

Life-cycle and population ecology of the freshwater mysid

Limnomysis benedeni

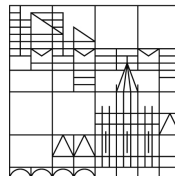


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„Der erste Schluck aus dem Becher der Naturwissenschaften
macht atheistisch,
aber auf dem Grund des Bechers
wartet Gott.“

Werner Heisenberg, Träger des Physik-Nobelpreises

Table of content

Chapter I	General Introduction	1
Chapter II	A review of spatio-temporal patterns of the colonisation of Lake Constance with alien Macrozoobenthos	11
	English abstract	11
	1 Einleitung	11
	2 Vorgehensweise	14
	3 Die Neozoen im Makrozoobenthos des Bodensees	16
	4 Diskussion	22
Chapter III	Seasonal shifts in the life-cycle of the ponto-caspian invader <i>Limnomysis benedeni</i> (Crustacea: Mysida) - a physiological adaptation	25
	Abstract	25
	Introduction	26
	Methods	27
	Results	30
	Discussion	36
Chapter IV	Embryonic development time of the freshwater mysid <i>Limnomysis benedeni</i> Czerniavsky as a function of water temperature	41
	Abstract	41
	Introduction	42
	Methods	43
	Results	45
	Discussion	47
Chapter V	Estimating instantaneous birth and mortality rates of an invasive freshwater mysid in the field	51
	Abstract	51
	Introduction	52
	Material and methods	54
	Results	56
	Discussion	58
Chapter VI	Nutritional ecology of the invasive freshwater mysid <i>Limnomysis benedeni</i> - field data and laboratory experiments on food choice and juvenile growth	61
	Abstract	61
	Introduction	62
	Methods	63
	Results	69
	Discussion	73
Chapter VII	General Discussion	77
	Summary	83
	Zusammenfassung	87
	References	91
	Acknowledgements	113
	Record of achievement / Abgrenzung der Eigenleistung	115
	Curriculum vitae & Publications	117

Chapter I

General Introduction

Limnomysis benedeni Czerniavsky is one of the few freshwater mysids. The order Mysida is part of the Peracarida, a superorder of the Crustacea (Westheide & Rieger 1996). Its main distribution range is located in marine ecosystems; only 6.7 % of all mysid species live in freshwater systems (Porter et al. 2008). In the sea, their focal habitats are shallow waters and estuaries; additionally some species are living in the pelagial and the deep sea. Most of these species are common and have frequently been explored (for overview see Mauchline 1980, Porter et al. 2008). In the worldwide increasing capture of native ecosystems by invasive species (Carlton & Geller 1993, Kinzelbach 1995, Chandra & Gerhardt 2008), the subphylum Crustacea plays an important role. It includes the most successful species among aquatic alien invaders (Hänfling 2011). Moreover, some mysids from the brackish estuaries spread upstream and captured many freshwater systems in Europe and North America (Audzijonyte et al. 2006, Wittmann 2007, Wittmann & Ariani 2008). Among them, *L. benedeni* is one of the most widespread mysid invaders in Central Europe; the latest reports come from eastern France (Wittmann & Ariani 2008). *L. benedeni* originates from the area of the Black Sea and the estuaries of the Danube, Dniester and Dnieper (Bacescu 1954, Audzijonyte et al. 2009). As indicated by its original habitat, the species is euryhaline and tolerates salinities up to 19 PSU (Komarova 1989, Ovcarenko et al. 2006). Although it avoids current velocity greater than 0.5 m s^{-1} , its main distribution is in larger rivers (Wittmann 1995, Wittmann & Ariani 2000). The probable distribution corridors to Western Europe were the Danube, the Main and the Rhine rivers and respectively the opening of the connection between them in 1992, the Rhine-

I – General Introduction

Main–Danube Canal (Kinzelbach 1972, Bij de Vaate et al. 2002, Audzijonyte et al. 2009). Besides the anthropogenic caused appearance in the shallow Lake Balaton (Wonyárovich 1955), the population of *L. benedeni* in Lake Constance is the only known from a larger lake, especially from a deep one. Lake Constance is a pre-alpine lake, situated in Central Europe. The shoreline belongs to Germany, Switzerland and Austria. With 253 m depth and ~50 km³ water volume, Lake Constance is the third largest lake in Central Europe. The lake consists of two basins, the larger and deeper Upper Lake Constance and the smaller and shallower Lower Lake Constance, that are connected by the Seerhein near Konstanz (Fig. 1). The largest contributing river is the Alpen Rhine, located in the eastern part in Austria. In the western part of the Lake, the river Rhine is leaving the lake towards the North Sea (IGKB 2004).

In the last decades, the rate of occurrence of invasive species in freshwater systems increased in high numbers (Richardson & Pysek 2008). Highly affected ecosystems are those like the river Rhine, which have a large drainage area, high water exchange between different sections and many man made connections to other river systems (Tittizer et al. 2000, Bij de Vaate et al. 2002). From the eighteenth century onward, a total of 45 non-indigenous macroinvertebrate species have been recorded in the freshwater sections of the Rhine (Leuven et al. 2009). These invasive species highly counted as potential invaders for Lake Constance. A short way after the lake the Rhine falls act as a natural barrier, hence introduction of these species to the lake were most likely caused by human activities. General introduction ways for alien species are transport via ships or boats (Pollux et al. 2003, Martens & Grabow 2008, Briski et al. 2011), trading with aquaristic products (van Kleef et al. 2006), net fishery and fish stocking (Müller & Falkner 1984), or human activities like angling or diving (Drake & Mandrak 2010). With the detection of the mysid *Katamysis warpachowskyi* in 2009 (Hanselmann 2010), the first alien species unknown from the Rhine appeared in Lake Constance (Hanselmann 2011b). This can be taken as proof that at least one other introduction pathway (not only from the Rhine) to Lake Constance exists (Hanselmann 2011a). For both mysids, transport via boats is a possible reason for the high dispersal over Europe (Wittmann 1995, Reinhold & Tittizer 1998). In the first decades of the



Mesocosm at the Limnological Institute (Chapter III)



Experimental setup for Chapter IV and VI

Fig. 1 Geographical situation at Lake Constance and some experimental setups

last century, several benthic mysids including *L. benedeni* were introduced in lakes of Eastern Europe (for example in Lake Balaton) to enhance the fish population for a better catching yield (Wonyárovich 1955). However as a central finding after all these years, the introductions of mysids have had a low effect on the fish community at best and dramatically decreased the fish populations

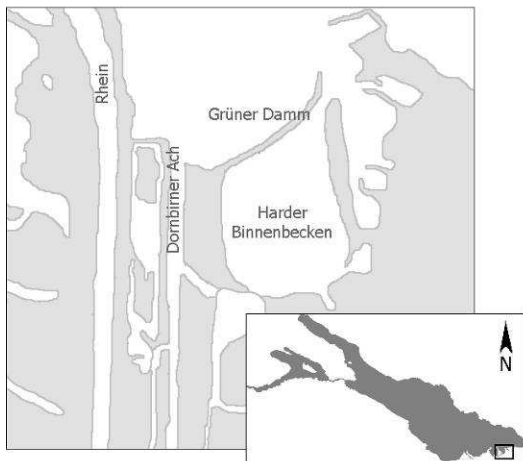
I – General Introduction

and the whole ecosystem at worst (Arbaciauskas et al. 2010, Ellis et al. 2011). Introducing new species always has the risk, that the effect of the species on the ecosystem is never completely predictable. Nevertheless, it is important to know the potential impact of invasive species to take precautions and to raise the public awareness for this problem (Shirley & Kark 2006, Richardson & Pysek 2008, Strayer & Dudgeon 2010, Kulhanek et al. 2011). The occurrence of alien species in ecosystems, especially in freshwater systems, is highly correlated with a decrease of diversity and ecosystem stability (Sala et al. 2000, Chandra & Gerhardt 2008, Strayer & Dudgeon 2010). New species can e.g. disturb evolved food webs or the nutritional balance, bring new diseases and parasites with them or displace native species (Kinzelbach 1995, Reinhardt et al. 2003, Ellis et al. 2011, Peeler et al. 2011, Poulin et al. 2011). The ratio of new species is very often correlated with an increase in human activities (Essl et al. 2011).

L. benedeni was first found in Lake Constance in 2006 in the eastern part of the lake near the influx of the Alpen Rhine in Austria (Fritz et al. 2006). The sampling site was on the “Grüner Damm” (Fig. 2), a man made dam built to protect the harbor of Hard (Vorarlberg). Since 2005, restoration management was established with bushes, a natural embankment and stones of different gravel size under water (Rey et al. 2009, Hanselmann 2011a). The western side of the dam is exposed to wind and waves from the lake because it is in the direct way of the predominant wind direction (Bäuerle et al. 1998). Tourists and residents use the dam for local recreation activities. In a former project on the development of fish eggs in 2005 (LUBW (Ed.) 2008), the restoration of the littoral was carried out and the littoral habitat consists now of stones with gravel size from ~0.5 cm to ~30 cm, mixed up with larger rocks (unpublished data). The original separation of the stones has become neutralized because of wind and wave activity. Within this former project, the benthic community was examined, and *L. benedeni* was discovered (Fritz et al. 2006).

Autecology of *L. benedeni*

In freshwater systems, most mysids show an ecological behavior that mostly cannot be classified as planktic or benthic in comparison to the established community designations; their behavior and habitat use is neither congruent



Map modified after Hanselmann 2008



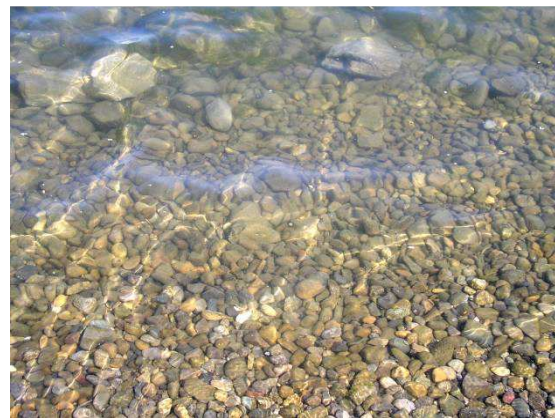
July 2009 (high water level)



May 2007 (higher water level)



February 2008 (lower water level)



Substrate at the sampling side

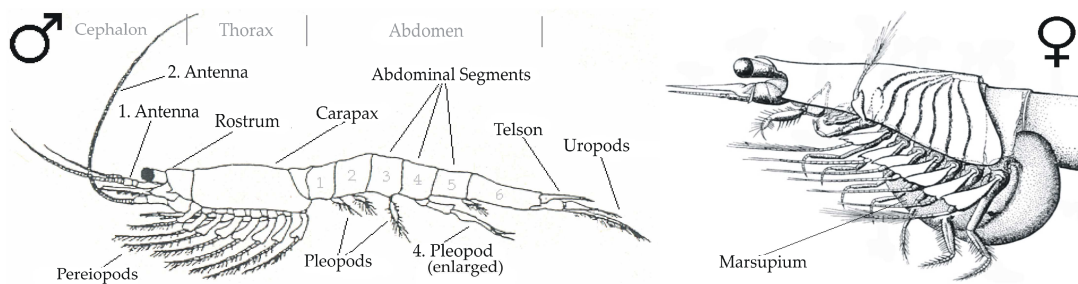
Fig. 2 Characteristics of the sampling site “Grüner Damm” in Lake Constance

to the zooplankton nor typical benthic organisms (e.g. Wittmann 1977, Bowers et al. 1990, Saltzmann 1996).

Nevertheless, some freshwater mysids are clearly pelagic and could be classified as zooplankton species. They can show vertical migration (Viherluoto et al. 2000, Scharf & Koschel 2004, Boscarino et al. 2009) and can be strong predators (Ellis et al. 2011). However, many mysid species in the freshwater are

found in the littoral or shallower regions (Porter et al. 2008). These species on the other hand, do not show habitat preferences or behavior like typical benthic organisms, e.g. amphipods (Hesselschwerdt et al. 2008). They mainly dwell associated with large structures, sitting on stones or swimming in the water column over macrophytes or over ground (Bacescu 1954, Mauchline 1980). Because of their swimming skills, these mysids have been classified as nektobenthic (Porter et al. 2008). *L. benedeni* is a nektobenthic species, and often found over macrophytes or associated with boats or quay walls (Reinhold & Tittizer 1998, Kelleher et al. 1999, Wittmann et al. 1999, Bogut et al. 2007, Wittmann 2007). First laboratory experiments confirm these findings; *L. benedeni* prefers highly structured habitats (Gergs et al. 2008). As a special phenomenon, the species forms swarms in Lake Constance during the colder season when no reproduction occurs (M. Mörtl and A. Huber, personal communication, and personal observations). A similar phenomenon was described only from a Turkish lake (Wittmann 1995). No additional observations on swarming or migration of *L. benedeni* in Lake Constance are reported so far.

Mysid species can feed on phyto- and zooplankton as well as on periphyton, detritus or benthic organisms (Bacescu 1954, Mauchline 1980). Only in pelagic species that show diel vertical migration, the feeding time is correlated with the light (Viherluoto & Viitasalo 2001). It seems that, in combination with their habitat preferences and migration activities, most freshwater mysids occupy a niche that intensifies the benthic-pelagic coupling (Rasmussen et al. 1990, Kotta et al. 2003, Sato & Jumars 2008), and/or resuspension of organic matters from the bottom to the water column (Bowers et al. 1990, Lindén & Kuosa 2004, Lesutiene et al. 2008, Lindström & Sandberg-Kilpi 2008). Both mechanisms are key processes in energy- and nutrient flow. *L. benedeni* is said to feed on pelagic algae and benthic organic material in the field (Wittmann & Ariani 2000, Wittmann 2002b) and, in combination with their swimming behavior, to be a nektobenthic mysid; first laboratory studies support these observations (Gergs et al. 2008, Aßmann et al. 2009).



Morphologic scheme of adult males and females with special focus on sexual dimorphism; modified after Kelleher *et al.* (1999), Kaestner (1967) and Hanselmann (2008)



Telson of an adult

Female with opened marsupium and larvae

Fig. 3 Morphologic characteristics of *Limnomysis benedeni*

The taxonomic differentiation between the mysid species is mainly based on the form of the telson (Mauchline 1980, Eggers *et al.* 1999). *L. benedeni* has an emarginated one with larger spines (Fig. 3). The distinguishing mark uniting all Peracarida is the marsupium of the females (Fig. 3). It is a brood pouch on the ventral side of the thorax, build of the sternites of the thorax and two pairs of oostegites. Oostegites are epipodites that were reshuffled to lamellae and moved inwards (Westheide & Rieger 1996). Through moving the oostegites, the female is able to adjust the size of the chamber when the larvae grow (Wittmann 1978). Directly after moulting, the females transport the eggs via the oviduct into the marsupium, where the males have to fertilize them (Wittmann 1982). For every new clutch, a new copulation has to take place, because females are not able to store spermatophores. While mating, the males drop a package of spermatophores into the marsupium or the oviduct from the females with the help of their enlarged fourth pleopod (Wittmann 1982). The marsupium and the enlarged fourth pleopod are distinguishing features for the sexes of the adults (Fig 3). From studies with *Leptomysis lingvura*, it is known that fertilization has to take place within 2-4 h after eggs enter the marsupium; after this period, the

I – General Introduction

eggs are not able to develop any longer (Wittmann 1982). All embryonic stages and larval moults occur in the marsupium except the last larval moult, that takes place directly after release into the water (Mauchline 1973, Wittmann 1984). In a preliminary study, I could show that the larval stages in *L. benedeni* are the same as described for other mysid species (Hanselmann 2008). Length measurement is done from the top of the rostrum to the end of the telson (Fig. 3). Adults in spring often reach a body length of ~10 mm (Gergs et al. 2008). The reproduction period and the frequency of clutches are highly variable within the Mysida and correlated with the climate regime (Wittmann 1984). Differences in the life cycle between species may be substantial, particularly in brood size (1–350 eggs/brood), generation time (a few weeks to 2 years), embryonic development time (a few days to several months) and pattern of reproduction (in cohorts or continuous) (e.g. Bacescu 1954, Mauchline 1980, Johnston et al. 1997). After Wittmann (1984), the life cycle of a mysid is highly correlated with the annual water temperature and therefore with the geographical position. Mysids in temperate zones like Lake Constance should reproduce in the warmer season with two or more broods per reproduction period, and greater numbers of larvae per brood in spring. Observations of single samples showed that *L. benedeni* probably confirms this finding (Bacescu 1954, Kelleher et al. 1999, Wittmann & Ariani 2000), but no detailed life cycle is described yet.

Aims and objectives

The aim of this study was to investigate and analyse the basic life-cycle characteristics and community interactions of the invasive mysid *Limnomysis benedeni* in Lake Constance. Thereby, the focus was to generalize the findings and transfer them to the species in general to be able to estimate the effect and requirements of *L. benedeni* on an ecosystem.

Because many alien makrozoobenthos species have invaded Lake Constance in the last decades and were often found near the place of discovery of *L. benedeni*, I analyzed the invasion history of Lake Constance to detect potential introduction ways and conspicuous patterns. The result was a review of all known alien makrozoobenthos species in Lake Constance with analyses of the species' origin, discovery sites and introduction ways (**Chapter II**).

Since no complete seasonal data set on a population of *L. benedeni* is available, the year-round life cycle is still unknown. Knowledge about the life cycle, its triggers and relations to environmental factors is necessary to reliably describe a community and understand the functioning of aquatic ecosystems in general. In a first step to answer this question, we combined field samplings and mesocosm experiments to obtain data on the life cycle of the population of *L. benedeni* in Lake Constance, covering an entire seasonal cycle at a high temporal resolution. Additionally, we obtained information about the factors that we expected could be responsible for the patterns observed (predation and temperature) by including mesocosm experiments and stomach analyses from potential fish predators in the field (**Chapter III**).

Because temperature is the most important factor that influences physiological processes in freshwater ecosystems, we analysed the relation between embryonic development time and water temperature. Many life-cycle characteristics like e.g. generation time, number of broods or the duration of the reproduction period depend on the embryonic development time (Mauchline 1973, Wittmann 1984). The correlation was determined in laboratory studies with different water temperatures and in different seasons (**Chapter IV**). Based on this function, a calculation of the components of population dynamics like instantaneous birth rates and mortality rates was done. Required data (like population growth rates, eggs per female, clutch size, temperature) were measured in the field to calculate a realistic mortality rate. As an important aim, we wanted to show that the formula by Edmondson (1971), modified after Paloheimo (1974) to calculate the instantaneous birth rate for zooplanktic species, is also capable for the nektobenthic species *L. benedeni* (**Chapter V**).

Interactions of a new species with the native food web via resource utilization (e.g. preferences, predation, and competition) are a strong indicator for estimations of the damage potential of an alien species and therefore for long-term developments of the invaded ecosystem. Therefore, we investigated the food preferences of *L. benedeni* in the field by stomach analyses, defined juvenile growth rates with different naturally available food sources in laboratory experiments and studied whether the feeding mode coincides with the known preference for benthic habitats (**Chapter VI**).

Chapter II

A review of spatio-temporal patterns of the colonisation of Lake Constance with alien Macrozoobenthos

A. J. Hanselmann

Lauterbornia (2011) 72: 131-148

English abstract

Since 1958, 14 alien species of the Macrozoobenthos have invaded the littoral of Lake Constance (Germany, Switzerland, Austria). A majority among them are Mollusca and Malacostraca (Crustacea) and they originate in the ponto-caspis. It is remarkable that formerly, their first records were made mainly in the Upper Lake Constance, but since 10 years has shifted to bay of Bregenz. We classify the species after their origins and taxonomy, the place where they were first found in Lake Constance, discuss possible ways of distribution and describe their so far known impacts on the ecosystem of the lake.

1 Einleitung

Die Bedeutung invasiver Arten, nicht nur auf ein lokales Ökosystem, sondern vor allem auch auf die weltweite Arten-Diversität, ist in den letzten Jahren immer mehr in den Fokus des wissenschaftlichen und öffentlichen Interesses gerückt (Geiter et al. 2002, Reinhardt et al. 2003, Richardson & Pysek 2008). Die Einwanderung gebietsfremder Arten wird als zweitwichtigster Faktor für den weltweiten Verlust der Biodiversität angesehen (Sala et al. 2000); die jährlichen Kosten, die allein durch aquatische Neozoa bzw. deren Eindämmung und Kontrolle verursacht werden, liegen weltweit bei mehr als 1,4 Trilliarden Dollar bzw. rund 5 % des Weltwirtschaftsvolumens (Chandra & Gerhardt 2008). Es ist

II – Review of alien species

klar, dass menschliche Aktivitäten die Ausbreitung vieler Arten begünstigen bzw. erst ermöglichen. Beispielsweise ist die Anzahl der aktuellen Neozoen einer Region korrelierbar mit den Handelsaktivitäten der letzten Dekaden (Essl et al. 2011) oder den Aktivitäten der Angler in einer Region (Drake & Mandrak 2010). Die Verbreitungswege, die einer invasiven Art offen stehen, sind vielfältig. Durch den Bau von Kanälen zur Schifffahrt werden Flusssysteme miteinander verbunden (Bij de Vaate et al. 2002, Audzijonyte et al. 2008), welche Arten zur aktiven Einwanderung nutzen können, oder die die passive Einschleppung über den Schiffsverkehr erleichtern (Pollux et al. 2003, Martens & Grabow 2008, Leuven et al. 2009). Mitte des letzten Jahrhunderts war es auch üblich, Arten als Fischnährtiere bewusst auszusetzen, in der Hoffnung, den Fischereiertrag zu erhöhen (Wonyárovich 1955). Es zeigte sich jedoch, dass diese Maßnahmen im besten Fall geringe Auswirkungen hatten, im schlechtesten Fall das genaue Gegenteil bewirkten und ganze Ökosysteme komplett veränderten (Arbaciauskas et al. 2010). Im Extremfall kann eine invasive Art einheimische Arten sogar fast komplett verdrängen (Ketelaars et al. 1999, Ellis et al. 2011). Immer häufiger kommt es auch zur (meist unbeabsichtigten) Ausbreitung von Arten, die in Zuchtanlagen oder für die Aquaristik eingeführt wurden, oder über diese Importe passiv eingeschleppt werden (Müller & Falkner 1984). Zu letzteren zählen vor allem Krankheiten und Parasiten, welche nicht nur für Wirbellose oder Fische gefährlich sein können, sondern auch für den Menschen (Peeler et al. 2011, Poulin et al. 2011). Aus diesem Grund ist es wichtig, auch rückblickend die Einwanderungsgeschichte und den Einfluss von fremden Arten auf ein Ökosystem zu verstehen, da auf diese Weise Abschätzungen über das weitere Ausbreitungs- und Schadenspotential einer Art getroffen werden können (Kulhanek et al. 2011). Dieses Wissen kann dazu beitragen, die weitere Ausbreitung der invasiven Art zu verhindern. Der Bodensee ist der drittgrößte Binnensee Mitteleuropas. Sein größter Zufluss ist der "Alpenrhein" im östlichen Teil, sein Abfluss der "Rhein", der den See im Westen verlässt. Mit maximal 254 m ist der Voralpensee ungewöhnlich tief. Seine Uferlänge beträgt 273 km, seine Länge 63 km, und er ist an seiner breitesten Stelle 14 km breit. Der Bodensee besteht aus zwei Seebecken, dem kleineren und flacheren Untersee am Ausfluss des Rheins und dem größeren und tieferen Obersee, welche durch den Seerhein

miteinander verbunden sind (Abb. 1). Rund 15 % der Seeoberfläche liegen über dem Flachwasserbereich (Litoral) (IGKB 2004). Die Belange des Bodensees werden von den Anliegerstaaten Deutschland (Bundesländer Baden-Württemberg und Bayern), Österreich (Bundesland Vorarlberg), der Schweiz (Kanton Thurgau und St. Gallen) und dem Fürstentum Lichtenstein durch die Internationale Gewässerschutzkommission für den Bodensee (IGKB) geregelt.

