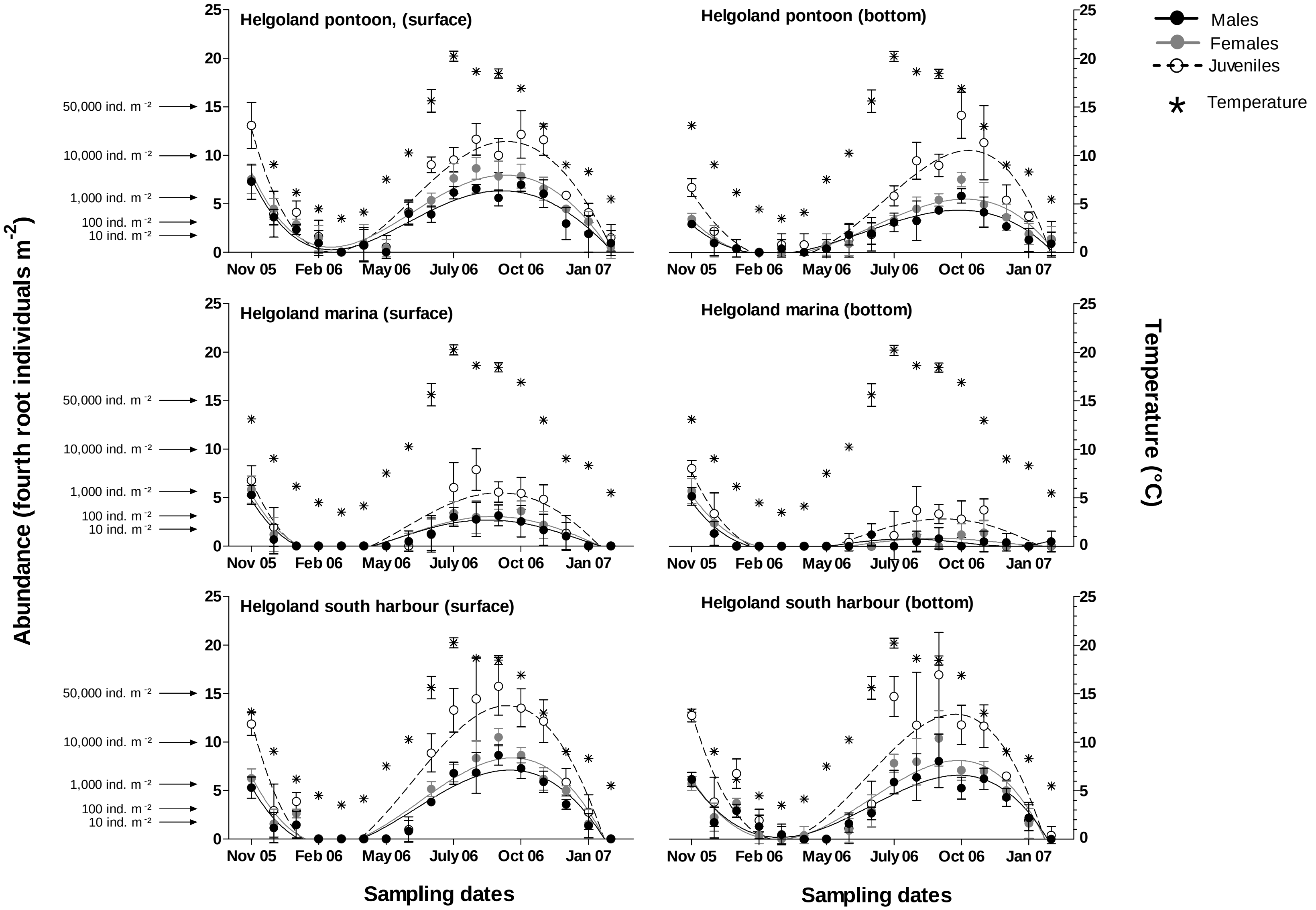

Fig. II-7: Seasonal abundance of male, female and juvenile *Caprella mutica* during the 17 months study period at three German sites Helgoland pontoon, Helgoland marina and Helgoland south harbour. Abundances from surface populations (left column of graphs) and bottom populations (right column of graphs) are presented. Symbols represent average fourth root ind. m^{-2} (± SD; N = 5). Curves are fourth order polynomials depicting population progression over time.

Tab. II-3: Results of PERMANOVAs testing the effect of site (Oban fish farm, Oban marina, Oban pontoon and Helgoland pontoon, Helgoland marina and Helgoland south harbour, respectively), season (winter, spring, summer and autumn) and orientation (surface and bottom) on the density and population structure of *Caprella mutica* at Oban and Helgoland. Bold P values indicate significant differences.

	Source of variation	**df**	**SS**	**MS**	**F**	**P**
Oban	Site	2	16687.09	8343.55	13.94	< **0.01**
	Season	3	196761.41	65587.14	109.62	< **0.01**
	Orientation	1	101.01	101.01	0.17	0.85
	Site * Season	6	31919.89	5319.98	8.89	< **0.01**
	Site * Orientation	2	4308.85	2154.43	3.60	**0.02**
	Season * Orientation	3	4269.07	1423.02	2.38	0.54
	Site * Season * Orientation	6	6767.40	1127.90	1.89	0.58
	Residuals	96	57439.74	598.33		
Helgoland	Site	2	26935.80	13467.90	20.99	< **0.01**
	Season	3	59299.97	19766.66	30.81	< **0.01**
	Orientation	1	2541.97	2541.97	3.96	**0.01**
	Site * Season	6	39304.32	6550.72	10.21	< **0.01**
	Site * Orientation	2	5471.33	2735.66	4.26	< **0.01**
	Season * Orientation	3	2822.68	940.89	1.47	0.17
	Site * Season * Orientation	6	8066.97	1344.49	2.10	**0.02**
	Residuals	96	61584.75	641.51		

Sex ratio

At both locations, females were more abundant than males at most sites and seasons. The female preponderance was strongest during summer, autumn and early winter months, but rarely significant (P for most comparisons > 0.05). The average share of males was 40% (Fig. II-8). In short periods of male preponderance the males never significantly dominated the females.

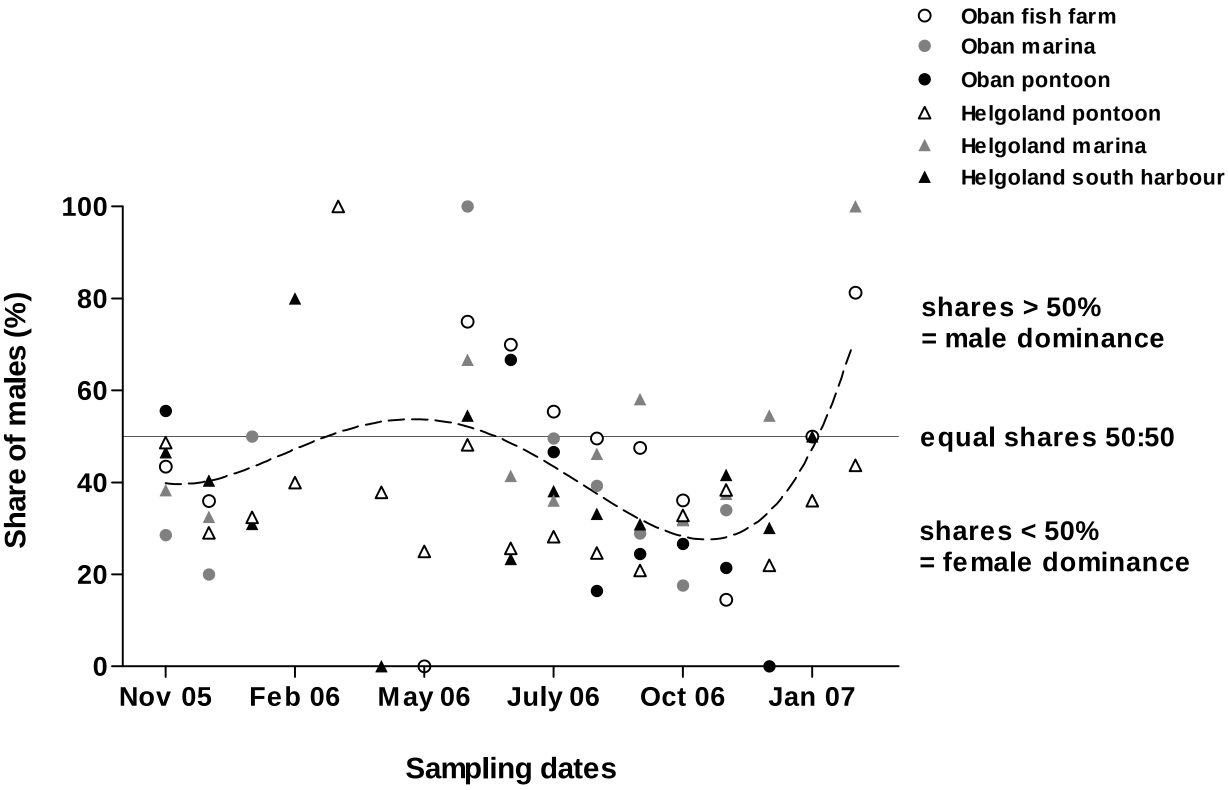

Fig. II-8: Share of males (males/ (males + females)) of *Caprella mutica* pooled for each sampling month from all sites within each location. Data from surface and bottom populations were pooled. The horizontal line indicates equal sex ratios at 50% shares of males. The curve is a fourth order polynomial calculated from all sampling events with sites as replicates per sampling date, depicting change and intensity of male and female preponderance over time.

Size-frequency distribution

At the Scottish study sites, individuals were significantly larger at Oban fish farm (largest male: 41.3 mm and female: 16.8 mm) than at Oban marina and Oban pontoon (each $P < 0.01$), while the latter two did not differ ($P > 0.05$). On average, the largest individuals were found at Helgoland marina, followed by Helgoland south harbour and Helgoland pontoon (each $P < 0.01$) (Appendix Tab. II-6).

Apart from seasons with low abundances (e.g. spring or winter), adult sexes tended to show unimodal size distributions at most sites. Males' size distributions were more strongly skewed towards larger size classes than the females' size distributions (Fig. II-9 and II-10, Appendix Tab. II-6).

At almost all sites within the two study locations, juveniles of the two smallest size classes (2 and 4 mm) typically dominated the entire winter populations with proportions of up to about 80%. Proportions of juveniles and adults from medium size classes (6 to 12 mm) were each around 10% of the population or lower. Percentages of individuals from higher size classes > 12 mm did not exceed 2% (Fig. II-9 and II-10).

In spring, *C. mutica* was generally absent from Oban sites. At Helgoland marina only four specimens were found. These were assigned to size classes larger than 6 mm. At Helgoland pontoon and Helgoland south harbour population densities were higher in spring. At these sites, the high juvenile proportions of the populations (70-80%) typically decreased from winter to spring to a total of about 40-50%. At the same time the proportions of all adult size classes increased and adult individuals grew up to 26 mm (Fig. II-10). During summer and autumn, again juveniles of the two small size classes (2 and 4 mm) dominated the populations with shares of between about 50 and 80% at all sites and both locations. The majority of summer and autumn adults were found in size classes between 6 and 12 mm and proportions of the populations in each of those size classes were typically below 10%. Proportions of adults in larger size classes (> 12 mm) of the population were typically around 0.5%.

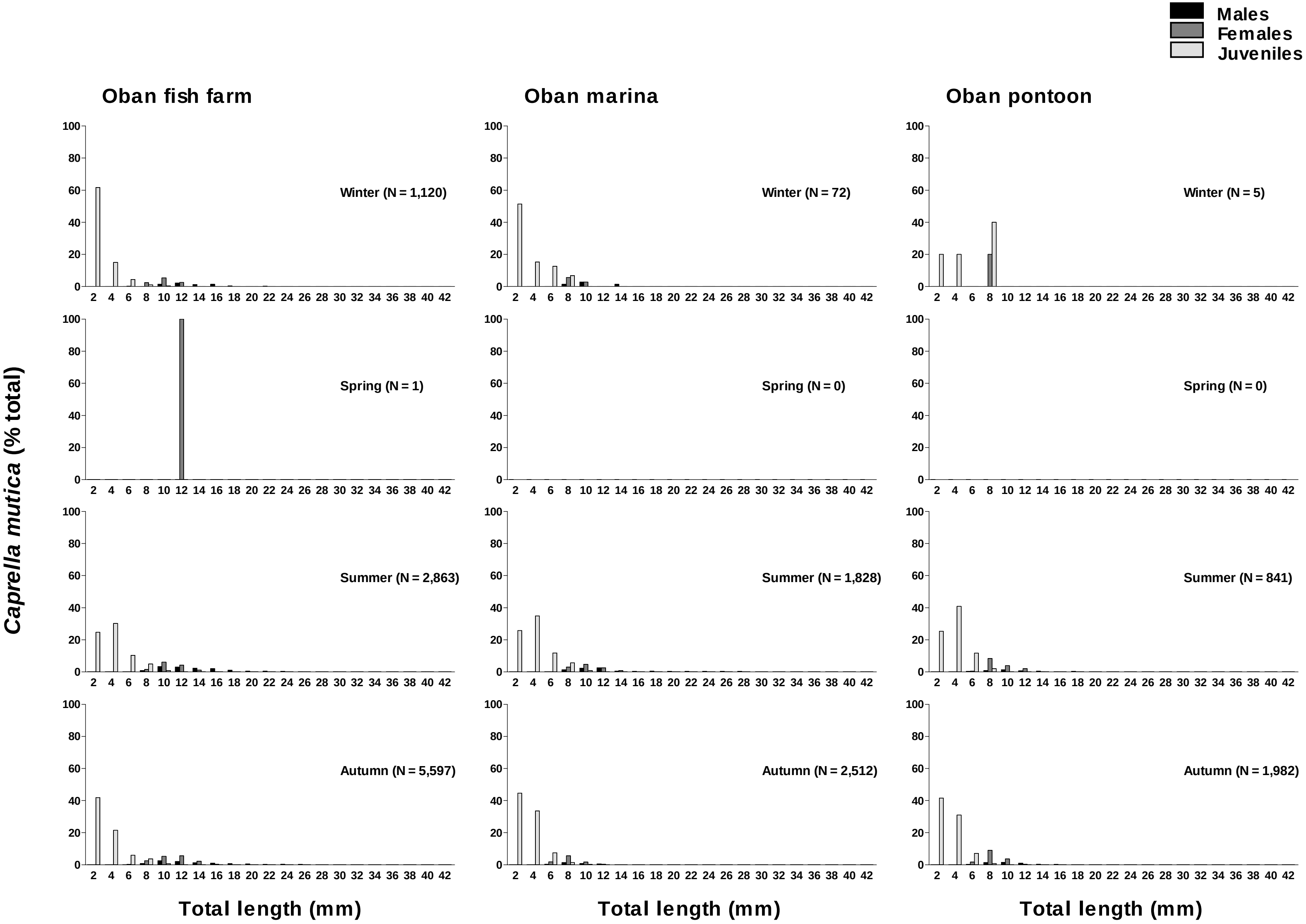

Fig. II-9: Seasonal size-frequency distribution of male, female and juvenile *Caprella mutica* at Oban fish farm, marina and pontoon. Data from surface and bottom populations are pooled. Percent shares of males, females and juveniles of the total population are shown for each size class.

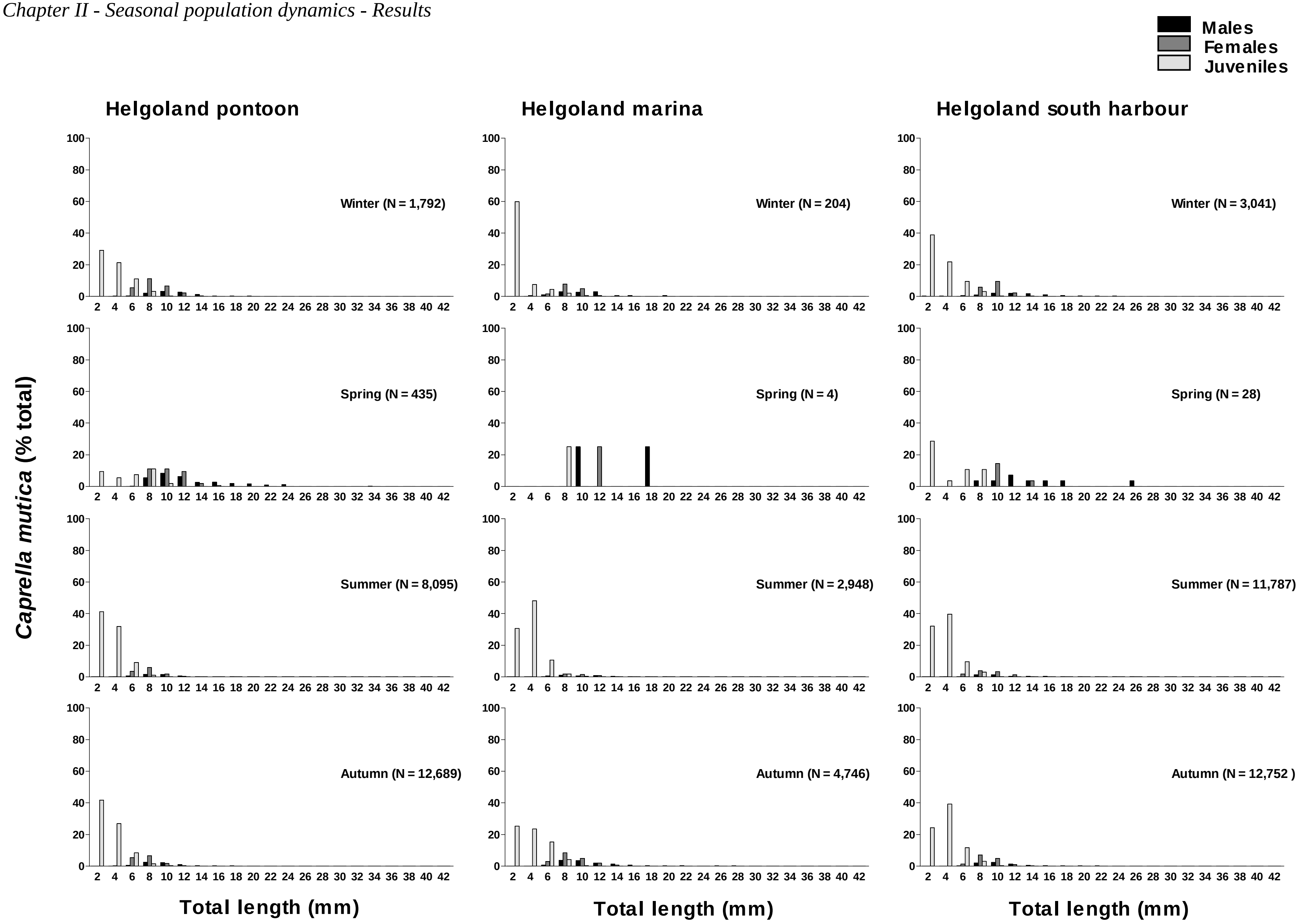

Fig. II-10: Seasonal size-frequency distribution of male, female and juvenile *Caprella mutica* at Helgoland pontoon, marina and south harbour. Data from surface and bottom populations are pooled. Percent shares of males, females and juveniles of the total population are shown for each size class.

Discussion

Temperature effect

Temperature is known to have a strong influence on the development and reproduction in numerous aquatic species (Korringa, 1957; Bentley and Pacey, 1992; Olive, 1995; Erikson Wiklund and Sundelin, 2001). Typically, reproductive and developmental rates (e.g., maturation time and duration of brooding cycles) decelerate or are suspended during periods of cold water temperatures, whereas an overall increase in reproductive activity comes into effect as soon as a criticial, species-specific temperature threshold is exceeded (Olive, 1995).

The present study found that more than any other factor, temperature significantly influenced the population dynamics of *C. mutica*. The results showed that the pattern of seasonal increase and decrease in total abundance was tightly synchronized with the annual seawater temperature at both study locations. At all sites the abundances of both, surface and bottom populations increased at the beginning of the summer when temperatures were between 10 and 12°C and reached their peaks typically in late summer or early autumn (September to November), when temperatures were highest. Along with temperature drops from November onward, densities declined during early winter and even decreased to zero at some sites during late winter and spring, when temperatures were lowest.

Apart from temperature, the intensity and duration of light is known to induce sexual activity particularly in gammarid amphipods (Dunn et al., 1996). However, because day-length and temperature are generally coupled, numerous authors proposed a synergetic effect of the variables temperature and light on reproduction (Roux, 1970; Armitage and Landau, 1982; DeCoursey, 1983). In fact, while studying the onset and termination of reproduction in the amphipod *Hyatella azteca*, De March (1976) showed that only photoperiod determined whether reproduction was continued or discontinued but that temperature influenced the rate of all changes.

While the effect of light and the daily photoperiod on the population dynamics of *C. mutica* was not investigated explicitly, its influence can not be categorically excluded here. However, as the results showed that the population dynamics were clearly in phase with the annual sea water temperature, this factor is likely to play a superior role in determining temporal variability in population abundances.

Effects of study locations (Oban vs. Helgoland)

The two study locations differed strongly in temperature range. While the Oban sites reached minimum temperatures of about 7°C, maximum temperatures were at about 14°C. In contrast, the temperature range at Helgoland was more than twice as large as at Oban, reaching higher summer (give mean summer temperature as for Oban) and lower winter temperatures (give mean winter temperature as for Oban).

The overall abundances were higher at Helgoland sites than at Oban sites. At first view, this might coincide with higher summer temperatures observed at Helgoland. However, when comparing the six sites individually, densities were not necessarily higher at all Helgoland sites. For example, highest annual average densities were found at Helgoland south harbour. About half as much were found at Oban fish farm and at Helgoland pontoon. Abundances were ten times lower at Oban marina and Oban pontoon, whereas lowest population densities were found at Helgoland marina.

Although the total abundances varied seasonally at all study sites, the overall population dynamics were not affected by the different temperature regimes at Oban and Helgoland. It rather seems that a temperature threshold which lies within the ranges of both study locations (about 10 to 12°C), is responsible for the increase or decrease in reproductive activity causing the observed populations dynamics. More so, as the observed pattern of seasonal dynamics was similar for native populations as well (Fedotov, 1991) were temperature ranges are even larger as in the German Bight (between -1.8 and 25°C; Schevchenko et al., 2004). Similar findings were reported by Rajagopal et al. (1999) who found the breeding season of the invasive amphipod *Corophium curvispinum*, introduced to the stretches of the lower river Rhine, to be initiated by rising water temperature during spring time.

Although the seasonal population dynamics were in phase with temperature at both study locations, all Helgoland sites showed a slight delay of abundances relative to temperature. This, however, was only obvious when the populations reached highest densities during early autumn and when temperature was already decreasing. While this shift did not affect the overall course of seasonal increase and decrease of population abundances, it is likely that the larger temperature range at Helgoland caused a delayed population response to decreasing temperatures. High reproductive activity in late autumn may have led to a release of brooded hatchlings contributing to extended periods of high densities while temperatures already started to decrease. Similar findings were reported by Gerten and Adrian (2002), who found delayed responses to warm water periods in the abundances of different freshwater copepods. The delayed population response later in the year observed at Helgoland sites may also be responsible for the persistence of populations throughout the winter while in Oban populations usually went extinct during the cold season.

Orientation (surface and bottom)

While *C. mutica* was found at the Helgoland study sites throughout the whole year, populations were absent from the Oban sites during the entire spring period (March-May) with the exception of a female singleton from Oban fish farm found in May 2006. The almost complete absence in spring might not be representative because of the loss of three sets of samples from Oban fish farm in the present study during heavy spring storms. In a previous study from 2004 to 2005, Ashton (2006) found a total of 908 individuals at this study site during spring. This difference might further be on account of natural annual variation within the population probably as a consequence of variable environmental conditions. The overall decrease in population abundance over winter and spring is, thus, most likely on account of natural stochastic processes (Fagan et al., 2002) under which older specimens die off and reproductive activity decreases leading to decelerated population growth. In addition, exceptional forces such as storms and heavy winds during winter and spring seasons may physically remove settlement structures along with individuals of *C. mutica* resulting in local population decline.

In her studies, Ashton et al. (2007b) found 100% mortality of *C. mutica* within 48 h at salinities lower than 16 psu. Heavy rainfalls and strong fresh water run-offs, particularly from Loch Etive at the Oban study sites, are known to create surface several metres strong layers of fresh water (Edwards and Edelsten, 1977). Unfavourably reduced salinity conditions may cause potential migration to deeper habitats (e.g. on the fish farm nets at Oban fish farm) or even decease of *C. mutica* where sites are not deep enough (e.g., Oban marina and Oban pontoon). According to the exponential population growth at the onset of summer at all study sites, however, it is highly unlikely that populations went completely extinct at the Oban study sites and that summer recruitment was entirely on account of re-introductions for example from local boating traffic.

In the present study, potential differences in seasonal abundances of *C. mutica* particularly during colder months were investigated at the surface level and from a depth of about 3 to 4

m. Seasonal vertical migration has been described for the different crustaceans (e.g., the portunid crab *Liocarcinus depurator* or the blue crab *Callinectes sapidus* and fish species (e.g., bay anchovy *Anchoa michilli* or spot *Leistomus xanthurus*) as a response to cold surface layers as opposed to milder deep water bodies (Szedlmayer and Able, 1996; Gibson and Robb, 1993). However, when comparing surface and bottom populations from the present study sites, there was no clear overall pattern detectable in the population density of *C. mutica*. Only one site, Helgoland pontoon, showed consistently lower abundances at all seasons in depth (with low adult and high juvenile proportions) than at the surface (with high adult and low juvenile proportions). In contrast, at other sites, depth related differences in abundance were not present or only detectable during particular seasons. The overall abundances of surface populations were typically higher than abundances in the depth during warm seasons (summer: Helgoland marina, autumn: Oban pontoon) than during cold seasons (winter: Oban fish farm). This trend may indicate downward migrations of *C. mutica* during colder seasons. In fact, in his studies on seasonal dynamics of *C. mutica* in its native range, Fedotov (1991) suggested migrations to shallower waters during spring time, when temperature is at a minimum. In its native habitats, *C. mutica* is distributed to a depth of about 13 m (Fedotov, 1991). Given potential migration to shallower waters during cold seasons, the presently investigated depth of 3 to 4 m might not be deep enough to detect seasonal migration processes. In addition, the ropes connecting the surface and bottom meshes might have offered the potential for permanent small scale migrations of *C. mutica* throughout all seasons and thus might have obscured differences between the surface and bottom populations.

In preliminary sampling studies in winter 2005/06, a large population of *C. mutica* was found in the extended shank part of a navigational buoy in the vicinity of Helgoland at water temperatures of approximately 3°C. The population consisted of several thousand individuals of all sizes and stages. This observation contradicts to the above described findings of generally low population abundances or even local extinction of *C. mutica* during cold seasons. Takeuchi and Hirano (1992) suggested that the seasonal occurrence of caprellid amphipods may depend on the availability of substratum (e.g. macroalgae) to cling to. The presence of native fouling species may play a crucial role in serving as settlement substrata and shelter for *C. mutica*. This might have biased the results of the present study in which clean meshes were repeatedly offered for settlement and which were barely fouled during winter or spring months, potentially not being attractive for *C. mutica*. The shank population of *C. mutica* was clinging to dense piles of gammarid amphipod tubes which covered the inside of the shank. The finding suggests that *C. mutica* is physiologically able to persist throughout colder periods in large numbers. The occurrence of the shank population, however, may only represent a random finding which offered *C. mutica* food and shelter throughout wintry periods of adverse physical conditions, during which substratum is typically rare (Takeuchi et al., 1990). Shallow water habitats, however, may offer similarly sheltered conditions but have not been investigated presently. It seems probable that overwintering populations of *C. mutica*, particularly at the Oban study sites, were not detected in our experimental set-up, however, persisted at shallower waters, seeking shelter from exposed to strong physical forces in undisturbed habitats.

Sex ratio and size-frequency distribution

When densities of *C. mutica* were high (from summer to early winter) the female shares of the populations were generally more pronounced than the male shares. This pattern was also found by Fedotov (1991) for native populations and by Ashton (2006) for introduced populations. Lewbel (1978) suggested highly aggressive and even lethal interactions between male individuals to have caused female biased sex ratios in *Caprella gorgonia* and this may be relevant for *C. mutica* as well. In addition, results from predator-prey interactions (this work, Chapter IV) revealed selective predation of common predators on large males of *C. mutica* over medium sized males or females. Intensive predation of large sized males was suggested for the amphipod *Dikerogammarus villosus* (Devin et al., 2004) and, likewise, might have contributed to female preponderance in field populations of *C. mutica*. While female biased sex ratios are common for different amphipod species (Costello and Meyers, 1989), this trait might not be an important factor determining the success of *C. mutica* in its new habitats. However, as female preponderance generally increases the reproductive capacity of a population (Devin et al., 2004), this trait might significantly support rapid colonization and establishment of *C. mutica* in new areas, particularly during warm seasons.

High population densities of *C. mutica* found all through summer, autumn and winter were typically accompanied by large proportions of small sized juveniles. After winter, proportions of adult size classes increased indicating that winter hatchlings stemming from high reproductive activity during late autumn, grow over winter. They potentially reach maturity during spring and subsequently contribute to the reproduction process and thus, to an exponential population growth during early summer. This highlights the capability of *C. mutica* to establish large populations from potentially small numbers of founder individuals under favourable temperature conditions. In fact, studies on life history traits of *C. mutica* have indicated that rapid growth, short maturation time and high reproductive frequency at seawater temperatures between 14 and 16°C have significantly contributed to the invasion success of this species (Cook et al., 2007b; this work, Chapter III). Similarly, Berezina and Panov (2004) found population densities of the Baikalian amphipod *Gmelinoides fasciatus*, introduced to the Gulf of Finland basin, to undergo exponential population increases within short time spans when temperatures were favourable.

Effects of habitat characteristic (sites)

a) Exposure and currents

While Oban fish farm is located in the open water of the Firth of Lorne, the other two Scottish sites were situated within the natural enclosure of Dunstaffnage Bay. Floerl and Inglis (2003) studied the effect of harbour design on the recruitment and propagule pressure on fouling communities dispersed via planktonic larvae. The authors showed that recruitment in enclosed marinas was several orders of magnitudes higher, than in unenclosed marinas. Floerl and Inglis (2003) found that complex water circulation patterns created by enclosed marina designs retained water bodies for up to 12 h d^{-2}. As a consequence, the authors concluded increased settlement of propagules on available surfaces. In contrast, unenclosed areas, or relatively wide or open bays may experience currents or fluxes passing by rather than retaining them. In a current study, Jahnke et al. (submitted) found that population abundances of *C. mutica* were higher in unenclosed than in enclosed marinas. The authors found habitats with strong currents to be more suitable for filter feeders such as *C. mutica*. When transcribed to the present study, this may be relevant for the unenclosed Oban fish farm. However, the two naturally enclosed sites in Dunstaffnage Bay experience comparably high circulating currents as well. Hence, populations of *C. mutica* do not seem limited in available food to filter feed on. Despite this, however, when retained in enclosed habitat for too long, water bodies of reduced salinity resulting from heavy rain falls and freshwater run-offs from adjacent Lochs could create unfavourable conditions for *C. mutica*. In this case natural enclosures may provide less suitable habitats for *C. mutica* as opposed to the unenclosed Oban fish farm and may account for reduced population densities.

At Helgoland, differences in population abundances of *C. mutica* were probably not influenced by currents and water circulations. As all three sites were located within enclosed harbour facilities with narrow openings, populations would be expected to experience similar conditions and thus, similar densities. This, however, was not the case.

b) Boating activity

The passage and the temporary mooring of yachts and other vessels with heavily fouled hulls may serve as important dispersal vectors of *C. mutica* on different geographical scales supporting the species' establishment in its introduced habitats (Ashton et al., 2006a, 2006b). In the present study the different frequency of boating activities (e.g., berthing or launching) at the sites under study seemingly influenced the population abundances of *C. mutica*. At Oban marina, Helgoland marina and Helgoland pontoon, which were regularly frequented by boating traffic, the abundances of *C. mutica* were comparably low. In contrast, Oban fish farm and Helgoland south harbour, both isolated sites attended only by few working boats, harboured far larger population of *C. mutica*. Intensive boating traffic and thus anthropogenic disturbances in harbour facilities may account for lower population densities compared to weakly disturbed sites. Similar findings were reported by Turner et al. (1997), who attributed the loss of cover by common solitary ascidians to marina operations and boating activities.

The only site deviating from this pattern was the isolated Oban pontoon that harboured comparably small populations of *C. mutica*. The pontoon is only attended for experimental usage by staff members of the Scottish Association for Marine Science and not used for berthing or mooring and therefore remains widely undisturbed. This may have accounted for its heavy fouling as this was probably the most intensively fouled site of all. A high native species diversity may enhance the probability for competitive or predatory interactions and may have significantly affected abundances of *C. mutica*.

c) Food availability

In the present study the amount of food supply available for *C. mutica* was not investigated. However, it is unlikely that the German study sites experienced strong differences in food availability in relation to each other. Water bodies are generally well mixed around the island of Helgoland (Wiltshire and Manly, 2004) and the harbour basins are subject to high turbidity during tidal exchange of water masses or storm induced circulations. Therefore, high amounts of suspended matter are likely to be available year round at all three sites (Chrapkowski-Llinares, 2005). The food availability at Helgoland may therefore be of minor importance causing differences in the population densities of *C. mutica*. In contrast, at the Scottish sites, the enhanced supply of salmon feed and thus the organic enrichment at Oban fish farm may have led to significantly higher population abundances of *C. mutica* as opposed to the non-fish farm sites. The organic enrichment of the seabed through sedimenting food pellets or faecal excretions is the most widely encountered impact of culturing fish in cages (Gowen and Bradbury, 1987; Karakassis et al., 2000). For example, Brown et al., (1987) found that the infaunal polychaetes *Capitella capitata* and *Scolelepis fuliginosa* dominated nutrient enriched sediments underneath fish farm cages containing high contents of proteins and lipids, whereas the abundances were far lower at the experimental control sites. Organically enriched sediments underneath fish farm cages might be of major importance for infaunal species. However, surrounding waters have been found similarly enriched by mariculture waste products (Navarro et al., 2008) and may affect epibenthic species in similar ways. In fact, Stirling and Okumus (1995) found organically enriched waters to significantly increase size and abundance of mussels (*Mytilus edulis*) suspended from salmon fish farm cages. This may hold true for *C. mutica* as well, as highest abundances and maximum body sizes were obtained at Oban fish farm.

d) Architecture and settlement space

At Helgoland south harbour, the ropes with the sampling meshes were fixed to weighted buoys in isolation from any other structures in direct proximity. This site supported highest population densities of *C. mutica* in the present study. Similarly, the isolated Oban fish farm harboured second highest abundances in the present study. In contrast, sites with directly neighbouring harbour walls or extensive surfaces of submerged berth-constructions contained relatively lower densities of *C. mutica*.

Settlement and recruitment success of invaders increases significantly with increasing availability of open resources, such as space (Stachowicz et al., 2002). Harbour walls and large surfaces of submerged pontoons offer, thus, extensive settlement space for *C. mutica*. The observed low densities at these sites may, therefore, simply reflect a dilution of densities in *C. mutica* while spreading onto available alternative surfaces as compared to when space is limited on isolated structures. The success of *C. mutica* must therefore be seen in view of the species' ability to colonize a variety of different microhabitats wherever space is available. Broad tolerances to environmental conditions and high phenotypic plasticity have been attributed to be qualities of successful invaders (Cohen and Carlton, 1995; Füreder and Pöckl, 2007) and hold true for *C. mutica* (Ashton et al., 2007b). In addition, the ability, to establish large populations when space is limited suggests reduced intraspecific effects in *C. mutica* highlighting a further common successful characteristic of invasive species (Holway et al., 1998; Tsutsui et al., 2000). Reduced intraspecific competition is thought to be associated to low genetic variation in small founder populations of non-native species when firstly introduced to new habitats (genetic bottleneck) as opposed to high genetic variability in native established species (Tsutsui et al., 2000; Lee, 2002). This might be advantageous when performing in density dependent interspecific interactions with native species (Tsutsui and Suarez, 2003). In fact, in their studies on intra- and interspecific competition of two ispod species, Franke and Janke (1998) gave indication that when one species out of a pair of potential competitors suffers less from intraspecific competition, that species will more likely be superior in interspecific competitive interactions.

Caprella mutica is well known for its great invasive capacity from numerous locations around the world. The present study highlights how anthropogenic influences, environmental conditions, architectural habitat settings and demographic traits of the introduced species may locally affect invasion success. Using this study as a descriptive starting point, further studies on the life history traits and on predaceous or competitive relationships with other species were conducted and presented in the following three Chapters to provide mechanistic interpretations of the invasion success of *C. mutica* in its new areas.

Appendix

Tab. II-4: Seasonal abundance of ind. m^{-2} (mean ± SD, N = 5) and percentages of *Caprella mutica* during the 17 months study in Oban. Samples are grouped into seasons (winter: December - February, spring: March - May, summer: June - August, autumn: September - November).

			Males		**Females**		**Juveniles**		**Total**		**Males**	**Females**	**Juveniles**
			mean	**± SD**	**mean**	**± SD**	**mean**	**± SD**	**mean**	**± SD**	**%**	**%**	**%**
Oban fish farm	Surface	Winter	5.3	7.3	18.7	17.9	34.7	45.8	58.7	67.1	9.1	31.8	59.1
		Spring	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-	-	-
		Summer	2780.7	1449.9	2374.7	753.3	11562.8	4421.2	16718.2	6293.1	16.6	14.2	69.2
		Autumn	2760.7	253.9	4450.0	650.4	10286.0	2365.9	17496.7	2982.4	15.8	25.4	58.8
	Bottom	Winter	202.7	17.4	296.0	76.2	2432.0	1240.6	2930.7	1250.9	6.9	10.1	83.0
		Spring	0.0.	0.0	2.7	6.0	0.0	0.0	2.7	6.0	0.0	100.0	0.0
		Summer	4013.8	1453.3	3538.0	1684.3	23000.3	2585.2	30552.2	4686.8	13.1	11.6	75.3
		Autumn	3586.7	765.5	3684.0	603.6	15621.3	9036.6	22892.0	8419.8	15.7	16.1	68.2
Oban marina	Surface	Winter	2.7	3.7	6.7	6.7	76.0	82.7	85.3	90.0	3.1	7.8	89.1
		Spring	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-	-	-
		Summer	202.0	106.2	302.0	167.2	2012.0	936.6	2516.0	1152.8	8.0	12.0	80.0
		Autumn	154.0	139.0	478.0	307.2	2106.0	1214.2	2738.0	1567.2	5.6	17.5	76.9
	Bottom	Winter	1.3.	3.0	1.3	3.0	6.7	11.5	9.3	11.2	14.3	14.3	71.4
		Spring	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-	-	-
		Summer	176.0	179.5	146.0	107.8	1042.0	813.4	1364.0	1085.7	12.9	10.7	76.4
		Autumn	54.0	25.1	184.0	145.7	2280.0	1141.7	2518.0	1180.3	2.1	7.3	90.5
Oban pontoon	Surface	Winter	0.0	0.0	1.3	3.0	2.7	3.7	4.0	6.0	0.0	33.3	66.7
		Spring	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-	-	-
		Summer	213.0	255.7	377.5	321.7	2678.0	3153.9	3268.2	3680.3	6.5	11.5	81.9
		Autumn	134.0	57.3	480.0	66.3	2202.0	312.2	2816.0	324.5	4.8	17.0	78.2
	Bottom	Winter	0.0	0.0	0.0	0.0	2.7	3.7	2.7	3.7	0.0	0.0	100.0
		Spring	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-	-	-
		Summer	14.0	11.4	46.0	42.8	496.0	727.3	556.0	774.6	2.5	8.3	89.2
		Autumn	54.5	51.4	98.0	79.5	996.0	859.3	1148.5	976.2	4.7	8.5	86.7

Tab. II-5: Seasonal abundance of ind. m^{-2} (mean ± SD, N = 5) and percentages of *Caprella mutica* during the 17 months study at Helgoland. Samples are grouped into seasons (winter: December - February, spring: March - May, summer: June - August, autumn: September - November).

			Males		**Females**		**Juveniles**		**Total**		**Males**	**Females**	**Juveniles**
			mean	**± SD**	**mean**	**± SD**	**mean**	**± SD**	**mean**	**± SD**	**%**	**%**	**%**
Helgoland pontoon	Surface	Winter	86.1	50.8	199.9	96.2	435.8	119.2	721.8	219.1	11.9	27.7	60.4
		Spring	102.5	88.7	121.7	117.5	120.0	116.1	344.2	315.2	29.8	35.4	34.9
		Summer	1222.2	165.5	3662.2	1875.4	12050.0	4911.2	16934.4	5074.2	7.2	21.6	71.2
		Autumn	2218.3	618.5	3684.2	872.2	22815.0	5614.2	28717.5	6277.0	7.7	12.8	79.4
	Bottom	Winter	16.1	10.8	67.2	84.2	249.4	200.7	332.8	280.0	4.8	20.2	75.0
		Spring	7.5	4.6	4.2	4.2	15.0	18.1	26.7	20.7	28.1	15.6	56.3
		Summer	151.9	129.5	239.7	164.6	3661.7	2583.0	4053.3	2844.3	3.7	5.9	90.3
		Autumn	567.5	194.2	1480.0	489.7	20785.8	9747.3	22833.3	10260.5	2.5	6.5	91.0
Helgoland marina	Surface	Winter	7.2	9.1	11.7	17.1	27.8	30.6	46.7	56.4	15.5	25.0	59.5
		Spring	1.7	3.7	0.8	1.9	0.0	0.0	2.5	5.6	66.7	33.3	0.0
		Summer	107.8	63.2	142.2	90.7	2730.0	1381.7	2980.0	1484.9	3.6	4.8	91.6
		Autumn	301.7	188.6	459.2	266.5	1460.8	635.3	2221.7	1059.8	13.6	20.7	65.8
	Bottom	Winter	4.4	5.0	6.1	3.6	56.1	64.0	66.7	64.3	6.7	9.2	84.2
		Spring	0.0	0.0	0.0	0.0	0.8	1.9	0.8	1.9	0.0	0.0	100.0
		Summer	3.3	5.0	17.8	33.7	274.4	298.7	295.6	322.6	1.1	6.0	92.9
		Autumn	204.2	110.1	335.8	254.2	1245.8	396.2	1785.8	625.5	11.4	18.8	69.8
Helgoland south harbour	Surface	Winter	41.1	20.1	129.4	43.8	385.6	179.0	556.1	163.9	7.4	23.3	69.3
		Spring	1.7	2.3	1.7	2.3	3.3	4.6	6.7	6.3	25.0	25.0	50.0
		Summer	1888.9	949.5	2995.6	1292.8	34362.2	16125.3	39246.6	17489.4	4.8	7.6	87.6
		Autumn	2843.2	764.8	5429.8	764.5	38248.5	6464.3	46521.5	7068.9	6.1	11.7	82.2
	Bottom	Winter	105.0	62.5	177.2	71.1	871.1	545.9	1153.3	549.3	9.1	15.4	75.5
		Spring	5.0	4.6	3.3	3.5	9.2	18.3	17.5	25.2	28.6	19.0	52.4
		Summer	1390.0	1086.3	3238.9	1877.3	31867.7	26840.9	36496.6	29086.3	3.8	8.9	87.3
		Autumn	2664.1	1538.7	5466.4	2535.8	44284.9	19953.1	52415.4	23441.2	5.1	10.4	84.5

Tab. II-6: Summary statistics of length (mm) in male, female and juvenile *Caprella mutica* during the 17 months study at Oban and Helgoland. Samples are grouped into seasons (winter: December - February, spring: March - May, summer: June - August, autumn: September - November).

		Males						**Females**						**Juveniles**					
		mean	**SD**	**median**	**min**	**max**	**N**	**mean**	**SD**	**median**	**min**	**max**	**N**	**mean**	**SD**	**median**	**min**	**max**	**N**
Oban fish farm	Winter	13.5	2.9	12.9	8.3	22.4	77	10.1	1.3	10.0	6.6	13.2	118	2.7	1.4	2.2	1.0	10.8	925
	Spring	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-
	Summer	14.9	5.8	13.3	7.7	41.3	442	10.9	1.7	10.7	7.2	16.8	383	3.9	1.7	3.5	1.0	10.4	2,038
	Autumn	13.9	5.1	12.3	5.0	37.0	553	11.0	2.0	11.0	6.4	16.6	905	3.3	1.7	2.8	0.8	13.4	4,139
Oban marina	Winter	10.9	2.3	10.6	8.5	14.0	4	8.5	0.8	8.5	7.0	9.5	6	3.2	1.9	2.5	1.3	8.9	62
	Spring	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-
	Summer	13.6	5.7	11.6	6.0	32.1	175	10.1	1.8	9.8	6.0	15.3	210	4.0	1.7	3.6	1.2	11.0	1,443
	Autumn	9.0	1.9	9.0	5.9	14.9	77	8.1	1.3	8.0	5.0	12.5	242	3.3	1.3	3.0	1.0	9.4	2,193
Oban pontoon	Winter	-	-		-	-	-	7.1	-	7.1	7.1	7.1	1	5.5	2.8	5.4	2.7	8.4	4
	Spring	-	-		-	-	-	-	-		-	-	-	-	-		-	-	-
	Summer	12.2	4.7	10.8	6.5	27.4	40	9.0	1.6	8.7	5.9	14.2	129	3.8	1.4	3.6	1.2	8.3	672
	Autumn	10.5	2.7	10.1	6.8	21.4	94	8.4	1.2	8.4	5.8	12.2	289	3.2	1.3	3.0	1.0	9.3	1,559
Helgoland pontoon	Winter	10.6	2.3	10.4	5.8	19.3	175	8.4	1.7	8.2	4.9	13.7	456	3.6	1.8	3.2	1.1	9.1	1,161
	Spring	13.0	4.7	11.6	7.5	33.0	134	10.2	1.8	10.1	6.5	16.5	148	5.4	2.4	5.8	1.3	10.4	153
	Summer	9.4	2.6	9.1	4.9	22.5	388	7.8	1.4	7.5	4.5	13.5	941	3.3	1.3	3.0	1.0	8.6	6,766
	Autumn	9.6	2.5	9.3	5.3	24.0	858	7.5	1.5	7.3	5.2	14.9	1,830	3.3	1.4	2.9	0.9	11.0	10,001
Helgoland marina	Winter	10.3	3.0	9.8	6.5	19.1	21	8.6	1.7	8.6	4.7	13.9	32	2.5	1.6	2.0	1.2	10.3	151
	Spring	13.5	6.0	13.5	9.2	17.7	2.0	11.7	-	11.7	11.7	11.7	1	7.5	-	7.5	7.5	7.5	1
	Summer	10.9	2.9	10.6	6.4	19.2	100	9.1	1.8	9.0	5.3	13.4	144	3.6	1.3	3.4	0.9	11.2	2,704
	Autumn	11.1	4.0	10.0	5.4	32.1	604	8.8	1.9	8.6	4.6	15.3	897	4.0	1.8	3.6	0.9	10.5	3,245
Helgoland south harbour	Winter	12.7	3.8	12.3	4.8	28.5	264	9.4	1.4	9.5	4.5	14.8	549	3.3	1.7	2.8	1.0	9.7	2,228
	Spring	14.7	5.8	13.4	8.7	26.9	8	10.7	2.3	9.8	9.3	14.7	5	4.1	2.5	2.5	1.6	8.2	15
	Summer	12.0	5.0	10.3	5.6	34.9	522	8.8	1.9	8.7	3.9	16.2	1,264	3.6	1.4	3.3	1.0	10.4	10,001
	Autumn	10.9	3.4	10.0	5.2	39.1	925	8.8	1.5	8.6	4.7	13.9	1,826	3.8	1.5	3.5	0.9	10.3	10,001

Chapter III

Life history traits of *Caprella mutica* Schurin, 1935 (Crustacea, Amphipoda) - implications for invasion success and range expansion

Introduction

The marine caprellid amphipod *Caprella mutica* Schurin (1935) is indigenous to sub-boreal waters of north-east Asia (Sea of Japan) (Arimoto, 1976; Fedotov, 1991; Vassilenko, 2006). During the past 40 years, *C. mutica* has successfully established populations in many locations outside its native range (Ashton et al., 2007a, 2008a, 2008b). Records from the highest latitudes are from Ålesund, Norway at 62°N (ICES, 2003). *Caprella mutica* is expected to expand its range towards higher latitudes between 25 and 70°N (Ashton et al., 2007a), because of comparable annual seawater temperature ranges in this region and the species' native area (between -1.8 and 25°C; Schevchenko et al., 2004). Ashton et al. (2007a) suggested that the absence of *C. mutica* from these regions is because of restricted dispersal, rather than of physiological constraints.