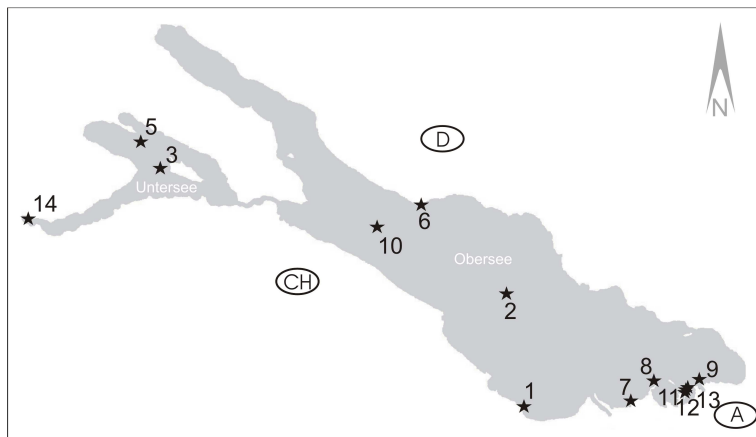


Abb./Fig. 1 Karte des Bodensees mit Markierungen der Erstfundorte der Neozoen. Die Nummerierung bezieht sich auf Tabelle 1 –

Map of Lake Constance with the place of first records of the invasive species. Numbering is explained in Tab. 1

Durch diesen Zusammenschluss war es auch möglich, die ab Mitte des letzten Jahrhunderts beobachtete Verschmutzung und durch erhöhten Nährstoffeintrag verursachte Eutrophierung des Bodensees rückgängig zu machen. Heute hat der Bodensee wieder seine ursprüngliche Phosphatkonzentration erreicht und gilt als oligotroph (IGKB 2004, Institut für Seenforschung an der Landesanstalt für Umwelt Messungen und Naturschutz B.-W. (LUBW) 2010). Am Bodensee gibt es seitens der IGKB starke Bestrebungen, die vielfältigen Nutzungswünsche (z. B. Freizeit, Fischerei, Trinkwasser, Naturschutz) zu vereinen, wobei mittlerweile ein starker Fokus auf der Umweltverträglichkeit liegt. Dies betrifft ebenfalls die Maßnahmen zur Renaturierung der Uferverbauungen (Rey et al. 2009), die in den letzten Jahren erfolgreich an mehreren Stellen durchgeführt wurden (LUBW (Ed.) 2008, Chovanec et al. 2010). Bereits im über Interreg IIIA geförderten EU- Projekt "Aquatische Neozoen am Bodensee" (ANEBO, 2003-2006 (Schröder 2008)) wurden u.a. zwei damals neu eingewanderte Arten einem Monitoring unterzogen, ihr Einfluss auf die Biozönose untersucht und Maßnahmen erarbeitet, um weitere Einschleppung zu unterbinden (Rey et al. 2005b). Die Wahrscheinlichkeit für die Einschleppung und Etablierung neuer Arten steigt weiterhin stetig, auch bedingt durch die Klimaveränderungen und den dadurch bedingten möglichen Anstieg der Wassertemperatur (Adrian et al. 2009). Eine vollständige Auflistung aller

II – Review of alien species

bisher in den Bodensee eingewanderten Neozoen des Makrozoobenthos, vor allem mit Auswertungen von Herkunft und Erstfundorten, ist bisher nicht veröffentlicht worden und wird hier vorgelegt.

2 Vorgehensweise

Mit dem Ziel, die Besiedlungsgeschichte der Neozoen des Makrozoobenthos im Litoral des Bodensees zu beschreiben, wurde eine (nach bestem Wissen und Gewissen) vollständige Liste aller seit 1958 eingewanderten Arten angelegt (Tab. 1). Aus der Zeit davor stammt nur der Fund von *Gammarus roeselii* Gervais, welchen Gervais bei Paris entdeckte und beschrieb (Gervais 1835). *G. roeselii* gilt mittlerweile in Mitteleuropa als heimisch (Josens et al. 2005) und wird aus diesem Grund hier nicht mit aufgeführt. In Tab. 1 sind ebenfalls die invasiven Decapoda aufgeführt, die jedoch wie auch die Süßwasserqualle *Craspedacusta sowerbyi* Lankester aufgrund ihrer größeren Mobilität und fehlender Literatur nur am Rande behandelt werden. Neozoische Fischarten (Vertebrata) wie der Kaulbarsch *Gymnocephalus cernuus* (Linnaeus) und der Blaubandbärbling *Pseudorasbora parva* (Temminck & Schlegel 1846) (LUBW (Ed.) 2008) kommen ebenfalls im Bodensee vor und sind Gegenstand vielfältiger Untersuchungen (z. B. D. Schleuter & Eckmann 2008). An dieser Stelle sollen vor allem die Neozoen des Makrozoobenthos behandelt werden, da von den anderen Arten meist kein Erstfundort bzw. Einschleppungsjahr bekannt ist. Die invasiven makrozoobenthischen Arten wurden nach dem Jahr der ersten Fundmeldung sortiert. Dies muss nicht das Jahr der Einschleppung sein, da einige Arten bei ihrer Entdeckung bereits größere Populationen ausgebildet hatten. Der beschriebene Erstfundort (soweit vorhanden) ist in eine Karte des Bodensees eingetragen (Abb. 1), die systematische Gruppierung der Arten (in Klassen) in Abb. 2 und die Herkunft der Neozoa in Abb. 3 dargestellt. Des Weiteren werden mögliche Einschleppungswege diskutiert und auf die bisher bekannten oder möglichen Auswirkungen der Invasionen auf das Ökosystem Bodensee eingegangen.

Tab. 1: Aquatischen Neozoen des Makrozoobenthos, die seit dem 19. Jahrhundert in den Bodensee eingewandert sind. V = mögliche Verbreitungsvektoren (A = Aquaristik, F = Fischbesatz, S = Schiffe/Boote, W = Wanderungen, B = Besatz) K = Nummer in der Karte in Abb. 1 (Macrozoobenthic invasive species who invaded Lake Constance since the 19th century. V = distribution vectors (A = fishkeeping, F = fish management, S = ship/boats, W = migration. B = exposure by humans) K = number in Fig. 1

Wissenschaftlicher Name	Deutscher Name	Gruppe	Jahr	Herkunft	V	Erstfundort	Literatur	K
Viviparus ater (De Cristofori & Jan 1832)	Italienische Sumpfdeckelschnecke	Gastropoda	1958	Südalpen	S,A	Arbon	Herold 1958, Kiefer 1972	1
Dreissena polymorpha (Pallas 1771)	Wandermuschel, Zebramuschel	Bivalvia	1966	Pontocaspis	S	Obersee	Siessegger 1969 Hofmann 1970	2
Potamopyrgus antipodarum (J. E. Gray 1843)	Neuseeländische Zwergdeckelschnecke	Gastropoda	1972	Neuseeland	F,A	Untersee	Stojaspal 1975, Schmid 1977, 3 Crozet 1980	3
Girardia tigrina (Girard 1850)	Tigerplanarie, Gefleckter Strudelwurm	Turbellaria	1986	Nordamerika	A	keine Angabe	Siessegger & Schaeffer 1992	4
Haitia acuta (Draparnaud 1805)	Spitze Blasenschnecke	Gastropoda	1988	Südwesteuropa	S,A	Metnau	Fiedler 1988, Schmid 2002	5
Dikrogammarus villosus (Sowinsky 1894)	Großer Höckerflohkrebs	Amphipoda	2002	Pontocaspis	S	Immenstaad	Mürle & al. 2004	6
Branchiura sowerbyi Beddard 1892	Kiemenvurm	Oligochaeta	2003	Südasien	A,S	Großraum Rohrspitz	Rey & al. 2005, S. Werner pers. Mitt.	7
Corbicula fluminea (O. F. Müller 1774)	Grobgerippte Körbchenmuschel	Bivalvia	2003	Asien	S,A	Rohrspitz	Werner & Mörtl 2004	8
Gyraulus parvus (Say 1817)	Kleines Posthörnchen	Gastropoda	2004	Nordamerika	A	Bregenzerach, Rohrspitz	Rey & al. 2005	9
Proasellus coxalis (Dollfus 1892)	Mittelmeer-Wasserassel	Isopoda	2005	Mittelmeer	S	Untersee und westl. Obersee	ANEBO 2011	10
Limnomysis benedeni Czerniavsky 1882	Donau-Schwembegamele	Mysida	2006	Pontocaspis	A,F	Hard	Fritz & al. 2006	11
Crangonyx pseudogracilis Bousfield 1958	Schreitender Flohkrebs	Amphipoda	2008	Nordamerika	S,F	Hard	Hanselmann & Gergs 2008	12
Katamysis warpachowskyi Sars 1877	Gefleckte Schwembegamele	Mysida	2009	Pontocaspis	A,F	Hard	Hanselmann 2010	13
Caspiobdella fadejewi (Epshtein 1961)	Donau-Fischegel	Hirudinea	2010	Pontocaspis	S,F	Stein am Rhein	ANEBO 2011	14
Craspedacusta sowerbyi Lankester 1880	Süßwasserqualle	Coelenterata		Ostasien	A,F		ANEBO 2011	
Astacus leptodactylus Eschscholtz 1823	Sumpfkrebs	Decapoda		Südeuropa	B		ANEBO 2011	
Eriocheir sinensis H. Milne Edwards 1853	Wollhandkrabbe	Decapoda		Ostasien	B,W		ANEBO 2011	
Orconectes limosus (Rafinesque 1817)	Kamberkrebs, Amerikanischer Flusskrebs	Decapoda		Nordamerika	B,W		ANEBO 2011	
Pacifastacus leniusculus (Dana 1852)	Signalkrebs	Decapoda		Nordamerika	B,A		ANEBO 2011	

3 Die Neozoen im Makrozoobenthos des Bodensees

Im Folgenden soll auf die einzelnen Neozoen des Makrozoobenthos näher eingegangen werden und eventuelle Einschleppungsvektoren, sowie bisher bekannte Auswirkungen auf das Ökosystem, dargestellt werden. Die Anordnung und Nummerierung der Arten entspricht der Reihenfolge des Erscheinens im Bodensee und findet sich so auch in Abbildung 1 mit dem Erstfundort und in Tabelle 1.

Nr. 1. *Viviparus ater*

Die Sumpfdeckelschnecke ist das am längsten bekannte Neozoon im Bodensee, dessen Fund 1958 in der Literatur dokumentiert ist (Kiefer 1972). Da sie aus Seen der Südalpen stammt, und sie auch im Zürichsee bereits länger bekannt war, liegt der Verdacht nahe, dass sie von dort eingeschleppt wurde (Kiefer 1972). Mit einer maximalen Schalenhöhe von über 4 cm zählt sie zu den größten Süßwassermollusca (Staub & Ribi 1995) und ist der größte Vertreter der Gastropoda im Bodensee.

Nr. 2. *Dreissena polymorpha*

Die Wander- oder Zebrauschel ist das bekannteste Neozoon des Bodensees, das bei ihrem Erstfund auch bereits große Teile des Obersees besiedelt hatte (Siessegger 1969, F. Hofmann 1970). Seit ihrer Einschleppung Mitte der 1960er Jahre hat sie so gut wie jedes verfügbare Hartsubstrat bis in 30 m Wassertiefe besiedelt und stellt mittlerweile rund 90 % der Biomasse im Litoral dar (Mörthl 2004). Sie ist eine beliebte Nahrungsquelle für überwinternde Wasservögel, deren Anzahl seit der Einschleppung der Muschel um das vierfache angestiegen ist (Werner et al. 2005). Im Litoral nimmt *D. polymorpha* eine Schlüsselrolle im Nahrungsnetz ein. Durch ihre Filtrieraktivität stellt sie als "keystone species" pelagische Nahrung in Form von Pseudofaeces für die benthischen Organismen, z.B. Amphipoda, zur Verfügung (Gergs & Rothhaupt 2008b, Gergs et al. 2009), gleichzeitig bietet sie als "ecosystem engineer" durch ihre Schalen anderen Invertebraten ein attraktives Habitat (Mörthl & Rothhaupt 2003, Gergs & Rothhaupt 2008a, Gergs et al. 2011). Mit Hilfe ihrer Byssusfäden heftet sich *D. polymorpha* auch an Boote, bietet damit für andere

Makroinvertebraten Zwischenräume, in denen sie den Überlandtransport von Booten überleben können (Martens & Grabow 2008) und fördert so die Verbreitung invasiver Arten. Ihr wirtschaftliches Schadenspotential ist hoch, da sie beispielsweise durch ihre freischwimmenden Veligerlarven auch in Wasser-Ansaugstutzen von Kraftwerken oder Trinkwassergewinnungsanlagen eindringen und diese zusetzen kann (Nalepa & Schloesser 1993). Im Bodensee soll sie ausserdem durch die Besiedlung der Schalen für den Rückgang der Unionidae verantwortlich sein (Rey et al. 2005a).

Nr. 3. *Potamopyrgus antipodarum*

Seit 1972 im Bodensee bekannt (Stojaspal 1975, Schmid 1977, Crozet et al. 1980), ist die Neuseeländische Zwergdeckelschnecke mittlerweile massenhaft im Bodensee zu finden (Roth 1987, Mörtl 2004). Sie wurde um 1850 per Schiff nach Europa eingeschleppt, und hat sich durch ihre erfolgreiche Lebensweise (Alonso & Castro-Díez 2008) seitdem in nahezu jedem Bach oder Teich verbreitet (Bößnek 1997). Die Ausbreitung erfolgt hauptsächlich durch den Besatz mit Forellen (Müller & Falkner 1984).

Nr. 4 *Girardia tigrina*

Die aus Nord-Amerika stammende Planaria (Syn. *Dugesia tigrina*) ist wahrscheinlich durch den Import von Aquarienpflanzen oder Zierfischen nach Europa eingeschleppt worden (Essl & Rabitsch 2002, Sluys et al. 2010). Sie ist im Bodensee nachgewiesen, jedoch ohne Angabe von Fundort und genauem Datum (Rey et al. 2005a).

Nr. 5 *Haitia acuta*

Der wahrscheinlichste Verbreitungsweg dieser südwest-europäischen Schnecke (Syn. *Physa/Physella acuta*) (Jungbluth & von Knorre 2008) ist die Verschleppung durch Aquarianer und Pflanzen für Botanische Gärten. In Baden-Württemberg ist sie das erste Mal 1899 in einem Teich des Botanischen Gartens Tübingen entdeckt worden (Schmid 2002). Auch der Erstfund im Bodensee 1988 beruht offenbar auf der Verschleppung durch Aquarianer (Fiedler 1988, Schmid 2002). *H. acuta* gilt als Überträgerin der Cercarien von *Trichobilharzia* sp., einem parasitischen Trematoden, der in die Haut von

II – Review of alien species

Menschen eindringen und beim Menschen die "Badedermatitis" auslösen kann (Leighton et al. 2000).

Nr. 6: *Dikerogammarus villosus*

Die Amphipoda-Art ist ein erfolgreiches Neozoon (Pöckl 2007), welches durch seine räuberische Ernährungsweise in vielen Gewässern starke Veränderungen in der Biozönose verursacht hat (Dick & Platvoet 2000). Die Verbreitung von *D. villosus* in Europa scheint den üblichen Einwanderungswegen der pontocaspischen Arten (Bij de Vaate et al. 2002) zu folgen, der Überlandtransport wird wahrscheinlich durch *Dreissena polymorpha* begünstigt (Martens & Grabow 2008). Im Bodensee wurde die Art 2002 entdeckt (Mürle et al. 2004); etwa zur gleichen Zeit ist sie auch in den Zürichsee gelangt (Steinmann 2006). Im Bodensee zeigten sich bereits kurz nach seiner Entdeckung erste Auswirkungen. Die Abundanz der etablierten Amphipoda-Art *Gammarus roeselii* fiel bereits zwei Jahre nach der Entdeckung von *D. villosus* um mehr als 95 % ab, sobald dieser im selben Habitat vorhanden war (Rey et al. 2005a). Der Grund dieser Abnahme ist der starke Prädationsdruck, den die als räuberisch bekannte Art (Dick et al. 2002) auf den omnivoren *G. roeselii* ausübt (Hesselschwerdt et al. 2009, van der Velde et al. 2009). Dieser kann sich nur mittels Abwanderung in andere Habitate schützen (Hesselschwerdt et al. 2008). Es wird davon ausgegangen, dass *D. villosus* auch auf andere Arten des Makrozoobenthos einen Einfluss hat. Den Fischen des Bodensees, die sich bisher von *G. roeselii* ernährten, scheint die Einwanderung von *D. villosus* keine Probleme zu bereiten. Sie fressen alternativ die neue Amphipoda-Art (Eckmann et al. 2008).

Nr. 7. *Branchiura sowerbyi*

Die Oligochaeta-Art stammt aus Süd-Asien (Paunovic et al. 2005) und ist wahrscheinlich mittels Fischen (Aquaristik oder Teichbesatz) oder Schiffen nach Europa eingeschleppt worden und bis Schweden zu finden. Sie ist seit 2003 im Bodensee bekannt, lebt im Sediment und gehört zu den Neozoen, die im östlichen Teil des Sees gefunden wurden (Rey et al. 2005a, S. Werner pers. Mitt.).

Nr. 8. *Corbicula fluminea*

Diese asiatische Muschel wurde über Amerika nach Europa eingeschleppt und ist im Rhein weit verbreitet (Schmidlin & Baur 2007). In der Aquaristik spielt *C. fluminea* eine zunehmend wichtigere Rolle und ist in vielen Fachhandlungen und im Online-Handel käuflich zu erwerben (persönliche Beobachtung). Die Einwanderung der Muschel 2003 in den Bodensee hat lokal große Veränderungen des Bodensee-Habitats verursacht. *C. fluminea* besiedelt vor allem sandige Weichsubstrate und ist daher auch hauptsächlich am Rohrspitz im östlichen Teil des Sees zu finden, ihrem Erstfundort (Werner & Mörtl 2004). Dort geht das Ufer in einer lang gestreckten, flachen und sandigen Bucht in den See über. Als "ecosystem engineer" verändert *C. fluminea* durch ihre Schalen auch das Habitat (Werner & Rothhaupt 2007, Sousa et al. 2009), da diese auch nach dem Absterben der Muschel als Hartstrukturen auf dem Sand verbleiben. Auf diese Art ermöglicht es die Muschel lithophilen Arten sandige Substrate zu besiedeln (Werner & Rothhaupt 2007, Hesselschwerdt et al. 2008). Die Art selbst wird sich vermutlich im Bodensee jedoch nicht in der gleichen Dichte etablieren wie im Rhein (Schöll 2000, Weitere et al. 2009). Sie kommt zwar mit den Nahrungsverhältnissen zurecht (Vaughn & Hakenkamp 2001, Basen et al. 2011), erleidet jedoch durch den niedrigen Wasserstand und die niedrige Temperatur im Winter und durch den Fraßdruck durch Wasservögel große Verluste (Werner & Rothhaupt 2008).

Nr. 9. *Gyraulus parvus*

Die Schnecke wurde durch den Aquarienhandel aus Nordamerika eingeschleppt (Laman et al. 1984) und ist immer noch dabei, sich in Baden-Württemberg auszubreiten (Schmid 2002). In Amerika ist *G. parvus* ein Überträger von *Gigantobilharzia* sp., der die "Badedermatitis" auslösen kann (Leighton et al. 2000). Im Bodensee ist sie seit 2004 und sowohl in der Bregenzer Bucht als vermutlich auch im Untersee zu finden (Rey et al. 2005a). Ihr nächstliegender bekannter Nachweis ist im Mindelsee bei Radolfzell, in dem sie schon länger nachgewiesen ist (Schmid 1983), eine Einschleppung von dort mittels Booten, Angel- oder Tauchausrüstung gilt als möglich. Der verifizierte Erstfundort liegt jedoch am anderen Ende des Sees (Bregenzer Bucht) (Rey et al. 2005a).

Nr. 10. *Proasellus coxali*

Die Mittelmeerassel ist im Rheinsystem und weiten Teilen Deutschlands verbreitet und seit 2005 mittlerweile auch an mehreren Stellen des Bodensees zu finden (ANEBO 2011). Sie gilt als unauffällig, scheint die einheimische Wasserassel *Asellus aquaticus* (Linnaeus) trotz ihrer geringeren Umweltansprüche nur gering zu schädigen und kann auch mit dieser koexistieren (Flössner 1987, Costantini & Rossi 1998).

Nr. 11. *Limnomysis benedeni*

Die Schwebegarnele wurde im Herbst 2006 zum ersten Mal im Bodensee nachgewiesen (Fritz et al. 2006). Ihr Erstfundort lag in Vorarlberg am sogenannten Grünen Damm und sie war der erste Vertreter der Mysida im Bodensee. Ursprünglich stammt *L. benedeni* aus der pontocaspischen Region, und hat sich über das Donau-Main-System und den Rhein bereits bis in die Niederlande und Frankreich ausgebreitet (Audzijonyte et al. 2009). Am Oberrhein war sie 2004 bis Niederhausen (Rhein-km 253,5) bekannt (Rey et al. 2005b). Durch die sprunghafte Ausbreitung kommen als Verbreitungsweg entweder Aquarianer oder Schiffe in Frage. Wittmann (1995) wies *L. benedeni* in Donau-Häfen an Schiffsrümpfen nach. Seit ihrem Erscheinen am Grünen Damm hat sich *L. benedeni* im ganzen See ausgebreitet und besiedelt heute in großer Anzahl den ganzen See (Hanselmann et al. 2011b). Die Art ist durch ihren Lebenszyklus sehr gut an die klimatischen Bedingungen des Bodensees angepasst (Hanselmann et al. 2011b). Freilanduntersuchungen zeigen, dass *L. benedeni* von Flussbarschen (*Perca fluviatilis*) gefressen wird, wobei die Fische große Individuen bevorzugen (Hanselmann et al. 2011b). Durch ihre Bevorzugung von kleineren bzw. feinen Partikeln (Algen, Detritus, Aufwuchs) als Futter und ihre nektobenthische Lebensweise (Wittmann & Ariani 2000, Gergs et al. 2008, Aßmann et al. 2009) kann man es als unwahrscheinlich ansehen, dass *L. benedeni* ähnliche Auswirkungen haben könnte wie räuberische bzw. planktische Mysida (Ellis et al. 2011).

Nr. 12. *Crangonyx pseudogracilis*

Die Amphipoda-Art wurde im November 2007 am Grünen Damm zum ersten Mal im Bodensee nachgewiesen (Hanselmann & Gergs 2008). Die Art war davor in Österreich nicht verbreitet (Essl & Rabitsch 2002). *C. pseudogracilis* stammt ursprünglich aus Nord-Amerika (Crawford 1937), ist jedoch bereits Anfang des letzten Jahrhunderts in weite Teile Europas eingewandert, seit 1993 im Oberrheingebiet bekannt und besiedelt dort insbesondere Auengewässer (Martens & Grabow 2006). Seit 2007 hat sich *C. pseudogracilis* nicht sehr weit in andere Teile des Bodensees ausgebreitet. Das Fundgebiet erstreckt sich nur von Neuem Rhein bis Bregenzer Ach (ANEBO 2011). Hier jedoch und vor allem am Grünen Damm ist er sehr erfolgreich (Hanselmann, unpublizierte Daten).

Nr. 13. *Katamysis warpachowskyi*

Die Schwebegarnele ist ebenfalls eine Mysida-Art aus der Pontocaspis (Wittmann & Ariani 2008). Im März 2009 wurde sie am Grünen Damm in Hard entdeckt (Hanselmann 2010). Dieser Fund ist deshalb außergewöhnlich, weil es der erste Schritt der Art aus ihrem ursprünglichen Flusseinzugsgebiet heraus ist. Sie ist zwar in den letzten Jahren die Donau aufwärts gewandert (2008 Erstfund in Passau, Wittmann 2008), da diese jedoch in das Schwarze Meer mündet, stellt erst der Fund im Bodensee, also im Rheineinzugsgebiet, den Sprung über die Europäische Wasserscheide dar. Es wird erwartet, dass sich die Art im Bodensee und langfristig auch im weiteren Verlauf des Rheines etablieren wird. Mit *L. benedeni* ist bereits eine Mysida-Art im Bodensee vorhanden, doch ist bekannt, dass beide Arten gut koexistieren können und auch in der Donau zusammen vorkommen (Wittmann 2007). Die Entwicklung der Population bei Hard seit 2009 bestätigt diese Annahme. *K. warpachowskyi* hat sich innerhalb kürzester Zeit etabliert und stellt teilweise bereits etwa 40 % der Mysida (Hanselmann 2011a). Mittlerweile ist auch ihre Verbreitung im Bodensee weiter fortgeschritten, die letzten Fundmeldungen vom Dezember 2010 bestätigen ein Vorkommen in der gesamten Bregenzer Bucht (ANEBO 2011).

Nr. 14. *Caspiobdella fadejewi*

Der Fischegel muss mit Wander- oder Besatzfischen aus dem Hochrhein in den Bodensee gelangt sein (Bernauer & Jansen 2006). Im Rheinsystem ist er seit 1998 bekannt (Geissen & Schöll 1998) und wurde 2010 kurz oberhalb des Rheinfalls am Ausfluss des Bodensees entdeckt (ANEBO 2011). Seine Verbreitung aus der Pontocaspis nach Europa (Bernauer & Jansen 2006) wurde wahrscheinlich ebenfalls durch die Öffnung des Rhein-Main-Donau-Kanals begünstigt. Da er nun den Sprung über den Rheinfall (vermutlich mittels Booten oder Wanderfischen) geschafft hat, wird erwartet, dass seine Ausbreitung im Bodensee rasch fortschreitet.

4 Diskussion

Seit 1958 sind im Bodensee 14 neue Neozoen des Makrozoobenthos entdeckt worden (Tab. 1). Zusätzlich sind weitere invertebrate Neozoen im Bodensee bekannt wie die Süßwasserqualle *C. sowerbyi* und vier Decapoda-Arten (Tab. 1). Damit wurden insgesamt 19 invertebrate Neozoen gefunden. Etwa 1/3 der Arten des Makrozoobenthos gehören zu den Peracarida (Crustacea: Malacostraca), wobei sowohl Amphipoda, Mysida als auch Isopoda vertreten sind (Abb. 2).