Along north-western European coasts, maximum population densities of *C. mutica* exceed 200,000 ind. m^{-2} in summer when seawater temperatures are between 16 and 20°C (Ashton, 2006; Chapter II). In late winter and early spring, populations nearly become extinct in the southern North Sea when temperatures drop to about 3°C or below (Chapter II). Occasionally, however, winter populations of several thousand ind. m^{-2} are found in sheltered habitats (e.g. in the shank of a navigational buoy; pers. obs.). These contradictory reports on winter abundances of *C. mutica* suggest that other environmental factors such as the availability of habitat and food may strongly control the occurrence of *C. mutica*.

The physiological ability of a species to reproduce and establish sustainable populations in a new area depends primarily on abiotic environmental parameters such as temperature or salinity (Lennon et al., 2001; Sakai et al., 2001; Stachowicz et al., 2002; Füreder and Pöckl, 2007). Knowledge on the thermal tolerance of *C. mutica* and the species' performance over the thermal range of a region is of paramount importance for (i) understanding the mechanisms of the invasion process, (ii) understanding its success in its new ranges, and (iii) predicting possible future range expansion to higher latitudes.

So far, only a single laboratory study has investigated the life history of *C. mutica* in European populations. Cook et al. (2007b) provided detailed information on survivorship, life cycle, growth and reproduction at ambient summer temperatures of 14°C. However, no information is available on life history traits of *C. mutica* along a thermal gradient including winter temperatures.

Herein, I studied life history traits of *C. mutica*, such as survival, development and reproduction at different temperatures that cover the annual thermal range in north-western European waters. The study aims to provide a mechanistic interpretation of the successful establishment of *C. mutica* in north-western European coastal waters and to estimate its distributional boundaries at high latitudes.

In detail, the aims of the study were:

(i) to investigate how seasonal temperatures of north-western European coastal waters (4 to 16°C) influence survival, development and reproduction of *C. mutica*, and

(ii) to investigate the physiological limitations of reproduction (‘theoretical biological zero’).

Material and Methods

From September to November 2007, individuals of *C. mutica* were collected from submerged areas of pontoons in the South-harbour of the Island of Helgoland, German Bight, North Sea, and transferred to the laboratories of the Helgoland Marine Biological Station. Ambient water temperatures were between 16.8°C (September) and 11.5°C (November).

Ovigerous females of *C. mutica* were identified by the presence of embryos in their brood pouch (Fig. III-1c and d) and maintained individually in 100 ml vials with a piece of gauze (1.5 x 4.0 cm, mesh width: 1 mm) to cling to at 16°C and a light-dark cycle of 16:8 hours. Sea water was changed daily. The females were fed *ad libitum* with a mix of freshly hatched *Artemia*-nauplii (cultivated at 20-30 ml cysts per 5 l seawater) and diatoms (*Thalassiosira rotula*). The diatoms were cultured in F ½ medium following standard protocols by Guillard and Ryther (1962). 10 ml silicate solution ($Na_2SiO_3 \bullet 9 H_2O$) per 10 l were added to enhance growth to approximately 400-450 single cells or 60-70 colonies of cells per ml (measured by repeated counts at visually determined optimal diatom densities with a FlowCAM® by Fluid Imaging Technologies). The mixed diet of live planktonic prey and diatoms was chosen according to stomach content analyses of *C. mutica* by Sano et al. (2003), and was assumed to represent a suitable food source for the filter feeding caprellids. The females were inspected daily for hatched offspring.

Over a period of 7 weeks, a total of 480 hatchlings were produced by 42 different females and classified after Takeuchi and Hirano (1991, 1992) as Instar I, with consecutive instars relating to subsequent moults. Under a light-dark regime of 16:8 hours, 192 hatchlings each were reared individually at a constant temperature of 16°C and 10°C, respectively, and 96 hatchlings were reared at a constant temperature of 4°C. The temperatures represented mean summer (16°C), spring/ late autumn (10°C) and winter (4°C) temperatures in the German Bight, North Sea (Wiltshire and Manly, 2004). For better handling due to small body size, the hatchlings were reared in 15 ml vials for their first three instars and given single strands drawn from a piece of gauze to cling on. On the day of their third moult (first day of Instar IV) they were transferred to 100 ml vials and offered a piece of gauze (1.5 x 4.0 cm, mesh width: 1 mm). On a daily basis the water was changed and the animals were fed *ad libitum* (freshly hatched *Artemia* nauplii and diatoms, see above). Beakers and gauze were exchanged weekly or when required. In daily inspections by eye and under a dissection microscope survival and moulting was recorded. If possible, exuviae were retained to count the number of flagellar segments of Antenna I. The body length of an animal was measured 24 hours after moulting from head (base of antennae) to the distal part of the abdomen to the nearest 0.1 mm. Measurements were conducted with the computer based imaging software ‘analySIS’, Version 3.2 (Soft Imaging System GmbH, Münster, Germany) connected to a dissection microscope.

Sexual differentiation and maturity of females, i.e. the development of oostegites on the ventro-lateral margin of pereonites III and IV and the development of eggs in the ovaries were recorded (Fig. III-1). Modified from Takeuchi and Hirano (1991), female stages were classified as immature, premature and mature, and differentiated by the presence and morphological development of the oostegites and eggs (Fig. III-1). In immature (juvenile) females, ovaries with developing eggs and oostegites are still missing (Fig. III-1a). In premature (subadult) females the first clutch of eggs is distinctly visible in the ovaries located in pereonites III and IV. Oostegites positioned at the same pereonites are present but underdeveloped (Fig. III-1b). Mature (adult) females have fully developed brood pouches formed by the oostegites (mostly with eggs/embryos inside) and newly differentiating eggs in the ovaries are normally visible (Fig. III-1c and d).

In the experiments a number of juveniles perished before sexual differentiation was possible. Despite this, data from these juveniles were included in the analyses.

Because maturity of male individuals is difficult to assess by means of morphological characters, the study concentrated on the females. Males were, thus, randomly taken from the field and used in the experiments only for mating purposes (see below).

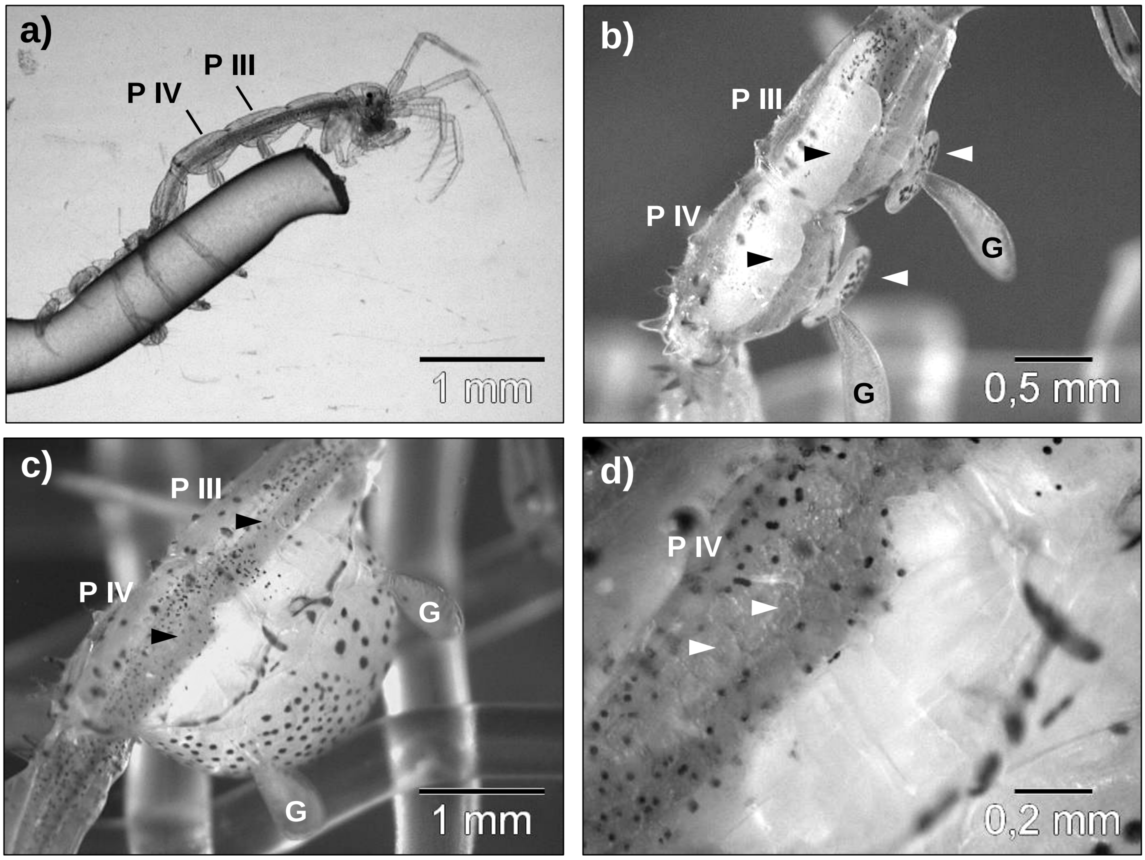

Fig. III-1: Characteristics of maturation in different developmental stages of *Caprella mutica* (P III and IV = pereonites III and IV; G = gills); a) immature (juvenile) specimen; b) premature (subadult) female with distinct differentiation of eggs (black arrows) in the ovaries and underdeveloped oostegites (white arrows); c) mature (adult) female with a fully developed brood pouch (hosting embryos near to hatching) and newly differentiating eggs in the ovaries (black arrows); d) high resolution section of newly differentiating eggs (white arrows) from image c.

Due to time constraints and to prevent loss of replicates over time because of increased mortality, a second set of experiments concentrating on reproduction was established at the same time. In this experiment, females were not introduced as hatchlings but as subadult specimens. Therefore, the first experiment was terminated when the females reached maturity.

Under the dissection microscope, females collected from the field (see above for sampling method) were scrutinized for prematurity. Methodological procedure on maintenance was as described above. However, in addition to the three experimental temperatures, two further temperatures, 20 and 26°C, were added for more reliable calculation of temperature dependent functions. 36 females each were assigned to 4, 10, 20 and 26°C, and 50 females to 16°C. Females were placed at 4, 10 and 16°C without acclimatization. Females were acclimatized to 20 and 26°C in daily increments of 2°C starting at 16°C. Average body length of all premature females was 8.0 ± 0.8 mm (mean ± SD, N = 194).

For mating purposes, sufficient numbers of adult males from the field were maintained for approximately seven days under the same conditions as the females. After acclimatization randomly selected single adult males were placed with each subadult female for the remainder of her lifespan. Only males visibly larger than the experimental females were chosen in order to ensure maturity. Dead males were replaced.

Data acquisition for reproduction started with the females’ parturial moult, i.e. when females moulted into their first adult instar and became mature. In daily visual inspections under a dissection microscope, survival, growth and moultings (see methods above) were recorded. Along with moult cycles, the reproductive cycles were documented as the duration of embryonic development until hatch, the duration until newly differentiating eggs appeared in the ovaries after moulting (onset of oogenesis) and the duration of oogenesis (i.e. development and maturation of eggs until oviposition). The relationship between the duration of embryonic development (or other reproductive traits as well) and temperature was used to estimate the ‘theoretical biological zero’, i.e. the theoretical temperature at which the duration of the respective trait is theoretically infinite and thus reproduction ceases (Tong et al., 2000). The hatchlings per clutch were counted and removed from the vial.

Statistical analysis

Statistics were performed at the 95 % confidence level using computer software GraphPad Prism (3.0).

Survival

The effect of temperature on the survival of reared hatchlings and subadult females from the field (duration in days) was plotted against time. Testing the null hypothesis that there is no linear trend between median survival at different temperatures, a Chi square logrank test for trend was applied to %-survival data.

Development

To test for temperature effects on moult cycle durations and growth per instar in reared individuals and adult females, ANCOVAs were applied to untransformed data. For better comparison and availability of all treatments, to create balanced data sets and improve normality (Kolmogorov-Smirnov test, $P > 0.05$) and homogeneity of variances (Bartlett's test, $P > 0.05$), only data up to Instar VI were used for the reared individuals. For the same reasons, only the first four adult stages (instars) were chosen in the analyses of adult females.

Reproduction

According to Tong et al. (2000) and Grubert (2005), the ‘theoretical biological zero’ was estimated by plotting the reciprocal duration of embryonic development (1/ days) against the experimental temperature (°C). Data consisted of the average duration of embryonic development per reproductive female and reproductive cycle. Linear regression was applied and extrapolated back to the intersection with the x-axis, which indicates the temperature at which the duration of embryonic development is theoretically infinite and, thus, reproduction ceases. In order to find other traits limiting reproduction at low temperatures, data on the duration until onset of oogenesis and on its completion were treated in the same way.

At all experimental temperatures, the number of released hatchlings differed between successive brood cycles. However, statistical assumptions could not be met by data transformation, data sets were unbalanced and non-parametric analyses failed to represent the actual situation. The effect of temperature on the numbers of offspring per instar, therefore, remained descriptive.

Results

Survival

Juvenile *C. mutica* survived significantly longer at 4°C than at 10 and 16°C (P for both comparisons < 0.01; P between 10 and 16°C > 0.05; Fig. III-2, Appendix Tab. III-1). Experimental populations declined to half their initial sizes (median survival time) after 35 days at 4°C with mortality rates of about 1.4 % per day (Fig. III-2). At 10 and 16°C median survival time was reached in 13 and 11 days, respectively, at daily mortality rates of approximately 4.4%. Experiments were terminated when females reached maturity at the age of 61.0 days at 10°C and 37.5 days at 16°C. At 4°C juveniles did not mature and the experiment ended after 112 days when all individuals had perished.

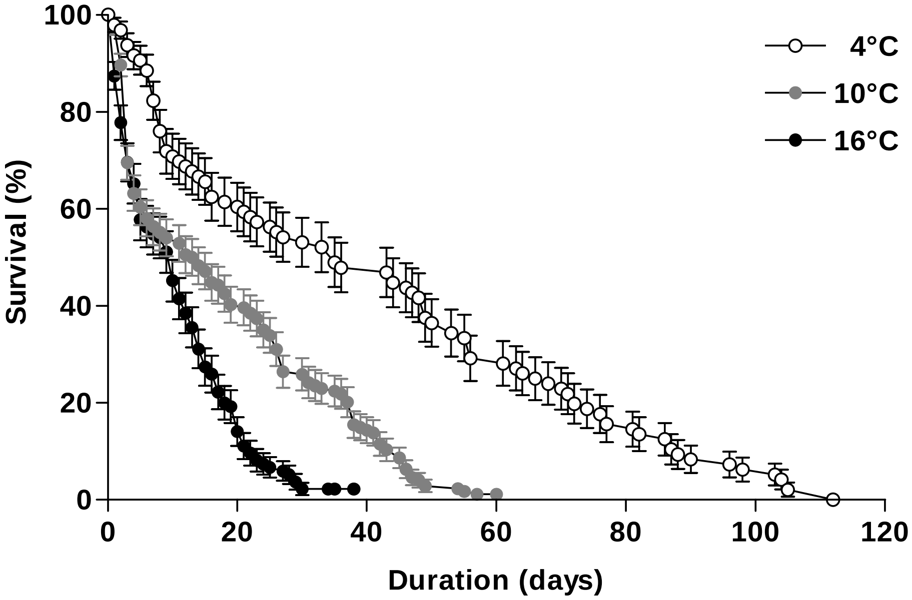

Fig. III-2: Survival of female juveniles and juveniles of undetermined sex of *Caprella mutica* reared from hatch at 4, 10 and 16°C. Experiments were terminated at onset of maturity. Mean values ± SE of percentage survival is shown, initial N = 96 (4°C), 176 (10°C) and 154 (16°C).

Survival of adult females did not differ between 4, 10 and 16°C (P > 0.05; Fig. III-3, Appendix Tab. III-2). *Caprella mutica* maintained at these temperatures declined to half their initial number after 23 to 47 days, and went extinct after 107 to 132 days, with average mortality rates of 1.3% per day. At higher temperatures individuals died significantly earlier (P for both < 0.01). At 20°C, median survival time was reached after only nine days with an average mortality rate of approximately 6% per day. At 26°C, the experimental animals experienced highest mortality rates of about 33% per day. 50% of the individuals had died after only two days. At both 20 and 26°C, individuals went extinct in less than 50 days.

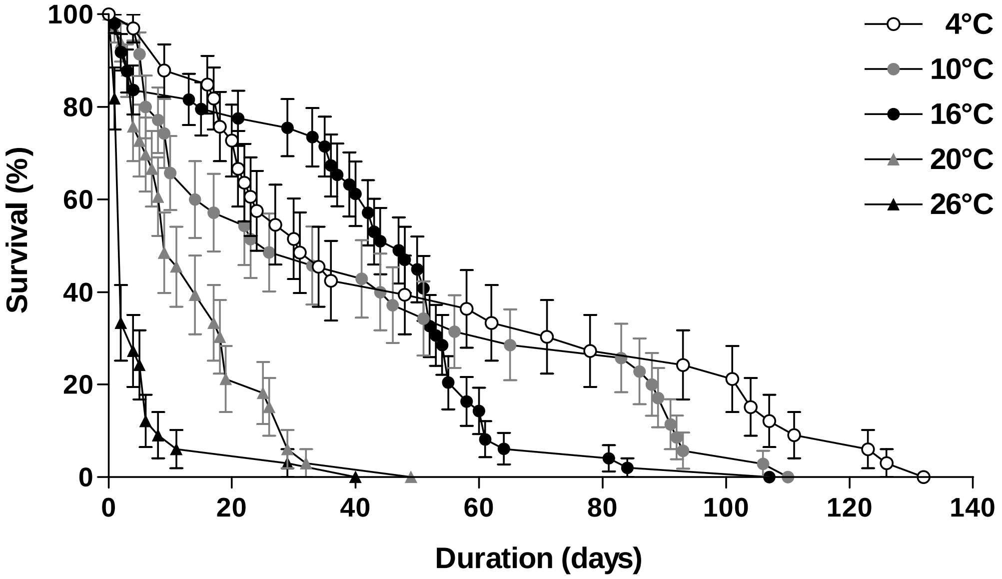

Fig. III-3: Survival of adult females of *Caprella mutica* maintained at 4, 10, 16, 20 and 26°C. Mean values ± SE of percentage survival is shown, initial N = 36 (4, 10, 20, 26°C) and 50 (16°C).

Development

Juveniles

At 4°C juveniles moulted up to six times at approximately two to three week intervals (Fig. III-4, Appendix Tab. III-1). From the total of 96 individuals, sex could only be identified in two females at Instar V after 57 and 61 days, respectively. All individuals reared at 4°C remained immature.

At 10°C, only two females reached maturity at Instar VII after 56 and 66 days, respectively. Both females had passed through four juvenile stages and one premature stage. All other females passed through four to eight juvenile stages before reaching one premature stage. A single individual experienced nine juvenile stages before decease (Fig. III-4, Appendix Tab. III-1). Juvenile moult cycles lasted on average one week. After sexual differentiation at Instar V, durations of moult cycles increased to about two weeks at Instar VIII.

At 16°C, juveniles moulted approximately every three to four days. After sexual differentiation at Instar V, the duration of female moult cycles increased to approximately 10 days at adult instars (Fig. III-4, Appendix Tab. III-1). The earliest females reached maturity at Instar VII after approximately 21 days, while others completed maturation no later than Instar IX after approximately 46 days (Fig. III-4). The majority of mature females at 16°C (43.0 %) had undergone five juvenile stages and one premature stage before becoming mature. Only a few females passed four or six juvenile stages and one premature stage before maturation. In addition, five females extended prematurity over two stages after having passed through four or five juvenile stages (Appendix Tab. III-1).

Temperature significantly affected instar duration in individuals reared at 4, 10 and 16°C ($P < 0.05$). The duration of moult cycle intervals decreased significantly with increasing temperature (P for all pair wise comparisons < 0.01).

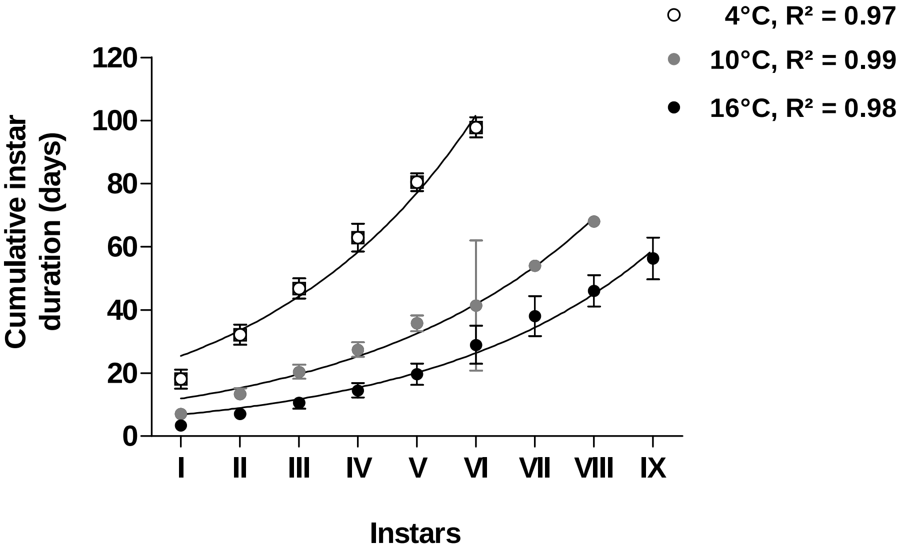

Fig. III-4: Cumulative instar durations of *Caprella mutica* reared at 4, 10 and 16°C. Mean values ± SD are shown; initial N = 96 (4°C), 176 (10°C) and 154 (16°C). Non-linear exponential growth curves depict cumulative instar duration per temperature.

At hatch, individuals from all the experimental temperatures measured about 1.3 mm in length. Females reared at 4°C grew up to an average maximum size of 3.5 mm, while growth rates remained steady at about 0.4 mm per instar (Fig. III-5, Appendix Tab. III-2). At 10°C growth increased by approximately 0.8 mm per instar and females reached a maximum size of 7.4 mm at Instar IX. At 16°C hatched females grew up to 8.1 mm at

Instar IX, with growth rates of about 0.9 mm per instar. While growth per instar was similar in individuals reared at 10 and 16°C (P > 0.05), individuals reared at 4°C were significantly smaller at all instars (P < 0.01 for both comparisons; Fig. III-5).

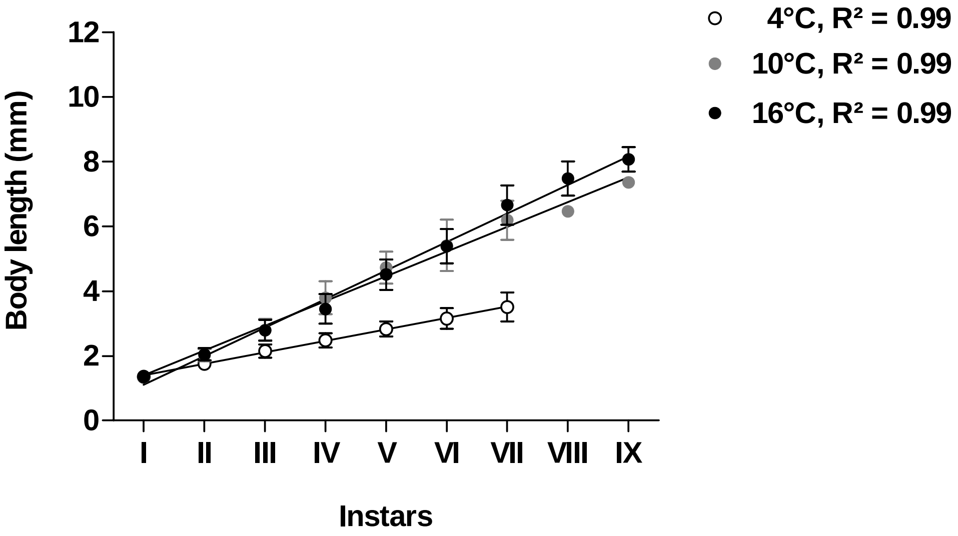

Fig. III-5: Growth per instar in *Caprella mutica* reared at 4, 10 and 16°C. Mean values ± SD are shown; initial N = 96 (4°C), 176 (10°C) and 154 (16°). Linear regression models are fitted to the temperature treatments.

Adult females

When introduced to the experiment as premature specimens, females reached a maximum of 11 adult instars at 16°C, seven at 4°C and each six at 10 and 20°C. At 26°C, females perished during their fifth instar (Fig. III-6, Appendix Tab. III-2). Durations of adult moult cycles were longest in females at 4°C (approximately 39 days) and decreased with increasing temperatures, lasting on average 18.7 days at 10°C and 10.6 days at 16°C. At 20 and 26°C females moulted approximately every 8.6 days. Statistical analysis revealed similar instar durations at 16, 20 and 26°C (P for each comparison > 0.05), but significantly shorter instar duration when compared to 4 and 10°C (P < 0.05 for each comparison; Fig. III-6).

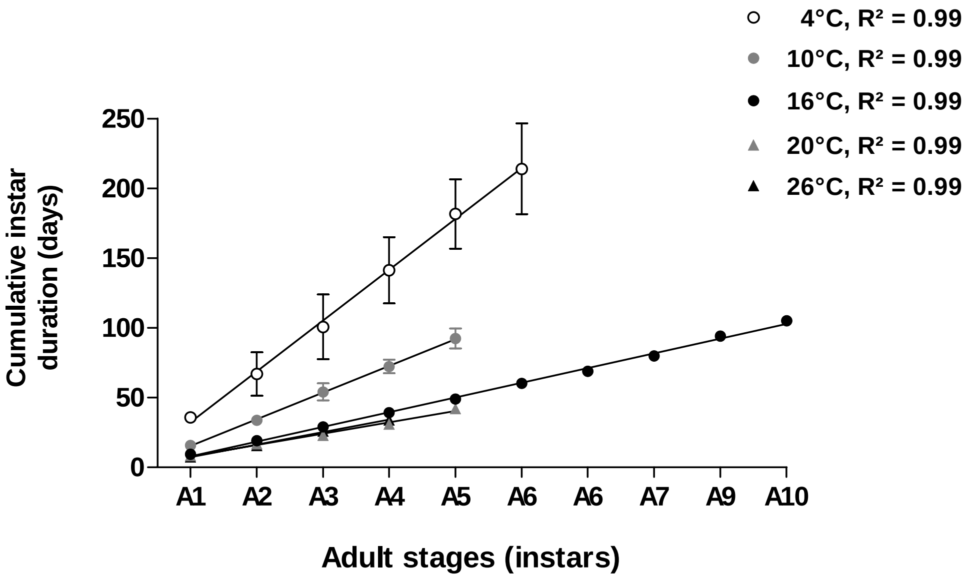

Fig. III-6: Cumulative instar durations of adult female *Caprella mutica* maintained at 4, 10, 16, 20 and 26°C. Mean values ± SD are shown; initial N = 36 (4, 10, 20, 26°C) and 50 (16°C). A_n = adult stages. Linear regression models are fitted to the temperature treatments.

Females at 4°C revealed highest growth rates per instar of about 0.8 mm and reached a maximum average size of 14.0 mm at the last experimental instar (Fig. III-7, Appendix Tab. III-2). At all other temperature treatments, sizes were smaller at comparable instars. Yet, statistical analysis revealed differences in growth per instar only between females at the lowest (4°C) and highest temperatures (20 and 26°C) (P for both comparisons < 0.01). When related to growth per time interval instead of instar, however, weekly growth rates were highest at 10°C with 0.7 mm as opposed to all others, in which a maximum of 0.3 mm was found.

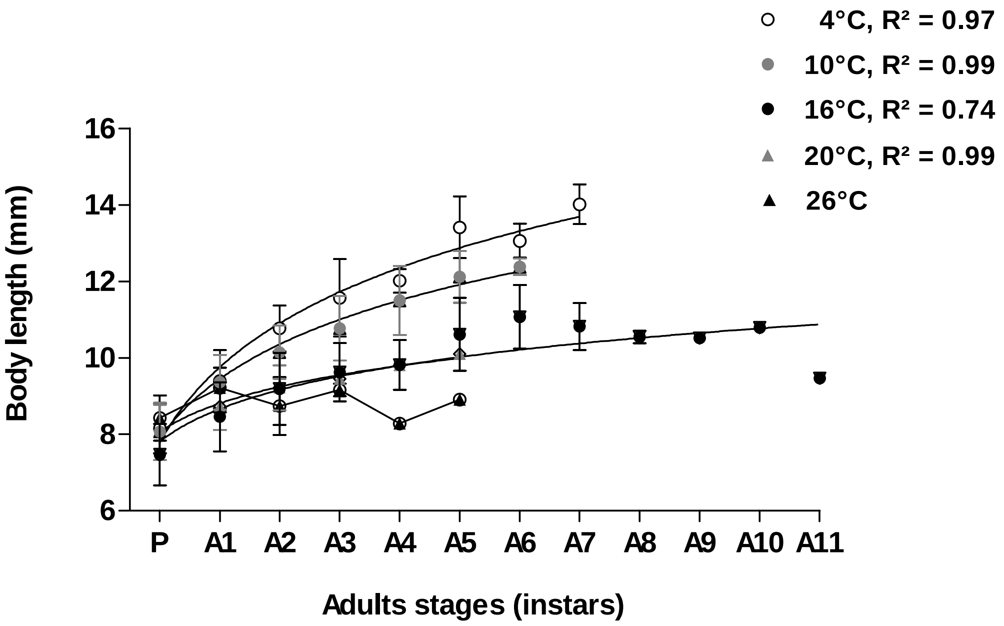

Fig. III-7: Growth per instar in *Caprella mutica* maintained at 4, 10, 16, 20 and 26°C. Mean values ± SD are shown; initial N = 36 (4, 10, 20, 26°C) and 50 (16°C). P = premature stage, A_n = adult instars. Logarithmic regression curves are applied to 4, 10, 16 and 20°C. At 26°C the model failed to fit the data. A connecting line was applied for better visualization.

Reproduction

The reciprocal durations of individual reproductive traits were strongly related to temperature and increased with decreasing temperature (Fig. III-8). Extrapolation of the linear model for the duration of embryonic development revealed a 'biological zero' of 1.1°C ($R^2 = 0.96$), indicating that development is theoretically infinite and reproduction ceases at this temperature (Fig. III-8). Similarly, the 'biological zero' of the duration until onset of oogenesis after moulting was 1.2°C ($R^2 = 0.52$). Oogenesis ceases theoretically at an even lower temperature of -2.6°C ($R^2 = 0.82$).

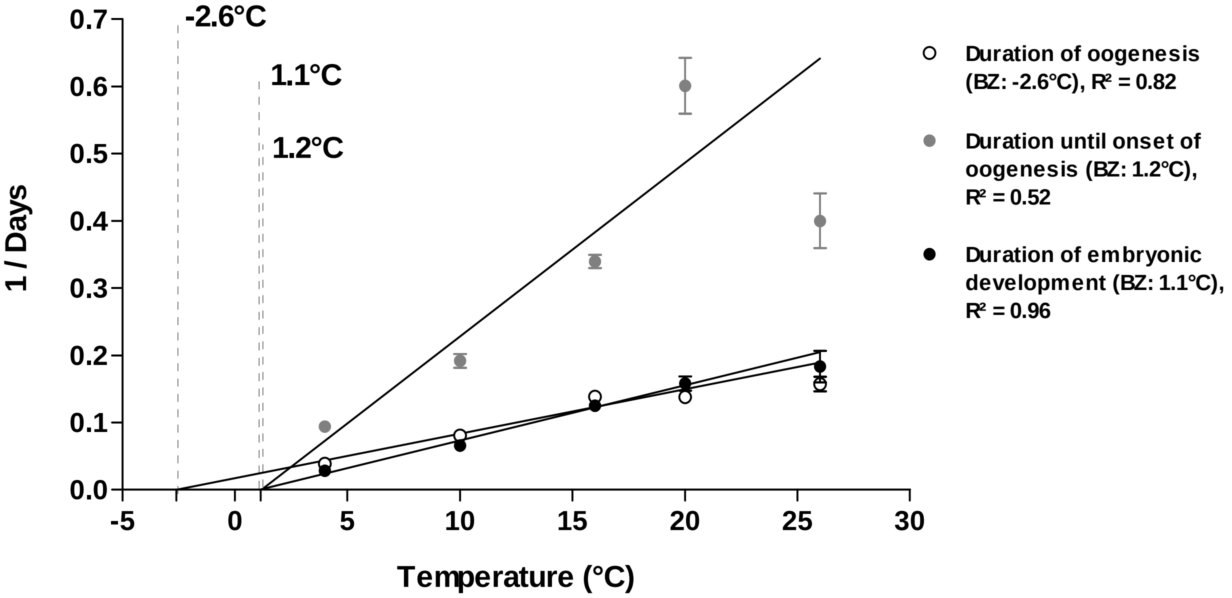

Fig. III-8: Linear regression analysis on the reciprocals of the duration of oogenesis, the duration until onset of oogenesis after moulting and the duration of embryonic development in *Caprella mutica* plotted against temperature (°C). Duration is shown as 1/days (mean ± SD). The 'theoretical biological zeros' (= BZ) represent the intersection of the x-axis after extrapolation of the linear regression.

The average generation time (i.e. the duration from hatch of a female until that specific female produced new hatchlings) was calculated for *C. mutica* as the total time required for maturation (see section on development above) and the duration of embryonic development of the first brood. This was only possible for 10 and 16°C and equated to approximately 70 and 45 days, respectively.

At 16°C, females produced eight consecutive clutches before broods were repeatedly aborted (Fig. III-9, Appendix Tab. III-2). Following their parturial moult, females at 10 and 26°C produced four successive clutches. At 4°C, females reproduced twice, while at 26°C only one brood produced live hatchlings. Apart from the 26°C treatment, broods consisted of an average of about 30 live hatchlings at first instar. A maximum of 85 hatchlings was counted at 10°C (Instar I). The numbers of broods decreased with consecutive broods. At the same time, the number of dead hatchlings increased per instar (Fig. III-9, Appendix Tab. III-2). While abortions occurred at all stages and temperatures, the number of abortions increased with the number of brood cycles. In four females at 4°C and two females at 20°C all embryos were aborted. Abortions occurred at any time during pregnancy. In some cases, abortion of the eggs was due to the male's death shortly before successful mating. A male successor was often allotted too late for successful mating. The females, therefore, either reabsorbed their eggs without oviposition or aborted the unfertilised eggs after oviposition. However, re-absorption of eggs was also observed in cases when males were present. In a total of seven older females oogenesis ceased shortly before death at 4, 10 or 16°C. However, females at 4°C occasionally developed new eggs after one or two cycles of suspended oogenesis.

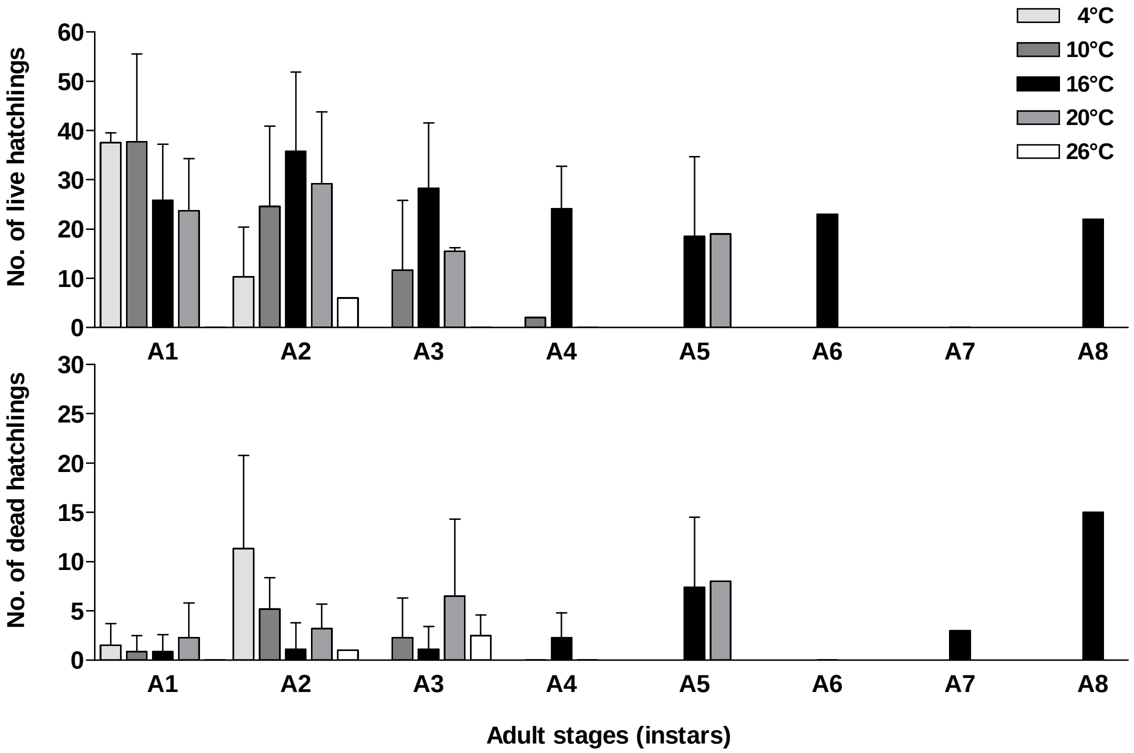

Fig. III-9: Number of live (upper graph) and dead (lower graph) hatchlings of *Caprella mutica* produced per adult instar at different temperatures (mean ± SD; N varied according to surviving numbers of females, see Appendix Tab. III-2) $A_{1\text{-}8}$ = adult Instars I - VIII.

Figure III-10 visualizes the developmental pathways of *C. mutica* and gives a chronology of different processes during the respective stages.

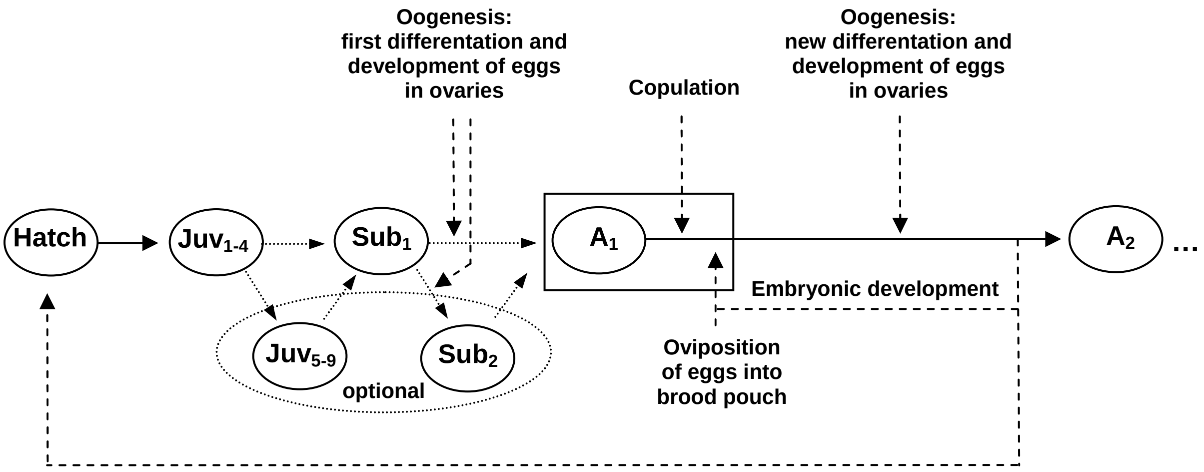

Fig. III-10: Schematic overview of the life cycle and chronology of processes (coarsely dotted arrows) in female individuals of *Caprella mutica*. After hatching (= Hatch), juveniles typically proceed through five (16°C) immature instars (juvenile stages = Juv_5) and then pass through one premature instar (subadult stage = Sub_1). Optional numbers of juvenile and subadult stages are indicated. All instars following parturial moult were characterised as adult instars ($A_{1\text{-}n}$). The square box around A_1 indicates processes taking place within a relatively short time period - independent of temperature.

Discussion

In marine benthic crustaceans from temperate regions, developmental traits (e.g. growth and moult cycle intervals) decelerate when water temperature declines (Dexter, 1971; Rees, 1975; Gutow and Franke, 2001). Moulting intervals are prolonged and maturation is protracted. In the present study, mortality of juvenile *C. mutica* was lower at 4°C than at 10 and 16°C. In addition, individuals remained smaller at the low temperatures than they did at higher temperatures. At constant 4°C, *C. mutica* did not reach maturity, while at 10 and 16°C individuals passed through their parturial moult after about two months or less.

During winter periods, ectotherms may chiefly require assimilated energy for maintaining basic metabolic functions, rather than for maturation or reproduction. For example, Pörtner et al. (2001) found cold-induced shifts in energy budgets of Atlantic cod *Gadus morhua* and common eelpout *Zoarces viviparous* leading to decreased growth and fecundity. Due to the permanent excess supply of food to *C. mutica* in the experiments, however, this seasonal pattern of energy allocation is probably not a direct consequence of winter resource limitation. In preliminary starvation experiments (not presented here) hatchlings of *C. mutica* survived seven weeks of starvation at 16°C indicating excessive yolk reserves in newborns, which may enable them to overcome periods of low food availability. Since energy requirements of ectotherms declines with decreasing temperatures (Eriksson Wiklund and Sundelin, 2001), juvenile *C. mutica* probably survive even longer starvation periods at lower temperatures in the field. Seasonal periods of water temperatures below 4°C last on average about two months in the southern North Sea (Franke et al., 1999; Wiltshire and Manly, 2004). This is far shorter than the time taken for the experimental populations to go extinct at constant 4°C. Accordingly, individuals that hatch in winter or early spring are able to survive periods of low temperatures and resource limitation at the cost of growth and development. High numbers of survivors will allow for eruptive population growth in early summer after rapid maturation of the individuals in spring.

Caprella mutica typically reaches maturity at Instar VII. Some individuals, however, delayed maturity undergoing additional juvenile and premature stages at 10 and 16°C. Gimenéz et al. (2004) explained alternative developmental pathways in the life cycle of the estuarine crab *Chasmagnathus granulata* to be a function of metabolic processes and environmental conditions. The authors found that larvae with initially low biomass underwent more larval stages than conspecifics with higher initial biomass. They suggested that the amount of biomass in hatched larvae depends on the amount of energy assimilated during embryogenesis. The present results may indicate similar processes in *C. mutica*. When food resources for ovigerous females are scarce during late winter and early spring (Greve and Reiners, 1988) less energy is invested into oogenesis. This may result in additional immature and/or premature stages, and thus slower development, of juvenile *C. mutica* which allocate resources to maintenance rather than to development and early reproduction. In summer, however, optimal food supply of reproductive females may allow for rapid growth and early maturation of juveniles. This is supported by investigations on the seasonal dynamics in European populations of *C. mutica*. The studies found that low abundances during winter and spring (typically below 100 ind. m^{-2}) increased exponentially to several 10,000 or even 100,000 ind. m^{-2} when ambient water temperatures increased to approximately 14°C or even 20°C and food supply is plentiful during late summer and autumn (Ashton, 2006; Chapter II).

In the present study, *C. mutica* reproduced successfully at experimental temperatures between 4 and 26°C, with highest numbers of consecutive broods were recorded at 16°C. The number of hatchlings produced at early reproductive instars was similar at experimental temperatures from 4 to 20°C. In addition, the number of offspring generally decreased with consecutive instars. This pattern was surprising, as field studies on *C. mutica* have shown positive relationships between brood size and the size of the female (Fedotov, 1991; Ashton, 2006). Fedotov (1991) and Ashton (2006) reported maximum numbers of more than 300 eggs per single clutches. The observed pattern and the comparably low numbers of hatchlings might therefore represent a laboratory artefact. The results from the present experiments suggest, however, that temperature has a greater effect on the reproductive frequency than on the clutch size. As reproductive frequency was highest at 16°C, the highest overall numbers of offspring were produced at this temperature. In view of exponentially increasing population densities during summer, increased mortality of hatchlings at summer temperatures are obviously outweighed by high positive net reproductive rates.

The duration of the reproductive cycles was constant at temperatures from 16 to 26°C indicating that a minimum time period is required for embryonic development and oogenesis. Similar results have been found for copepod species, in which embryonic development did not accelerate beyond a certain threshold temperature (Herzig, 1983). However, fewer broods and, thus, less hatchlings were produced at 20 and 26°C. Eriksson Wiklund and Sundelin (2001) studied temperature effects on reproduction in the amphipod *Monoporeia affinis*. The authors found that high metabolic demands of the females at high temperatures led to smaller amounts of lipids available for gonad maturation. Accordingly, reproductive output might be controlled in *C. mutica* by the amount of energy left for oogenesis after the basic metabolic requirements of the female have been met.

It is unknown whether populations of *C. mutica* can persist at temperatures beyond 20°C. Mortality of adult females increased significantly at 20 and 26°C and only few hatchlings were produced at 26°C. Similarly, Ashton et al. (2007b) found that high water temperatures increased mortality in *C. mutica* and that temperatures of 30°C caused 100% mortality in adult specimens within 48 hours.

In contrast to temperatures exceeding 20°C, the minimum temperature theoretically limiting reproduction in *C. mutica*, was calculated to be 1.2°C when food was constantly available. Typically, the ‘biological zero’ refers to the relation between temperature and the duration of embryonic development (Tong et al., 2000). It predicts, that the duration of embryonic development is theoretically infinite at a specific temperature and thus reproduction ceases. In contrast, the present results revealed suspended oogenesis in *C. mutica* to be the actual physiological limitation for reproduction at low temperatures. Regardless of the specific traits responsible for reproductive cessation, however, the ‘biological zero’ must be seen as a strictly theoretical limit of the physiological ability to reproduce. In case of *C. mutica*, it is likely that reproduction is suspended at a somewhat higher temperature slightly below 4°C.

Hence, when winter temperatures drop below 4°C, ovigerous females may still release their current broods, but might be unable to produce new clutches of eggs until temperatures increase back to at least 4°C or before they perish. Depending on the time (and temperature) at which females become mature and thus, carry broods before the temperature drops below 4°C, a few individuals might survive over winter and contribute to increased reproduction in early spring. However, while the present experiments showed that juvenile *C. mutica* are unable to mature at 4°C (see above) and perish within four months at this temperature, field populations can only persist throughout the year when winter seawater temperatures below 4°C last less than four months. In addition, minimum summer temperatures between > 4 and 10°C must last for at least 61 days, as this was found to be the average maturation time at 10°C.

The potential range expansion towards high latitudes (up to 70°N) would therefore include habitats along the Arctic Circle, where summer temperatures are reported to fluctuate between 3 and 4°C in April and 15-16°C in July (Freiwald and Henrich, 1994; NOAA/ National Weather Service). On average, temperatures around 10°C and above may last at least 2.5 months at the Arctic Circle and, therefore, would be sufficient for maturation of *C. mutica* (NOAA/ National Weather Service). However, if a subsequent decrease in temperature to about 4°C persists for too long (> four months), adult females may not survive for repeated reproduction and hatched juveniles will not mature before perishing. As most specimens hatch during warmer periods (spring/ summer), females may naturally perish during colder (winter) periods at an average life expectancy of about six months (two months until maturation at 10°C and approximately four months of survival as adult). Populations at latitudes around 70°N and beyond, therefore, may be more prone to regular extinction events and recruitment will rely strongly on regular introductions as opposed to self-sustaining reproduction.

According to its physiological ability not only to perform along a wide thermal range but especially at low temperatures, *C. mutica* may be able to survive transits periods of low temperatures in refrigerated containers or cargo compartments containing aquaculture species for export-import trading purposes. This may enhance the probability for local and global dispersal to new areas within short periods of time.

Considering global warming trends, average surface temperatures are expected to rise between 1.8 to 4.0°C by the year 2100 (Bates et al., 2008) and may increase the chance of *C. mutica* establishing populations at latitudes around the Arctic Circle or even beyond. This is of paramount importance as the warming arctic areas (Zhang, 1998; Fyfe et al., 1999; Kerr, 2002a) provide longer ice-free periods during summer and thus, may enhance shipping passages along northern routes (Rahmstorf and Ganopolski, 1999; Kerr, 2002b) and open pathways for potential introductions. It is, however, unlikely that *C. mutica* will establish in Arctic regions in the near future, as prevailing water temperatures do not exceed 4°C during summer periods (NOAA/ National Weather Service).