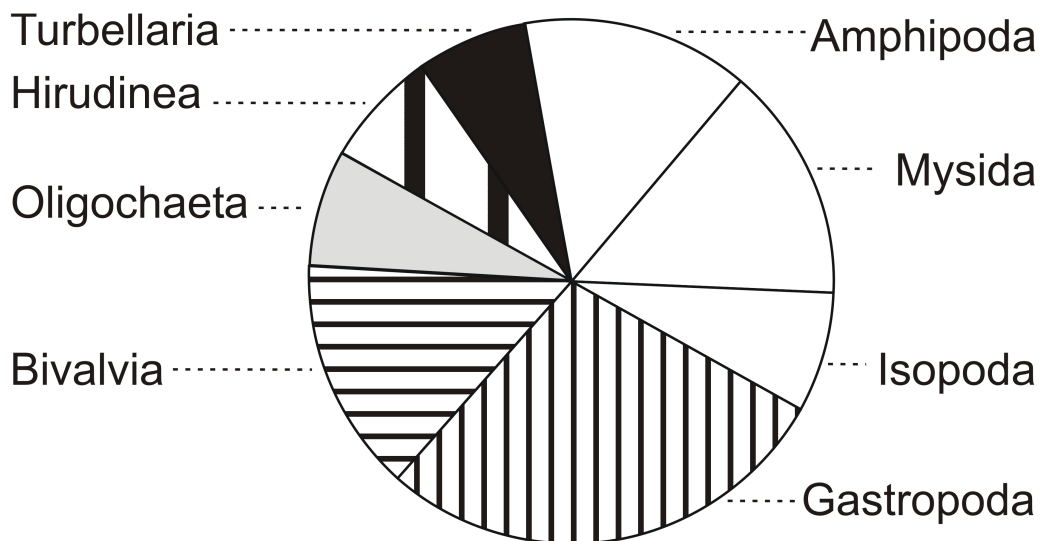


Abb./Fig. 2: Taxonomische Einordnung der Neozoen des Makrozoobenthos des Bodensees (n = 14) – Taxonomic classification of the invasive species in Lake Constance

Ein weiteres knappes Drittel zählt zu den Mollusca, von denen sowohl Gastropoda als auch Bivalvia gefunden wurden. Die Dominanz der Crustacea

und Mollusca innerhalb der Neozoa findet sich auch z.B. in der Gesamtbetrachtung aller österreichischen (Moog et al. 2008) bzw. französischen (Devin et al. 2005) Neozoen. Der größte Teil der hier behandelten Neozoen des Bodensees kommt ursprünglich aus anderen Teilen Europas (8 Arten) (Abb. 3).

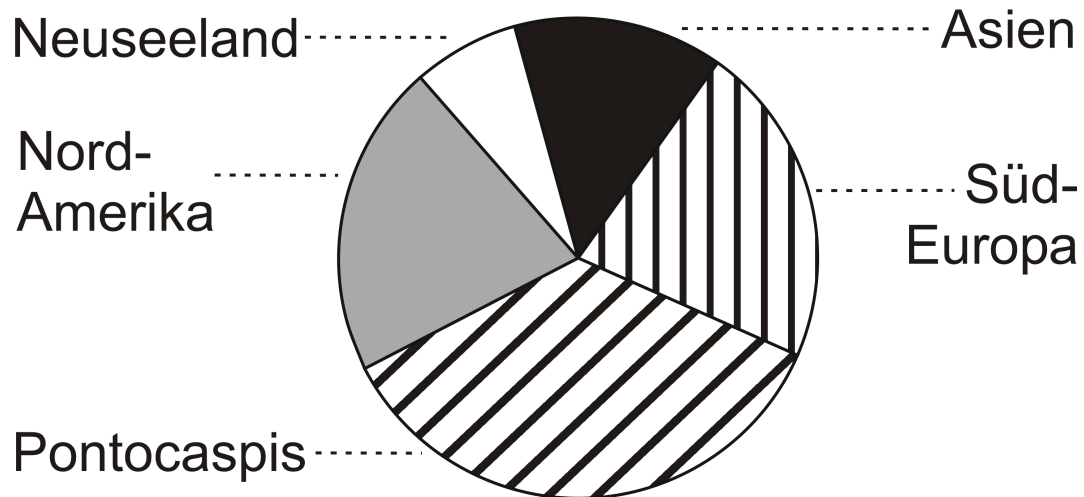


Abb./Fig. 3: Aufteilung der Neozoen des Makrozoobenthos des Bodensees nach ihrem Herkunftsgebiet (n = 14) – Origin of the invasive species in Lake Constance

Die Pontocaspis ist die Region, aus der die meisten Arten (5) stammen, die anderen Neozoa verteilen sich auf die Ursprungsregionen Süd-Europa, Nord-Amerika, Asien und Neuseeland. Für die pontocaspischen Arten kommen drei Inland-Korridore als Verbreitungswege nach Mitteleuropa in Frage. Der Nord-Korridor geht über die Wolga in den baltischen Raum, der Zentral-Korridor über den Dnjepr zur Oder, Ems und in den Rhein und der Süd-Korridor über Donau, Rhein-Main-Donau-Kanal in den Rhein (Bij de Vaate et al. 2002). Letzterer gilt als ursächlich für die meisten pontocaspischen Neozoen im Bodensee.

Auffallend ist, dass die Anzahl der Neozoen in den letzten 10 Jahren stark angestiegen ist (Tab. 1), und diese Neozoen seither vermehrt in der Bregenzer Bucht bzw. im österreichischen Teil des Sees gefunden wurden (Abb. 1). Bisher war es so, dass die Neozoen des Rheins alle als potentielle Einwanderer für den Bodensee galten. Zwar war dieser durch den Rheinfluss als natürliche Barriere vor ihnen geschützt, doch haben menschliche Aktivitäten für die Arten hier neue Verbreitungsvektoren erschlossen (Martens & Grabow

II – Review of alien species

2008). Viele Erstfundorte lagen dementsprechend im Untersee bzw. westlichen Teil des Obersees (Abb. 1). Insofern war es ein besonderes Alarmzeichen, als 2009 die *Katamysis warpachowskyi* (Mysida) im Bodensee gefunden wurde (Hanselmann 2010). Sie ist im Rheineinzugsgebiet bis dahin unbekannt gewesen, und beweist, dass es noch andere Einschleppwege in den Bodensee geben muss. Im Fall von *K. warpachowskyi* liegt ein starker Verdacht auf Wanderbooten oder Freizeitsportlern (Angler, Taucher), da der nächste Verbreitungsnachweis 300 km entfernt bei Passau in der Donau liegt (Wittmann 2008). Dieser zweite Einwanderungsweg könnte auch erklären, warum sich der Schwerpunkt der Erstfunde in den letzten 10 Jahren vom Untersee und westlichen Obersee in die Bregenzer Bucht verlagert hat (Tab. 1). Gleichzeitig stieg die Anzahl der Erstfunde deutlich. Leider war es nicht möglich, diesen neuen Einschleppweg in den Bodensee zu identifizieren, es besteht jedoch weiterhin der Verdacht der Boote und Angler als Verbreitungsvektoren. Die Bregenzer Bucht ist reich frequentiert mit Freizeitbooten, auch durch die großen dort stattfindenden jährlichen Wettbewerbe (Hanselmann 2011a). Ein direktes Einschleppen mit dem normalen Fischbesatz im Bodensee wird nahezu ausgeschlossen (Hanselmann 2011a), weitere Aufklärungsarbeit ist hierzu noch zu leisten.

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Chapter III

Seasonal shifts in the life-cycle of the ponto-caspian invader *Limnomysis benedeni* (Crustacea: Mysida) - a physiological adaptation

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Abstract

The mysid *Limnomysis benedeni*, one of the most important ponto-caspian invaders, was found in Lake Constance (southern Germany) in 2006. As part of larger studies to evaluate the effects of *L. benedeni* on the ecosystem, we studied its life-cycle strategies over an entire seasonal cycle in intervals of 3–5 weeks, addressing factors (predation, temperature) which we expected to be most important triggers of the observed changes. The size class distribution and the reproductive pattern indicated that the life cycle of *L. benedeni* changes seasonally. During winter (November to March), the mysid invested energy in growth and delayed reproduction until April, when the population was dominated by adults. In summer (June to September), the adults reproduced at a smaller body size and the population was disproportionately dominated by juveniles. In a mesocosm experiment that excluded fish predators, the mysids followed the same seasonal patterns of growth and energy investment as in the field population, but the size class distribution differed. Even in summer, the population in the mesocosm was dominated by adults. Stomach analyses of fish showed that *L. benedeni* is preyed upon by juvenile *Perca fluviatilis*, which fed size selectively on larger mysids. In conclusion, our results suggest predation was the reason for the dominance of juveniles and the observed size class distribution in summer. In contrast, the smaller adults in summer were most

III – Seasonal life-cycle shifts

likely a physiological adaptation, perhaps evolved to avoid predation or as a reaction on metabolic losses at higher temperatures.

Introduction

The life cycle of a species summarizes its various energy investments and presumably optimizes fitness. An animal has a limited amount of energy, and the allocation of this energy to growth or reproduction leads to different life-cycle strategies (Stearns 1989). Local and temporal variations in life cycles are influenced by differing or changing environmental conditions, in terms of both abiotic factors such as temperature and water chemistry, and biotic factors such as food availability, competition, and predation. To reliably describe a community and understand the functioning of aquatic ecosystems in general, it is necessary to start with gaining knowledge about the life cycle of the respective species. The sum of these findings allows you then, for example, to estimate the impact of invasions by alien species. Life cycles vary in timing of reproduction and maturation, rate of growth, and clutch size among others. Since these life-cycle characteristics can vary considerably within the range of a species, investigating field patterns of local population structure and life cycle is essential for describing the species (for a summary, see Begon et al. 1998, Krebs 2001). The mysid *Limnomysis benedeni* Czerniavsky, 1882 is one of the most invasive mysids in Europe although little is known about the factors affecting its life cycle and life-cycle traits. It has been characterized as necto-benthic (Porter et al. 2008) and phyto-lithophilic (Dediu 1966) with a preference for smaller particles (Gergs et al. 2008, Aßmann et al. 2009). This common invader originates in the brackish estuaries of the Black and Caspian Seas and has spread widely in Eastern and Central Europe since the early twentieth century; the large Rivers Danube and Rhine serving as invasion corridors (Bij de Vaate et al. 2002, Wittmann & Ariani 2008, Audzijonyte et al. 2009).

The mysid was found for the first time in the eastern part of Lake Constance in 2006, near the influx of the river Rhine in Austria (Fritz et al. 2006). Mysids can be a good food source for fish (Mauchline 1982, Chigbu & Sibley 1998, Lindén et al. 2003), and like other mysids, *L. benedeni* was introduced to lakes in Northern and Eastern Europe in the early 20th century

(Bacescu 1954, Wonyárovich 1955, Lasenby et al. 1986) to enhance fish production, although the expected benefit was not always realized (Langeland et al. 1991). Nevertheless, *L. benedeni* is an important food source for the two Sander species in Lake Balaton, for instance (Specziár 2005).

The particular life cycle of different species within the crustacean order Mysida vary inter alia with climate regime (Wittmann 1984). Differences between species may be substantial, particularly in brood size (1–350 eggs/brood), generation time (a few weeks to 2 years), embryonic development time (a few days to several months) and pattern of reproduction (in cohorts or continuous) (e. g. Mauchline 1980, Wittmann 1984, Johnston et al. 1997). In temperate areas, such as in Central and Eastern Europe, mysids usually reproduce in the warmer season, with two or more broods per reproduction period, and greater numbers of larvae per brood in spring (Mauchline 1973, Mauchline 1980, Wittmann 1984). This might also be true for *L. benedeni*, as indicated by initial findings in Lake Constance in spring and summer 2007 (Gergs et al. 2008), in the River Rhine in both the Netherlands (Kelleher et al. 1999) and France (Wittmann & Ariani 2000), and in the Danube basin (Bacescu 1954). However, in all these studies, only one or two single samples were analysed, and sampling was not consistent over an entire seasonal cycle. Since no complete seasonal data set on the population is available, the year-round life cycle of *L. benedeni* is still unknown. Here, we combined field samplings and mesocosm experiments to obtain data on the life cycle of *L. benedeni* in Lake Constance, covering the entire seasonal cycle at a high temporal resolution. We also evaluated information about the factors that we expected could be responsible for the patterns observed (predation and temperature).

Methods

Field sampling

We chose as the study site the location where *L. benedeni* was first found in Lake Constance in summer 2006 (Fritz et al. 2006) because we expected the most stable population there. The study ran from October 2007 until November 2008, with sampling intervals of 3–5 weeks. Because of the higher water

III – Seasonal life-cycle shifts

temperature in summer, we sampled more frequently then. The substratum at the sampling site is very homogeneous with stones and rocks along ca. 900 m shoreline. We collected *L. benedeni* at about 0.5 m depth by kick sampling (mesh size 200 μm) and measured body size, brood size and stage composition (juvenile, female or male). The mysids were immediately fixed in 96% ethanol in the field. 5 additional breeding females were caught on 9 July 2008 and 9 October 2008 to be able to calculate an average for the brood size. Water temperature was recorded on every sampling date from 8 October 2007 to 6 November 2008 (MultiLine F/SET-3, WTW, Weilheim, Germany). The presence and estimated age of any perch in spring and summer was verified by snorkelling. For this, an area of 15 x 5 m was observed and schools of perch were assigned as present or not.

Mesocosm

The outdoor mesocosm is located in Konstanz, close to the Limnological Institute. It consists of a concrete basin (1 x 1 m, 60 cm water depth, 600 l) with a flow-through of filtered (200 μm) lake water (~1.5 l/min). Stones from the nearby littoral zone of the same size as found at our field site (4-10 cm) served as a substratum. We collected the stones in May 2008 and cleaned them with a hard water jet to remove possible predators. On 29 May 2008, we added to the mesocosm 500 *L. benedeni* originating from our field sampling site in Austria. This number is comparable to field abundances (A. Hanselmann, unpublished data). On 4 August and 10 October 2008, we collected the mysids by kick sampling, and measured body size and stage composition (see above). Algae and biofilm were seen on the substrate every time and the constant water flow from the lake (lake seston < 200 μm) provided additional food. Supported by a quick check of the gut fullness of some mysids (for methods see Gergs et al. 2008), we concluded that no food limitation or crowding occurred in the mesocosm.

Laboratory analyses

We measured the body size of the sampled mysids using a measurement program developed by the electronic facilities of the University of Konstanz (G.

Heine). Individuals were photographed under a stereomicroscope with an attached fire-wire camera (The Imaging Source, Bremen, Germany) connected to a computer, and directly measured. The body size was the mean of three measurements from the top of the rostrum to the end of the telson, excluding spines (e.g. A. Schleuter et al. 1998). The animals were arranged according to length classes (class width 0.5 mm). We distinguished three groups in the population: juveniles, adult females, and adult males. Juveniles and adults were separated not by size but rather by indicative morphological features. Adult males were recognized by the remarkably longer 4th pleopod. Females carrying offspring were recognized by their marsupium (brood pouch), and females without offspring were recognized by the oostegites (lamellae at the ventral end of the thorax, which form the brood pouch) or the normal 4th pleopod (Mauchline 1980). We also counted the brood size of the females. The ash-free dry mass (AFDM) of non preserved eggs was determined by drying at 105° C for 24 h, followed by combustion at 550° C for 8 h. AFDM of the females was calculated with the equation from Gergs et al. (2008).

Analysis of perch stomachs

To investigate the predation of perch (*Perca fluviatilis* L.) on *L. benedeni* in the field, we collected young 0+ perch at our sampling site with a beach seine (mesh width 5 mm) on 29 July 2009. The fish were stored on ice for transportation (max. 2 h) and the stomach was removed in the laboratory immediately and preserved in 96% ethanol. The wet weight of the fish and the total length was noted. By means of a stereomicroscope, the stomach contents were analyzed. It was noted if the stomachs contained *L. benedeni* and ingested *L. benedeni* were separated into two classes, juveniles > 5.0 mm and adults > 5.0 mm. At the same date, we collected and measured *L. benedeni* as described above and classified them the same way as the animals in the stomachs.

Statistical analyses

All statistical analyses were made using R (R Development Core Team 2008). Before calculating any statistical test, we checked for homogenous variances. In

III – Seasonal life-cycle shifts

all calculated ANCOVAs, the body size was the independent variable and the date the co-variable. To analyze the differences in the adult body size between the two generations (summer and winter), we calculated a two-way ANCOVA after transforming the data with $1/x$. The independent variable was the generation. In addition, each temporal development of adult body size in winter and summer was calculated with a one-way ANCOVA including correlation coefficients. Differences between the length of males and females were determined with two-way ANCOVA; the independent variable was the sex. Seasonal characteristics were determined with oneway ANCOVAs including correlation coefficients for each sex. A t test was used to compare brood sizes in spring and summer: to accordance of the mean body size in the mesocosm and the field was tested with a Mann–Whitney U test owing to significant variances. The Mann–Whitney U test was also used to examine the differences between the proportion of body mass and egg mass on the total female biomass of the winter and summer females. The proportions of large *L. benedeni* in the field and in the fish stomachs were compared using the z ratio for the significance of the difference between two independent proportions. To compare the mean size of the perch eaten small or large mysids, a t test was calculated.

Results

Field observations

The temperature at the sampling site at 0.5 m depth (Fig. 1) varied greatly over the year. The highest temperature (22.9° C) was at the end of July, and the lowest temperature (5.0° C) was in January and February. The weather on the sampling dates was always fair with calm waves, except for 9 March, 2008 when strong winds and waves prevailed. From July

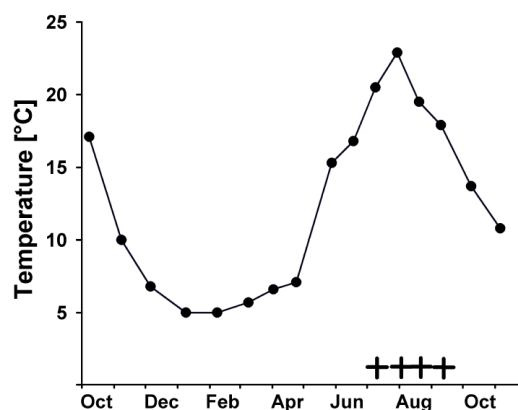


Fig. 1: Water temperature at 0.5 m depth (line with dots) and occurrence of juvenile *Perca fluviatilis* (+) at the sampling site in Austria. Lines between the sampled temperature values (dots) are interpolated

until September 2008, we found perch (0+) in the littoral zone (Fig. 1). No other fish species was recognized. In July, the perch were smaller but more abundant than in September, when the largest perch were present.

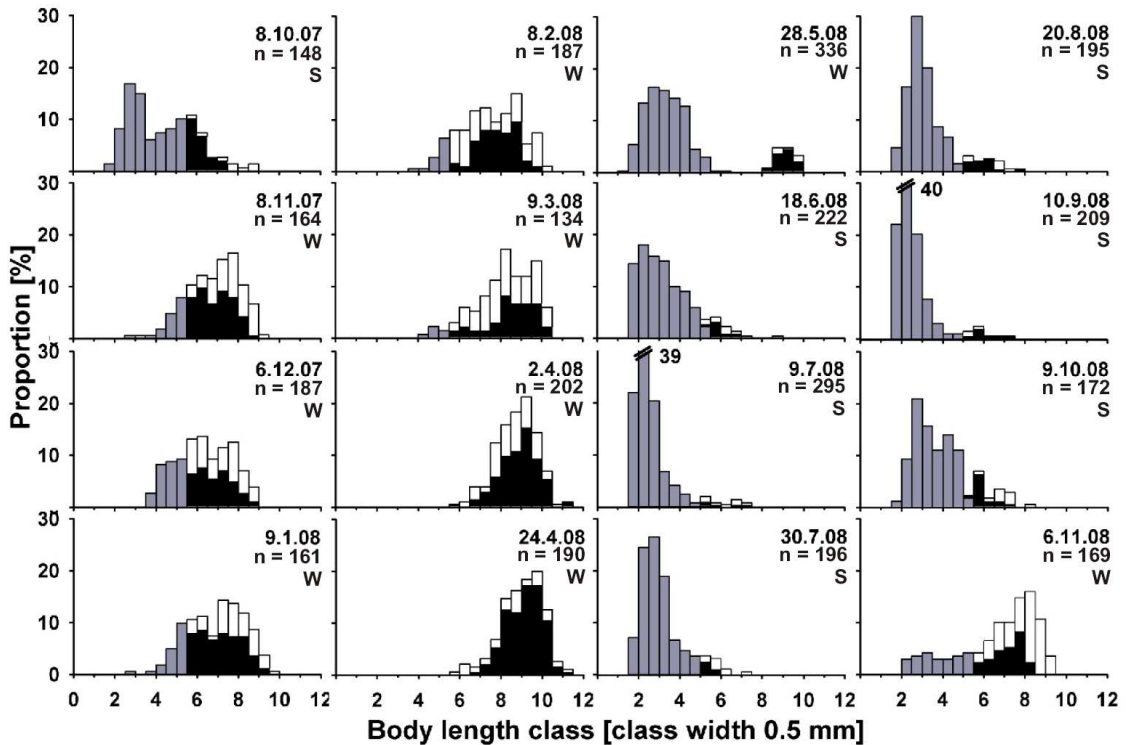


Fig. 2 Development of the body size of *Limnomysis benedeni* (measured from the apex to the end of the telson, see “Methods” section) from a qualitative subsample at 0.5 m depth over 14 months; n = number of measured individuals; gray bar juveniles, white bar males, black bar females; W winter generation, S summer generation (for definitions, see text)

Population characteristics in the field

The stage and size class composition of the *L. benedeni* population changed during the year (Fig. 2). In the winter half year, from November until the end of April, the mean body size of all individuals increased, and in late winter and spring, adults dominated (percent composition of adults in March = 96%). The first juveniles were observed at the end of May (Fig. 2). After that the juveniles began to dominate. During summer, juveniles dominated the population, and the entire length distribution was skewed toward smaller individuals (percent composition of juveniles at the end of July = 92%). Only few animals reached sexual maturity. In November, the adults dominated again (percent composition of adults = 76%). The sex ratio in 24 April and 28 May is more in favor of females compared to the other samplings.

III – Seasonal life-cycle shifts

The body size of the three smallest juveniles showed little variation and did not vary between winter (1.65 ± 0.14 mm in May) and summer (1.72 ± 0.14 mm) generations. In contrast, adult body size varied markedly between the generations (Fig. 3; Table 1, date x generation: $P < 0.001$). In winter, the body size increased as the season advanced (Table 1, date: $P < 0.001$, coef is positive). The mean body size in spring (24 April, 2008) was 9.0 ± 0.1 mm (females 9.1 ± 0.8 mm, males 8.6 ± 0.1 mm). During summer, the adult mean length did not vary between the sampling dates

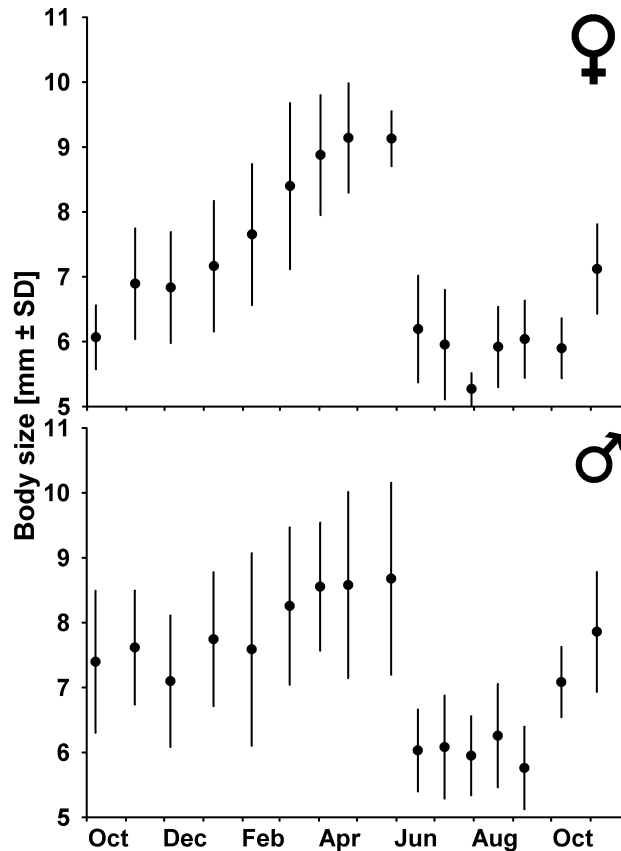


Fig. 3: Body size of adult *Limnomysis benedeni* (mean \pm SD) over the entire sampling period from 8 October 2007 to 6 November 2008. Refer to the text for an explanation of which mysids were counted as adult

(Table 1, date: $P = 0.176$). The mean body size was 6.1 ± 0.2 mm (females 5.9 ± 0.3 mm, males 6.4 ± 0.6 mm). In autumn, the adults grew larger again. The maximum body size in summer (8.5 mm, observed in 18 June, 2008) was lower than the maximum body size in winter/spring (11.4 mm, observed in 24 April, 2008).