The (calculated) temperature range at which *C. mutica* is theoretically able to reproduce (1.2 to 26°C) is similar to the ranges at which *C. mutica* is found in its native and new areas (-1.8 to 25°C, for review: Ashton et al., 2007a, 2008a). In its European habitats in the southern North Sea, temperatures range between about 3.5°C in winter and approximately 20°C in summer (Wiltshire and Manly, 2004), and therefore typically lack extreme temperatures at which reproduction is restricted in *C. mutica*. Temperate regimes, therefore, provide excellent conditions for *C. mutica* to persist during cold periods, reproduce at high levels during summer and thus, establish populations all year round, reflecting the species' successful spread and establishment in these habitats. Despite this, however, non-natives are not similarly successful in all habitats. This study has shown temperature to be among the driving forces determining seasonal population dynamics of *C. mutica* on a physiological basis and reflecting its invasion success. Other environmental factors, for example reduced salinity, have proven to be restrictive and even lethal for *C. mutica* (Ashton et al., 2007b), potentially limiting its dispersal to estuaries under strong freshwater influence. Ultimately, biotic factors, such as the availability of settlement substratum and food resources and the ability to persist in interactions with other species will determine the realised niche of *C. mutica* in its new areas.

Appendix

Tab. III-1: Summary statistics of survival and development per instar in *Caprella mutica* reared at 4 and 10°C (mean ± SD). Depending on the particular trait listed, N varies between the numbers of survivors at the beginning and the end of each instar. (n.a. = not available).

			Instars								
			I	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**
4°C	Juveniles	No. of survivors at beginning	96	60	48	35	25	12	4		
		No. of survivors at end	60	48	35	27	12	4	0		
		% Survivors at end	62.5	50.0	36.5	28.1	12.5	4.2	0.0		
		Duration of instars (days)	18.1 ± 3.0 (60)	14.2 ± 1.5 (48)	15.1 ± 1.5 (35)	16.3 ± 2.8 (27)	16.7 ± 2.7 (12)	18.5 ± 0.6 (4)	-		
		Cumulative duration of instars (days)	18.1 ± 3.0 (60)	32.2 ± 3.2 (48)	46.8 ± 3.2 (35)	62.9 ± 4.4 (27)	80.2 ± 3.0 (12)	97.8 ± 3.2 (4)	-		
		Body length (mm)	1.4 ± 0.1 (96)	1.7 ± 0.2 (60)	2.2 ± 0.2 (48)	2.5 ± 0.2 (35)	2.8 ± 0.2 (25)	3.2 ± 0.3 (12)	3.5 ± 0.4 (4)		
		No. of flagellar segments, Antenna I	2.0 ± 0.0 (58)	4.0 ± 0.0 (43)	5.1 ± 0.4 (27)	6.1 ± 0.4 (8)	8.0 ± 0.0 (2)	n.a.	-		
	Females	No. of survivors at beginning					2	2			
		No. of survivors at end					2	0			
		% Survivors at end					100.0	0.0			
		Duration of instars (days)					23.0 ± 4.2 (2)	-			
		Cumulative duration of instars (days)					82.0 ± 1.4 (2)	-			
		Body length (mm)					3.0 ± 0.0 (2)	3.2 ± 0.3 (2)			
		No. of flagellar segments, Antenna I					n.a.	-			
		Maturity stage (% juveniles)					100.0 (2)	100.0 (2)			
		Maturity stage (% prematures)					0.0	0.0			
		Maturity stage (% mature)					0.0	0.0			
10°C	Juveniles	No. of survivors at beginning	192	115	101	83	18	5			
		No. of survivors at end	115	101	83	65	5	0			
		% Survivors at end	59.9	52.6	43.2	33.9	2.6	0.0			
		Duration of instars (days)	7.0 ± 1.6 (115)	6.2 ± 0.7 (101)	7.0 ± 0.9 (83)	7.6 ± 1.3 (65)	8.6 ± 0.9 (5)	-			
		Cumulative duration of instars (days)	7.0 ± 1.6 (115)	13.2 ± 0.7 (101)	20.2 ± 2.1 (83)	27.3 ± 2.3 (65)	36.4 ± 2.1 (5)	-			
		Body length (mm)	1.3 ± 0.1 (192)	2.0 ± 0.2 (115)	2.8 ± 0.3 (101)	3.8 ± 0.5 (83)	4.6 ± 0.6 (18)	5.3 ± 1.4 (5)			
		No. of flagellar segments, Antenna I	2.0 ± 0.0 (84)	4.0 ± 0.1 (73)	6.0 ± 0.2 (60)	8.3 ± 0.5 (25)	11.1 ± 0.7 (2)	-			
	Females	No. of survivors at beginning					30	28	6	1	1
		No. of survivors at end					28	6	1	1	0
		% Survivors at end					93.3	20.0	3.3	3.3	0.0
		Duration of instars (days)					8.9 ± 1.6 (28)	12.0 ± 6.6 (6)	11.0 (1)	14.0 (1)	-
		Cumulative duration of instars (days)					35.8 ± 2.6 (28)	48.3 ± 10.4 (6)	54.0 (1)	68.0 (1)	-
		Body length (mm)					4.8 ± 0.4 (30)	5.4 ± 0.7 (28)	6.2 ± 0.6 (6)	6.5 (1)	7.4 (1)
		No. of flagellar segments, Antenna I					10.9 ± 0.5 (15)	14.1 ± 0.8 (4)	n.a.	n.a.	-
		Maturity stage (% juveniles)					100.0 (30)	50.0 (14)	50.0 (3)	100.0 (1)	100.0 (1)
		Maturity stage (% prematures)					0.0	50.0 (14)	16.7 (1)	0.0	0.0
		Maturity stage (% mature)					0.0	0.0	33.3 (2)	0.0	0.0

Tab. III-1 (continued): Summary statistics of survival and development per instar in *Caprella mutica* reared at 16°C (mean ± SD). Depending on the particular trait listed, N varies between the numbers of survivors at the beginning and the end of each instar. (n.a. = not available).

			Instars								
			I	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**
16°C	Juveniles	No. of survivors at beginning	192	142	131	111	7				
		No. of survivors at end	142	131	111	85	0				
		% Survivors at end	74.0	68.2	57.8	44.3	0.0				
		Duration of instars (days)	3.3 ± 0.9 (142)	3.7 ± 1.4 (131)	3.7 ± 1.3 (111)	4.2 ± 0.8 (85)	-				
		Cumulative duration of instars (days)	3.3 ± 0.9 (142)	7.0 ± 1.8 (131)	10.5 ± 2.0 (111)	14.5 ± 1.3 (85)	-				
		Body length (mm)	1.3 ± 0.1 (192)	2.1 ± 0.2 (142)	2.8 ± 0.3 (131)	3.5 ± 0.4 (111)	4.8 ± 1.0 (7)				
		No. of flagellar segments, Antenna I	2.0 ± 0.1 (90)	4.1 ± 0.4 (67)	5.9 ± 0.4 (51)	8.2 ± 0.0 (21)	-				
	Females	No. of survivors at beginning					41	40	25	19	13
		No. of survivors at end					40	25	19	13	9
		% Survivors at end					100.0	63.4	46.3	31.7	22.0
		Duration of instars (days)					5.2 ± 2.1 (40)	8.7 ± 4.4 (25)	8.7 ± 2.1 (19)	9.6 ± 2.5 (13)	9.8 ± 3.2 (9)
		Cumulative duration of instars (days)					19.7 ± 3.4 (40)	28.9 ± 6.1 (25)	38.1 ± 6.3 (19)	46.1 ± 5.0 (13)	56.3 ± 6.6 (9)
		Body length (mm)					4.5 ± 0.5 (41)	5.4 ± 0.5 (40)	6.7 ± 0.6 (25)	7.5 ± 0.5 (19)	8.1 ± 0.4 (13)
		No. of flagellar segments, Antenna I					11.4 ± 1.2 (22)	14.7 ± 1.9 (16)	17.6 ± 1.7 (15)	18.7 ± 1.6 (11)	20.8 ± 1.1 (8)
		Maturity stage (% juveniles)					100.0 (41)	60.0 (24)	8.0 (2)	0.0	0.0
		Maturity stage (% prematures)					0.0	40.0 (16)	68.0 (17)	15.8 (3)	0.0
		Maturity stage (% mature)					0.0	0.0	24.0 (6)	84.2 (16)	100.0 (13)

Tab. III-2: Summary statistics of reproductive traits in female *Caprella mutica* maintained at 4, 10 and 16°C. Number in brackets indicates N at the respective instars. Mean ± SD are shown. Ad_n = adult instars; n.a. = not available.

		Adult instars (parturial moult onward)										
		Ad_1	**Ad_2**	**Ad_3**	**Ad_4**	**Ad_5**	**Ad_6**	**Ad_7**	**Ad_8**	**Ad_9**	**Ad_{10}**	**Ad_{11}**
4°C	No. of survivors at beginning	27	15	11	3	3	3	2				
	No. of survivors at end	15	10	3	3	3	2	0				
	% Survivors at end	41.7	27.8	8.3	8.3	8.3	5.6	0.0				
	Body length (mm)	9.4 ± 0.8 (27)	10.8 ± 0.6 (15)	11.6 ± 1.0 (11)	12.0 ± 0.3 (3)	13.4 ± 0.8 (3)	13.1 ± 0.4 (3)	14.0 ± 0.5 (2)				
	No. of flagellar segments, Antenna I	15.9 ± 1.6 (24)	17.6 ± 1.7 (12)	21.9 ± 14.3 (9)	20.3 ± 1.0 (3)	22.3 ± 1.0 (3)	23.5 ± 0.6 (2)	23.8 ± 0.5 (2)				
	Duration of instars (days)	35.9 ± 2.5 (15)	37.6 ± 3.8 (10)	37.0 ± 0.0 (3)	40.7 ± 0.6 (3)	40.3 ± 1.5 (3)	40.0 ± 2.8 (2)	n.a.				
	Cumulative duration of instars (days)	35.9 ± 2.5 (15)	66.9 ± 15.6 (10)	100.7 ± 23.2 (3)	141.3 ± 23.8 (3)	181.7 ± 24.8 (3)	214.0 ± 32.5 (2)	n.a.				
	Duration of embryonic development (days)	35.0 ± 2.1 (11)	38.0 ± 0.0 (3)	-	-	-	-	-				
	No. of live juveniles	37.5 ± 20.5 (11)	10.3 ± 10.1 (3)	-	-	-	-	-				
	No. of dead juveniles	1.5 ± 2.2 (11)	11.3 ± 9.5 (3)	-	-	-	-	-				
	Duration from last moult until beginning ofoogenesis (days)	10.9 ± 2.3 (20)	11.5 ± 4.1 (13)	11.7 ± 4.5 (6)	17.0 ± 1.0 (3)	14.7 ± 1.5 (3)	16.7 ± 7.5 (3)	16.0 (1)				
	Duration of oogenesis until next oviposition (days)	25.9 ± 3.0 (15)	26.8 ± 5.8 (11)	24.7 ± 3.2 (3)	25.3 ± 0.6 (3)	27.3 ± 0.6 (3)	28.0 ± 2.8 (2)	n.a.				
	Duration of egg resorption of non-ovipositioned eggs (days)	-	14.0 (1)	7.0 (1)	-	12.0 (1)	7.0 (1)	12.0 (1)				
	Duration from oviposition until abortion (days)	20.2 ± 10.9 (6)	31.1 ± 11.8 (8)	16.0 ± 9.1 (6)	21.3 ± 15.6 (3)	32.7 ± 6.0 (3)	17.3 ± 15.1 (3)	4.0 (1)				
10°C	No. of survivors at beginning	31	19	17	11	9	3					
	No. of survivors at end	19	17	11	9	3	0					
	% Survivors at end	52.8	47.2	30.6	25.0	8.3	0.0					
	Body length (mm)	9.4 ± 0.7 (31)	10.1 ± 0.7 (19)	10.8 ± 0.8 (17)	11.5 ± 0.9 (11)	12.1 ± 0.7 (9)	12.4 ± 0.2 (3)					
	No. of flagellar segments, Antenna I	16.0 ± 1.4 (23)	16.9 ± 1.9 (15)	18.4 ± 1.7 (17)	19.5 ± 1.3 (11)	21.0 ± 1.6 (8)	21.3 ± 2.3 (3)					
	Duration of instars (days)	15.8 ± 0.6 (19)	18.0 ± 2.4 (17)	21.1 ± 0.6 (11)	19.3 ± 1.2 (9)	19.3 ± 2.5 (3)	n.a.					
	Cumulative duration of instars (days)	15.8 ± 0.6 (19)	33.8 ± 2.4 (17)	54.1 ± 6.2 (11)	72.3 ± 4.8 (9)	92.3 ± 7.2 (3)	n.a.					
	Duration of embryonic development (days)	14.8 ± 0.8 (20)	16.0 ± 1.6 (10)	18.3 ± 2.5 (3)	13.0 (1)	-	-					
	No. of live juveniles	37.7 ± 17.9 (20)	24.6 ± 16.3 (10)	11.7 ± 14.2 (3)	2.0 (1)	-	-					
	No. of dead juveniles	0.9 ± 1.6 (20)	5.2 ± 3.2 (10)	2.3 ± 4.0 (3)	0.0 (1)	-	-					
	Duration from last moult until beginning ofoogenesis (days)	4.7 ± 1.2 (25)	6.7 ± 1.8 (18)	6.8 ± 2.1 (12)	7.7 ± 0.9 (10)	6.4 ± 1.7 (7)	5.0 (1)					
	Duration of oogenesis until next oviposition (days)	12.1 ± 1.1 (19)	12.1 ± 1.9 (17)	15.1 ± 5.9 (11)	12.7 ± 1.5 (9)	14.7 ± 2.5 (3)	n.a.					
	Duration of egg resorption of non-ovipositioned eggs (days)	-	-	-	-	-	-					
	Duration from oviposition until abortion (days)	-	13.3 ± 3.3 (7)	13.0 ± 7.4 (10)	12.2 ± 2.3 (9)	10.6 ± 1.3 (5)	3.0 (1)					
16°C	No. of survivors at beginning	45	41	39	33	26	9	3	2	2	1	1
	No. of survivors at end	41	39	33	26	9	3	2	2	1	1	0
	% Survivors at end	83.7	79.6	67.3	53.1	18.4	6.1	4.1	4.1	2.0	2.0	0.0
	Body length (mm)	8.5 ± 0.9 (45)	9.2 ± 0.9 (41)	9.6 ± 0.8 (39)	9.8 ± 0.7 (33)	10.6 ± 1.0 (26)	11.1 ± 0.8 (9)	10.8 ± 0.6 (3)	10.5 ± 0.2 (2)	10.5 (1)	10.8 (1)	9.5 (1)
	No. of flagellar segments, Antenna I	13.1 ± 1.5 (27)	15.2 ± 1.7 (36)	16.9 ± 1.2 (37)	18.3 ± 1.3 (32)	19.9 ± 1.4 (22)	20.9 ± 1.0 (7)	22.0 ± 2.4 (3)	23.3 ± 2.1 (2)	23.0 (1)	24.0 (1)	n.a.
	Duration of instars (days)	9.4 ± 1.0 (41)	9.7 ± 0.9 (39)	10.0 ± 0.9 (33)	10.6 ± 1.1 (26)	10.6 ± 1.0 (9)	12.3 ± 1.5 (3)	9.5 ± 0.7 (2)	11.0 ± 0.0 (2)	12.0 (1)	11.0 (1)	n.a.
	Cumulative duration of instars (days)	9.4 ± 1.0 (41)	19.1 ± 1.6 (39)	29.0 ± 1.8 (33)	39.4 ± 2.4 (26)	49.0 ± 2.4 (9)	60.3 ± 2.9 (3)	69.0 ± 2.8 (2)	80.0 ± 2.8 (2)	94.0 (1)	105.0 (1)	
	Duration of embryonic development (days)	8.0 ± 0.6 (36)	8.0 ± 0.9 (36)	7.9 ± 0.5 (27)	8.1 ± 0.5 (14)	8.0 ± 0.5 (8)	7.0 ± 0.0 (2)	9.0 (1)	7.0 (1)	-	-	-
	No. of live juveniles	25.9 ± 11.3 (36)	35.8 ± 16.1 (36)	28.3 ± 13.3 (27)	24.1 ± 8.7 (14)	18.5 ± 16.2 (8)	23.0 ± 0.0 (2)	0.0 (1)	22.0 (1)	-	-	-
	No. of dead juveniles	0.9 ± 1.7 (36)	1.1 ± 2.7 (36)	1.1 ± 2.3 (27)	2.3 ± 2.5 (14)	7.4 ± 7.1 (8)	0.0 ± 0.0 (2)	9.0 (1)	15.0 (1)	-	-	-
	Duration from last moult until beginning ofoogenesis (days)	3.0 ± 0.6 (41)	3.1 ± 0.6 (40)	3.1 ± 0.8 (38)	3.0 ± 0.9 (32)	3.3 ± 1.0 (21)	4.4 ± 1.5 (5)	3.0 ± 0.0 (2)	3.0 ± 1.4 (2)	7.0 (1)	4.0 (1)	-
	Duration of oogenesis until next oviposition (days)	7.3 ± 0.7 (41)	7.5 ± 0.8 (39)	7.9 ± 1.1 (33)	8.6 ± 1.3 (26)	8.5 ± 1.2 (10)	8.7 ± 1.2 (3)	8.0 ± 0.0 (2)	9.0 ± 1.4 (2)	6.0 (1)	8.0 (1)	n.a.
	Duration of egg resorption of non-ovipositioned eggs (days)	-	-	4.0 ± 0.0 (2)	5.0 ± 0.0 (3)	6.7 ± 1.5 (3)	5.5 ± 2.1 (2)	-	-	-	-	-
	Duration from oviposition until abortion (days)	4.8 ± 2.6 (6)	4.0 ± 4.2 (2)	4.9 ± 2.1 (9)	6.5 ± 2.1 (17)	5.5 ± 2.8 (11)	6.3 ± 1.2 (3)	7.0 (1)	5.0 (1)	6.0 (1)	6.0 (1)	-

Tab. III-2 (continued): Summary statistics of reproductive traits in female *Caprella mutica* maintained at 20 and 26°C. Number in brackets indicates N at the respective instars. Mean ± SD are shown. Ad_n = adult instars; n.a. = not available.

		Adult Instars (parturial moult onward)					
		Ad_1	**Ad_2**	**Ad_3**	**Ad_4**	**Ad_5**	**Ad_6**
20°C	No. of survivors at beginning	31	15	7	2	1	1
	No. of survivors at end	15	7	2	1	1	0
	% Survivors at end	41.7	19.4	5.6	2.8	2.8	0.0
	Body length (mm)	8.7 ± 0.6 (31)	9.2 ± 0.6 (15)	9.4 ± 0.1 (7)	9.8 (1)	10.1 (1)	n.a.
	No. of flagellar segments, Antenna I	15.8 ± 1.1 (28)	17.3 ± 1.9 (10)	18.3 ± 1.4 (4)	21.0 ± 1.4 (2)	22.0 (1)	22.0 ± 1.4 (1)
	Duration of instars (days)	8.3 ± 1.2 (15)	8.8 ± 1.3 (6)	7.5 ± 0.7 (2)	9.0 (1)	11.0 (1)	n.a.
	Cumulative duration of instars (days)	8.3 ± 1.2 (15)	16.9 ± 1.8 (6)	23.0 ± 1.4 (2)	31.0 (1)	42.0 (1)	n.a.
	Duration of embryonic development (days)	6.3 ± 0.7 (15)	6.6 ± 1.1 (5)	6.0 ± 0.0 (2)	-	7.0 (1)	-
	No. of live juveniles	23.7 ± 10.6 (15)	29.2 ± 14.6 (5)	15.5 ± 0.7 (2)	-	19.0 (1)	-
	No. of dead juveniles	2.3 ± 3.5 (15)	3.2 ± 2.5 (5)	6.5 ± 7.8 (2)	-	8.0 (1)	-
	Duration from last moult until beginning ofoogenesis (days)	1.9 ± 0.7 (25)	1.6 ± 0.7 (12)	3.8 ± 2.9 (5)	4.0 (1)	4.0 (1)	-
	Duration of oogenesis until next oviposition (days)	7.3 ± 1.2 (15)	8.4 ± 0.9 (6)	6.0 ± 0.0 (6)	6.0 (1)	8.0 (1)	n.a.
	Duration of egg resorption of non-ovipositioned eggs (days)	4.0 (1)	4.0 (1)	4.0 (1)	-	-	-
	Duration from oviposition until abortion (days)	1.8 ± 1.3 (5)	3.0 ± 2.0 (3)	3.5 ± 2.1 (2)	6.0 (1)	-	-
26°C	No. of survivors at beginning	5	2	2	1	1	
	No. of survivors at end	2	2	1	1	0	
	% Survivors at end	5.6	5.6	2.8	2.8	0.0	
	Body length (mm)	9.2 ± 0.5 (3)	8.7 ± 0.8 (2)	9.2 ± 0.2 (2)	8.3 (1)	8.9 (1)	
	No. of flagellar segments, Antenna I	16.5 ± 0.8 (5)	16.8 ± 1.9 (2)	18.3 ± 2.1 (2)	18.0 (1)	18.0 (1)	
	Duration of instars (days)	7.5 ± 0.7 (2)	8.0 ± 1.4 (2)	9.0 (1)	8.0 (1)	n.a.	
	Cumulative duration of instars (days)	7.5 ± 0.7 (2)	15.5 ± 2.1 (2)	26.0 (1)	34.0 (1)	n.a.	
	Duration of embryonic development (days)	-	5.0 (1)	5.5 ± 0.7 (2)	-	-	
	No. of live juveniles	-	6.0 (1)	0.0 ± 0.0 (2)	-	-	
	No. of dead juveniles	-	1.0 (1)	2.5 ± 2.1 (2)	-	-	
	Duration from last moult until beginning ofoogenesis (days)	2.7 ± 0.6 (3)	2.5 ± 0.7 (2)	3.5 ± 2.1 (2)	2.0 (1)	-	
	Duration of oogenesis until next oviposition (days)	5.5 ± 0.7 (2)	6.5 ± 0.7 (2)	8.0 (1)	7.0 (1)	n.a.	
	Duration of egg resorption of non-ovipositioned eggs (days)	-	-	-	-	-	
	Duration from oviposition until abortion (days)	0.5 ± 0.6 (4)	4.0 (1)	-	3.0 (1)	-	

Chapter IV

Testing the enemy release hypothesis - consequences for habitat specific distribution in the non-native amphipod *Caprella mutica* Schurin, 1935

Introduction

When arriving in a new range, the local abiotic environmental conditions (e.g. temperature or salinity) determine at first whether a non-native species is able to survive and has the potential to become established (Richardson et al., 2001). Long term successful establishment, however, depends on whether the non-native species is able to persist in biotic interactions with the recipient community (Sakai et al., 2001; Füreder and Pöckl, 2007). The enemy release hypothesis (ERH) is often used to explain invasion success of non-native species in their introduced ranges (Keane and Crawley, 2002; Shea and Chesson, 2002). It suggests that non-native species may become more abundant in their new areas as compared to their native ranges if natural enemies (i.e. predators, parasites or pathogens), normally controlling abundance and distribution, are absent (Elton, 1958; Keane and Crawley, 2002). For example, comparing 26 host species of different animal taxa, Torchin et al. (2003) found twice as much parasites in populations in native ranges than in introduced populations. Moreover, introduced populations were less heavily parasitized than native equivalents in the same range.

Contrarily to the ERH, the biotic resistance hypothesis (BRH) argues that communities resist invasions due to community diversity (Stachowicz et al., 1999), superior native competitors or abundant predators (Crawley et al., 1999). For example, the blue crab *Callinectes sapidus* predates readily on the European green crab *Carcinus maenas* introduced to North America, limiting the non-native's abundance and geographic range (DeRivera et al. 2005). Although treated as contrasting hypotheses, the ERH and the BRH are not mutually preclusive, because they differently refer to causes for spreading success and restricted dispersal (Hüls, 2005). In fact, Agrawal et al. (2005) found contrasting results in a common garden experiment by repeated examination of herbivore damage in introduced and native field plants. In a first experiment, the introduced plants showed higher damage, whereas it was the opposite result in the repeated set. DeWalt et al. (2004) found enemy release to be on account of variable environmental conditions leading to spatial and seasonal variation in life cycles of enemy species. The authors suggested that net effects of enemies might vary in space and time and thus, create enemy free (or enemy reduced) ‘invasion opportunity windows’. In fact, natural enemies acting as biotic resistors were considered to determine habitat distribution of introduced species in their new ranges (DeWalt et al., 2004), potentially closing invasion opportunity windows. This may lead to the occurrence of non-natives in certain habitats of a recipient area, where they are typically not found in their native range.