Table 1: Changing of adult body length in winter and summer and differences between these generations, analyzed by one-way and two-way ANCOVAs

	Two-way ANCOVA			One-way ANCOVA				One-way ANCOVA			
	Winter/summer			Winter				Summer			
	<i>P</i> value	df	<i>F</i>	<i>P</i> value	coef	df	<i>F</i>	<i>P</i> value	coef	df	<i>F</i>
date	0.049782*	1	3.9	<0.001***	0.0122	1	497.6	0.176	0.0022	1	1.9
generation	<0.001***	1	979.5								
Date x generation	0.001**	1	10.5								

coef correlation coefficient

Asterisks indicate the significance level (**<0.001, ** 0.001–0.01, * 0.01–0.05)

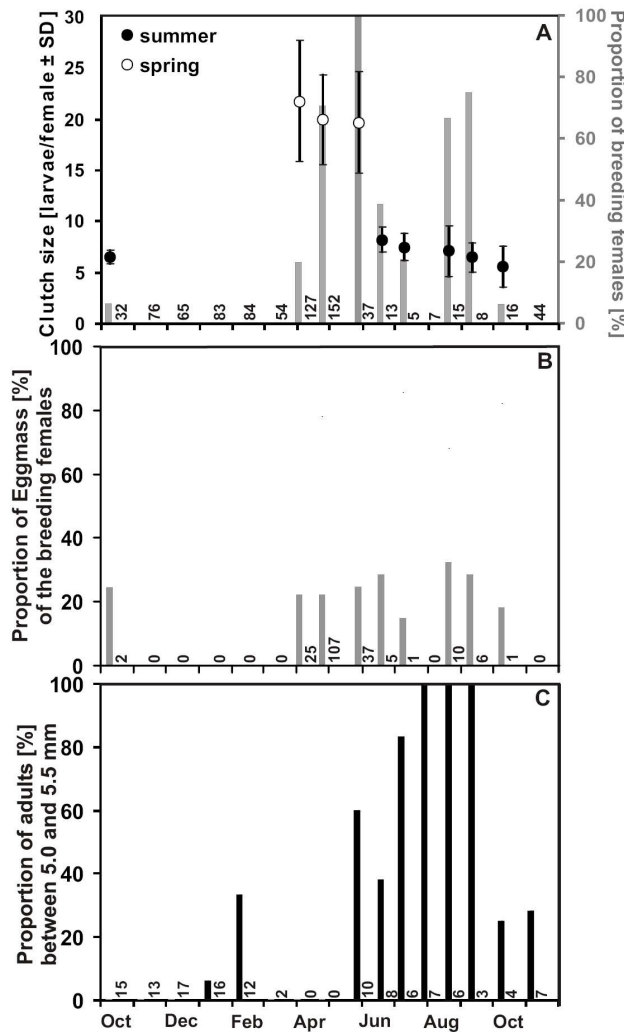


Fig. 4: **A.** Dots: Brood size as the mean (\pm SD) of all breeding females per sampling date, separated into spring (white) and summer (black) breeding females. Bars: proportion (%) of breeding females among all females. Numbers are the sum of all females in the sample. **B.** Proportion (%) of egg mass on the total female biomass (mean of all gravid females). Numbers are the sum of breeding females in the sample. **C.** Proportion (%) of mysids between 5.0 and 5.5 mm classified as adult males or females. After a proportion of 50% were identified as adults, the mysids were considered as belonging to the summer generation. Numbers indicate all individuals in this length class

The size at maturity differed between spring (adults from winter half year) and summer (Fig. 4C). In the size class between 5.0 and 5.5 mm from October to April, 0-33% of the animals were adult females or males; from May to September, all animals (100%) of this size class were adults (Fig. 4C). For further calculations, we therefore defined as juveniles all animals ≤ 5.5 mm in body size during the winter period, and ≤ 5.0 mm during the summer period. The proportion of egg-carrying females (% of all adult females) changed with the season (Fig. 4A). No broods were found during winter until March. In April and May, when the animals from winter were breeding, nearly all females were carrying a brood. The proportion decreased in June, was apparently zero in late July, and increased again in August. The very low sample sizes of adults in July may have made it difficult to detect any gravid

females. Reproduction stopped in late October; the last breeding females were observed on 9 October 2008. The significant difference in brood size with season (t test, $P > 0.001$) paralleled the difference in female mean length between summer and winter: spring females carried 20.5 ± 1.1 eggs/gravid female on average while summer females carried 6.9 ± 0.9 eggs/gravid female (Fig. 4A). The mean proportion of the eggs on the total biomass of the breeding

III – Seasonal life-cycle shifts

Table 2: Changing of adult body length in adult females and males in winter and summer, analyzed by one-way and two-way ANCOVAs

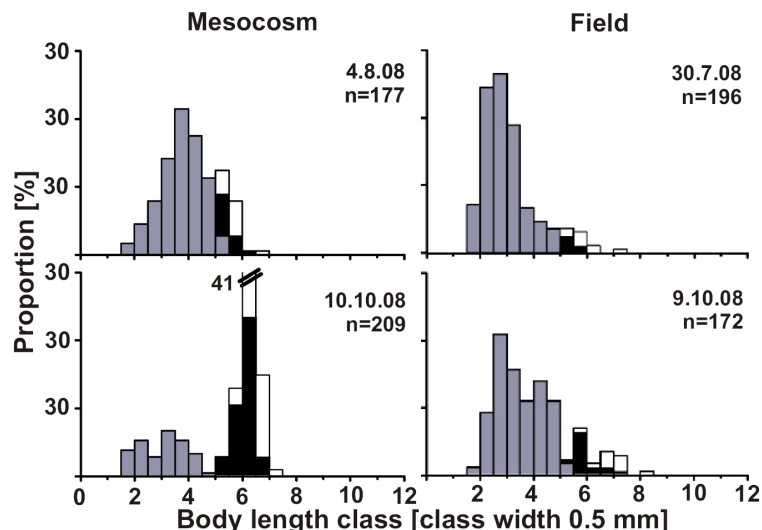
Season	Two-way ANCOVA			One-way ANCOVA				One-way ANCOVA			
	Males/females			Males				Females			
	P value	df	F	P value	coef	df	F	P value	coef	df	F
<i>Winter</i>											
date	<0.001***	1	572.6	<0.001***	0.0079	1	65.1	<0.001***	0.0146	1	647.0
sex	0.782	1	0.1								
Date x sex	<0.001***	1	39.7								
<i>Summer</i>											
date	0.161	1	2.0	0.006**	0.0075	1	8.3	0.671	-0.0008	1	0.2
sex	0.005**	1	8.3								
Date x sex	0.011*	1	6.7								
<i>Summer, excluding October</i>											
date	0.404	1	0.7	0.606	-0.0021	1	0.3	0.567	-0.0018	1	0.3
sex	0.422	1	0.7								
Date x sex	0.960	1	<0.1								

coef correlation coefficient

Asterisks indicate the significance level (***<0.001, ** 0.001–0.01, * 0.01–0.05)

females (Fig. 4B) was $23.6 \pm 5.8\%$. No differences between the winter females ($22.8 \pm 1.4\%$) and the summer females ($24.3 \pm 6.8\%$) could be found (U test $P = 0.548$). The life-cycle characteristics of adult males and females differed in some respects (Fig. 3; Table 2). During winter, all adults increased in size (Table 2, date: $P < 0.001$ each, coef is positive), but the females increased in size more than the males (Table 2, date x sex: $P < 0.001$) as indicated by correlation coefficients (Table 2). In summer, males and females again differed in body length (Table 2, date x sex: $P = 0.011$). The females did not increase in length (Table 2, date: $P = 0.671$), whereas the males did (Table 2, date: $P = 0.006$). This difference, however, arose only from the data of the last

Fig. 5: Body size (measured from the apex to the end of the telson, see “Methods” section) of *Limnomysis benedeni* in summer and autumn in the mesocosm experiments running over 19 weeks, compared with the population in the field (see Fig. 2). juveniles (grey), males (white), females (black)



sampling of males in October 2008. The same ANCOVA calculated without this date was not significant (date x sex: $P = 0.96$), so the mean length of the adults did not change during summer (Table 2).

Mesocosm data

The size structure of the mesocosm population differed from the size structure of the field population (Fig. 5), measured on the same dates. In contrast to the field population, no length class dominated clearly in the mesocosm population in August. The length classes were distributed in a bell-shaped manner (Fig. 5). In October, at the end of the reproduction period, most individuals were of adult size. However, the adult mean body size did not differ from the field data (U test, $P < 0.001$). In the mesocosm, the body size on 4 August 2008 was 5.5 ± 0.3 mm (males 5.5 ± 0.4 mm, females 5.4 ± 0.3 mm), and on 10 October 2008 it was 6.2 ± 0.4 mm (males 6.4 ± 0.3 mm, females 6.1 ± 0.3 mm).

Stomach analysis of perch

The mean standard length of the perch captured with the beach seine was 6.1 ± 0.5 cm, the mean wet weight 2.4 ± 0.6 g. The population of *L. benedeni* at the same time showed an equal size distribution as in the year before (Fig. 2). In comparison with the available population of *L. benedeni*, the perch clearly preferred the larger mysids (Fig. 6). The proportion of large mysids in the field population was 0.0815 (15 individuals out of 184 in the sample).

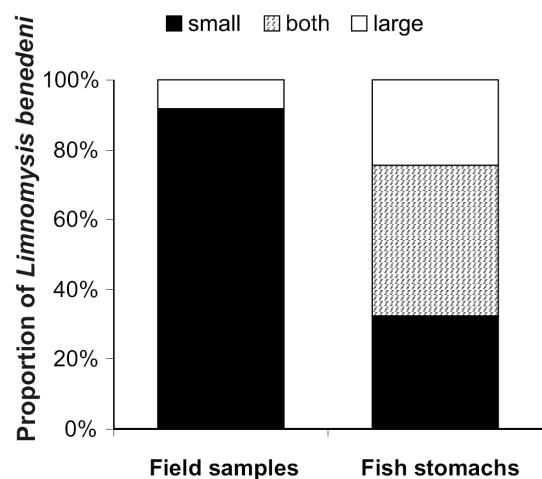


Fig. 6: Proportion of small (black, <5.0 mm) and large (white, >5.0 mm) *Limnomysis benedeni* consumed by young *Perca fluviatilis* compared with the size-distribution of *L. benedeni* in the field; some (shade) perch consumed both small and large *L. benedeni*

A total of 139 perch were caught. 118 of these fishes had mysids in their stomachs, indicating that *L. benedeni* was used as a food item by most fish (85%). 38 fish had ingested only small mysids; 51 fish had ingested both small

III – Seasonal life-cycle shifts

and large mysids; 29 fish had ingested only large mysids. These numbers show that large mysids were found disproportionately more frequent in the perch stomachs. Even a very conservative assessment, considering only the 29 perch that had exclusively ingested large mysids, indicates that this number is exceedingly high; the proportion of large *L. benedeni* in the fish stomachs was significantly higher than the proportion of large *L. benedeni* in the field sample (z ratio, $P < 0.01$). No significant difference was found between the size of the fish fed on small or on large mysids (t test, $P = 0.84$).

Discussion

During a 1-year period, the population of *L. benedeni* in Lake Constance underwent substantial changes in their life-cycle characteristics (maximal body size, stage composition, reproductive activity, clutch size, energy investment). These differences allowed us to separate the adults into two groups, which reflect the two life-cycle strategies of the species: the “winter generation”, which lacks eggs from November to March and reproduces from March to May, and the “summer generation”, which reproduces continuously from June to October. As clearly shown by our data, *L. benedeni* reproduces not in cohorts. Therefore it is important to note that here in this context a generation is a group of animals of unspecific age and different life stages and not a cohort.

We can summarize two important and newly described phenomena in the life cycle of *L. benedeni*. First, the adults in summer in the field are underrepresented in comparison with the predation-less mesocosm population, suggesting that they suffered huge mortality, and that only a small proportion of *L. benedeni* reproduced in the field. Second, the summer generation reached a smaller size at maturity compared to the winter generation and had a smaller brood size in accordance with a smaller body size, leading to a different life-cycle pattern. In the following, we explain these two different phenomena. All considerations and conclusions on the life cycle of *L. benedeni* depend on the assumption that our samples are representative of the population. We think that there is good evidence for the representativeness of our samples. At our sampling site, the bank is very homogeneously covered with gravel and rocks and there is, as a matter of fact, no choice of different substrate types.

Quantitative benthic invertebrate samplings at comparable sites in the littoral zone of Lake Constance indicated very similar size distributions of *L. benedeni* in various sampling depths (0.5-5 m; C. Fiek, personal communication). Despite the rareness of mature animals in summer (Fig. 4), the remaining number of adults can account for the maintenance of the population (A. J. Hanselmann, unpublished data), without a need for immigration to sustain the local population.

Life-cycle characteristics

Winter generation

In winter and early spring (November 2007–April 2008), the mysids invested their energy in increasing their body size and not in reproduction (Fig. 4B), until the end of this period in April, when the winter generation developed a large brood (Fig. 4A). The stronger length development of females in winter probably prepares the individual for a larger reproduction success. The benefit of a larger size in spring is greater for females than for males; with a larger marsupium they can produce larger broods and larger animals also accumulate larger energy reserves that can be converted to eggs (Gorokhova & Hansson 2000, Atkinson & Hirst 2007). In a previous study, Gergs *et al.* (2008) showed that in *L. benedeni*, the clutch size correlates well with the length of the female. As already described in this previous study, the sex ratio also changed in spring (Fig. 2) and the females dominated in April. Gergs *et al.* (2008) assumed that the females live longer and so have the chance to grow larger. By the end of May (2008), all mysids from the winter generation “disappeared” (Fig. 2). “Disappearing” means that the number of the large adults decreased markedly from April until June. We hypothesize that these adults die, of either natural senescence or predation. Migration into deeper water or the pelagic zone could also be an occurring (Boscarino *et al.* 2009), but in our opinion an improbable explanation, because *L. benedeni* has not been described as pelagic (Wonyárovich 1955, Dediú 1966). In addition, no observations of migration into deeper water were available, and we never found any large adults during the summer that had potentially drifted upwards by waves (Rinke *et al.* 2009).

III – Seasonal life-cycle shifts

Summer generation

The first juveniles from May (Fig. 2) reached sexual maturity in about 1 month and produced their first brood in June. The adult summer individuals showed different characteristics compared to the winter adults. Their length at maturity was smaller (Fig. 4C), a pattern also known from other species (Hilton et al. 2002). In addition, they did not reach the length of the adults in April (Fig. 3). Since the proportion of biomass that entered egg production was comparable to that of adults in April, their brood size was only one third of that of the winter generation. The females with brood invest in somatic growth about 75% of their energy budget (Fig. 4B), which is one fourth less than females without a brood. They continuously reproduced, developed several broods until October 2008, and therefore it was not possible to follow discrete peaks of the length histogram. Wittmann (1984) predicted such a pattern for mysids in the Middle European climate zone. During their reproduction period, the length distribution was clearly affected by mortality, as shown by comparing the field and mesocosm populations (Fig. 5). Despite the fact that during summer only few animals reached maturity in the field (Fig. 4), the remaining number of adults can well account for the number of juveniles. This was indicated by calculation of birth rate using temperature dependent egg development times (A. J. Hanselmann, unpublished data). With a larger sample size, the probability to find some gravid females will increase in summer. None of the previous studies with *L. benedeni* described the seasonal changes in life cycle or has a comparable time resolution of the field data. Nevertheless, when we include the single samples from these previous studies (Table 3; Bacescu 1954, Kelleher et al. 1999, Wittmann & Ariani 2000, Gergs et al. 2008), they follow well the patterns we describe here, but they lack a long-term dataset. The females of most mysid species grow larger than the males, but *L. benedeni* is said to show a reverse pattern (Mauchline 1980, Wittmann 2002a). Our data support this only in part, because we could show that the length proportions changed with the season. Only during summer time the males had a larger mean body size, in winter it reversed and the females grew larger. The impression of the previous studies that the males were larger, could have arisen from their larger range of body sizes and the according larger size maximum; the standard deviations from the females body size seems to be smaller (Fig. 3). It becomes apparent,

that the patterns described here, are an attribute of the whole species, and not only of the population in Lake Constance. Therefore, the adult mysids change their energy allocation, spending their available energy on growth during winter and on reproduction in summer.

Table 3 General survey of the adult body length, the brood size, and the reproduction period of *Limnomysis benedeni* on several dates and from various populations and regions invaded by the species (single samples, except present study)

Date and location (reference)	Body length ♀/♂ (mm ± SD) or min–max (mm)		Brood size (eggs/♀ ± SD) or min–max (eggs/♀)		Reproduction period (months)
	Spring	Summer	Spring	Summer	
2008 Lake Constance (present work)	9.0 ± 0.1/8.6 ± 0.1 11.4 (max)	6.1 ± 0.4/6.6 ± 0.6 8.5 (max)	20.5 ± 1.1 35 (max)	7.1 ± 1.6 10 (max)	Apr–Oct
2007 Lake Constance (Gergs et al., 2008)	9.4 ± 0.6/8.6 ± 0.6	6.7 ± 0.8/6.5 ± 0.7	28.4 ± 5.7	8.7 ± 2.9	Apr–Oct
1998 Rhine (France) (Wittmann & Ariani, 2000)	–	6.1 ± 0.7/6.8 ± 0.4	–	7.4 ± 2.3	–
1997 Rhine (Netherlands) (Kelleher et al., 1999)		6–13	12–40		Mar–Nov
1954 Danube (drainage basin) (Bacescu, 1954)	10–15 (winter)	7–10	20–40		Mar/Apr–Oct/Nov

Mortality of adults in the field

Our data show that perch prey size-selectively on large mysids, suggesting that fish predation causes high adult mortality. The stomach analyses of young perch in summer 2009 verified this hypothesis and showed that the larger *L. benedeni* undergo a size selective predation pressure. In general, young perch are dominant in the littoral of Lake Constance in summer, but not present in winter (Wang & Eckmann 1994, Imbrock et al. 1996) and no other fish species could be observed during our study. The perch might prefer the larger prey because they are visual hunters (Thorpe 1977, D. Schleuter & Eckmann 2006). The gape height of young perch with about 5 mm (perch of 62 mm, Guma'a 1978) was large enough to feed on adult *L. benedeni* and perch are known to feed well on other mysids (Mauchline 1982, Borcharding et al. 2007). The smaller adult body size of *L. benedeni* in summer was not caused by size-selective predation as a direct mortality factor. In the mesocosm, where no fish were present, the length of the mysids remained as small as in the field with the same small size at maturity. Therefore we hypothesize that the differences to the winter generation are physiological adaptations by the mysids (Atkinson &

III – Seasonal life-cycle shifts

Hirst 2007). Either water temperature or the photoperiod could be responsible (proximate) triggers. The ultimate factor could be predation by fish (Woodward & Warren 2007). An alternative hypothesis is that smaller sizes at higher temperatures result from increasing metabolism and therefore respiration losses. In other species, mainly Crustaceans, the age and/or size at maturity decreased with higher temperatures (Brown et al. 2004). In addition, it is a common phenomenon that colder environments result in larger body size (Wolfenbarger 1999, Fockedey et al. 2005). We conclude that predation is the reason for the dominance of the juveniles and the shifted length distribution in summer, but not for the shorter mean and maximum lengths of adults, their associated smaller clutch size or their smaller size at maturity. These are physiological adaptations, perhaps evolved to avoid negative effects of predation or as adaptations to unfavorable high temperature conditions with higher respiration loss. Also, the actual trigger for this life-cycle shift is not yet known and needs further investigations.

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Chapter IV

Embryonic development time of the freshwater mysid *Limnomysis benedeni* Czerniavsky as a function of water temperature

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Abstract

The numbers of alien species in freshwater systems and their detrimental impacts on the stability of ecosystems and global species diversity are increasing. To predict and assess such impacts, a thorough knowledge of the autecology and life cycle of the alien species is required. *Limnomysis benedeni* is common and one of the most invasive mysids in Europe. Here we show a clear dependency of the development time of the brood of *L. benedeni* on water temperature. In laboratory experiments (one in spring 2008 and two in 2009, in spring and summer) under controlled conditions, we determined embryonic development times and the probability of survival of the females and juveniles at water temperatures ranging from 4 to 25° C. At 6.5 and 25° C, the probability of survival of both the females and the larvae was lower than at 10, 15, or 20° C. Since the development time is one of the key characteristics of the life cycle and is therefore necessary to calculate, for example, birth and mortality rates, we determined an equation for the development time as a function of the water temperature. This information will be useful to understand the distribution potential of this invasive species.

Introduction

With increasing numbers of alien species in freshwater systems such as the River Rhine (Leuven et al. 2009), their detrimental impact on both the stability of ecosystems and the global diversity of species is also increasing (Sala et al. 2000). To be able to predict the impacts of alien species on resident species and communities, detailed information on their autecology and life cycle is required. The expansion of an invasive species is often enabled or limited by the temperature, especially with a possible influence of climate change (Vermonden et al. 2010).

Many common alien species in Central Europe are freshwater Crustacea, including Mysida (Leuven et al. 2009). In contrast to marine mysids, many life-cycle properties of freshwater mysids, e.g., development times of the brood, growth rates, and mortality rates, are still unknown. This information is important to determine the influence of an alien species on the invaded ecosystem and to understand the distribution potential of an invasive species. The generation time is related to the duration of the reproduction period, the age at maturity, the number of broods, the brood size, and the body length of the adults (Ishikawa & Oshima 1951, Murano 1964, Davis 1966, Mauchline 1973, Wittmann 1984).

Limnomysis benedeni Czerniavsky, 1882, is one of the most invasive mysids in Europe; it is a common invasive species, originates in the brackish estuaries of the Black Sea and Caspian Sea, and has spread nearly throughout Eastern and Central Europe since the early twentieth century (Bij de Vaate et al. 2002, Wittmann & Ariani 2008, Audzijonyte et al. 2009). The mysid was found for the first time in Lake Constance in 2006 (Fritz et al. 2006). The species has been characterized as a necto-benthic (Porter et al. 2008), phyto-lithophilic (Dediu 1966), suspensions feeder (Gergs et al. 2008, Aßmann et al. 2009). In winter, in Lake Constance, the population does not reproduce, and the adults invest in body growth. In spring and summer, the species reproduces continuously. In spring, the large overwintering females produce large egg clutches. In summer, adults reach maturity at a size smaller than that in winter and produce smaller clutches (Hanselmann et al. 2011b).

In general, the life cycle of a mysid is strongly correlated with the climate regime in its environment (Wittmann 1984). Within the order Mysida, the

life-history trades, including, e.g., development time, generation time, and clutch size, vary widely. In temperate zones, as in Central Europe, with seasonal fluctuating water temperature, species of the family Mysidae, including *L. benedeni*, normally reproduce only during the summer (Wittmann 1984). The common attribute of the superorder Peracarida, to which the family belongs, is that brood development takes place in a brood pouch of the females, the marsupium, which is built by the sternites of the thorax and a pair of oostegites (Westheide & Rieger 1996). Larval development occurs inside the marsupium. Eggs are fertilized by the male directly after the female lays them in the marsupium and embryonic development and all larval stages except the last larval moult take place inside the marsupium. Just before the last larval moult, the female sets the larvae free and the last larvae molt takes place directly after the larvae leave the marsupium. This development is similar for all mysid species (Mauchline 1973, Wittmann 1984). The adult females protect their brood, provide it with oxygen by pumping movements of the oostegites, and are to a small extent responsible for the spatial arrangement of the larvae in the brood pouch (Wittmann 1978, Mauchline 1980). Each developing larva feeds on yolk invested by the mother in its egg (Morgan 1980), but the diameter of the eggs, as a proxy of the yolk mass, plays a subordinate role for the development time of other mysid species in comparison with the water temperature (Wittmann 1981b).

We determined to what extent mysid embryonic development time depends on water temperature in laboratory experiments under controlled conditions at different water temperatures. Furthermore, we determined the probability of survival of the females and juveniles.

Methods

Experimental set-ups

To measure the relationship between temperature and the development time of the brood in the marsupium, we chose a temperature range from 4 to 25° C. We ran three experiments, one in spring 2008 (run I, starting on April 24, at 4, 10, 15, 20, and 25° C) and two in 2009, in spring (run II, starting on April 30, at 6.5,

IV – Embryonic development time

10, 15, and 20° C) and summer (run III, starting on July 30, at 15 and 20° C). Run III was carried out to see whether the eggs from the smaller summer clutches have development times comparable to the eggs from the larger spring clutches. Three climate chambers and two climate cabinets (plant growth chamber KBW 720, Binder GmbH, Tuttlingen) were used to provide a stable water temperature; the overall tolerance was $\pm 0.3^\circ$ C. In all experiments, the same light conditions with a diurnal light rhythm of 12 h-12 h (day-night) and the same experimental setup were used. Day length in the field was about 14 h in April and 15 h in July.