In the marine environment, human mediated introductions generally occur by transportation of marine organisms in ballast water or sediments of ocean going cargo ships or among fouling communities on boat hulls (Ruiz et al., 1997; Floerl et al., 2005). Commercial shipping ports and recreational boating harbours therefore provide first habitats in a colonisation corridor of introduced species (Bax et al., 2002; Floerl et al., 2005). For example, for several years the introduced Asian Sea Squirt *Styela clava* was exclusively found on man-made structures in the harbours of Sylt, Germany, before it established permanently in natural native mussel bed communities (Buschbaum 2002). Artificial substrata close to ports of arrival (e.g. pontoons, berths, harbour constructions or aquaculture facilities) may, therefore, serve as ‘stepping stones’ for invaders before spreading into natural habitats (Apte et al., 2000; Wilhelmsson and Malm, 2008).

Generally, submerged man-made structures close to ports of arrival undergo regular exchange and re-deployment for cleaning and mending purposes, which may result in enhanced disturbance creating available resources (i.e., space) for native fouling communities on such structures. Davis et al. (2000) theorized that a community will be more susceptible to invasion if disturbance, grazing, or other factors periodically lead to an increase in available resources for invaders, thus enhancing the probability for successful establishment.

In cases were the spread of an introduced species into natural habitats is limited by biotic resistance of natural communities, artificial substrata may serve as the only possible habitat, providing enemy free refuges and opening invasion opportunity windows with available resources and reduced competition, thus facilitating invasion success (Glasby et al., 2007). Support is given by Page et al. (2006) who found three exotic species (the bryozoan *Watersipora cf. subtorquata,* the anemone *Diadumene* sp. and the amphipod *Caprella mutica*) in high densities on offshore oil platforms in the Santa Barbara

Channel, California, where they were entirely absent from natural habitats. As first sightings of *C. mutica* on the Californian coast date back to the early 1970s (USGS, 2005). this suggests that biotic or abiotic factors may limit this species in spreading into natural habitats.

Caprella mutica Schurin, 1935 a marine caprellid amphipod indigenous to north-east Asia is typically reported from sublitoral zones inhabiting different macroalgae but also aquaculture structures in Otsuchi Bay (Fedotov, 1991; Kawashima et al., 1999; Vassilenko, 2006). Maximum abundances in its native area range between 1,200 and 2,600 ind. m^{-2} (Fedotov, 1991; Vassilenko, 2006). In the last 40 years, *C. mutica* has successfully spread to numerous locations world-wide, probably with shippings of Japanese oysters *Crassostrea gigas* (Thunberg, 1793) or in ballast water (Willis et al., 2004; Cook et al., 2007a).

In its new ranges, populations of *C. mutica* have been found in fouling communities typically on artificial substrata such as the underneath side of pontoons or boat hulls, ropes, buoys or nets, offshore oil platforms and wind parks (Willis et al., 2004; Buschbaum and Gutow, 2005; Dong Energy et al., 2006; Page et al., 2006; Cook et al., 2007a). Maximum population densities of *C. mutica* exceeding 300,000 ind. m^{-2} were reported from the west coast of Scotland (Ashton, 2006). Typically, European populations amount to some 60,000 ind. m^{-2} in summer and autumn periods, outnumbering native populations more than twentyfold (Ashton, 2006; Schneider, 2007; this work, Chapter II). Findings of *C. mutica* from natural benthic habitats are rare and seemingly sporadic. Small populations or single specimens have been found in kelp communities (*Laminaria* spp.) along the north coast of Scotland (S. Dworjanyn, pers. comm.) and attached to floating macroalgae (Ashton, 2006).

According to the above, the question arises whether the observed habitat distribution (artificial versus natural habitats) in European populations of *C. mutica* is determined by biotic resistance (natural benthic predators) and restricted to artificial structures which provide enemy free invasion opportunity windows.

To answer these questions, predation pressure on *C. mutica* exerted by two types of predators, an omnivorous benthic crustacean and a common rockfish, were studied in laboratory experiments.

In detail, the following questions were addressed:

(i) Do shore crabs (*Carcinus maenas* (Linnaeus, 1758)) and goldsinny wrasse (*Ctenolabrus rupestris* (Linnaeus, 1758)) predate on *C. mutica*?

(ii) If so, are there differences in selective feeding behaviour due to size, sex or densities of *C. mutica*?

(iii) Are predation rates different when *C. mutica* is offered at the bottom of an aquarium tank as opposed to structures near the surface?

Material and Methods

Preliminary aquarium-based feeding experiments for best handling, choice of predators and setup were run on the west coast of Scotland at the Dunstaffnage Marine Laboratory, Scottish Association for Marine Science. Main experiments were conducted from July until October 2007 at the laboratory facilities of the Helgoland Marine Biological Station, Island of Helgoland, German Bight, North Sea. Shore crabs *C. maenas* and goldsinny wrasse *C. rupestris* were chosen as benthic and nektonic predators, respectively (Elner, 1981; Ropes, 1988; Sayer et al. 1995, 1999). For wrasse, tapered fish creels (length: 1.5 m, width: 0.5 m) baited with different flatfish were deployed over night at 4 m depth in the Northeast Harbour of Helgoland. Shore crabs were trapped using commercial lobster pots baited with crushed mussel and deployed in the vicinity of the island over night.

Until usage, both predators were maintained in separate flow-through tanks (45 x 66 x 38 cm; 80 l) at ambient water temperatures ranging from 9.9 to 13.9°C over the entire experimental period and at a constant light:dark regime of 12:12 h. Predators were fed regularly with pieces of fish or mussel tissue. Wrasse were between 9.0 and 13.0 cm in length. Shore crabs between 3.9 and 6.2 cm in carapax width and 3.3 and 5.1 cm in carapax length.

Caprella mutica was collected by scraping fouling organisms off submerged areas of pontoons in the South Harbour of Helgoland. The specimens were maintained on their settlement substratum from the field (the ascidians *Ciona intestinalis* and *Ascidiella aspersa* and different algal species) in 10 l flow-through aquarium tanks until usage (max. two to three days).

All experiments were conducted in individual 45 x 66 x 38 cm (80 l) aquarium tanks using single predator species per trial. Temperature and light conditions were as described above. Prior to the actual experiments the predators were starved and adapted to the experimental conditions for 24 h. Each tank was furnished with a perforated brick (5 x 10 x 25 cm) as substratum and shelter. A net fragment (approx. 15 x 15 cm, mesh width 7 cm, strength 0.7 cm) was fixed to the brick in an upward position, approximately reaching the surface level (Fig. IV-1). In all experiments, defined numbers of *C. mutica* (see below) were offered on artificial turf structures (Aquatic plastics, London) providing about 30 cm² of surface to cling to (Shucksmith, 2007). The turfs mimicked filamentous algae from fouling communities amongst which *C. mutica* is commonly found in the field. Artificial mimicks were used instead of natural substrata to prevent chemical cues or associated epibiota potentially influencing the predators' feeding behaviour.

In a first experiment, *C. mutica* was offered in different size and sex groups, either separately or mixed, to test for selective feeding behaviour (Tab. IV-1). Measured from head (base of antennae) to the distal part of the abdomen to the nearest 1.0 mm, the following reference sizes of *C. mutica* were regarded representative: 25 mm for large males, 12 mm for medium males and females, and 5 mm for juvenile individuals. For best comparison of prey biomass, numbers of caprellids introduced to the experiments were inversely related to size (Caine, 1991). Ten large males were chosen as reference density and multiplied with their reference size, resulting in an estimated calculation factor of 250. This factor was applied to the other experimental groups in order to calculate appropriate densities (Tab. IV-1). The proportions of adults and juveniles (50+50) in the mixed trials reflect actual shares and field densities in *C. mutica* during summer periods (Schneider, 2007; this work, Chapter II).

Tab. IV-1: Experimental design for numbers of *Caprella mutica* used in different size and sex groups. The calculation factor is highlighted in bold writing.

Type of trial	Sex / size group	Reference size (mm)	Calculation of density estimates	Densities used in the experiments per 30 cm^2
single group	large males	25	**250**/25 = 10	10
single group	medium males	12	**250**/12 = 20.8	20
single group	females	12	**250**/12 = 20.8	20
single group	juveniles	5	**250**/5 = 50.0	50
mixed group	all above groups together	see above	see above	10 + 20 + 20 + 50 = 100

Prior to each experimental run, the caprellids were transferred onto individual turf structures, each placed individually in a 10 x 10 x 5 cm container filled with seawater. The animals were left to settle and cling on the turf for a minimum of 30 min. The containers were then carefully submerged into the experimental tanks with the respective predators and the structures carefully lowered to the tank floor. After one hour of feeding, the predators were removed from the tanks. The number of surviving caprellids was recorded after thorough inspection of all structures (i.e. the brick, net and turf, tank walls and floor). Five replicates were run for each experimental combination described above in presence and absence (control) of the respective predator.

In a second experiment, feeding trials on low (20 individuals), medium (45 individuals) and high (90 individuals) densities of *C. mutica* were run. Only conspicuous individuals were used, i.e. adult and subadult specimens with a minimum size of 6 mm. Juveniles were omitted in this experiment as predation rates were found negligibly small (see results of first experiment). Density treatment was fully crossed with the factor orientation to test whether predation rates differed when prey was offered at the water surface as opposed to the tank floor. Therefore turfs were attached to submerged underneath sides of plastic panels fixed at surface level (Fig. IV-1). The panels closely neighboured the net fragments on the bricks. This was considered a realistic access to prey for the shore crabs, as they were observed clinging to the nets during preliminary studies and adaptation periods. For transfer of counted caprellids, the panels were laid across 10 x 10 x 5 cm containers filled with seawater, so that the turf blades would extend into the water allowing caprellids to cling to. Otherwise, methodological procedure and number of replicates and controls were as described above.

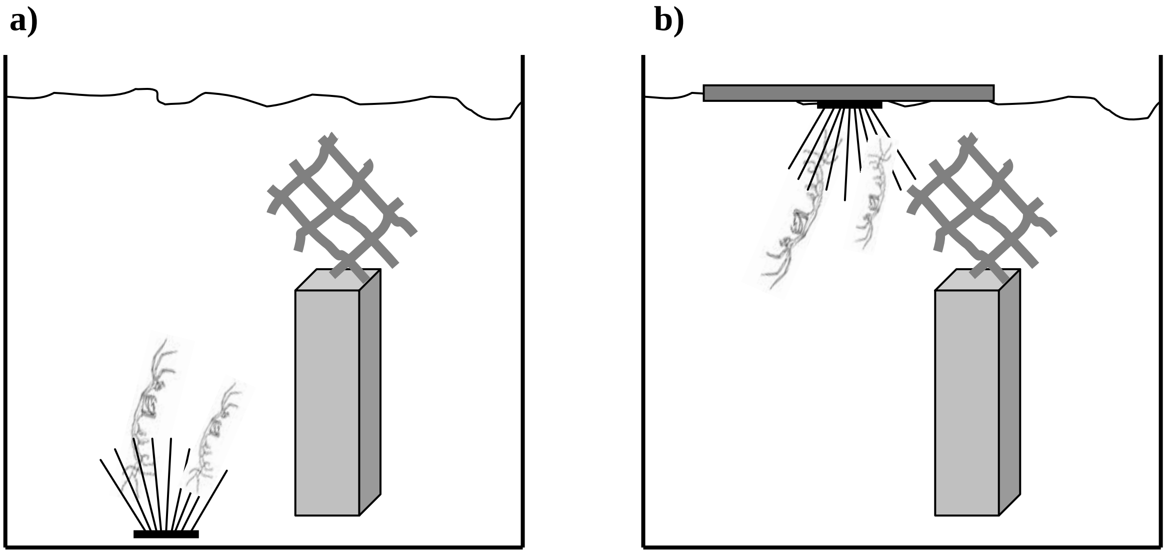

Fig. IV-1: Sketch overview of the experimental tanks with bricks, nets and turfs. Sizes do not represent realistic dimensions. a) Caprellids on turfs are offered on the tank floor (this setup was also used for the selective feeding experiments) and b) turfs are attached to the submerged side of a floating panel and caprellids are offered from near the surface.

Statistical analysis

Statistical analyses were run at the 95 % confidence level using computer software GraphPad Prism (3.0) and STATISTICA (7.0).

To test for differences in selective feeding behaviour, separate two-way-ANOVAs were applied to the single and the mixed group trials, with predator species and prey groups as fixed factors. Percentages of consumed individuals of each group were used as response variable. Arcsin transformation on the square root of the data (Zar, 1996) was performed to meet the assumptions of normal distribution (Kolmogorov-Smirnov test, $P > 0.05$) and homogeneity of variances (Cochran's test, $P > 0.05$ for all but one group in the mixed trials). Significant differences within factors and interaction of factors were compared with Tukey's post-hoc test.

Differences in density dependent feeding on the tank floor (bottom) and at water surface (top) were analysed using a three-way-ANOVA with predator species, prey densities and orientation as crossed fixed effects factors. The absolute number of consumed caprellids was used as response variable. For normal distribution (Kolmogorov-Smirnov test, $P > 0.05$) and homoscedasticity (Cochran's test, P for all groups > 0.05) data were log+1 transformed. Significant differences within factors and interaction of factors were compared with Tukey's *post-hoc* test.

Results

Shore crabs and wrasse consumed comparable numbers of caprellids in the single and the mixed treatments (single groups: $P = 0.98$; mixed groups: $P = 0.22$; Fig. IV-2a and b, Tab. IV-2, Appendix Tab. IV-3). More caprellids were consumed in the experimental time period, when higher overall numbers of caprellids were offered. Feeding was selective in both treatments (P each < 0.01; Fig. IV-2a and b, Tab. IV-2). In relation to the numbers of *C. mutica* offered per group, both predators consumed relatively more large males than medium males, females or juveniles in the single group trials ($P < 0.05$ for all comparisons with large males; Fig. IV-2a). Although relatively more medium sized males and females were consumed than juveniles, this difference was not significant. When all prey groups were offered together, again relatively more large males were consumed than specimens from the other groups. However, this was significant only between large males and juvenile specimens ($P < 0.05$; Fig. IV-2b). No significant interaction between the factors was found.

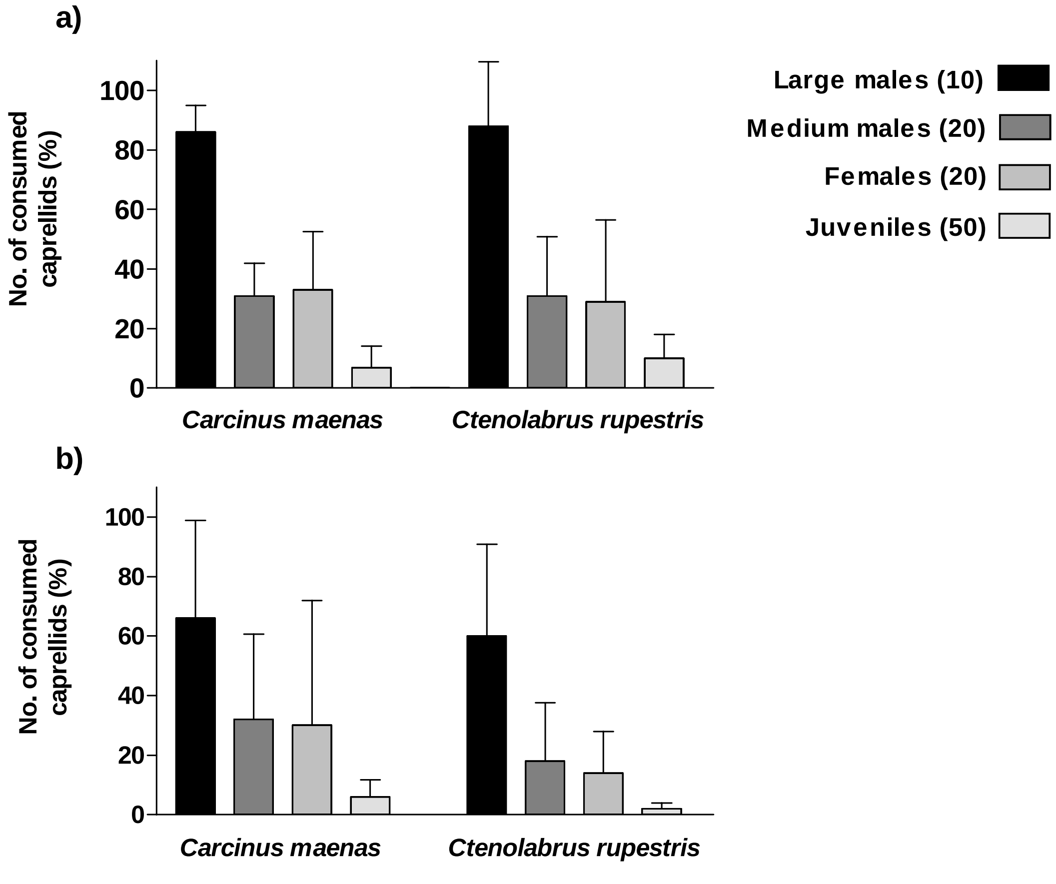

Fig. IV-2: Percentage of consumed specimens of *Caprella mutica* by *Carcinus maenas* and *Ctenolabrus rupestris* for a) single and b) mixed prey groups; mean ± SD (N = 5).

The density dependent feeding trials revealed no difference in the numbers of caprellids consumed by shore crabs or wrasse (predator species: P = 0.30; Fig. IV-3, Tab. IV-2, Appendix Tab. IV-3). Moreover, the analyses showed no difference in prey consumption at different densities (prey density: P = 0.07; Fig. IV-3, Tab. IV-2). The latter contradicts with the results of the selective feeding trials, in which more caprellids were consumed when higher numbers were offered. When data are pooled for the analysis of main factors in high factorial designs, actual situations are often obscured by compensation of differences within other factors' levels. However, these are mostly unravelled, when interactions of main factors are significant. For the present results this was the case, and the significant interaction revealed clear differences in the feeding behaviour of the two predator species at different densities (P < 0.01; Fig. IV-3, Tab. IV-2). While *C. maenas* consumed more caprellids at high densities as compared to low or medium densities, no differences were found between the latter two groups. *Ctenolabrus rupestris* fed significantly more at medium densities as compared to high or low densities; further significant differences could not be detected. Both predators consumed similar numbers of caprellids at low densities (P > 0.05 for low densities). At medium densities, the wrasse consumed significantly more caprellids than the shore crab. At high densities, however, the shore crab consumed more prey than the wrasse (P < 0.05 for medium and high densities).

More bottom dwelling caprellids were consumed than surface dwelling specimens (factor orientation: P < 0.01; Fig. IV-3, Tab. IV-2). The non-significant interaction between the factors predator species and orientation confirmed, that this was true for both predator species (P = 0.81; Fig. IV-3, Tab. IV-2). The interaction between prey density and orientation revealed orientation to affect consumption of caprellids at different densities (P < 0.01; Fig. IV-3, Tab. IV-2). At the tank floor, more caprellids were consumed at high densities than at low densities (P < 0.01). Orientation did not influence feeding at medium or low densities (P > 0.05 for medium and low densities). Surface feeding was not affected by prey density (P > 0.05). The interaction of all three factors was not significant (P = 0.19; Fig. IV-3, Tab. IV-2).

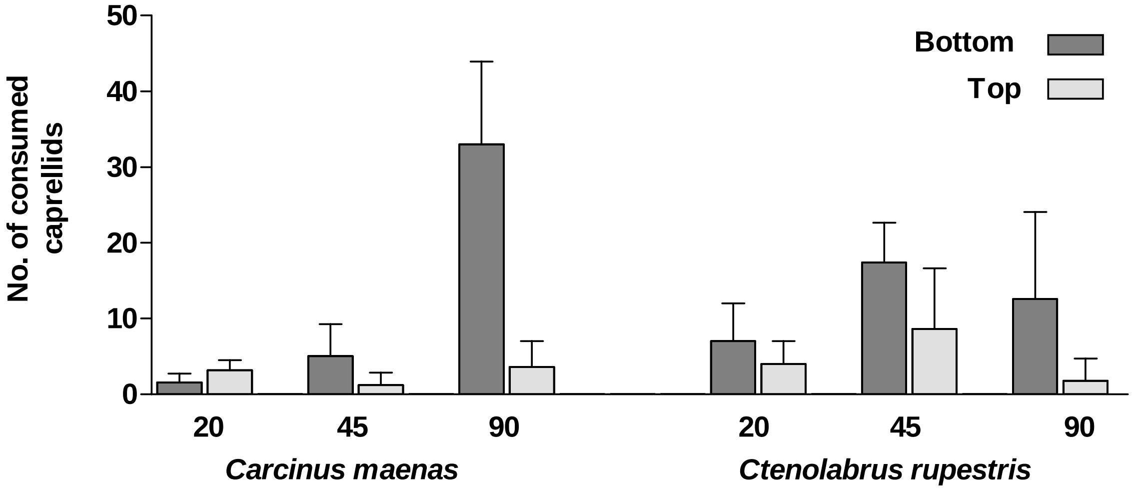

Fig. IV-3: Number of consumed specimens of *Caprella mutica* by *Carcinus maenas* and *Ctenolabrus rupestris* at different densities offered at the tank bottom and at surface level; mean ± SD (N = 5).

Tab. IV-2: Results of three multi-factorial ANOVAs used to test *Carcinus maenas* and *Ctenolabrus rupestris* for selective feeding behaviour in individual and mixed trials of *Caprella mutica* and density dependent feeding at the tank bottom and near the surface. Significant P values are in bold writing.

Source of variation	**df**	**SS**	**MS**	**F**	**P**
Selective feeding: single groups					
Predator species	1	0.00	0.00	0.00	0.98
Prey group	3	5.88	1.96	28.05	**< 0.01**
Predator species * Prey group	3	0.10	0.03	0.49	0.69
Residuals	32	2.24	0.07		
Selective feeding: mixed groups					
Predator species	1	0.21	0.21	1.56	0.22
Prey group	3	3.94	1.31	9.69	**< 0.01**
Predator species * Prey group	3	0.04	0.01	0.09	0.97
Residuals	32	4.34	0.14		
Density dependent feeding					
Predator species	1	0.12	0.12	1.10	0.30
Prey density	2	0.61	0.31	2.76	0.07
Orientation	1	2.38	2.38	21.39	**< 0.01**
Predator species * Prey density	2	2.27	1.36	12.24	**< 0.01**
Predator species * Orientation	1	0.01	0.01	0.06	0.81
Prey density * Orientation	2	1.49	0.74	6.69	**< 0.01**
Predator species * Prey density * Orientation	2	0.39	0.19	1.74	0.19
Residuals	48	5.34	0.11		

Discussion

The results showed that shore crabs and goldsinny wrasse readily fed upon *C. mutica.* Large males were preferred over medium sized specimens, while juveniles were not consumed. Shore crabs do not hunt visually but rely on mechano- and chemoreceptors (Waterman, 1961 and references therein). By sensing water currents and vibrations, larger prey organisms such as male *C. mutica* are more likely to be detected than small juveniles when typically swaying in the water column. Ropes (1968) found that crab size influenced feeding behaviour in shore crabs. This suggests that young stages of *C. maenas* might more readily prey on juvenile *C. mutica* than adult crabs. This, however, was not tested in the present study.

When offered different densities of conspicuous caprellids, *C. maenas* ingested less than 10% from bottom and surface habitats at low and medium prey densities. At high densities, however, nearly half the experimental population was consumed when feeding from the bottom, while only about 5% caprellids were consumed from the surface. This suggests that (i) populations of *C. mutica* exceeding a certain density are more likely to be tracked by *C. maenas* and (ii) are more efficiently regulated by benthic predators in bottom-near habitats than close to the surface.

In contrast, fish are visual predators commonly predating on amphipod species (Caine, 1979, 1991; Takeuchi and Hirano, 1992). Similar to the present results on *C. rupestris,* Caine (1991) found shiner perch *Cymatogaster aggregata* to ingest larger volumes of *Caprella laeviuscula* with increasing caprellid body length. In earlier studies, Caine (1979) reported from *Obelia* sp. habitats, that more males (52.2%) of *C. laeviuscula* were found in fish stomachs of different species than females (39.0%) or juveniles (8.8%).

Large specimens may be more conspicuous than smaller specimens that often hide amongst the inner ramifications of their hosts (e.g. turfs of bryozoans and hydrozoans, or different filamentous algae). This was observed for *C. mutica* in field populations (pers. obs.) and during the feeding trials, suggesting that smaller specimens require higher search and handling effort and are, thus, less worthwhile prey. However, although remaining speculative, this might again not be the case for younger or smaller fish.