For each temperature, 50 brood-carrying females (except in run III, which had 35 at 15° C and 40 at 20° C because fewer breeding females were available) were kept individually in 1 l glass jars with 750 ml filtered (30 μ m) and slightly aerated lake water. We used the green alga *Scenedesmus obliquus* (Turpin) (SAG 276-3a, Göttingen, Germany) as food, which was added *ad libitum* (4 ml suspension, ~1 mg/l carbon) twice a week. During earlier experiments, we measured that this was more than the females were able to consume. Once a week, the glasses were cleaned carefully with a soft brush and the water was replaced.

The gravid females were freshly caught in the eastern part of Lake Constance in Austria near the confluence of the Rhine River at ~0.5 m depth. For determining the clutch size and categorizing the stages of the larvae in the marsupium at the beginning of each set of experiments, a sample of the population was caught via kick-sampling and directly fixed with 96% ethanol. The females caught for the experiments were adapted overnight to the respective temperature and placed into the glass jars the next morning. Because *L. benedeni* neonates are released during the night (Mauchline 1980), the water in the glass jars was checked for neonates once each morning; hatched juveniles and their mother were directly fixed in 96% ethanol and counted. If a female died, it was not removed unless the decomposition process inhibited larval development. Inhibiting conditions occurred when the decay of the dead mother started to pollute the water (visible pollution or smelling water).

Calculations and statistics

For the development time at each temperature (D_T), the number of remaining egg-carrying females was plotted against time. The x-axis intercept of the linear regression ($y = 0$) is the calculated development time for the respective temperature. These D_T values were then plotted against the temperature to obtain the relationship between development time and temperature. The probability of survival at each temperature was calculated for females and larvae. For larvae, the mean brood size of hatched larvae of each replicate was compared to the mean brood size at the beginning, which was determined in the field, as described above; the field brood sizes of the runs differed. The optimal temperatures were calculated from the first derivation of the nonlinear regression that described the correlation.

A linear-regression model was calculated for each temperature in each experiment, and a nonlinear regression model was calculated for the relationship between development time and temperature and for the probabilities of survival (R Development Core Team 2008).

Results

Development time

At all temperatures except 4° C, juvenile mysids hatched, and we could determine the development times of *L. benedeni* in the marsupium (Fig. 1). For these resulting development times, the linear regression of time versus the number of remaining females was significant (Table 1). When the measured development times were plotted against the temperature, a significant negative exponential curve was obtained ($y = 122.549 \times e^{-0.127}$, $P < 0.001$; Fig. 2; Table 2). The validity of this equation ends below 6.5° C because at the next lower tested temperature at 4° C in run I, no juvenile *L. benedeni* were found, all females died within 60 days, and the experiment was stopped after 80 days. For temperatures above 25° C, the equation is not tested. In the summer experiments (run III), the hatching of the juveniles started immediately, whereas in the spring experiments (run I and II), the first juveniles were found after several days (Fig. 1).

IV – Embryonic development time

Clutch size and probability of survival

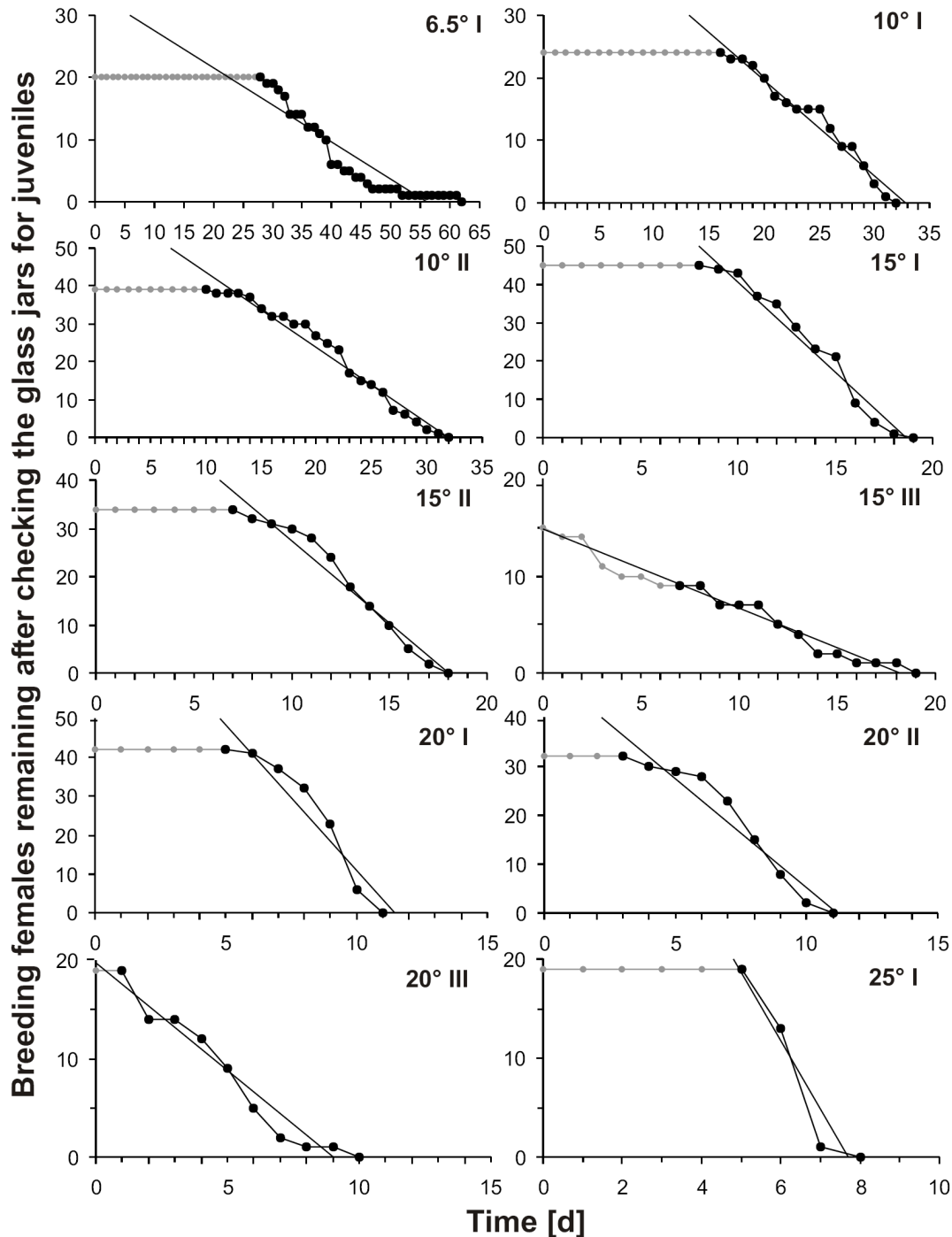


Fig. 1: Breeding females of *L. benedeni* remaining after checking the glass jars for juveniles every morning (see “Methods”) during the experiments. Lettering indicates the temperature (6.5° – 25° C) and the time (run I–III) of each experiment. Please pay attention to the different x axis scaling. Data represented by black dots were used in the linear regression

The brood size of the mysids caught in the field at the beginning of each experiment was 20 ± 4.5 larvae/female in run I, 18.2 ± 5.1 larvae/female in run II, and 6.2 ± 2.2 larvae/female in run III. The mean brood sizes (hatched juveniles) at all temperatures (Table 1) decreased as the development time

increased. The probability of survival of both the mother ($R^2 = 0.62$) and the larvae ($R^2 = 0.83$) at each temperature tested is described with a nonlinear-regression curve (Fig. 3; Table 2). At 6.5 and 25° C, the probability of survival of the mothers (Fig. 3a) and of the larvae (Fig. 3b) was lower than at 10, 15, and 20° C. The optimal and maximum temperature for survival of both the mothers and the larvae was 15.9° C (Table 2).

Discussion

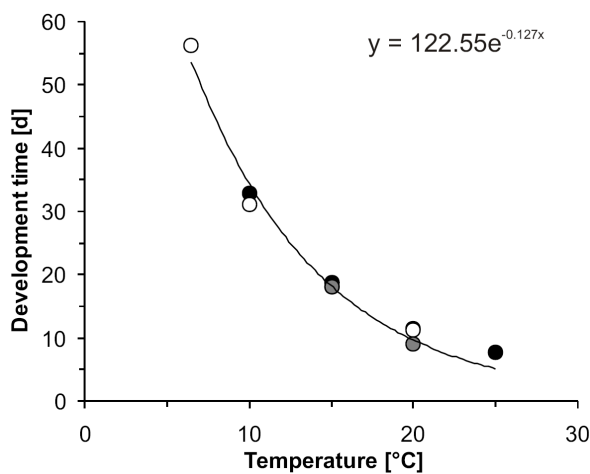


Fig. 2: Development time of *L. benedeni* at the indicated temperatures and time. Results from Fig. 1 were combined in an exponential curve (black dots run I, white dots run II, grey dots run III; see text for dates of each set of experiments)

Our experiments, which provide the first determination of the embryonic development time of a freshwater mysid, revealed a clear dependency of the development time of the brood of *L. benedeni* on the water temperature. The tested temperatures between 4 and 25° C represent the range observed in the littoral of Lake Constance (Stich & Brinker 2010, Hanselmann et al. 2011b) and in most lakes in temperate zones in which *L. benedeni* is found (Wittmann & Ariani 2008, Audzijonyte et al. 2009).

At 4° C, eggs did not develop. The coldest temperature at which the larvae developed to juveniles was at 6.5° C, which is close to the temperature measured in the field at which the first breeding females were found in spring 2008 (6.6° C, Hanselmann et al. 2011b). Because of the negative exponential relationship, fluctuations at lower temperatures cause much higher changes in the development time than fluctuations at higher temperatures. Therefore, the speed at which water warms in spring and the higher water temperatures in winter that will probably be caused by climate warming (Straile et al. 2003) should have a greater influence on population growth, abundance, and the length of the reproductive period of the mysids than fluctuations in the maximum summer temperatures.

IV – Embryonic development time

Table 1 Results of the linear-regression model for the development time in each experiment (D_T), the percent of surviving females ($\%$), and the corresponding mean brood size (mean number of hatched juveniles per female \pm SD) of *L. benedeni*

Temperature ($^{\circ}$ C)	Run I				Run II				Run III			
	D_T (d)	R^2	P value	Brood size	D_T (d)	R^2	P value	Brood size	D_T (d)	R^2	P value	Brood size
6.5	-	-	-	-	56.16	0.86	< 0.001	7.7 \pm 4.8	-	-	-	-
10	32.88	0.97	< 0.001	18.1 \pm 5.0	31.19	0.97	< 0.001	12.5 \pm 6.4	-	-	-	-
15	18.66	0.97	< 0.001	11.9 \pm 3.9	18.18	0.96	< 0.001	18.1 \pm 6.0	18.17	0.97	< 0.001	6.0 \pm 2.8
20	11.45	0.91	0.008	17.9 \pm 4.8	11.17	0.92	< 0.001	11.9 \pm 4.2	9.02	0.94	< 0.001	12.2 \pm 1.9
25	7.70	0.92	0.04	12.2 \pm 4.0	-	-	-	-	-	-	-	-

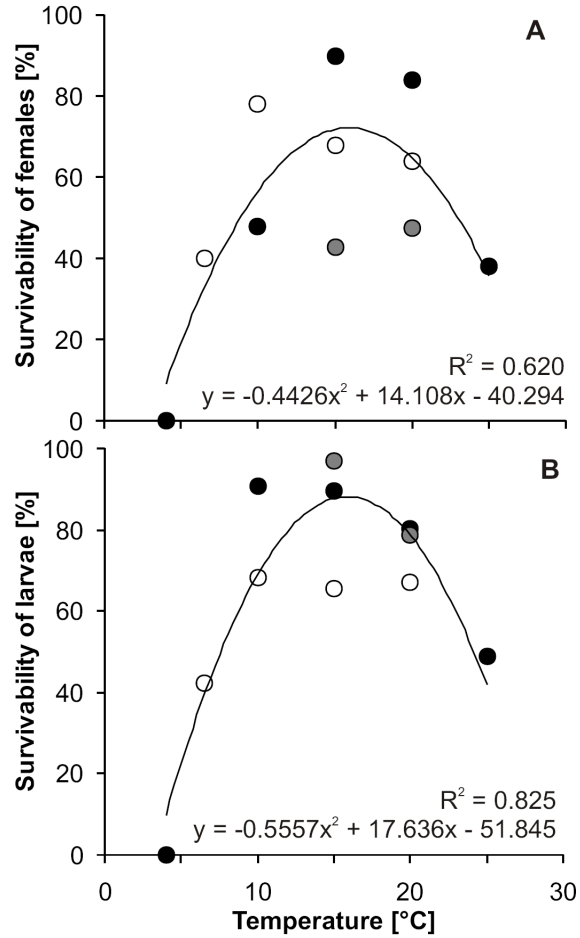


Fig. 3: Probability of survival of females a and larvae b at the temperatures indicated in three experiments (filled circle run I, open circle run II, filled gray circle run III; see text for dates of each set of experiments)

The summer temperatures, on the other hand, influence the distribution and survival of *L. benedeni*. Because of decreasing productivity over 20 $^{\circ}$ C, as observed by the lower survival at 25 $^{\circ}$ C, the establishment, density, and continuing dispersion of the mysids could be limited by increasing summer temperatures (Adrian et al. 2009). *L. benedeni* is well adapted to the temporal conditions in Lake Constance, as indicated by the maximal survival of larvae and adults at 15.9 $^{\circ}$ C. The mean temperature in the

Table 2: Results of the nonlinear-regression model on the probability of survival of females and larvae of *L. benedeni*, with calculations of the optimal temperature (maximum) and of the temperature-dependent development time

	Parameter	Estimated value	SE	T value	P value	R ²	Maximum (°C)
Optimal temperature						Formula $f = ax^2 + bx + d$	
<i>Females</i>	<i>a</i>	-0.443	0.140	-3.159	0.013	0.6196	15.94
	<i>b</i>	14.108	4.079	3.459	0.009		
	<i>d</i>	-402.950	26.823	-1.502	0.171		
<i>Juveniles</i>	<i>a</i>	-0.556	0.103	-5.421	<0.001	0.8247	15.87
	<i>b</i>	17.635	2.985	5.909	<0.001		
	<i>d</i>	-51.841	19.627	-2.641	0.030		
Temperature-dependent development time						Formula $f = a \times e^{bx}$	
	<i>a</i>	122.549	8.27	14.81	<0.001	0.985	
	<i>b</i>	-0.127	0.006	-19.58	<0.001		

field during the reproduction period in 2008 was $15.6 \pm 5.7^\circ \text{C}$, with a minimum of 6.6°C at the beginning on April 2 and a maximum of 22.9°C in midsummer on July 30 (Hanselmann et al. 2011b). This could also explain the rapid increase in *L. benedeni* after its introduction in Lake Constance (Hanselmann, unpublished observations).

One precondition for this type of experiment is continuous reproduction. Because we started the experiments early in the year at the beginning of the reproduction period, there was a plateau, i.e., no hatching, at the beginning of runs I and II. Because of this pattern, we conclude that at the beginning of the spring experiments, the clutch age distribution was skewed toward younger clutches, whereas in the summer samples (run III), clutch ages were more evenly distributed, i.e., unlike the spring samples, the summer samples contained relatively old clutches that hatched immediately in the first day after the start of the experiment. Nevertheless, we assumed for all experiments that the clutch that hatched last was fertilized just before the females were caught. As the decline of breeding females, respectively the hatching of the juveniles during our experiments, is well described by a straight line (Fig. 1), we concluded that the reproduction was continuous and that our sampling size of 50 females was large enough to include a newly breeding female.

The deviation at 20°C in run III (summer) from runs I and II (spring) could possibly be caused by the lower number of females. At the end of July,

IV – Embryonic development time

when we started the experiment, only few breeding females were found. At this time, the abundance of the population of *L. benedeni* in Lake Constance was lower probably because of size-selective predation by juvenile perch on the large-length classes of the mysid (Hanselmann et al. 2011b). Because of reduced adults available in the field, it could be that in our sampling no female was included with a clutch fertilized the night before. So the last clutch could be fertilized some days before catching, which would lead to an underestimation of the development time. The described equation (Fig. 2) could therefore, underestimate but never overestimate the egg development time.

Compared to previous methods, such as storing the eggs out of the marsupium in petri dishes (Manton 1928, Modlin 1979, Wittmann 1981a, Johnston et al. 1997, Fockedey et al. 2006, Ghekiere et al. 2007), our experimental method avoided the stress of removing the larvae from the marsupium and handling them during water exchange. We reduced negative effects resulting from possible oxygen deficits by allowing the female to care for the brood. Therefore, we introduced a facile method for working in vivo with the larvae of *L. benedeni*, which can be used to answer ecotoxicological questions (Verslycke et al. 2007).

In our future studies on population processes of *L. benedeni*, we intend to quantify the changes in population size over time, and finally develop a model based on the mysids characteristics (inter alia rates in relation to environmental factors such as the embryonic development time, growth rates, and birth rates) to calculate and predict population dynamics and mortality rates.

Acknowledgments

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Chapter V

Estimating instantaneous birth and mortality rates of an invasive freshwater mysid in the field

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Abstract

The freshwater mysid *Limnomysis benedeni* (Crustacea: Mysida) is an alien species in Lake Constance with high, fluctuating abundances. It reproduces continuously instead of building cohorts, which makes it difficult or impossible to determine population dynamics. Population dynamics are an excellent tool for understanding an ecosystem and the role species play in it. It is especially important to know the potential that invasive or alien species have for modifying an ecosystem. The mortality rate is the most difficult population rate to determine but is useful for estimating the impact of possible predators or other mortality factors on a species. Direct field measurements of the main population characteristics (abundance, biomass, clutch size, sex ratio) were combined with general ecological equations developed for species with other ecological behaviours. We estimated the instantaneous mortality rate (d) of the population of *L. benedeni* in the littoral of Lake Constance by calculating the instantaneous birth rate and the population growth rate. The equations used served well for the estimations. During the reproduction period in summer, the instantaneous mortality rate was high, but the instantaneous birth rate was high enough to balance the population growth rate. The instantaneous mortality rates reinforced the known life-cycle patterns of *L. benedeni* and confirmed the assumption that the life-cycle shift in summer is an adaption to the high predation on the

V – Calculating birth and mortality rates

population by fish. With the calculated population rates, we will now be able to continue defining the role of this invasive species on the whole ecosystem.

Introduction

Any population is subject to the numerous influences stemming from its natural environment. Distribution, life-cycle and population dynamics are often governed by environmental conditions, such as temperature, oxygen or food availability, and species interactions (Krebs 2001, Wiens & Graham 2005). In aquatic systems, the water temperature is of prime importance. If the environmental conditions comply with the demands of the species, the population growth depends on processes that add individuals to the population or that remove them. The main processes are birth, mortality, emigration and immigration. The birth rate depends on the fitness of the species and is often correlated with the temperature (e. g. Margalef 1955, Shaw & Bercaw 1962, Wolfinbarger 1999). Species often migrate to avoid predation or unacceptable environmental conditions or for foraging (McLaren 1963, Stich & Lampert 1981, Boscarino et al. 2009). The population rate that is most difficult to determine is the mortality rate. Mortality can occur owing to natural senescence, predation (Benard 2004, Rinke et al. 2008), parasitism (Ebert 2005), and because of incalculable environmental risks, e.g. turbulence or randomly changing temperatures (H. Hofmann et al. 2008, Stoll et al. 2010).

To quantify all these processes directly, much data, manpower and time are required and are often not possible. Nevertheless, an estimation of the components of population dynamics is useful for understanding an ecosystem and the role a species plays in it. Simplifications of the basic assumptions are an elegant way to reach this goal by calculations and reduce the needed field data. Some population parameters, such as growth, production and mortality can be calculated from life-table analyses if the species of interest reproduces in cohorts (Gentile et al. 1982, Mees et al. 1994, Sudo et al. 2011). But for species that reproduce continuously, these analyses are not possible because no distinct age classes can be observed. To calculate population rates for such a species, much more data on the life cycle has to be experimentally determined.

One such species that reproduces continuously is the mysid *Limnomysis benedeni* (Czerniavsky) (Crustacea: Mysida). *L. benedeni* is one of the few freshwater mysids of Central Europe (Mauchline 1980); only 6.7 % of all mysids live in freshwater ecosystems, and most species are found in brackish estuaries or in the oceans (Porter et al. 2008). *L. benedeni* originated in the Ponto-Caspian region (Bij de Vaate et al. 2002, Audzijonyte et al. 2006) and invaded nearly all of Europe (Wittmann 2007, Wittmann & Ariani 2008, Audzijonyte et al. 2009). It was first found in Lake Constance in 2006 (Fritz et al. 2006) and spread throughout the lake within two years (Hanselmann et al. 2011b). Like most inland mysids, *L. benedeni* lives nectobenthically, i.e. associated with the ground or large structures, and is part of the macrozoobenthos. Observations in the field and laboratory experiments have shown that the species prefers structured habitats like macrophytes, stones, boats or quay walls (Kelleher et al. 1999, Gergs et al. 2008). *L. benedeni* is phyto-litophilic and preferentially feeds on smaller particles (Wittmann & Ariani 2000, Gergs et al. 2008, Aßmann et al. 2009). Reproduction occurs in the warmer season from April to September, which leads to a life-cycle shift of the adults. In the winter generation, the adults grow large and reproduce only once with a large clutch in early spring; the summer generation reproduces continuously with a smaller size at maturity, and smaller body and clutch sizes (Hanselmann et al. 2011b). As the mysid is not pelagic, the only known migration process is the aggregation of huge swarms in winter in the open water of the littoral zone (LUBW (Ed.) 2008). These swarms in Lake Constance can be several metres high but are always associated with the ground, and have been observed only in the littoral zone but never in the pelagic zone (LUBW (Ed.) 2008, Mörtl, M., Huber, A., pers. comm.). Similar aggregations have been reported only from one other deep lake, Lake Akgöl in Turkey (Wittmann 1995).

To help to define the role of the invasive *L. benedeni* in the Lake Constance ecosystem, we estimated the instantaneous mortality rate (d) of the population in the littoral. We measured the main population characteristics abundance, biomass, clutch size and sex ratio and analysed them using general ecological equations develop

Material and methods

Data collection

Mysids were sampled at the man-made dam “Grüner Damm” situated in the eastern part of Lake Constance near the confluence of the river Rhine in Austria, Central Europe. During a 3-year period, 24 sampling sets were collected at a depth of about 0.5 m. From November 2007 until November 2008, samples were taken every 3–5 weeks. In 2009, the sampling interval was 3 months, and in 2010, samples were collected every month in spring and once in November. During the period of continuous sampling in 2007 and 2008, the water temperature was recorded by loggers (HOBO Pendant 64k Temp/Light data logger, Onset) newly set at 0.5 m depth on every sampling date to compensate for fluctuations in the lake level; these data were used for the calculations of the population dynamics.

To measure abundance, we used an underwater Surber sampler (Mörtl 2004) with a quadratic frame (25 × 25 cm, 40 cm height, mesh size 200 µm) to obtain quantitative samples (three replicates per day). All animals and stones inside the frame were collected and stored in cold water for transport. In the laboratory, the macroinvertebrates were brushed from rocks, and all organic matter was collected with a 200 µm sieve. The organic fraction was fixed in 96% ethanol. Afterwards, *L. benedeni* was identified and counted under a stereomicroscope.

The samples from the Surber sampler were not suitable for measuring the biomass, clutch size and sex ratio because the individuals were too battered. We therefore took a qualitative subsample of the population in the field via kick-sampling (mesh size 200 µm) and stored the animals directly in 96% ethanol. The sex, clutch size and body length of the subsample under a stereomicroscope were recorded. The biomass was calculated from the body length according to the correlation of Gergs *et al.* (2008). To compare the clutch sizes of the winter or summer generation between the different years, the mean clutch size was determined. In this context, a generation means a group of individuals of unspecific age, not a cohort (Hanselmann *et al.* 2011b). The reproduction period is defined as all dates on which females are carrying clutches.

Calculations

One way to determine the instantaneous mortality rate (d) of a continuously reproducing species in the field is to calculate it indirectly by determining other factors. If no immigration or emigration is observed or if both are assumed to be constant, the mortality rate can be estimated by subtracting the observed population growth rate (μ) from the instantaneous birth rate (b) (Krebs 2001):

$$d = b - \mu.$$

To calculate the birth and growth rates, we used several formulae known from ecological theories and earlier research. To calculate the population growth rate (μ) between two sampling dates, the abundance (N) on both dates (t_1 and t_2) is required. For a population with exponential growth, the growth rate is calculated according to a well-known ecological principle (Begon et al. 1998, Krebs 2001):

$$\mu = \frac{\ln(N_{t_2}) - \ln(N_{t_1})}{t_2 - t_1}.$$

To calculate the instantaneous birth rate (b), we chose the egg-ratio method of Edmondson (1971), modified by Paloheimo (1974):

$$b = \frac{\ln(E + 1)}{D}.$$

This method considers the average number of eggs per individual (including all adults and juveniles) (E), calculated from the mean clutch size and the proportion of females carrying clutches within the total population in the field, and the experimentally derived development time (D) of these eggs at the ambient temperature. The formula is devised for zooplankton communities and serves well for them (Lampert 1988, Bennett & Boraas 1989, Stockwell & Johannsson 1997, Ooms-Wilms et al. 1999). The prerequisites for this calculation of continuous reproduction and a constant age structure of the embryonic stages are met by the population of *L. benedeni* (Hanselmann et al. 2011b). For further derivations, we refer the reader to books on general ecology (e.g. Begon et al. 1998, Krebs 2001, Lampert & Sommer 2007).