Similar to the shore crabs, *C. rupestris* consumed more caprellids from the bottom than from the surface, with highest numbers (nearly 50%) ingested at medium prey densities.

In the present study predation rates were higher on prey offered at the bottom as opposed to the surface. At the bottom, both benthic and nektonic predators depleted experimental populations of *C. mutica* offered in medium or high densities, resembling approximately 15,000 and 30,000 ind. m^{-2} in the field. When transcribed to the field, the results suggest that predatory regulation from both benthic and nektonic predators may be responsible for the comparably low numbers of *C. mutica* found in bottom-near natural habitats.

In contrast to the low densities found in natural bottom-near habitats, maximum densities of *C. mutica* exceed several 10,000 to even more than 300,000 ind. m^{-2} on artificial substrata directed away from the sea bed (Ashton, 2006; this work, Chapter II). The share of juveniles in those populations was between 50 and 70% under favourable climatic conditions (this work, Chapter III).

Shore crabs are rarely found on structures off the ground (pers. obs), suggesting artificial constructions to be refuges from benthic predators and thus, allowing for mass occurrences of *C. mutica* on those structures. Under laboratory conditions, *C. rupestris* consumed about 25% of the experimental population at medium densities from near the surface. According to the densities described above, however, this amount of consumed caprellids does not seem to affect its population growth in the field. High reproductive activity of *C. mutica* may ensure constant production of hatchlings leading to exponential population growth outweighing consumption rates of nektonic predators. More so, as wrasse consumed significantly less individuals when highest densities were offered in the experiments as compared to medium densities.

The observed habitat distribution of *C. mutica* in its new areas clearly differs from the patterns in its native ranges (Fedotov, 1991; Kawashima et al., 1999; Vassilenko, 2006). In natural habitats, both, native and introduced populations most likely experience strong predatory regulation. On artificial structures, however, invasion opportunity windows provide refuges of low predation pressure to *C. mutica*, allowing for exponential growth of thriving populations. Accordingly, Australian studies showed that pier pilings and pontoons harboured more non-native species than surrounding natural rocky habitats (Glasby et al., 2007). Holloway and Connell (2002) found different communities settling on artificial substrata deployed at seabed level than at water surface in Sydney Harbour. Species composition may play a crucial role in determining whether habitats resist or facilitate the establishment of non-native species, thus creating enemy-reduced invasion opportunities. Because of seasonal launching and recovery or regular cleaning of many artificial constructions, these habitats may be characterised highly disturbed while regularly providing free settlement space. Serving as ‘stepping stones’ or ‘beach heads’ for further spread of introduced species, artificial structures may provide habitats of reduced predation and competition pressure due to highly available resources (e.g. space) at first arrival (Connell, 2001; Airoldi et al., 2005; Bulleri and Airoldi, 2005; Glasby et al., 2007).

In the case of *C. mutica*, it seems doubtful whether this species will accomplish an invasive potential in natural habitats similar to that found in its enemy-reduced artificial habitats. And as deployments of artificial structures in marine and estuarine environments (e.g. offshore wind parks) are steadily increasing (Wilhelmsson and Malm, 2008), it seems unlikely that these ‘invasion opportunity windows’ will be shut down for *C. mutica* and other non-natives in the near future.

On a large geographical scale *C. mutica* may be considered a highly successful invader having escaped natural predators from its native areas, thus, supporting the enemy release hypothesis On a small scale, however, *C. mutica* experiences strong biotic resistance and regulation in its new areas by natural predators, which determines the species’ distribution and closes ‘invasion opportunity windows’ in natural habitats.

Appendix

Tab. IV-3: Numbers of *Caprella mutica* consumed by *Carcinus maenas* and *Ctenolabrus rupestris*. Mean ± SD are given (N = 5). Numbers in brackets indicate the number of caprellids introduced at the beginning of each experiment.

Predator	**No. of consumed individuals of *Caprella mutica***					
Carcinus maenas	Offered individually					
	Large males (10)	Medium males (20)	Females (20)	Juveniles (50)		
	8.6 ± 0.9	6.2 ± 2.2	6.6 ± 3.9	3.4 ± 3.6		
	Offered together					
	Large males (10)	Medium males (20)	Females (20)	Juveniles (50)	Total (100)	
	6.6 ± 3.3	6.4 ± 5.7	6.0 ± 8.4	3.0 ± 2.8	21.2 ± 16.6	
	Conspicuous random sexes, Bottom (20)	Conspicuous random sexes, Top (20)	Conspicuous random sexes, Bottom (45)	Conspicuous random sexes, Top (45)	Conspicuous random sexes, Bottom (90)	Conspicuous random sexes, Top (90)
	1.6 ± 1.1	3.2 ± 1.3	5.0 ± 4.2	0.8 ± 1.8	33.0 ± 10.9	3.4 ± 3.0
Ctenolabrus rupestris	Offered individually					
	Large males (10)	Medium males (20)	Females (20)	Juveniles (50)		
	8.8 ± 2.2	6.2 ± 4.0	5.8 ± 5.5	5.0 ± 4.0		
	Offered together					
	Large males (10)	Medium males (20)	Females (20)	Juveniles (50)	Total (100)	
	6.0 ± 3.1	3.6 ± 3.9	2.8 ± 2.8	1.0 ± 1.0	13.0 ± 8.3	
	Conspicuous random sexes, Bottom (20)	Conspicuous random sexes, Top (20)	Conspicuous random sexes, Bottom (45)	Conspicuous random sexes, Top (45)	Conspicuous random sexes, Bottom (90)	Conspicuous random sexes, Top (90)
	6.6 ± 5.1	3.6 ± 3.4	17 ± 5.2	8.2 ± 8.2	12.6 ± 11.5	1.6 ± 2.6

Chapter V

Density dependent interference competition between the non-native *Caprella mutica* Schurin, 1935 (Crustacea: Amphipoda) and its European native congener *Caprella linearis* (Linnaeus, 1767)

Introduction

Competition is considered a key factor in structuring communities (Amarasekare, 2002) as well as in determining invasion success of non-native species in their new habitats (Levine and D'Antonio, 1999; Levine et al., 2004). Intense interspecific competition is likely to occur, when competing species are closely related and exploit identical resources (Franke and Janke, 1998).

One of the main mechanisms of interspecific competition is exploitation. It involves one organism reducing the availability of a shared resource to another. The other main mechanism is interference, in which one organism reduces the ability of another to make use of a shared resource (Carothers and Jaksić, 1984). This is typically reached by overgrowth, predation or the extrusion of chemical repellents (Adams and Traniello, 1981; Schoener, 1983).

Interspecific aggression has been suggested a key factor controlling the invasion success of numerous taxa (Holway and Suarez, 1999; Dick, 1996; Dick et al., 1999). For example, Dick et al. (1999) observed that aggressive behaviour and differential predation in the non-native gammarid amphipod *Gammarus pulex* led to the displacement of the native *G. duebeni celticus* from preferred habitats in freshwater systems of Lough Neagh, Ireland. Holway et al. (1998) argued that the invasive Argentine ant *Linepithema humile* experienced less intraspecific aggression compared to native species. This might have significantly contributed to the competitive superiority of the non-native over resident species, particularly, when densities are high in space-limited habitats.

Within the last decade, the north-east Asian amphipod *Caprella mutica* Schurin, 1935, has successfully invaded different European coastal areas (Platvoet et al., 1995; Tierney et al., 2004; Willis et al., 2004; Buschbaum and Gutow, 2005; Cook et al., 2007a). It

commonly inhabits various fouling species on artificial, man-made structures (e.g., harbours or aquaculture facilities) in densities exceeding several 10,000 to 100,000 ind. m^{-2} in summer months (Ashton, 2006; Schneider, 2007; this work, Chapter II).
The native European congener, *Caprella linearis* (Linnaeus, 1767) typically inhabits natural benthic habitats, where it clings to macroalgae, bryozoans or hydroids (Sokolowsky, 1925; McCain, 1968; Moore, 1984; Laubitz, 1972; Guerra-García, 2002 Shucksmith, 2007; pers. obs.). Knowledge on field abundances of *C. linearis* is scarce. Few populations inhabiting sponges, mussels and hydroids in the natural rocky intertidal were found at the west coast of Scotland (Guerra-García, 2002) in densities similar to those of *C. mutica* (R. Shucksmith, pers. com.). Generally though, abundances of *C. linearis* are comparably low and spatially and temporally instable (H.-D. Franke, M. Janke, A. Röw, C. Wanke; pers. com). *Caprella linearis* also inhabits artificial substrata such as marina berths or pontoons, buoys, fishing creels and even shipwrecks, for example, around the island of Helgoland, German Bight (North Sea) (Sokolowsky, 1900; Harrison, 1944, Hayward and Ryland, 2006). Accordingly, encounter between *C. linearis* and *C. mutica* is most likely to occur on artificial structures. However, regular monitoring events around the island of Helgoland in the last five years have shown the native *C. linearis* to be widely absent from artificial structures. Instead, large populations of *C. mutica* are found where *C. linearis* has been previously recorded.

To date, no detailed studies are available on the biology and life history of *C. linearis* for comparison with *C. mutica*. Nevertheless, the two species are referred to as ecological equivalents based on their close taxonomic relation and their similar habitat and food requirements (Caine, 1974; Arimoto, 1976; Guerra-García, 2002; Sano et al., 2003; Nauwelaerts et al., 2007; Michel et al., 2007; Shucksmith, 2007). In fact, scrape samples taken from navigational buoys in the vicinity of Helgoland in 2006 confirmed the co-occurrence of *C. linearis* and *C. mutica* in the field for the first time (Franke, unpubl. data).
Artificial structures represent space-limited and often disturbed habitats. Disturbances may be caused by seasonal hauling, shifting and launching of structures. This may regularly shift native communities back into earlier successional stages, thus, making resources accessible (e.g., settlement space). The availability of resources and their fluctuations in space and time may severely influence the relative competitive performance of a non-native species and its native equivalent (Daehler, 2003) and may

strongly affect the outcome of competitive encounters (Davis et al., 2000; Agrawal et al., 2005). As a consequence, the impact non-native species may vary with the environment it has invaded (Phillips and Shine, 2006). In fact, the only study on competition between *C. mutica* and *C. linearis* found increased structural heterogeneity of settlement substratum to allow for the coexistence between the two species on spatially limited habitat patches (Shucksmith 2007). A reduction in structural heterogeneity led to the competitive exclusion of *C. linearis* by the non-native *C. mutica* particularly at high densities.

According to the above, it is possible that interspecific encounters between *C. linearis* and *C. mutica* have resulted in the competitive exclusion of the native *C. linearis* from artificial habitats within the harbours of Helgoland.

Shucksmith (2007) measured competition between *C. linearis* and *C. mutica* as a reduction in density of either species. This, however, did not reveal the specific mechanisms underlying this competitive interaction. Intraspecific effects within the two species may play a crucial role in the outcome of competitive encounters between *C. linearis* and *C. mutica*, especially when structural heterogeneity is low and space is limited.

Therefore, the aim of the present laboratory experiment was to evaluate the outcome and mechanism of interspecific encounter at different density combinations of *C. linearis* and *C. mutica* competing for space and measuring mutual displacement, mortality and predation rates.

The experiment was designed to determine,

(i) if displacement of *C. linearis* by *C. mutica* is density dependent,

(ii) if intraspecific effects influence the outcome of competitive encounter, and

(iii) if mutual predation is the underlying mechanism of interference competition between *C. linearis* and *C. mutica*.

Material and Methods

Collection of animals

In September 2006 native *C. linearis* were collected via SCUBA-diving from natural habitats in Loch Etive off the Lynne of Lorne (56°26.50'N, 5°24.00'W), west coast of Scotland along with their substratum, the hydroid *Tubularia indivisa*, on which they occurred in dense populations. *Caprella mutica* were collected from fouling communities attached to mooring lines and fish farm cages at Dunstaffnage fish farm in the Lynne of Lorne (56°26.55'N, 5°28.25'W). After transfer to the aquarium facilities of Dunstaffnage Marine Laboratory (Scottish Association for Marine Science) within 30 min after collection the two species were maintained separately on their substrata and additional plastic meshes (approx. 1 m², mesh width: approx. 1.0 mm) in large (approx. 450 l) aerated flow-through tanks at 14°C. The filter feeding animals (Caine, 1974; Sano et al., 2003) were fed daily with 500 ml of a solution of 80 g commercial planktonic feed/ l (®gamma foods, Tropical Marine Centre Ltd., UK) which was readily grasped by the caprellids with their antennae and first gnathopods.

For the experiments, specimens of different sizes ranging from 8.0 to 13.0 mm in length for *C. linearis* and from 9.0 to 17.0 mm for *C. mutica* and different sexes were selected randomly to best represent populations in the field (Hayward and Ryland, 2006; this work, Chapter II).

Experimental set-up and design

Forty round plastic containers (volume: 1 l) were each supplied with a mesh of 50 cm^2 (mesh size 1.0 mm) used as attachment structure for the caprellids. All containers were placed in a 100 x 75 x 25 cm aquarium tank supplied with a flow-through seawater system (300 ml/ min/ container) at 14°C. To avoid overflow and thus loss of caprellids, the upper sections of the containers were replaced by a mesh (mesh size 250 µm) to ensure constant water outflow and retention of animals and food particles.

Two initial densities of individuals were used in the experiments for the 'experimental resident species' and were chosen to reflect actual densities observed in the field for both species: low (5 ind. $mesh^{-1}$ = 1,000 ind. m^{-2}) and high densities (50 ind. $mesh^{-1}$ = 10,000 ind. m^{-2}). At the beginning of the trials, prior to the addition of the respective 'experimental competitor species', the 'experimental resident species' was placed on the structures for acclimatization and settlement for 30 min. Treatments comprised the addition of low (5) and high (50) densities of the ‘experimental competitor species’ according to Table V-1. Control trials were run for each species without the respective competitor at low (5) and high (50). Each treatment was replicated 5 times. During the experimental period, the animals were fed 10 ml of commercial planktonic feed per container to avoid competitive interference due to food limitation (see above for details on food). According to preliminary studies the amount of food was considered sufficient.

Tab. V-1: Densities of *Caprella linearis* and *Caprella mutica* in presence (trial) and absence (control) and of the respective other species.

	Densities	***Caprella linearis***		***Caprella mutica***
Trial	low + low	5	+	5
	low + high	5	+	50
	high + low	50	+	5
	high + high	50	+	50
Control	low	5	+	0
	high	50	+	0
	low	0	+	5
	high	0	+	50

After 24 h, the numbers of displaced individuals (i.e. the number of individuals not located on the settlement structure) from each species were recorded. In addition, the number of dead animals found after 24 hours were counted. In order to asses the proportion of predation from overall mortality, the numbers of missing individuals were calculated. Therefore, the numbers of all remaining individuals of each species (dead + alive) were subtracted from the initial number of the respective species. In this way, mortality events explained by interspecific effects (i.e. predation) could be separated from residual mortality assumed to be caused by intraspecific effects (see discussion).

Statistical analyses

All statistics were performed at the 95 % confidence level using computer software GraphPad Prism (3.0) and STATISTICA 7.

The number of displaced, dead and predated upon individuals were all analysed in the same way. For each data set, individual one-way ANOVAs were applied to both species (*C. linearis* and *C. mutica*), each at initially low and high densities to test for differences between the treatments, i.e. the absence (control) and the presence of low and high numbers of the respective other species (Tab. V-2). Tukey's pairwise comparisons tested for significant differences within species. For each treatment differences in displacement, mortality and predation between *C. linearis* and *C. mutica* were tested with Student's *t*-tests. Where assumptions for normal distribution of data ($P > 0.05$) and homogeneity of variances ($P > 0.05$) were not met, non-parametrical analyses were applied, i.e., the Kruskal Wallis test, the Dunn's test and the Mann-Whitney-U test.

Tab. V-2: Analysis designs (ANOVA) of each *Caprella linearis* and *Caprella mutica* in initially low (5) and high (50) numbers for displacement, intraspecific mortality and predation. Factor levels of each ANOVA are the absence (+ 0 = control), presence of low (+ 5) and presence of high (+ 50) numbers of the respective other species.

Initial densities of "resident species"				**Density treatments of "competitor species" (factor levels)**		
low	5	*C. linearis*	+	0	*C. mutica*	control
	5	*C. linearis*	+	5	*C. mutica*	low
	5	*C. linearis*	+	50	*C. mutica*	high
high	50	*C. linearis*	+	0	*C. mutica*	control
	50	*C. linearis*	+	5	*C. mutica*	low
	50	*C. linearis*	+	50	*C. mutica*	high
low	5	*C. mutica*	+	0	*C. linearis*	control
	5	*C. mutica*	+	5	*C. linearis*	low
	5	*C. mutica*	+	50	*C. linearis*	high
high	50	*C. mutica*	+	0	*C. linearis*	control
	50	*C. mutica*	+	5	*C. linearis*	low
	50	*C. mutica*	+	50	*C. linearis*	high

Results

Displacement

When the initial densities of the 'resident species' were low, neither the presence nor the abundance of the respective 'competitor species' affected the displacement of *C. linearis* and *C. mutica* (*C. linearis*: $F_{2,12} = 0.93$, $P = 0.42$; *C. mutica*: $F_{2,12} = 1.00$, $P = 0.40$; Fig. V-1a, Appendix Tab. V-3). When the initial numbers were high, the 'resident' *C. mutica* was never affected by the 'competitor' *C. linearis* ($H_{\text{Kruskal Wallis}} = 0.95$, $P = 0.62$; Fig. V-1b). In contrast, it was the other way round for the 'resident' *C. linearis*, which was displaced by the 'competitor' *C. mutica* when initial densities were high ($H_{\text{Kruskal Wallis}} = 8.88$, $P = 0.01$; Fig. V-1b). Exposed to high numbers of the 'competitor' *C. mutica*, about 20% (approximately eight individuals) of *C. linearis* were displaced, whereas the proportion of displaced individuals was halved when the numbers of *C. mutica* were low (Fig. V-1b). Because of high variations, however, the differences were statistically significant only between the high density treatment and the control ($P < 0.05$).

For each treatment the number of displaced individuals was compared between *C. linearis* and *C. mutica*. The results revealed that consistently more individuals of *C. linearis* were displaced by *C. mutica* than the other way round. Due to strong variations within the individual treatments this was statistically significant only for the control (+0) and the low (+5) treatments at low initial densities ($P < 0.05$; Fig. V-1a) and for the high (+50) treatment at high initial densities ($P < 0.05$; Fig. V-1b).

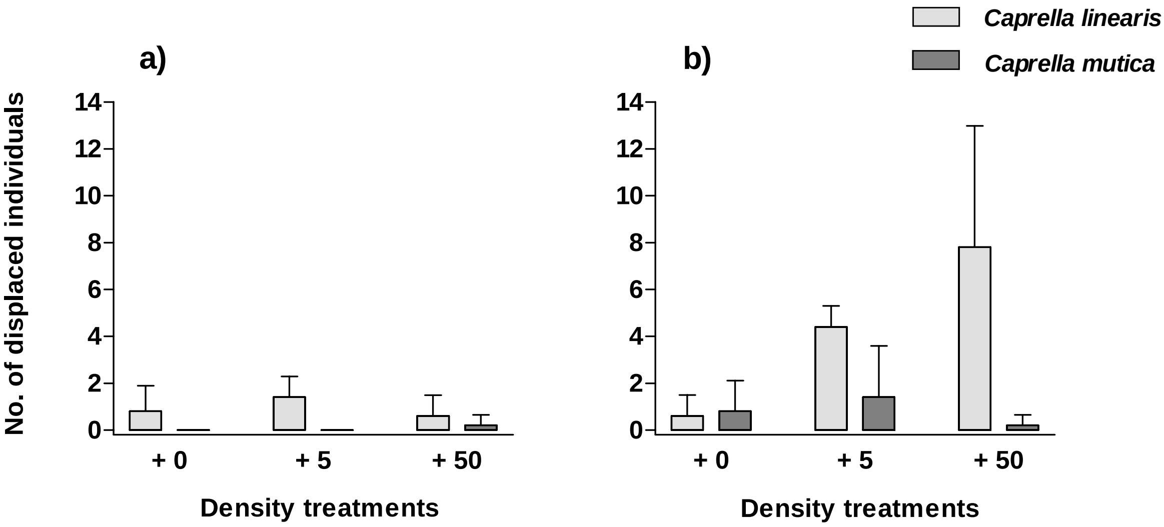

Fig. V-1: Number of displaced individuals (mean ± SD) of 'resident' *Caprella linearis* and *Caprella mutica* in a) initially low (5) and b) initially high (50) densities by the respective 'competitor species' after 24 h of encounter. The x-axes illustrate the absence (+ 0 = control) and the presence of low (+ 5) and high (+ 50) numbers of the respective 'competitor species'.

Residual mortality (intraspecific effects)

Neither the presence nor the density of the respective "competitor species" had an effect on the observed number of dead individuals of *C. linearis* and *C. mutica*, respectively. This result was independent of the initial density of the "resident species" (*C. linearis* init. low: $F_{2,12} = 0.44$, $P = 0.65$; *C. mutica* init. low: $F_{2,12} = 0.50$, $P = 0.62$; Fig. V-2a; *C. linearis* init. high: $H_{\text{Kruskal Wallis}} = 0.43$, $P = 0.81$, *C. mutica* init. high: $F_{2,12} = 0.88$, $P = 0.44$; Fig. V-2b, Appendix Tab. V-3).

When comparing *C. linearis* and *C. mutica* at each treatment at initially low densities, the numbers of dead animals were similarly low for both species (between 0.1 and 0.5 individuals) (P for all comparisons > 0.05, Fig. V-2a). At initially high densities, by contrast, the number of dead *C. linearis* (on average 8.6 individuals) was more than 6 times higher than the number of dead *C. mutica* (on average 1.4 individuals) in all treatments (for all comparisons $P < 0.05$, Fig. V-2b).

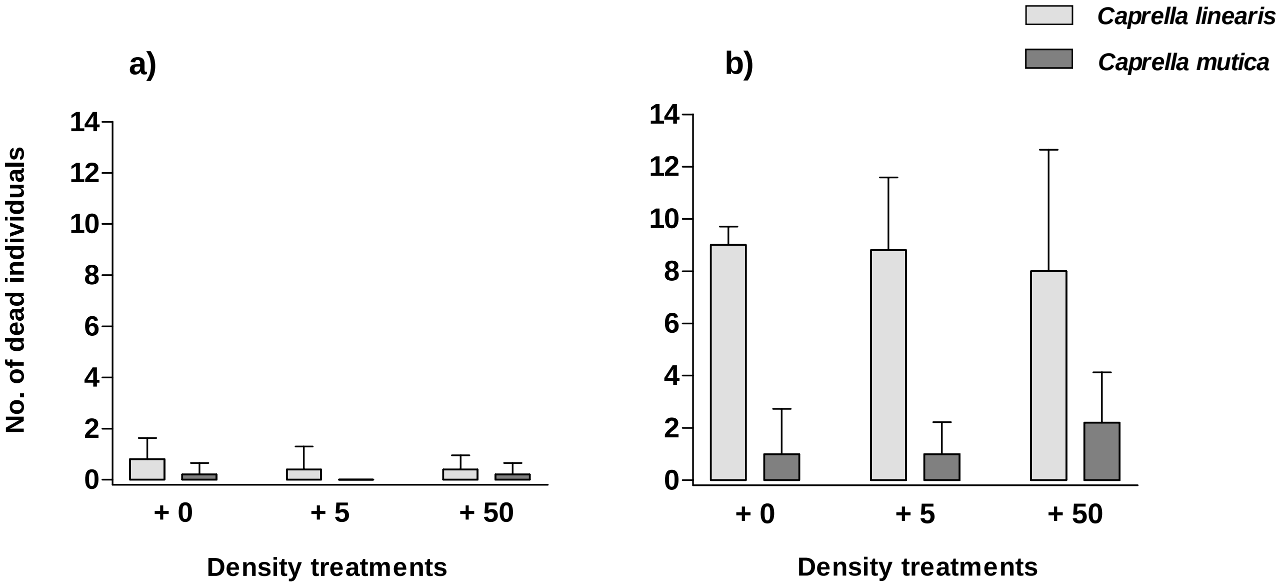

Fig. V-2: Number of dead individuals (mean ± SD) of 'resident' *Caprella linearis* and *Caprella mutica* in a) initially low (5) and b) initially high (50) densities after 24 h of encounter with the respective 'competitor species'. The x-axes illustrate the absence (+ 0 = control) and the presence of low (+ 5) and high (+ 50) numbers of the respective 'competitor species'.