The development time between two dates was calculated considering the temperature measured in the field and the relationship between temperature and development time determined in laboratory experiments (Hanselmann et al. 2011a). Because of the exponential correlation between temperature and

V – Calculating birth and mortality rates

development time (Hanselmann et al. 2011a), we calculated the development time for each day with the mean temperature from the last 24 h. A daily birth rate was then calculated, and for the time between two sampling dates, the mean of these daily birth rates was taken. To calculate the instantaneous mortality rate for the interval between two sampling dates, we also considered the average number of eggs per individual (E).

Statistics

To determine the differences in the clutch size within one generation between years and between generations, we calculated Kruskal-Wallis H-tests because of inhomogeneous variances and an unbalanced sample size.

Results

Abundance in the field 2007-2010

The abundance of *L. benedeni* in the field substantially changed during the 3-year sampling period (Fig. 1A). High peaks of abundance were observed in summer and winter, and in general, abundances were low in spring and autumn. Measurements of biomass (Fig. 1B) followed the abundance patterns except for the sample from May

Table 1 Mean clutch size of females at different life-cycle stages over 3 years. Reproduction occurred in summer (S for summer generation) or in spring (W for winter generation). Standard deviation was calculated if $n \geq 2$, but placed in parentheses if $n = 2$

Season and year	Clutch size [mean \pm SD]	n
W 2008	20.46 \pm 1.12	3
W 2009	18.27	1
W 2010	20.14 (\pm 1.48)	2
S 2008	6.98 \pm 0.99	5
S 2009	4.71 (\pm 0.40)	2

28, 2008, on which the highest biomass of all samples was found. This biomass was approximately two-fold higher than the next two samples, whereas the abundance on this date was similar to that of the following two samples (Fig. 1). For the highest abundance in July 2010, no biomass data are available.

The mean clutch size differed between the generations ($p = 0.003$). In spring (winter generation), the clutch size was about three-fold larger than in summer (19.99 ± 1.3 vs. 6.33 ± 1.38 larvae/female). Between the generations of different years, the clutch size did not differ (summer: $p = 0.053$, winter: $p = 0.304$).

Population dynamics in 2008

The abundance of *L. benedeni* during the reproduction period in 2008 (Fig. 2A) was very high in early summer, with a maximum of $3,776 \pm 818$ Ind/m² on July 30. Thereafter, the abundance decreased and stayed at a low level with a minimum of 5 ± 9 Ind/m² on October 9. The temperature in the beginning of April, when the first females carried a brood, was 6.6° C; the maximum temperature of about 20° C occurred in July and August; autumn temperatures were lower (Table 2).

The instantaneous growth rate (μ) was positive except from July to August and from the beginning of September to October (Fig. 2B, Table 2). The instantaneous birth rate (b) increased from spring to summer, decreased over the course of the summer, and increased again up to the end of August. In September, it began to decrease, reaching zero in winter (Fig. 2B, Table 2). The instantaneous birth rate was usually higher than the growth rate. Only in April and late October, i.e. the beginning and end of the reproduction period, was the birth rate lower, which resulted in apparent negative mortality rates (Fig. 2B). From May to the beginning of October, the mortality rates were variable but positive (Fig. 2B).

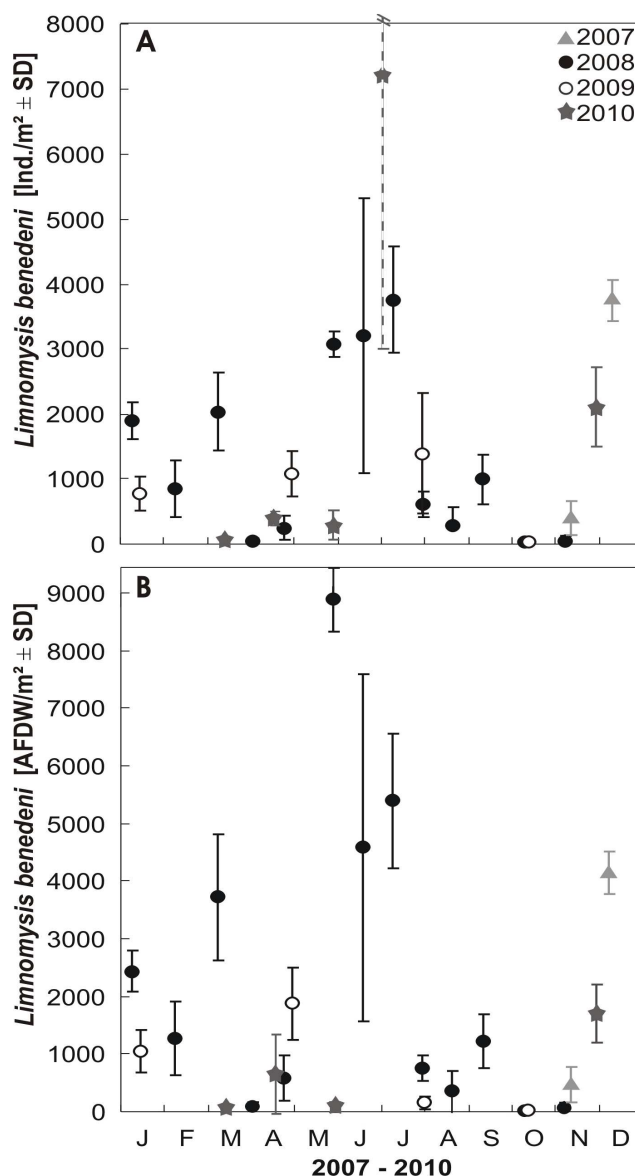


Fig. 1 Abundance and biomass of *L. benedeni* from November 2007 to December 2010. A) Abundance (individuals/m² ± SD) of *L. benedeni* at the sampling site. **B)** Biomass (ash-free dry weight, AFDW/m² ± SD) of *L. benedeni* at the sampling site. Abundance sample from July 2010 (dashed line) has no corresponding biomass data

Discussion

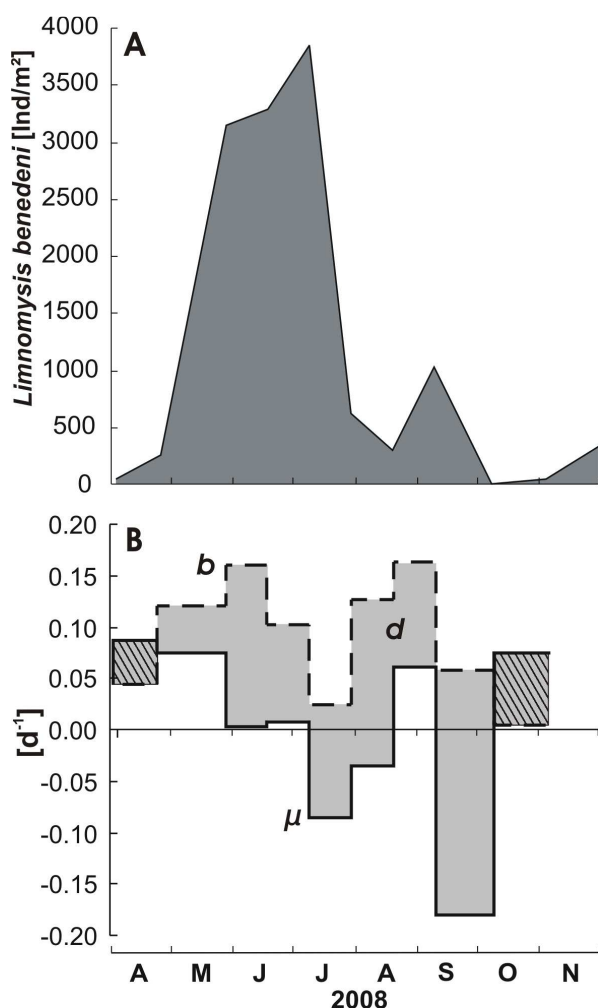


Fig. 2 Abundance, instantaneous birth and mortality rates, and population growth rate of *L. benedeni* in 2008. **A)** Abundance (individuals/m²) of *L. benedeni* during the reproduction period (April to November), indicated by the presence of egg carrying females. **B)** Instantaneous birth rate (*b*, dashed line) and population growth rate (μ , solid line) during the reproduction period. The difference between the lines (shaded area) is the instantaneous mortality rate (*d*). Hatched areas indicate a negative mortality rate

To our knowledge, our estimations of the birth and mortality rates of *L. benedeni* are the first reported for a necto-benthic freshwater mysid. We showed that the formula used for the instantaneous birth rate (egg-ratio method modified from Paloheimo (1974)), developed for planktonic species (zooplankton), is also well suited for benthic or necto-benthic species. The prerequisites for these calculations, e.g. continuous reproduction and a uniform distribution of embryonic development stages, occur with *L. benedeni* during summer (Hanselmann et al. 2011b). We also successfully calculated mortality rates for the population of the freshwater mysid in Lake Constance during the reproduction period in 2008. We made the assumption that a

large part of this mortality, beside the natural senescence, is caused by fish predation. As shown in previous studies, juvenile perch (*Perca fluviatilis*) prefer the large mysids as prey (Hanselmann et al. 2011b) and are present in the littoral zone of Lake Constance in high numbers from June/July to September (Wang & Eckmann 1994, Imbrock et al. 1996). Other predators, e.g. other fish or other invertebrates, probably do not play an important role because of lower

abundances (unpublished data). We hypothesize that the markedly high mortality in September (Fig. 2B) is caused by both increased fish predation because the perch present at that time are larger and a decrease in reproduction at the end of the reproduction period. Despite this high predation, especially on the large adult mysids during summer, the instantaneous birth rate was positive and high enough to stabilize the population (Fig. 2B).

Table 2 Data used for the calculations of instantaneous birth and mortality rates, and population growth rate of *L. benedeni* in 2008, shown in Fig. 2. Clutch size and temperature are the average between the two sampling dates; the development time is the average of daily-calculated development times with daily-measured temperatures. ♀+ = female carrying a clutch.

Date	Proportion of ♀+ (%)	Clutch size <i>E</i> (eggs/ind.)	Temperature (°C)	Development time <i>D</i> (d)	Birth rate <i>b</i> (d ⁻¹)	Population growth rate <i>μ</i> (d ⁻¹)	Mortality rate <i>d</i> (d ⁻¹)
9.3.2008	0						
2.4.2008	12.4	6.97	7.5	47.62	0.0436	0.0866	-0.0430
24.4.2008	56.3	13.36	13.8	22.42	0.1188	0.0739	0.0450
28.5.2008	78.7	8.68	17.0	14.31	0.1586	0.0020	0.1566
18.6.2008	22.7	1.20	21.8	7.84	0.1005	0.0076	0.0929
9.7.2008	7.1	0.27	19.9	9.85	0.0241	-0.0865	0.1106
30.7.2008	0.0	1.69	21.7	7.88	0.1257	-0.0360	0.1617
20.8.2008	47.6	3.46	20.4	9.26	0.1616	0.0594	0.1022
10.9.2008	54.5	1.87	15.2	18.31	0.0576	-0.1806	0.2382
9.10.2008	3.6	0.10	12.8	24.38	0.0039	0.0743	-0.0704
6.11.2008	0						

In spring (March to May) and autumn (November and December), the main wind direction on Lake Constance changes from west or north-west to east or south-east, which causes more intense wind and waves (Bäuerle et al. 1998) and therefore more turbulence in the littoral zone (H. Hofmann et al. 2008). Since *L. benedeni* seems to avoid current velocity over 0.5 m/s (Wittmann 1995), this turbulence could force the mysids to migrate and therefore be responsible for the negative mortality rates in April and the end of October (Fig. 2B). The swarms observed in the last years (LUBW (Ed.) 2008) could therefore, beside other reasons, be a response on turbulent conditions and one reason for the negative mortality rates. Because of these findings, we restricted our calculations to the warmer season, for which no information on

V – Calculating birth and mortality rates

emigration or immigration of mysids could be found. The fluctuating abundances in spring and autumn (Fig. 2A) confirm this assumption. The negative mortality rates observed in this study are therefore an indication of migration processes and should not be overvalued.

The maximum biomass in May 2008 was caused by larger adults, which started to reproduce. The adults in summer never reach the length of the animals in May and consist mainly of juveniles and small adults (Hanselmann et al. 2011b). This phenomenon is correlated with larger clutch sizes and larger size at maturity of the reproducing adults in spring (Table 1, (Hanselmann et al. 2011b)). The difference in size at maturity has been suggested to be related to the seasonal variation of mortality of different size classes, probably caused by fish predation and induced by temperature. Future studies will focus on estimating the mortality rate of different age classes and their productivity. To do this, growth rates of individuals in different life-cycle stages need to be determined.

Acknowledgements

We thank René Gergs for his support and help in the field, and Christian Fiek, Cornelia Welte and Katharina Greiner-Perth for their enthusiasm in counting and measuring *Limnomysis benedeni*.

Chapter VI

Nutritional ecology of the invasive freshwater mysid *Limnomysis benedeni* - field data and laboratory experiments on food choice and juvenile growth

A. J. Hanselmann, B. Hodapp, K.-O. Rothhaupt

Abstract

(1) In the environment, the introduction of alien species leads to changes in species composition. The functional traits of the biota thereby also change, which in turn will likely alter ecosystem processes, e.g. by modifying the availability, capture, and use of nutrients or by affecting the feeding relationships (trophic structure) within a community. The highly invasive freshwater mysid *Limnomysis benedeni* was introduced in Lake Constance (Central Europe) and is now established and abundant.

(2) We examined the feeding mode and food preference of adult *L. benedeni* collected from the field and from laboratory feeding experiments by analysing their stomach contents. In the second setup with two sets of laboratory growth experiments, we determined the growth of juveniles by feeding newly hatched juveniles with different natural food sources at different water temperatures.

(3) The stomach analyses showed clearly that *L. benedeni* fed on small organic matter of both benthic and pelagic origin and fed by both filtering and grazing. Juvenile growth was supported equal by natural biofilm, biodeposited material from *Dreissena polymorpha* and an algal suspension.

(4) We conclude that *L. benedeni* has no predatory impact on zooplankton in the field and probably affects the nutrient cycles in the littoral.

Introduction

In recent years, non-native and invasive species have received increased media as well as scientific attention (Chapin et al. 1997, Shirley & Kark 2006). Especially in freshwater systems, invasive species have a high potential to affect the diversity and stability of ecosystems (Sala et al. 2000) through changes in species composition, which cause changes in the functional traits of the biota. For example, the availability, capture, and use of nutrients or the feeding relationships (trophic structure) within a community can be altered. The supply of nutrients is an important “bottom-up” mechanism that controls the structure and dynamics of ecosystems (Chapin et al. 1997, Wikström & Hillebrand 2012). By using different resources, new species can open alternative paths of nutrient utilisation, and their predators can benefit (Werner et al. 2005). When new species consume resources on which native species depend, they can indirectly damage these native competitors (Chapin et al. 1997). In extreme cases with a “top-down” mechanism, they can disturb whole food webs (e.g. microbial communities) and potential prey can be affected (Ellis et al. 2011).

Many alien species in European freshwater systems are crustaceans (Devin et al. 2005, Moog et al. 2008). Among them, the mysids are of increasing importance because some have a high damage potential (Arbaciauskas et al. 2010, Ellis et al. 2011) and/or a rapid distribution potential (Wittmann 1984). *Limnomysis benedeni* Czerniavsky is one of the few freshwater mysids of Central Europe (Mauchline 1980) and is highly invasive (Audzijonyte et al. 2009). Originating in the Ponto-Caspian region (Bij de Vaate et al. 2002, Audzijonyte et al. 2006), the species has invaded nearly all of Europe (Wittmann 2007, Wittmann & Ariani 2008). After its first discovery in Lake Constance in 2006 (Fritz et al. 2006), the species spread throughout the lake within two years (Hanselmann et al. 2011b). It now forms large biomasses with a high potential impact on the lake ecosystem (Hanselmann et al. 2011a). The preferred habitat of *L. benedeni* is the littoral, where it lives nectobenthically, i.e. associated with the ground or large structures. Observations in the field and experiments in the laboratory have shown that *L. benedeni* prefers structured

habitats, such as macrophytes, stones, boats or quay walls (Kelleher et al. 1999, Gergs et al. 2008).

L. benedeni reproduces in the warmer season from April to September, which leads to a life-cycle shift of the adults. In winter, the adults grow to a larger size and reproduce once in spring, producing a large egg clutch; in summer, *L. benedeni* reproduces continuously with a smaller size at maturity, body and clutch size (Hanselmann et al. 2011b). As with other mysids, *L. benedeni* larvae develop inside the female marsupium, a brood pouch formed by two pairs of oostegites (Westheide & Rieger 1996); the development time is very sensitive to water temperature (Hanselmann et al. 2011a). Females are not able to store spermatophores; therefore, the eggs for each clutch have to be newly fertilized. Egg fertilization, embryonic development, and all larval moults occur inside the marsupium. Therein, the larvae gain all energy and nutrients from the yolk; the mother provides only oxygen by pumping fresh water into the marsupium. The last larval moult takes place directly after the larvae are released into the water. The juveniles start to feed actively during this last larval stage (Mauchline 1973, Wittmann 1981a, Wittmann 1984). Field observations and preliminary laboratory studies have indicated that *L. benedeni* is phyto-lithophilic and prefers smaller particles (Wittmann & Ariani 2000, Gergs et al. 2008, Aßmann et al. 2009). However, no detailed data on food utilization, feeding mode, growth and predatory impact in the field are available.

In this study, we tested the previously proposed hypotheses on the feeding mode and food preference of *L. benedeni* to determine their position in the food web. We analysed the stomach contents of adult *L. benedeni* collected from Lake Constance, and in laboratory experiments, we examined their feeding mode. Additionally, we fed juvenile mysids different natural food items and measured growth rates.

Methods

Field sampling

We collected all adult *L. benedeni* in the littoral of Lake Constance with a dip net at a depth of 0.5 to 1 m. The main collection site was at the Littoral Garden on

the western shore of Lake Constance near the Limnological Institute of the University of Konstanz (Germany). The habitat there is a mixture of sandy ground with Characea and stones, overgrown with the mussel *Dreissena polymorpha*. To compare the conditions at different stations in the lake, we chose a second sampling site at the eastern part of the lake at Hard (Vorarlberg, Austria). It is situated on a man-made dam near the confluence of the river Alpen-Rhine. At the second sampling site, the shore has a steeper decline than at the Littoral Garden, and the habitat consists mainly of stones.

For stomach content analyses, we collected the mysids on two dates (end of April and middle of June) at both sampling sites. Animals caught for immediate analysis were conserved in 96% ethanol directly on site to avoid further digestion of the stomach content. The animals used for laboratory experiments were caught in the Littoral Garden and then kept outside the Limnological Institute in an outdoor mesocosm consisting of a concrete basin with 2 × 2 m surface area, 60 cm water depth and flow-through of filtered (200 µm) lake water (~1.5 l/min). To compare it with the stomach content, Biofilm from the lake was collected in April by carefully scratching it from some stones, fixed with 96% ethanol and processed like the stomach content.

Preparation of the stomach and analysis of stomach contents

In mysids, the stomach is located directly under the carapax (Mauchline 1980) and is therefore easy to dissect out. We carefully removed the thin, translucent carapax viewed under a stereomicroscope. After removing the marsupium, legs, antennae and carapax, the gut was carefully clipped away from the stomach, and the stomach was taken out (Fockedey & Mees 1999, Wittmann & Ariani 2000). Any remaining connective tissue around the stomach was carefully removed. The stomach content was spread on a microscope slide with an eyelash glued to a small stick, and the sample was conserved with the mountant Euparal (Henkel 2006). The sample on the slide was covered with a cover glass and dried at 40 °C for 24 h to harden the mountant and to allow any air bubbles to diffuse out.

We analysed the stomach content using a light microscope (Axioskop, C. Zeiss) with 40-fold magnification in the dark-field modus. We recorded the

composition of the stomach content into categories of diatoms, inorganic material < 5 µm, inorganic material > 5 µm, organic material < 5 µm and organic material > 5 µm. Using the microscope's measuring grid, we determined the proportions of the different categories in the stomach in five randomly chosen subsample areas on the slide and calculated the mean. The diatoms from four subsample areas from some of the stomachs of mysids collected in the field were identified according to Streble & Krauter (2008) to the genus level or, when possible, to the species level and counted. To avoid counting an organism twice, we counted broken diatoms only when more than half of the organism was found. Exceptions were made when the counting of an organism twice could be definitely ruled out. Finally, we searched for special structures or species on the whole slide of the stomach contents.

Feeding mode experiments

To determine the feeding mode of *L. benedeni*, we placed three adults each in glass jars filled with 700 ml of filtered (0.2 µm) lake water; the water was aerated and the glass jars were held at 15 °C. The mysids were allowed to adapt for 24 h. Biofilm collected from ceramic tiles (4.7 × 4.7 cm) that had been incubated in the lake as described for the growth experiments below was fed *ad libitum* in one of two ways. To test for grazing, tiles with biofilm were added to the glass jar (one tile per jar). To test for filter feeding, the biofilm was scraped off the tiles and suspended in the water in the glass jar (biofilm from one tile per jar). Two hours after the biofilm was added, the animals were caught and immediately fixed in 96% ethanol. The animals were then dissected, and the stomach contents were analysed as described above. The number of replicates are given in the graphs. Eight subsamples of the biofilm were also fixed, analysed and compared with the stomach contents.

Growth experiments

We determined the growth rates of juvenile *L. benedeni* after their release from the marsupium. Two climate chambers and one climate cabinet (plant growth chamber KBW 720, Binder GmbH, Tuttlingen) were used to provide a stable

VI – Nutritional ecology

water temperature; the overall tolerance was ± 0.3 °C. In all experiments, the same light conditions with a diurnal light rhythm of 12 h/12 h (day/night) and the same experimental setup was used.

In the first experiment in summer 2009, we determined the growth rate as a function of the water temperature (10, 15 and 20° C). As food, a suspension of the green alga *Scenedesmus obliquus* and newly hatched nauplii of *Artemia* were added *ad libitum* twice a week. The glass jars were cleaned well once a week with a soft brush, and the water was replaced. Because *L. benedeni* neonates are released during the night (Wittmann 1984), the water in the glass jars was checked for neonates each morning. When juveniles were released, the mother was removed. Three of the juveniles were immediately fixed in 96% ethanol, and maximally five juveniles were left in the glass jar. Experiments began by feeding the juveniles fresh food added *ad libitum* (Hanselmann et al. 2011a) twice a week. The duration of the experiment was 36 days for all clutches.

In the main experiment in summer 2010 (13 May to 8 June), we estimated the growth rate of the juveniles under approximate field conditions and tested the suitability of four different food sources comparable to their natural food sources, which are predicted to play an important role in the lake: (1) To simulate planktonic algae, we fed a suspension of *S. obliquus* SAG 276-3a and *Nannochloropsis limnetica* Kr 98/3 (both Göttingen, Germany) grown in batch cultures. (2) To provide biodeposited pseudofaeces of zebra mussels (*Dreissena polymorpha*), which is a good and important food source for benthic invertebrates (Gergs & Rothhaupt 2008a, Gergs & Rothhaupt 2008b), we collected faeces and pseudofaeces in the field using ten modified sediment traps (Gergs et al. 2009) containing living *D. polymorpha*; the traps were fixed on pontoons in the littoral, and hung 1.5 m under the surface and 5 m above the ground. (3) To obtain natural biofilm, bare ceramic tiles (4.7 × 4.7 cm) were mounted on six metal plates (1 × 1 m). Nine tiles were placed in each of four cages (0.5 mm mesh size) per plate to exclude grazing animals. The plates were placed at an average depth of 1 m in the Littoral Garden two months before the experiments started. (4) To provide dead animal material, adult *L. benedeni* were placed in hot water for 10 s immediately before feeding them to the juveniles. To compare the quality of the food sources, we dried three

samples of each food source at 55 °C and analysed the particulate carbon and particulate nitrogen content with an NCS–2500 analyser (Carlo Erba Instruments, Italy).

The experiments were conducted at 15° C because this temperature is suitable for embryonic development (Hanselmann et al. 2011a). Brood-carrying females were freshly caught in the lake and kept individually in glass jars filled with 700 ml of filtered (30 µm) and aerated lake water. The cleaning of the glass jars and the experimental procedure with juveniles was the same as describes above, except the duration of the experiments. For each food source, 25 replicates were conducted and stopped successively to obtain a minimum of 4 replicates for each growth period (5, 10, 15 and 20 days). The body length (tip of the apex to the end of the telson, (Gergs et al. 2008) of all juveniles at the beginning and end of the experiments was measured using a stereomicroscope. One clutch was considered as one replicate. For each replicate, we calculated the difference in the mean body lengths of the juveniles fixed at the beginning and the end.

Data analyses

We calculated the growth function of juvenile *L. benedeni* in laboratory experiments using linear regression models for each suitable individual food source and for the mean growth with all suitable food sources. Because of an insufficient number of replicates, the data point at 5 days after adding the biodeposited material was not included in the mean growth calculations. We checked for differences in growth with different food sources using a two-way ANCOVA and a Tukey-HSD posthoc test. For a clearer outline, the specific growth rate (SGR) was calculated as weight increase

$$SGR = \frac{\ln(w_2) - \ln(w_1)}{\Delta d} * 100 \text{ (Busacker 1990),}$$

where w_1 and w_2 are the weight on the beginning and the end and Δd is the duration of the experiment. The body weight (ash-free dry weight) was calculated from the measured length (Gergs et al. 2008).

VI – Nutritional ecology

The selectivity (D) of feeding by *L. benedeni* in the field as well as in the laboratory experiment (feeding mode) was calculated for each animal with the electivity index recommended by Jacobs (1974; Jacobs D):

$$D = \frac{(r - p)}{(r + p - 2rp)}$$

where r is the proportion of the food category in the mysid diet and p is the proportion of the food category in the biofilm on the tiles. Selection is slightly positive with values from 0.25 to 0.5 and clearly positive with values from 0.5 to 1, and slightly negative with values from -0.25 to -0.5 and clearly negative with values from -0.5 to -1; numbers between -0.25 and 0.25 show no significant difference between food content in the stomach and the biofilm (Baltz 1990). When we analysed the diatoms, Jacobs D was only calculated for species that were found with a proportion of more than 0.05 in the stomachs or biofilm. The diet overlaps between different feedings and samples were calculated using Schoener's similarity index (S) (Schoener 1970), recommended by Wallace Jr. (1981):

$$S = 1 - 0.5 \left(\sum_{i=1}^n |p_{xi} - p_{yi}| \right),$$

where p_{xi} is the proportion of food category i in the diet of mysids x , p_{yi} is the proportion of food category i in the diet of mysids y , and n is the number of food categories. The index has values from 0 to 1; low values indicate low diet overlap, and values close to 1 indicate high diet overlap between feedings or samples.

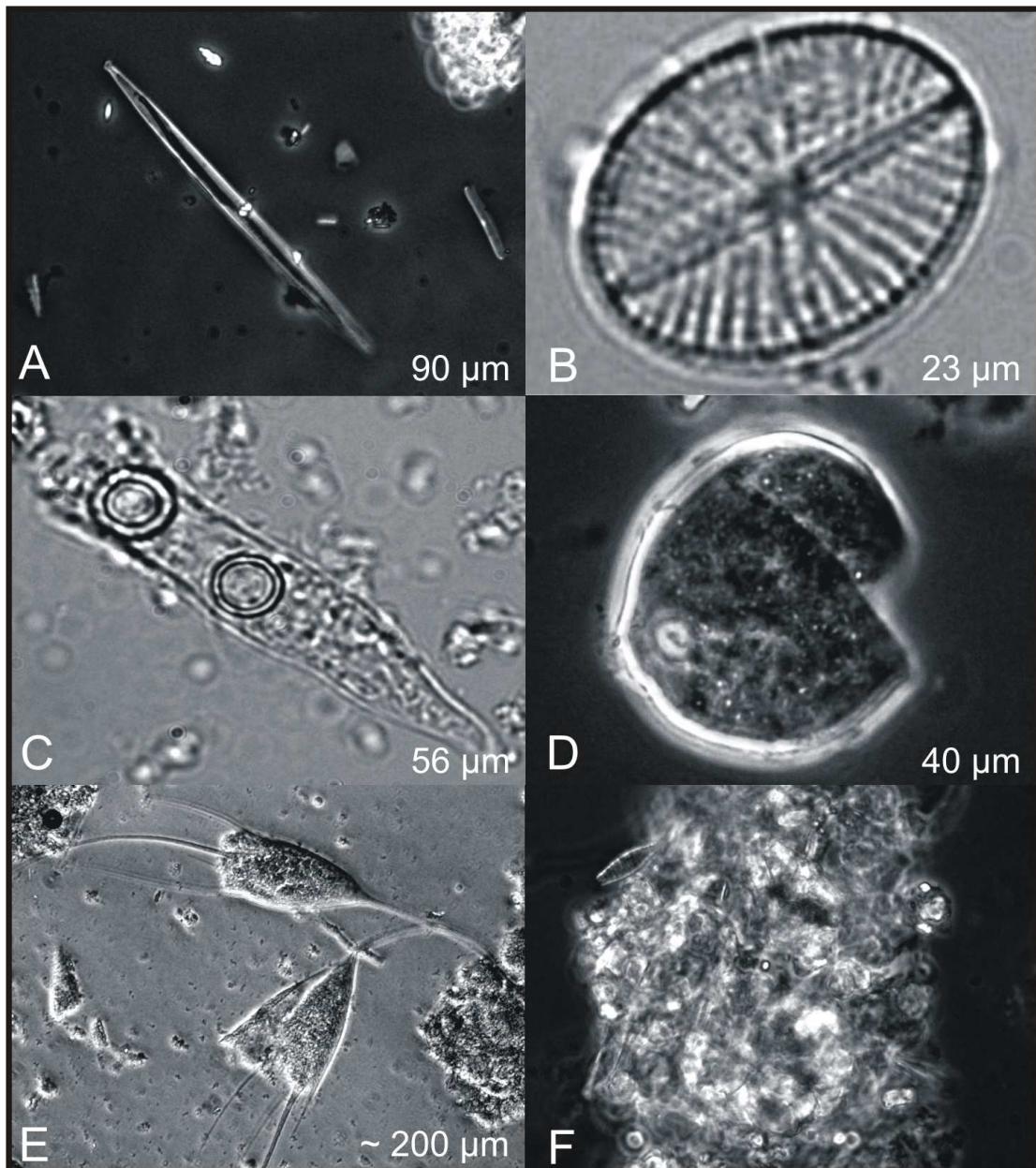


Fig. 1: Microphotographs of selected structures in stomach contents of *L. benedeni* collected from the lake. **A** *Fragilaria crotonensis* (in the right upper corner is some unidentified green organic material); **B** *Cocconeis* sp.; **C** *Dinobryon* sp.; **D** *Peridinium* sp. (green colour); **E** *Kellicottia* spp.; and **F** organic stomach content. The maximal length of the subject (μm), including spines, is indicated

Results

Stomach analyses

When we analysed the stomach contents of *L. benedeni* under the microscope, it became apparent that it was not possible to count every single species or cells that the mysids fed on. The stomach content was an aggregate of unidentifiable organic material (mainly of plant origin, as indicated by the green

VI – Nutritional ecology

colour) and inorganic material (silicate) (Fig. 1F). In addition to the diatoms (Fig. 1A and B), the organic fraction consisted of unidentifiable aggregated algal cells; only a few distinguishable plant structures could be identified (e.g. *Dinobryon divergens* and *Peridinium* sp. Fig. 1C and D). As an exception, in three stomachs, structures of animal origin were determined (the rotatoria *Kellicottia* spp., Fig. 1E). We found no other fragments or structures of animal origin. The largest structure found in the stomachs was a grain of sand with a length of 210 μm ; the largest organic fragment (*Kellicottia* spp.) was about 200 μm , including spines (Fig. 1E).

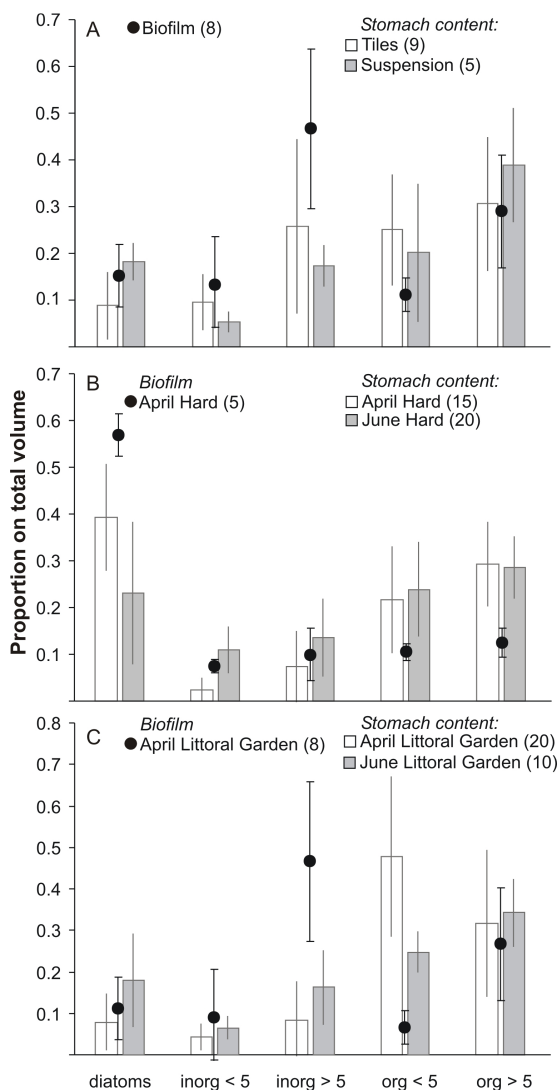


Fig. 2: Stomach content as a proportion of the total volume (\pm SD) of the stomachs of adult mysids (A) from laboratory experiments and (B; site Hard) and (C; site Littoral Garden) caught in the field, compared with the available biofilm. Bars indicate proportion of stomach content; points indicate proportion of biofilm. Numbers indicate replicates

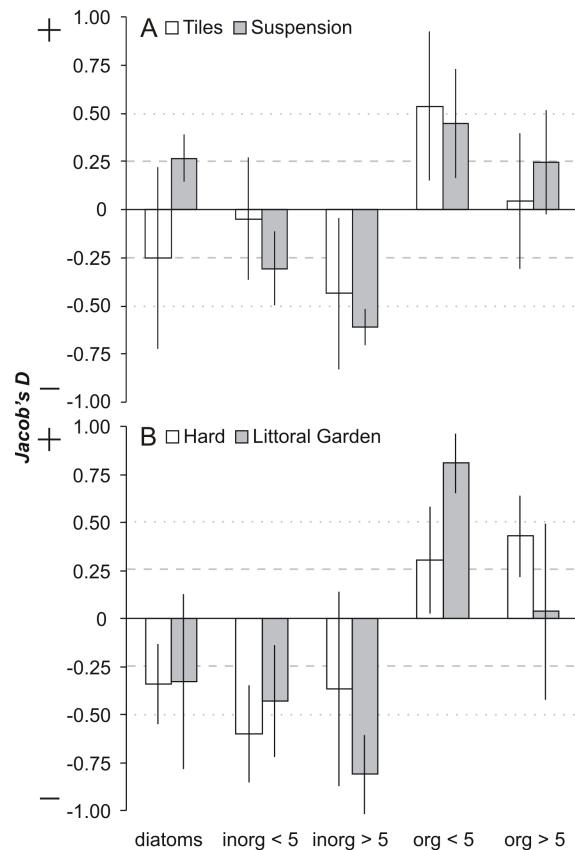


Fig. 3: Jacobs selectivity index D (\pm SD) from the stomach content (A) in the laboratory experiments and (B) in the field. + indicates preference, - indicates avoidance, grey dotted lines indicate significance levels (see methods)

The proportion of the different fractions in the biofilm in April differed between the sampling sites Hard and Littoral Garden ($S = 0.5$). In the Littoral Garden (Fig. 2C), the larger fractions >5 mm, especially the inorganic fraction, dominated, whereas in Hard (Fig. 2B), the diatoms comprised more than 50% of the biofilm. In both places, the organic fraction was slightly or clearly preferred, and the inorganic fraction was clearly avoided (Fig. 3B). In June, when no biofilm data are available, the proportions of the fractions in the stomach contents were comparable to those from April (Littoral Garden: $S = 0.77$, Hard: $S = 0.83$).

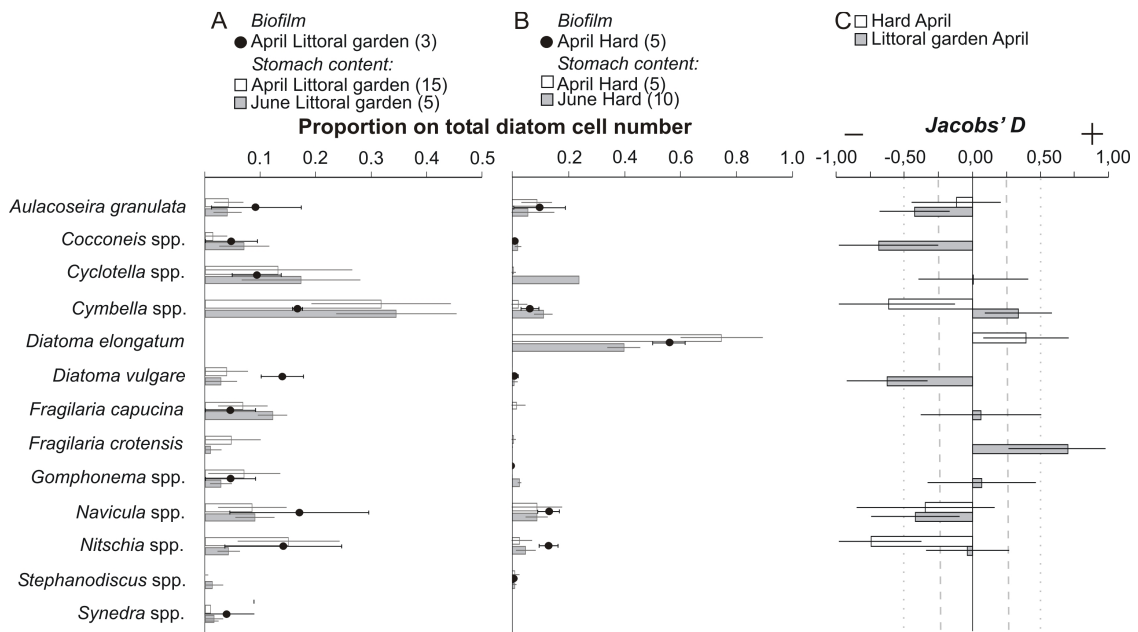


Fig. 4: A and B Diatom species as a proportion of the total diatom cell number (\pm SD) in the stomach contents of adult mysids collected in the field compared to the available biofilm collected at the sampling sites. Bars indicate stomach content, points indicate biofilm. Numbers indicate replicates. **C** Jacob's selectivity index D (\pm SD) from the diatom species in April. Only species with a proportion of the total diatom cell number > 0.05 were included. + indicates preference, - indicates avoidance, grey dotted lines indicate significance levels (see methods)

When we considered the diatoms in the field in April, the community in the biofilm differed between the two sampling sites ($S = 0.44$, Fig. 4A and B). Especially the two *Diatoma* species occurred only at one place. In Hard, *D. elongatum* clearly dominated the diatom community (Fig. 4B) and was ingested by *L. benedeni* with a slight preference. It is conspicuous that only one species (*Fragillaria crotonensis*) was significantly preferred by *L. benedeni* (Fig. 4C). At both sampling sites, two (different) species were clearly avoided, but no correlation was found with either the cell type (round or acicular) or the habitat (benthic or pelagic). The similarity between the diatoms in the stomach contents was higher when April and June at one sampling site were compared (Littoral

VI – Nutritional ecology

Garden: $S = 0.79$; Hard: $S = 0.6$) than the stomach contents on the same date when the two sites were considered (April: $S = 0.2$; June: $S = 0.52$).

In the laboratory experiments in which we fed the mysids the biofilm either on the tiles or suspended, the proportions of food categories in the stomach contents were highly similar ($S = 0.82$, Fig. 2A). In both cases, the small organic fraction was preferred, and the inorganic fraction was avoided (Fig. 3A).

Growth experiments

Three of the four used food sources served well for juvenile *L. benedeni* in the laboratory experiments (Fig. 5). We excluded the experiment with dead adult mysids as food from further calculations because all juveniles died latest after 15 days with a maximum length of 2.2 mm.

Table 1: Ratio of elementary carbon and nitrogen in the different food sources

Food source	C : N
Algae	4.36 ± 0.15
Biodeposited material	5.15 ± 0.06
Biofilm	22.33 ± 7.18
Dead adult mysids	3.82 ± 0.21

The C:N ratios of the feedings with algae, biodeposited material and dead adult mysids was similar (Table 1) and about fourfold lower than the C:N ratios of the feedings with biofilm.

The growth on the three suitable food sources did not significantly differ ($p = 0.735$ Table 3); only the elapsed time had a significant influence on the size increase ($p < 0.001$; Table 3). The function of the mean growth rate (mm/d) was highly significant ($R^2 = 0.814$, $p < 0.001$, Fig. 5). In growth experiments at the

different temperatures, the juveniles at 15 and 20° C had the same body length after 36 days (6.37 ± 0.46 and 6.16 ± 0.68 mm, Fig. 6). The specific growth rates in these experiments were slightly higher than in the other experiments with various food sources at 15° C (Table 2). The length at the start of the

Table 2: Specific growth rates SGR (ash-free dry wt., d^{-1}) with the different food sources and at different temperatures. The mean SGR was calculated from the three food sources at 15° C in 2010 (see text for explanations)

Food	Temperature (°C)	SGR (d^{-1})	Year
Alga + <i>Artemia</i>	10	6.932	2009
Alga + <i>Artemia</i>	15	10.547	2009
Alga + <i>Artemia</i>	20	10.875	2009
Algae	15	8.989	2010
Biodeposited material	15	9.009	2010
Biofilm	15	9.497	2010
Mean	15	9.165	2010

experiments, i.e. the length of the juveniles upon release from the mother, was nearly the same in all experiments (1.88 ± 0.01 in 2010 and 1.94 ± 0.09 in 2009).

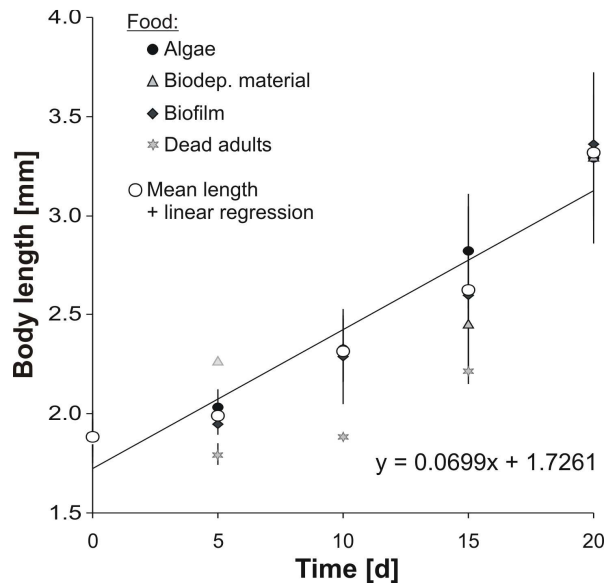


Fig. 5: Body length (mm \pm SD) of juveniles fed with different food sources at 15 °C in 2010. The data point after 5 days with biodeposited material was not included in the calculation because of the low number of replicates

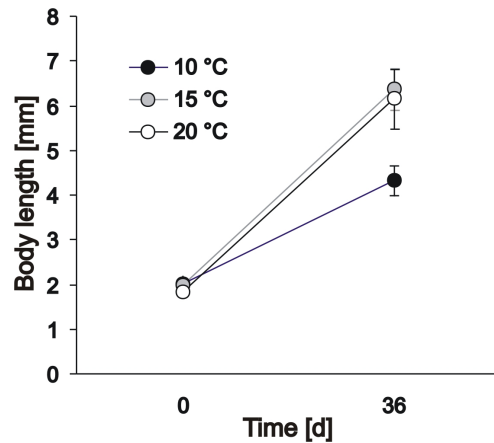


Fig. 6: Body length (mm \pm SD) of juveniles fed with an *Artemia-Scenedesmus* suspension at 10°, 15° and 20° C in 2009

Discussion

The stomach analyses from adult *L. benedeni* in the field show clearly that *L. benedeni* feeds on small organic matter of benthic as well as of pelagic origin. The largest particle found in a stomach was about 200 μ m, although the biofilm in the field contained larger structures. It is important to keep in mind that the stomach contents in the field and the collected biofilm have to be compared carefully, because the biofilm is not the only food source in the field for the mysids. *F. crotonensis*, a pelagic species (Streble & Krauter 2008) with high preference by *L. benedeni* in the Littoral garden, is found in the stomachs, but not in the biofilm (Fig. 6). But as seen in Fig. 2 and 3, the patterns in the biofilm and the stomachs followed nearly the same way. The mysids also adapt their feeding on the given conditions, as seen in the given similarities between the sampling sites. The only significant difference between biofilm and stomach

Table 3: Results of two-way Ancova calculated for the growth of the juveniles on different food sources in 2010. Asterisks indicate the significance level (**<math> < 0.001</math>, ** 0.001-0.01, * 0.01-0.05)

	<i>p</i> -value	<i>df</i>	<i>F</i> -value
Day	< 0.001	***	1 432.608
Food	0.735	2	0.310
Day x food	0.553	2	0.596

VI – Nutritional ecology

content is that on both sampling sites, *L. benedeni* avoided the inorganic material and preferred the small organic. This small organic matter could also originate from the water column (seston). While looking on the diatom community (Fig. 4), one can see that *L. benedeni* clearly fed on other food sources than the biofilm, too. The avoidance of inorganic material (sand, silicate), especially the large particles, is not surprising because of the lacking nutrients.

Natural biofilm, biodeposited material from *D. polymorpha*, as well as an algae suspension suit well for the juvenile growth of *L. benedeni*. Dead adults are not sufficient, most juveniles died in this treatment. The C-N-ratio could not be the reason that the dead animals do not suit as food source, their value is comparable to the algae and the biodeposited material (Tab. 1). The high carbon content of the biofilm could be caused by the containing inorganic carbon (carbonate), because only elementary carbon was measured.

The finding that (in the temperature experiments) the juveniles grown at 15 and 20° C (Tab. 2) had the same body length after 36 days is probably caused by the fact, that they reached maturity during the experiments (at about 5.5 mm, Hanselmann et al. 2011b). They therefore stopped their length growth and started to invest their main energy in reproduction. To transfer now the results from the relationship between temperature and growth rate to the growth rate with other food sources, is not possible. It is known from other mysids, that food with different nutrients have a different influence e.g. on the duration of the single moulting states of mysids and therefore on the growth rate (Gorokhova 2002), a phenomenon also known from zooplankton (Masclaux et al. 2009, Martin-Creuzburg et al. 2011, McFeeters & Frost 2011).

The fact that *L. benedeni* fed with a suspension of algae and *Artemia*, the only successful treatment with food of animal origin, showed a slightly higher SGR (Tab. 2), should not be overestimated. We are not sure that *L. benedeni* really fed predatory, because *Artemia* nauplii die after 3-4 h living in freshwater. It could also be possible that *L. benedeni* only fed on the dead *Artemia* lying on the ground of the glass. For this reason (and because *Artemia* has no natural occurrence in Lake Constance), the data from the experiments with *Artemia* could not be transferred to the field. In only three of 75 analysed stomachs collected in the field, fragments of animal species (Rotatoria, Fig. 4)) were

found. From other studies, it is known that mysids do not shred their food in a way that no identifiable structures remain. In stomachs from *Hemimysis anomala* (Borcherding et al. 2006) and *Mysis relicta* (Lehtiniemi et al. 2009), two predatory pelagic mysids, several zooplanktic species could be identified. In laboratory experiments with *L. benedeni*, the mysids were able to feed on *Daphnia*, but in choice with *S. obliquus* they prefer the green algae (Fink et al. 2012). This was supported by field observations that *L. benedeni* does not have a structuring effect on the zooplankton distribution (Lesutiene et al. 2005). So we conclude that in the field, *L. benedeni* feeds on small organic matter like algae (seston), biofilm, detritus, and biodeposited material from *D. polymorpha* or other benthic food sources up to a maximum diameter of about 200 µm. It seems that they have no ability or no need to compete for small zooplankton with other species, for example juvenile fish like *Perca fluviatilis* (D. Schleuter & Eckmann 2008) or predatory zooplankton like *Bythotrephes longimanus* (Straile & Hälbich 2000). Animal food seems to be more valuable, but is not the preferred one in the field. Another explanation could be a trade-off between hunting costs (food availability) and benefits (nutrient composition). In the littoral of Lake Constance, biofilm and algae are always available in high numbers. In addition, *L. benedeni* prefers a habitat where benthic food is best available (Gergs et al. 2008).