Predation (interspecific effects)

The native 'competitor' *C. linearis* never predated upon the non-native 'resident' *C. mutica* (Fig. V-3a and b). As this consistent result caused no variances, the ANOVA was not applicable in this case. No prominent differences between the treatments are, however, assumed from a visual inspection of the results. At initially high densities of *C. mutica* no differences between the treatments were detected relative to the control (init. high: $F_{2,12} = 1.91$, $P = 0.19$; Fig. V-3a and b, Appendix Tab. V-3).

In contrast, at both low and high initial densities of 'resident' *C. linearis,* the 'competitor' *C. mutica* predated upon *C. linearis* (init. low: $F_{2,12} = 4.80$, $P = 0.03$; init. high: $H_{\text{Kruskal Wallis}} = 6.96$, $P = 0.03$, Fig. V-3a and b). With increasing densities of the competitor *C. mutica*, the number of *C. linearis* predated upon approximately doubled from about 0.5 to 1.0 at initially low densities and from about 3.5 to 6.5 at initially high densities. However, because of high variation at both initial densities, differences were only significant between the control and the high density treatments (for both comparisons $P < 0.05$).

The number of individuals predated upon in the controls is assigned to cannibalism. Accordingly, the numbers of *C. linearis* eaten by *C. mutica* are probably slightly lower. This difference, however, is negligibly small (on average one individual, Fig. V-3b).

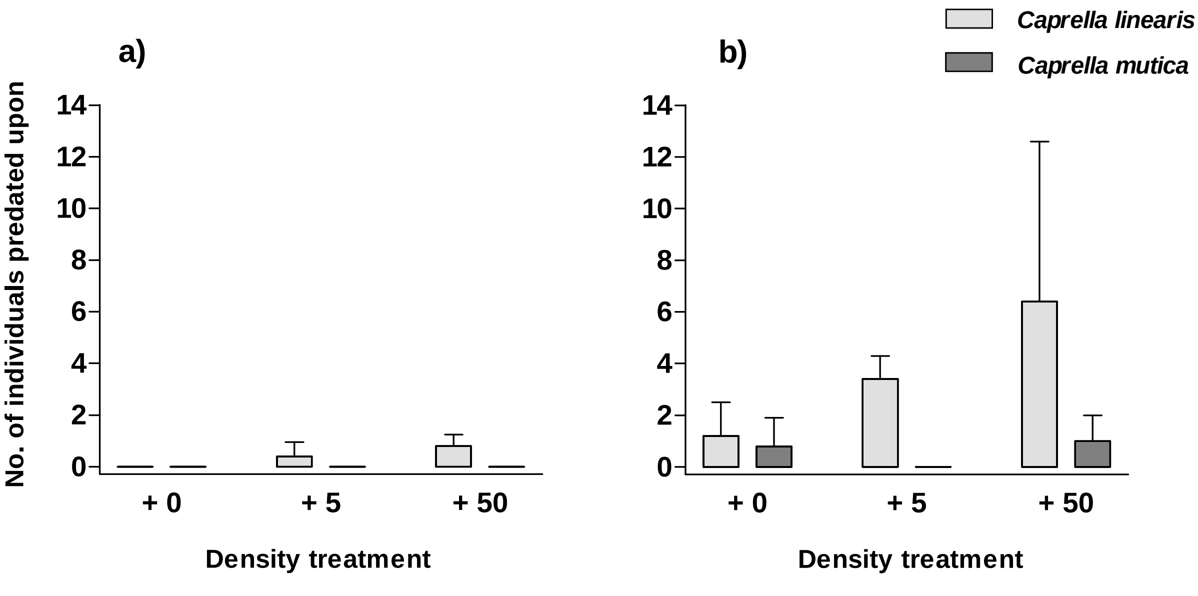

Fig. V-3: Number of individuals (mean ± SD) of 'resident' *Caprella linearis* and *Caprella mutica* in a) initially low (5) and b) initially high (50) densities, predated upon by the respective 'competitor species' after 24 h of encounter. The x-axes illustrate the absence (+ 0 = control) and the presence of low (+ 5) and high (+ 50) numbers of the respective 'competitor species'.

Discussion

In the present study, *C. mutica* was always less affected than *C. linearis*. *Caprella linearis* was significantly affected by the presence of *C. mutica*, particularly when the initial densities of the native *C. linearis* were high. However, in cases of initially low densities in which the presence of low or high numbers of *C. mutica* did not affect *C. linearis* as compared to the controls, the numbers of displaced or dead individuals were consistently higher in the native *C. linearis*, than in the non-native *C. mutica*.

The results from the present study suggest that competitive interactions between the inferior *C. linearis* and the superior *C. mutica* occur as soon as specific numerical proportions exceed a certain threshold in the overall densities of the two species.

These results showed that displacement, aggressive encounter and predatory behaviour of *C. mutica* towards *C. linearis* were minimal when initial densities of the latter remained low, independent of the number of added *C. mutica*. High initial densities of *C. linearis*, however, unavoidably led to enhanced predation by *C. mutica*, even when only low numbers of *C. mutica* encountered high numbers of *C. linearis*, and as a direct result, caused increased mortality in the native caprellid. The displacement from the preferred meshes (the shared resource space) may then, in turn, be the consequence of the aggressive behaviour by *C. mutica*.

When comparing the controls of initially low and high densities of *C. linearis*, the results revealed crowding effects to increase mortality. In contrast, this was not the case for *C. mutica*. The tolerance towards high densities may be important for *C. mutica* in establishing large populations. Numerical advantages may enhance exploitative abilities and may play a crucial role in dominating in density dependent competitive encounters with other species (Holway, 1999). For example, Underwood (1978) found that when competing for resources, the limpet *Cellana tramoserica*, suffering strongly from intraspecific interactions at high densities, was inferior towards the gastropod *Nerita atramentosa* Reeve, 1855, which suffered far less from intraspecific interactions at high densities. Another example is given by Holbrook and Schmitt (2002), who investigated the underlying biological mechanisms causing density-dependent mortality in two tropical damselfishes. The authors found intraspecific crowding to result in the displacement of less resistant individuals.

In the present study, the observed crowding in *C. linearis* at high densities and thus, the amount of dead individuals, was not affected by increasing numbers of *C. mutica*. Long-term effects of intraspecific interactions may negatively influence reproduction rates and biomass (Underwood, 1978). In the present study, however, increased mortality was observed already after 24 hours indicating intense intraspecific interference (aggression and lethal strikes).

Although the results revealed no influence of *C. mutica* on the numbers of dead individuals (residual mortality), not every incident of mortality in *C. linearis* could be separated from predation by *C. mutica*. Highly aggressive interaction between *C. mutica* and *C. linearis* may result in lethal attacks, but specimens must not necessarily be eaten at the same time. Therefore, predation without subsequent consumption could have inflated the amount of residual mortality in the present experiment. Despite this, however, it seems that intraspecific effects were consistently present, as soon as a certain density of *C. linearis* was reached (i.e., 50 individuals per 50 cm^2. The increased overall mortality (residual mortality and predation) of *C. linearis* is, therefore, the consequence of increased predation by *C. mutica*.

It has been theorized, that the elimination of the competitively inferior species is likely when interspecific interactions are stronger than intraspecific interactions (i.e. predation is greater than cannibalism in the present case) (Dick et al., 1999). In fact, in the present study, predation by *C. mutica* on *C. linearis* was greater than the effect of cannibalism within the controls of *C. linearis*. In the superior *C. mutica*, by contrast, intraspecific effects (cannibalistic behaviour) were very low and interspecific effects (predation by *C. linearis*) were not detectable.

The present study demonstrates that intraspecific pressure in *C. linearis*, which comes into effect at high densities of conspecifics, is overlaid by interspecific effects when encountering any number of *C. mutica*. More so, as the habitats on which the two species may encounter are highly restricted in available settlement space potentially increasing intraspecific effects. Intraspecific effects in *C. linearis* (e.g. increased cannibalism) may affect its ability to persist in interspecific competition for shared resources. As a response to the encounter with *C. mutica*, the native *C. linearis* experiences increased predation pressure (interference), and thus, displacement from the shared habitats. Similar results were reported from Coen et al. (1981), who studied the displacement of the caridean shrimp *Palaemonetes vulgaris* by the aggressive and predaceous *Palaemonetes floridanus*. The authors suggested intraspecific effects within the inferior shrimp to have influenced its ability to persist in interspecific competition with the superior shrimp.

The present results showed that, irrespective of the initial densities, at most 20% of the individuals of *C. linearis* were displaced, dead or predated upon after 24 h. Although longer time periods were not tested in the present experiments stronger impacts may be exopected over time. Yet, the observed impact of the superior *C. mutica* on the inferior *C. linearis* does not necessarily imply its extinction. In fact, coexistence was found feasible, as long as overall densities and the specific proportions remained below critical levels.

However, when population sizes are severely reduced, densities may fall below an ‘Allee threshold’ i.e., the critical threshold, below which a population cannot persist (Keitt et al., 2001). The Allee effect, described for numerous animal taxa, strictly refers to low densities in populations and may be generated by different factors. Examples are inbreeding in small populations or demographic stochasticity including severe sex-ratio fluctuations which may influence successful reproduction (Courchamp et al., 1999). The Allee effect may also occur by lower survival, such as when anti-predatory strategies become insufficient in small prey populations (Quinn et al., 1993; Courchamp et al., 1999). Allee effects may become relevant for *C. linearis* when densities are reduced, i.e. after having encountered its non-native congener *C. mutica* at critical densities in the field.

Combined effects of competitive encounter with *C. mutica*, Allee dynamics and stochastic processes may, therefore, strongly influence the survival of *C. linearis* and, thus, may endanger its regional persistence on artificial substrata, where space is limited. This may be particularly true for habitats around harbour constructions of Helgoland (i.e., mooring ropes, berths and pontoons), where *C. linearis* was found regularly prior to the presumed introduction of *C. mutica* dated back to the mid 1990s (H.-D. Franke, M. Janke, pers. comm.). Since 2004, however, regular sampling events on these structures have widely proved the absence of *C. linearis* while densities of the non-native *C. mutica* were high (Ashton, 2006; this work, Chapter II).

Artificial structures used as settlement space by numerous species, typically undergo physical disturbances due to high frequencies of boating traffic or marina operations (i.e.

launching and deployment of structures on a seasonal basis) (Byers, 2000a). In addition, natural forces such as storms, waves and heavy rainfalls may cause disturbances and thus, temporarily increased heterogeneity in the respective artificial habitats (Davis et al., 2000). Disturbances impact the niche relationships of organisms occupying a certain niche (Shea et al., 2004). For example, biomasses may be destroyed or removed, freeing up resources for other organisms to use and, according to the intermediate disturbance hypothesis, may promote the co-existence of competing species (Shea et al., 2004).

The observed presence of *C. linearis* and *C. mutica* on navigational bouys in the vicinity of Helgoland (Franke, unpubl. data), might, therefore, reflect a particular disturbance regime, that allows the co-existence of the two species. Irrespective of disturbance, the observed co-existence may also represent an early stage of competitive encounter, potentially reflecting a still ongoing process of displacement.

While *C. linearis* may be competitively excluded by *C. mutica* from space-limited artificial structures, intra- as well interspecific pressure may be reduced in natural benthic habitats due to available sidestep-habitats with less spatial restrictions compared to artificial structures.

Consequently, reduced encounter rate and competition between the two species in natural habitats might increase the probability of persistence of local populations of *C. linearis*. *Caprella mutica* is rare in natural European habitats and abundances are negligibly low as compared to densities on artificial habitats (pers. obs). The combination of space-unlimited habitats for shelter and low abundances of *C. mutica* in natural benthic habitats may, locally, reduce competition between *C. linearis* and *C. mutica* and thus, allow for co-occurrence in natural habitats (Shucksmith, 2007).

The results from the present study must be treated with care, as the experiments did not control for absolute density. For example, while the overall densities in the experimental treatments of species' encounter varied between 10 (5+5), 55 (50+5 and 5+50) and 100 (50+50), the controls tested only for initial densities (5 and 50). Yet, the experiments obtained species-specific responses to the tested treatments, which could be explained to a great extent.

In conclusion, the present study demonstrated that the non-native *C. mutica* successfully displaced the native *C. linearis* for space via interference competition. Asymmetric mutual predation was the mechanism of interference leading to enhanced mortality in the inferior *C. linearis*. This mechanism, however, only seemed to come into effect when increased densities of *C. linearis* caused high intraspecific pressure and thus, reduced its ability to withstand in interspecific encounter with *C. mutica*. The degree to which *C. linearis* then predated upon by *C. mutica*, increased with increasing numbers of the non-native competitor. While interspecific competition on space-limited, disturbed artificial habitats may endanger the persistence of local populations of *C. linearis*, natural habitats may allow for the coexistence between the two species. However, as populations of *C. linearis* generally occur in patchy distribution and are subject to strong annual fluctuations, the displacement of *C. linearis* from artificial structures may have permanent effects on the overall population densities of the native *C. linearis* in European coastal waters.

Appendix

Tab. V-3: Overview of displaced, dead and predated upon numbers of *Caprella linearis* and *Caprella mutica* at initially low (5) and high (50) numbers in the absence (+ 0), and presence of low (+ 5) and high (+ 50) numbers of the respective other species. Mean ± SD are given.

	Initial density		Density treatment	***Caprella linearis***	***Caprella mutica***
No. of displaced individuals	low (5)	+	0	0.8 ± 1.1	0.0 ± 0.0
	low (5)	+	5	1.4 ± 0.9	0.0 ± 0.0
	low (5)	+	50	0.6 ± 0.9	0.2 ± 0.4
	high (50)	+	0	0.6 ± 0.9	0.8 ± 1.3
	high (50)	+	5	4.4 ± 0.9	1.4 ± 2.2
	high (50)	+	50	7.8 ± 5.2	0.2 ± 0.4
No. of dead individuals	low (5)	+	0	0.8 ± 0.8	0.2 ± 0.4
	low (5)	+	5	0.4 ± 0.9	0.0 ± 0.0
	low (5)	+	50	0.4 ± 0.5	0.2 ± 0.4
	high (50)	+	0	9.0 ± 0.7	1.0 ± 1.7
	high (50)	+	5	8.8 ± 2.8	1.0 ± 1.2
	high (50)	+	50	8.0 ± 4.6	2.2 ± 1.9
No. of individuals predated upon	low (5)	+	0	0.0 ± 0.0	0.0 ± 0.0
	low (5)	+	5	0.4 ± 0.5	0.0 ± 0.0
	low (5)	+	50	0.8 ± 0.4	0.0 ± 0.0
	high (50)	+	0	1.2 ± 1.3	0.8 ± 1.1
	high (50)	+	5	3.4 ± 0.9	0.0 ± 0.0
	high (50)	+	50	6.4 ± 6.2	1.0 ± 1.0

Chapter VI

General Discussion

During the past 40 years, *Caprella mutica* has become established along numerous coastal areas world wide. In regions of introduction, *C. mutica* is typically associated with areas of human activity. Anthropogenic vectors such as shipping traffic, recreational boating and aquaculture serve as efficient dispersal mechanisms for *C. mutica* as this species lacks a planktonic larval stage. High densities of this species typically inhabit space-limited artificial structures and thus highly disturbed habitats reflecting its ability to colonize instable systems. High reproductive activity, rapid growth, early maturation and short generation times may significantly contribute to the successful establishment of *C. mutica* outside its native range. In addition, the wide environmental tolerances of *C. mutica,* as well as its omnivorous feeding behaviour provide excellent prerequisites for colonizing a variety of different microhabitats. The comparably large body size, as well as the highly aggressive behaviour, in conjunction with reduced intraspecific interaction may give this species' an advantage in interference competition with other species.

While *C. mutica* possesses many characteristics typically found in successful marine invaders (Lodge, 1993; Williamson and Fitter, 1996b; Ricciardi and Rasmussen, 1998; Van der Velde et al., 1998), the actual mechanisms of how these characteristics may support successful invasions of *C. mutica* and where they may be restrictive have been rarely studied.

The present thesis seeks to clarify which characteristics are responsible for the actual invasion success of *C. mutica* in its European habitats, as well as the underlying mechanisms, its mass occurrence on artificial structures and its ability to persist in interactions with other species.

The main findings from the present study were:

- Populations were found on a variety of different anthropogenic habitats.
- Local abundances of European populations vary with food availability and boating activity (disturbance) on site.

- Population densities of *C. mutica* were highly correlated with annual seawater temperatures.
- Population abundances on artificial structures ranged from 0 in winter to > 200,000 ind. m^{-2} in late summer/ autumn.
- High population abundances were accompanied by a high percentage of juveniles (up to 80%).
- *Caprella mutica* reproduced at temperatures ranging from 4 to 26°C. A theoretical biological zero was calculated to be 1.2°C.
- Populations were able to persist cold water periods because of high juvenile survival of winter hatchlings (4°C).
- At average European summer temperatures (16°C), hatchlings grew rapidly and matured within only three weeks.
- At 16°C reproductive frequencies were highest with approximately 30 hatchlings at early broods. Maximum number of hatchlings was 85 at 10°C.
- Annual seawater temperatures in European coastal areas represent optimal condition for year round persistence of *C. mutica*. Warming trends may promote range expansion towards high latitudes.
- Low intraspecific competition allowed for high population densities on isolated space-limited artificial structures.
- Isolated artificial structures largely disconnected from the seabed served as refuges with reduced predatory pressure compared to natural bottom-near benthic habitats.
- High benthic predation pressure restricted mass occurrences of *C. mutica* and thus, may prevent the spread into natural bottom-near benthic habitats.
- *Caprella mutica* successfully out-competed *C. linearis* from disturbed, space-limited artificial habitats.
- Interspecific interaction took place by interference when intraspecific effects when high densities of *C. linearis* provoked encounter with *C. mutica*.
- The encounter resulted in displacement and increased mortality of *C. linearis* because of enhanced predation by *C. mutica*.
- Independent of the non-native’s densities, coexistence between *C. linearis* and *C. mutica* was possible only when densities and intraspecific effects remained low in the native *C. linearis*.

- The overall persistence of local populations of *C. linearis* may be endangered on artificial habitats in European coastal areas by the presence of the introduced *C. mutica*.

One of the most prominent characteristics found in this study and related to the invasion success of *C. mutica* in its European habitats, was the species' predominant occurrence on artificial structures in areas of human activity, where populations increased exponentially over short time periods (< 3 months). Similar associations to artificial structures were reported for numerous other non-native species from different taxa (Wasson et al., 2005). For example, at half the sites studied by Neill et al. (2006) the green alga *Codium fragile* ssp. *tomentosoides*, introduced to the Chilean coast, was present only on artificial structures, suggesting that these habitats may act as corridors for the dispersal of this alga into natural benthic habitats.

Artificial structures typically colonized by *C. mutica* are largely disconnected from bottom-near habitats anchored only by chains (e.g., pontoons or fish farm cages) or are solid surfaces (e.g., solid berths, harbour walls or offshore wind farms) providing settlement space largely separated from natural benthic habitats. While often serving as first point of entry within the introduction process of marine non-natives (Carlton and Geller, 1993; Ruiz et al., 1997; Floerl et al., 2005), such habitats are generally subject to frequent anthropogenic disturbances. These include boating activities, marina related construction work and aquaculture or offshore wind farm operations (Vitousek et al., 1997). Accordingly, these habitats may experience severe environmental fluctuations (Byers, 2002a) with free resources, such as space or food (Davis et al., 2000). Typically anthropogenic disturbances are outside the magnitude, duration or frequency of disturbances that naturally affect ecosystems (Byers, 2002a). Anthropogenic activities transform ecosystems on time scales of years or even days. Hence, habitat alterations take place much faster than the evolutionary response of species (Byers, 2002a). Anthropogenic activities may skew the environmental conditions to which native species are well adapted. Hence, non-native species, often showing wide phenotypic plasticity and rapid adaptation to environmental changes (Sakai et al., 2001), may be superior in colonizing temporarily disturbed habitats and in performing in interactions with other species.

A vast amount of literature documents the link between biological invasions and anthropogenically disturbed habitats (Bossard, 1991; Hobbs, 1991; D'Antonio et al., 1999; Dukes and Mooney, 1999). It has been suggested that frequent disturbance may decrease the predatory and competitive abilities of native species, making them less capable of regulating growing populations of invading species (D'Antonio, 1993; Moyle and Light, 1996; Kotanen, 1997; Stylinski and Allen, 1999; Davis et al., 2000). Hence, disturbed habitats may create free niches or invasion opportunity windows for invading species (Parker et al., 1993, Carlton 1996, 2000). This was found to be true for *C. mutica* in the present study. The results suggested that populations of *C. mutica* in bottom near natural habitats are strongly controlled by benthic predators, whereas reduced predation pressure on artificial structures allowed for highly population densities.

The results from the competition experiment showed that the non-native *C. mutica* was the superior competitor when encountering high densities of *C. linearis.* The non-native's aggressive behaviour may account for the predaceous and lethal mechanism of interference competition between the two species. Competitive exclusion of the native was promoted by intraspecific interactions in *C. linearis* at high densities relative to *C. mutica*.

In the field this superiority might only come into effect when the two species encounter on space-limited artificial structures, representing temporal highly disturbed habitats to which *C. linearis* may be less adapted than *C. mutica*. Alternative refuges in spatially unlimited, natural benthic habitats may reduce intraspecific crowding effects in *C. linearis* and thus, the probability of competitive encounter (Roda et al., 2000; Jackson et al., 2001; Byers, 2002b) and promote co-existence of *C. linearis* and *C. mutica* (Shucksmith, 2007).

Decreased predation pressure and competitive superiority in *C. mutica* inhabiting artificial structures may be a prerequisite for the establishment of dense populations. Seasonal seawater temperatures in Europe matched with life history characteristics of *C. mutica* such as the ability to reproduce at low temperatures, the high survivorship of winter hatchlings and the enormous reproductive activity during summer. These traits substantially enhanced the invasive potential of *C. mutica*. The variability in population abundances between different study locations (i.e., Oban vs. Helgoland) and among sites within locations may depend on local environmental conditions such as current regimes or food availability. In addition, sites experiencing high boating traffic were found to harbour lower densities than those less frequented by boats.

The variable establishment success of *C. mutica* at different sites and locations does not diminish the potential risk of further range expansion. More so, as its distribution is expected to continue to increase on a global scale, while warming trends may support the dispersal to high latitudes. Yet, the invasion success of *C. mutica* in European coastal areas is determined by the presence of suitable habitats providing reduced risk of predation. Only on artificial structures, *C. mutica* can meet conditions under which its invasive potential allows for the establishment of high population densities.

While this knowledge may provide encouragement for control and management actions, the ongoing human globalisation (Perrings et al., 2005) and particularly ever-increasing number of anthropogenic constructions in marine and estuarine environments (e.g. offshore wind parks, maricultures and boating harbours) provide an increasing number of ‘invasion opportunities’ for *C. mutica* and non-native species in general along all coastal zones of the world (Carlton and Geller, 1993; Wilhelmsson and Malm, 2008). Artificial constructions may serve as first stepping stones for non-native species in a corridor of invasion processes after having breached geographical barriers by ocean going transits (Bax et al., 2002) accompanied by increasing amounts of floating anthropogenic debris (e.g. styrofoam, plastic and glass bottles, bags, buoys) in the world’s oceans and coastal areas (Thiel and Gutow, 2005a). For example, in the Mediterranean, about 2,000 floating items of anthropogenic debris (‘macrolitter’) per m^2 were reported (Morris, 1980). The dispersal of species associated with floating substrata is a natural process allowing for range extensions beyond the species’ native borders (Thiel and Gutow, 2005b). Hence, an increase in available anthopogenic debris will significantly enhance the efficiency of this dispersal mechanism on local and global scales and, at the same time, may provide suitable long-term habitats for non-native species to become established in new areas (Thiel and Gutow, 2005b).

In view of the above, not only the transportation and thus the chance for species of becoming introduced to new areas may apply to the ‘ecological roulette’ *sensu* Carlton and Geller (1993) but also the availability of suitable structures may substantially redefine the rules of this risky game for a steadily increasing number of global players.

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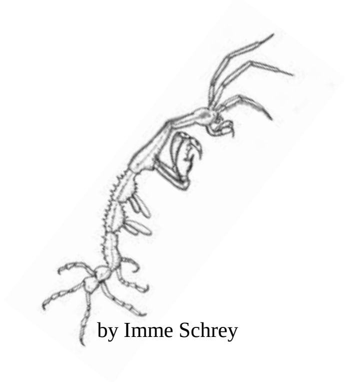
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