The feeding mode experiments in the laboratory confirm this feeding strategy. For the mysids, it makes not really a difference if the food is given as biofilm grown on tiles or as a suspension, which means distributed in the water column (Fig. 3a). *L. benedeni* is obviously able to feed on both benthic and pelagic food sources. The feeding mechanism is on the one side filtering the water column, on the other dispersing material from the ground. The way mysids could feed on sedimented material is described with *Mysis relicta*. In video analyses from submersible dives, Bowert et al. (1990) showed that mysids can swirl up the sediment with a stroke of their abdomen. They could also generate a current of water with their pereopods (Mauchline 1980, Hanselmann, personal observations). With their feeding activity over the ground, mysids are able to bioturbate the sediment and therefore improve the oxygen conditions in the sediment (Lindström & Sandberg-Kilpi 2008). This could be of great importance if lakes impend to become anoxic layers as a

VI – Nutritional ecology

reason of eutrophication. We suppose that *L. benedeni* is also able to resuspend benthic material in the water column and hereby increase the nutrient availability for planktic organisms as other mysids do (Lindén & Kuosa 2004), but this hypothesis will need further investigations.

In consuming planktic algae and biofilm, *L. benedeni* surely changed the nutrient availability in the littoral of Lake Constance since their massive establishment. It could be of great concern for zooplankton studies to focus on the question if possible competitors like *Daphnia* (Martin-Creuzburg et al. 2011) show changing in their life cycle or abundance in the last 5 years. In addition, the feeding on biofilm will surely affect the concerning community who consists of bacteria, fungi, algae, meiobenthos and other organisms (Peters & Traunspurger 2005, Hempel et al. 2009). Which effects the interventions of the mysids on this food web have is of great interest for understanding degradation processes and nutrient recycling (microbial loop) in a lake. As it is known that the juvenile perch in Lake Constance fed well on *L. benedeni* (Hanselmann et al. 2011b), long-term observations should be done to detect if the fish benefit from this new food source or if this effect will be negated (as it is a very often case (Arbaciauskas et al. 2010)) because *L. benedeni* only replaces the native prey (Eckmann et al. 2008).

In sum, *L. benedeni* has the potential to play an important role in the trophic relations in Lake Constance, via “bottom-up” mechanisms as well as via “top-down” control, and it seems necessary to further follow up and examine these processes.

Acknowledgments

We thank Monika Friedel and Stephan Rimmele for their help in the field and Karen A. Brune for editing the English language.

Chapter VII

General Discussion

Since its first discovery in Lake Constance in 2006, the freshwater mysid *L. benedeni* spread over the whole lake within 2-3 years. It has established a stable population in the littoral of the whole lake, reaching high biomasses and abundances. Like the majority of alien species in Lake Constance (**Chapter II**), the species originated in the ponto-caspian region. Perhaps its continuing dispersion and rapid establishment was forced and supported by the mussel *Dreissena polymorpha* that previously invaded Lake Constance. The “invasive meltdown theory” describes the phenomenon that one invaded species can benefit from the presence of an other one that beforehand has decreased the resistance potential of an ecosystem (Simberloff 2006). In such a case, adjustment processes to the new ecosystem can be easier, especially when the species “know” each other from their origin region. *D. polymorpha* is a wide-spread and common alien species (Nalepa & Schloesser 1993) and an active and important filter feeder, which produces nutrient rich pseudofaces (Gergs et al. 2009). In this work, I can show that *L. benedeni* benefits from this organic material (Chapter VI). In general, *L. benedeni* prefers a habitat with *D. polymorpha* in it (Gergs et al. 2008). For *Dikerogammarus villosus*, a ponto-caspian amphipod found in Lake Constance since 2003 (Mürle et al. 2004), a comparable behavior is described (Gergs & Rothhaupt 2008a); this species is also said to simplify the establishment of new species on an ecosystem (Ricciardi 2001, Dick et al. 2002). The finding that most of the latest invaders were first found in the eastern part of Lake Constance points out the importance of identifying the introduction ways. It is conspicuous that human activities are responsible, but no mechanism was clearly identified until now (Hanselmann 2011a). Only if we know the mechanisms, politics and society are able to establish rules that slow or avoid further invasions (Strayer & Dudgeon 2010). The increase in new findings in the last years emphasizes the importance of these projects.

VII – General discussion

In our field studies, we successfully described the life-cycle characteristics of *L. benedeni* (**Chapter III and IV**). The size class distribution and the reproductive pattern indicated that the life cycle of *L. benedeni* changes seasonally. During winter (November to March), the mysid invests energy in growth and delays reproduction until April, when the population is dominated by adults. In summer (June to September), the adults reproduce at a smaller body size and the population is disproportionately dominated by juveniles. The clutch size correlates well with the body length and is therefore larger in spring. The number of clutches per females during the reproduction period was not examined, but it is evident that *L. benedeni* reproduces continuously during summer and not in cohorts. The importance of predation by fish in the field was shown with a mesocosm experiment that excluded fish predators (Chapter III). The mysids followed the same seasonal patterns of growth and energy investment as in the field population, but the size class distribution differed. Even in summer, adults dominated the population in the mesocosm. We verified this with stomach analyses of *Perca fluviatilis* (perch) from the field. The 0+ perch fed well on *L. benedeni* with a significant preference for the larger mysids.

These two findings (high mortality of the summer adults and seasonal life-cycle shift) should be explained in different ways. Our results suggest that population losses via predation are the reason for the dominance of juveniles and the observed size class distribution in summer. In contrast, the smaller size at maturity in summer is a physiological adaptation, perhaps evolved to avoid the predation (as it is known from other species (Johnson & Belk 2001, Hilton et al. 2002)) or as a reaction on higher respiration losses with warmer temperatures. The laboratory studies on the embryonic development time (**Chapter IV**) confirm the importance of the environmental water temperature on the life cycle of the mysid. The determined temperature-development equation serves well for the temperatures in Lake Constance during the reproduction period of the mysids (6.5 – 25° C). It is not known if the temperature is a reason or a trigger for the seasonal life-cycle change, this question needs further investigations. It could be evolved e.g. as a reaction on metabolic losses at higher temperatures or to avoid predation. With this equation, we were able to estimate the mortality rates in the field (**Chapter V**) to quantify the high losses of adult mysids in summer in the field compared to the numbers of adults in the

mesocosm. The high mortality rates of *L. benedeni* correlated well with the appearance of juvenile perch in the littoral and therefore support the hypothesis that fish predation is an important trigger for life-cycle adaptations. If the predator affects the population via behavioural or physiological mechanisms (Beckermann et al. 2007) is also of high interest. In addition, it is an important and interesting finding that the formula by Edmondson (1971) and Paloheimo (1974) for calculating the instantaneous birth rate in zooplanktic species serves well for a nekto-benthic species like *L. benedeni*. In Chapter III and V, we showed that the species meets well the preconditions the formula requires. It becomes apparent that despite the small amount of sexually mature females in July, the reproduction rate is high enough for maintaining a population. Immigration is not necessary and unequal spatial distribution patterns were not observed. All examined population samples for the different purposes, taken at the same time but at distances of up to several hundred meters, had comparable age- and size class compositions.

One missing detail on the autecology and the ecological impact of *L. benedeni* was the feeding behavior. We examined it with stomach analyses and laboratory growth experiments with different natural food sources (**Chapter VI**). In Lake Constance, *L. benedeni* mainly fed on small organic material; no significant predatory impact was found. Even though the mysid is able to hunt small zooplankton in laboratory experiments (Gergs et al. 2008, Fink et al. 2012), animal food plays no role in their feeding behavior in the field. We found fragments of Rotatoria in only 2% of all counted stomachs. The organic material in the stomachs consisted mainly of algae from benthic and pelagic origin with the diatoms as the most important group. In comparison with the natural food sources, *L. benedeni* fed non-selective on organic particles smaller than ~ 200 µm both by filtering or grazing. They fed well on biofilm in the field as well as in laboratory growth experiments and we suppose a high disturbance potential of the mysid on the biofilm community. Pelagic mysids are known to force the benthic-pelagic coupling e.g. by transfer of organic matter by their migration behaviour (Lesutiene et al. 2008, Sato & Jumars 2008). We suppose that also *L. benedeni* affects this mechanism, although in a different scale. Biofilm is an important part of the lakes' nutrient cycle (microbial loop), and *L. benedeni* will probably affect the degradation processes of detritus and the

VII – General discussion

recycling of the essential elements. The semi-pelagic species *Mysis relicta* is known to improve benthic oxygen conditions via bioturbation over ground (Lindström & Sandberg-Kilpi 2008), a behavior that we could also observe for *L. benedeni*. By feeding on benthic and (sedimented) pelagic organic material in such enormous abundances in the littoral, *L. benedeni* could directly cause changes in the microbial community as well as in an indirect way in the planktic community. Additionally, they compete with other makrozoobenthos like amphipods. In Lake Constance, the native *Gammarus roeselii* and the invasive *Dikerogammarus villosus* both feed well on biodeposited material from *D. polymorpha* (Gergs & Rothhaupt 2008b), which is also used by *L. benedeni*. Another indication for the omnivory of *L. benedeni* is that the artificial green algae suspension in our growth experiments also served well for the juveniles. All these potential food sources were available (in parts) in Lake Constance during the whole year. This leads me to the assumption that the adults in summer (Chapter III), that are smaller than in winter and spring, are not bottom-up limited. This life-cycle shift was not caused by food limitation, and I can support the thesis that it is a physiological adaptation.

The mysids on their part were used as a food source by fishes. In the beginning of the 20th century, one tried to enhance the fish production of lakes by introducing alien mysids, especially in Eastern Europe. *L. benedeni* was introduced in Lake Balaton around 1950, for example (Wonyárovich 1955). The establishment was comparable to the findings from Lake Constance; they spread over the whole lake within three years and established high biomasses. The author supposed that the fishes profit from the new food source, but no data were published later. The semi-pelagic mysid *Mysis relicta* was introduced in many lakes in Sweden and North America, but no clear profit for the fish communities was found. In some lakes, fish grew larger and the yield was higher, but in other lakes, the mysids caused a massive decline of the fish population (Lasenby et al. 1986). In Flathead Lake in the western United States, the introduction caused a massive change in species composition of the whole ecosystem. The conspicuous findings were the effects over several trophic stages from zooplankton over kokanee to high predators like bald eagles and bears; the introduction of *M. relicta* caused a massive decline of all these species (Ellis et al. 2011). A comparative study in Lithuania on the effect of the

mysid introductions (*Paramysis lacustris*, *L. benedeni* and *Hemimysis anomala*) on the fish community in 13 lakes does not support the enhancement of fish production in Lithuanian lakes. Although the selected model fish (perch) assimilated the introduced species into diet and sometimes in large quantities, there was no subsequent influence on somatic growth rates when compared with perch from lakes without alien mysids (Arbaciauskas et al. 2010). As seen in Chapter II, the perch fed well on *L. benedeni* in Lake Constance, but at this stage of our research, no reliable statement for the long-term effects can be given. In further studies, the predation of perch on *L. benedeni* has to be quantified, and we should examine if *L. benedeni* suits as rich food source for perch. A new food source does not always have to result in higher growth or biomass of the perch. If *L. benedeni* serves well as food source, it could also have no significant effect on the perch because they only replace the natural food source. After the replacement of the native amphipod *Gammarus roeselii* with invasive *D. villosus* in Lake Constance, the perch switched to the new amphipod, but the amphipod proportion in the stomachs did not change (Eckmann et al. 2008). From my studies, I state that, as a reason of their feeding mode, *L. benedeni* will not cause a massive decline of the fish community as it is described for *M. relicta*. But I also suppose that the effect on the growth of the perch, if there is any, will be small in both ways, negative or positive. Perhaps the perch will profit from the new food source, but it could be that the effect will be negated because *L. benedeni* only replaces other prey species.

As *L. benedeni* is well adapted to the climate regime in Middle Europe, its continuing invasion to South and Western Europe (Wittmann & Ariani 2008) will be successful and the species can capture many new ecosystems. In sum, *L. benedeni* has the potential to play an important role in the trophic relations in Lake Constance, via “bottom-up” mechanisms as well as via “top-down” control, and it seems necessary to further follow up and examine these processes. The impact of *L. benedeni* as an invasive species is more caused in indirect respective more hidden ways, no spectacular effects or mechanisms were found. Nevertheless, the introduction of the mysid can cause massive changes in an ecosystem, and it is never possible to reliably forecast the effects by this invasive species.



Summary

Summary

The numbers of alien species in freshwater systems and their detrimental impacts on the stability of ecosystems and global species diversity are increasing. The introduction of alien species leads to changes in species composition inter alia. Functional traits of the biota thereby also change, which in turn will likely alter ecosystem processes, e.g. by modifying the availability, capture, and use of nutrients or by affecting the feeding relationships (trophic structure) within a community. To predict and assess such impacts, a thorough knowledge of the autecology and life cycle of the alien species is required. The mysid *Limnomysis benedeni*, one of the most important ponto-caspian invaders, was found in Lake Constance (southern Germany) in 2006. Since 1958, 14 alien species of the makrozoobenthos have invaded the littoral of Lake Constance. About 1/3 of the species belong to the Peracarida (including Amphipoda, Isopoda and Mysida), 1/3 to the Mollusca (Gastropoda and Bivalvia) and the last 1/3 to other groups of the makrozoobenthos. The main part of the alien species originated in the ponto-caspian region and it is remarkable that formerly, their first records were mainly made in the Upper Lake Constance, but since 10 years has shifted to bay of Bregenz.

The aim of the study was to gain knowledge on the possible impacts of *L. benedeni* on the littoral of Lake Constance. *L. benedeni* was not a well examined species, so basic studies on the autecology were necessary first. Studies on the life-cycle strategies over an entire seasonal cycle, addressing factors (predation, temperature) which we expected to be most important triggers of the observed changes, indicated that the size class distribution and the reproductive pattern of *L. benedeni* changes seasonally. During winter (November to March), the mysid invested energy in growth and delayed reproduction until April, when the population was dominated by adults. In

Summary

summer (June to September), the adults reproduced at a smaller body size and the population was disproportionately dominated by juveniles. In a mesocosm experiment that excluded fish predators, the mysids followed the same seasonal patterns of growth and energy investment as in the field population, but the size class distribution differed. Even in summer, the population in the mesocosm was dominated by adults. Stomach analyses of fish showed that *L. benedeni* is preyed upon by juvenile *Perca fluviatilis* in summer, which fed size selectively on larger mysids. Because of the smaller size at maturity, we state that the adults in summer really showed a physiological adaptation on the season, perhaps evolved to avoid predation or as a reaction on metabolic losses at higher temperatures, but the shifted length distribution was probably caused by the high fish predation.

L. benedeni shows a distinct dependency of the development time of the brood on water temperature. In laboratory experiments under controlled conditions, we determined embryonic development times and the probability of survival of the females and juveniles at water temperatures ranging from 4° to 25° C. At 6.5° and 25° C, the probability of survival of both the females and the larvae was lower than at 10°, 15°, or 20° C. With the determined equation for the development time as a function of water temperature, it was now possible to estimate population rates, e.g. birth and mortality rates. Direct field measurements of the main population characteristics (abundance, biomass, clutch size, sex ratio) were combined with general ecological equations developed for species with other ecological behaviours. *L. benedeni* reproduces continuously instead of producing cohorts, with high, fluctuating abundances. We estimated instantaneous mortality rates of *L. benedeni* in the littoral by calculating instantaneous birth population growth rates. The formulae used served well for the estimations. During the reproduction period in summer, the instantaneous mortality rate was high, but the instantaneous birth rate was high enough to balance the population growth rate. The instantaneous mortality rates reinforced the known life-cycle patterns of *L. benedeni* and confirmed the assumption that the life-cycle shift in summer is an adaptation to high predation on the population by fish.

The feeding mode and food preference of adult *L. benedeni* collected from the field and from laboratory feeding experiments were examined by

analysing their stomach contents. In a second setup with two sets of laboratory growth experiments, we determined the growth of juveniles by feeding newly hatched juveniles with different natural food sources at different water temperatures. The stomach analyses showed clearly that *L. benedeni* fed non-selective on organic particles smaller than ~ 200 µm both by filtering or grazing. They fed well on biofilm in the field as well as in laboratory growth experiments and we suppose a high disturbance potential of the mysid on the biofilm community. As a reason of their feeding mode, we conclude that *L. benedeni* has no predatory impact on zooplankton in the field and probably affects nutrient cycles in the littoral. *L. benedeni* seems to be a good food source for perch, but will not cause a massive decline of the fish community as it is describes from other mysids. However, the effect on the perch growing, if there is any, will be small in both ways, negative or positive. Perhaps the perch will profit from the new food source, but it could be that the effect will be negated because *L. benedeni* only replaces other prey species.

With this study, we contribute a huge step in understanding freshwater mysid ecology, life-cycle physiology and population dynamics. In sum, *L. benedeni* has the potential to play an important role in the trophic relations in the littoral, via “bottom-up” mechanisms as well as via “top-down” control, and will persist an important invasive species in Europe.



Zusammenfassung

Die Zahl der invasiven Arten in Süßgewässern und ihr störender Einfluss auf die Stabilität von Ökosystemen und die globale Artendiversität nimmt immer mehr zu, und ihre Einschleppung führt oft zu Veränderungen in der Artengemeinschaft. Da sich hierbei die funktionellen Beziehungen der Biota verändern, ändern sich auch die Prozesse innerhalb eines Ökosystems (z. B. Verfügbarkeit und Nutzung von Nahrung und Nährstoffen oder die Fraß-Beziehungen und damit die trophische Struktur einer Gemeinschaft). Um diese Auswirkungen vorhersagen und bewerten zu können, ist ein tiefer gehendes Wissen über die Autökologie und den Lebenszyklus der eingewanderten Arten nötig. Die Mysida *Limnomysis benedeni*, eine der wichtigsten Invasoren, die aus der Ponto-caspis stammen, wurde 2006 zum ersten Mal im Bodensee (Süddeutschland) entdeckt. Seit 1958 haben sich 14 fremde Arten des Makrozoobenthos im Litoral des Bodensees etabliert. Ungefähr 1/3 davon gehören zu den Peracarida (welche die Amphipoda, Isopoda und Mysida einschließen), 1/3 zu den Mollusca (Gastropoda und Bivalvia) und das letzte Drittel besteht aus den restlichen Gruppen des Makrozoobenthos. Der Hauptteil der fremden Arten stammt aus der Ponto-caspis, und es ist bemerkenswert, dass der Ort des Erstfundes anfangs vor allem im Obersee lag, seit 10 Jahren jedoch in der Bucht von Bregenz.

Ziel der Studie war es, die möglichen Auswirkungen von *L. benedeni* auf das Litoral des Bodensees zu untersuchen. Über *L. benedeni* war bisher nicht viel bekannt, und so war es nötig, mit grundlegenden Studien über die Autökologie der Art zu beginnen. Untersuchungen zum jahreszeitlichen Lebenszyklus, mit Schwerpunkt auf Faktoren, die wir als die wichtigsten Ursachen der Veränderungen einschätzten (Prädation und Temperatur), zeigten, dass die Größenklassenverteilung und die Reproduktion saisonal unterschiedlich sind. Im Winter (November bis März) investieren die Mysida ihre Energie in Wachstum und stellen bis April die Reproduktion ein. Ab April

Zusammenfassung

dominieren dann die adulten Tiere die Population. Die Adulten vermehren sich im Sommer (Juni bis September) schon bei einer kleineren Körpergröße und die Juvenilen dominieren die Population überproportional. In einem Mesokosmos-Experiment unter Ausschluss von Fisch-Prädation waren Wachstum und Energieinvestition der Adulten vergleichbar zur Freilandpopulation, nur die Verteilung der Größenklassen unterschied sich deutlich. Auch im Sommer dominierten die adulten Tiere die Population. Bei Magenanalysen von juvenilen Flussbarschen (*Perca fluviatilis*) im Sommer zeigte sich, dass diese *L. benedeni* gefressen hatten und dabei die größeren Tiere bevorzugten. Aufgrund ihrer geringeren Größe bei der Geschlechtsreife schlussfolgern wir, dass die Adulten im Sommer damit eine physiologische Anpassung an die Jahreszeit zeigen. Der Grund könnte die Vermeidung der Prädation sein oder eine Reaktion auf erhöhte Stoffwechselraten bei höheren Temperaturen. Die verschobene Größenklassenverteilung könnte jedoch durch die hohe Prädation der Fische verursacht sein.

Die Entwicklungsdauer der Larven von *L. benedeni* hängt deutlich mit der Temperatur zusammen. In kontrollierten Laborexperimenten wurden Entwicklungszeiten und Überlebensraten bei Temperaturen zwischen 4° und 25° C gemessen, wobei sowohl die Überlebensraten der Juvenilen als auch die der Weibchen bei 6,5° und 25° C niedriger waren als bei 10°, 15°, oder 20° C. Der ermittelte Zusammenhang zwischen Entwicklungsdauer und Wassertemperatur ermöglicht nun eine Abschätzung verschiedener Populationsraten wie Geburtenrate oder Mortalitätsrate. Dazu wurden wichtige Populationsparameter (wie Abundanz, Biomasse, Gelegegröße, Geschlechterverhältnis) mit Berechnungsmethoden für bereits etablierte Arten kombiniert. Das Besondere dabei ist, dass diese Arten eine andere ökologische Klassifizierung als *L. benedeni* haben. *L. benedeni* pflanzt sich mit hohen, aber schwankenden Abundanzen kontinuierlich fort und bildet keine Kohorten. Wir berechneten die momentane Mortalitätsrate von *L. benedeni* im Litoral mit Hilfe der Formeln für die momentane Geburtenrate und der Populationswachstumsrate, welche dafür gut geeignet waren. Während der sommerlichen Reproduktionsphase war die momentane Geburtenrate hoch genug, um die momentane Mortalitätsrate auszugleichen und das Populationswachstum zu stabilisieren. Der Verlauf der Mortalitätsrate bestätigt

den bisher bekannten Lebenszyklus von *L. benedeni* und stützt die Annahme, dass die Änderung der Lebenszyklusstrategie im Sommer eine Anpassung an die hohe Fisch-Prädation ist.

Mit Magenanalysen wurde die Art der Nahrungsaufnahme und die Futterpräferenz adulter *L. benedeni* aus dem Freiland und aus Laborversuchen untersucht. In einem zweiten Schritt wurden die Wachstumsraten von juvenilen *L. benedeni* bestimmt. Dabei wurden in zwei Durchgängen verschiedene natürliche Futtersorten bei mehreren Wassertemperaturen an Juvenile, die einen Tag alt waren, verfüttert. Die Magenanalysen zeigten deutlich, dass *L. benedeni* sowohl filtrierend als auch weidend unselektiv feines organisches Material kleiner als ~ 200 µm frisst. Da sie Biofilm sowohl im Freiland als auch im Labor gerne annehmen, vermuten wir vielfältige Störungen der Biofilmgemeinschaft durch die Mysida. Eine wichtige Schlussfolgerung aus ihrer Art der Nahrungsaufnahme ist, dass *L. benedeni* keinen Prädationsdruck auf Zooplankton im Freiland ausübt, jedoch wahrscheinlich die Nährstoffzyklen im Litoral beeinflusst. *L. benedeni* scheint für Flussbarsche eine geeignete Nahrungsquelle zu sein, und wird wahrscheinlich keine solch dramatischen Einbrüche der Fischgemeinschaft verursachen, wie es für andere Mysida bekannt ist. Der Effekt auf das Fischwachstum, sowohl negativer als auch positiver Art, wird gering sein. Die Flussbarsche könnten nur von der neuen Nahrungsquelle profitieren, solange *L. benedeni* nicht einfach ihre bisherige Beute ersetzt.

Mit dieser Studie tragen wir einen großen Beitrag zum Verständnis der Autökologie, dem Lebenszyklus und den Populationsdynamiken von Süßwasser-Mysida bei. *L. benedeni* hat das Potential eine wichtige Rolle in den trophischen Beziehungen des Litorals zu spielen, entweder durch „bottom-up“ oder „top-down“ Mechanismen. Die Art wird sich als eine wichtige invasive Spezies in Europa etablieren.



References

- Adrian, R., O'Reilly, C.M., Zagarese, H., Baines, S.B., Hessen, D.O., Keller, W., Livingstone, D.M., Sommaruga, R., Straile, D., Van Donk, Ellen, Weyhenmeyer, G.A. & Winder, M. (2009) Lakes as sentinels of climate change. *Limnology & Oceanography*, 54, 2283-2297.
- Alonso, A. & Castro-Díez, P. (2008) What explains the invading success of the aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca)? *Hydrobiologia*, 614, 107-116.
- ANEBO (2011) Arbeitsgruppe Aquatische Neozoen im Bodensee, www.neozoen-bodensee.de. *letzter Abruf Dezember 2011*.
- Arbaciauskas, K., Rakauskas, V. & Virbickas, T. (2010) Initial and long-term consequences of attempts to improve fish-food resources in Lithuanian waters by introducing alien peracaridan species: a retrospective overview. *Journal of Applied Ichthyology*, 26, 28-37.
- Aßmann, C., Von Elert, E. & Gergs, R. (2009) Effects of leaf litter and its fungal colonization on the diet of *Limnomysis benedeni* (Crustacea: Mysida). *Hydrobiologia*, 636, 439-447.
- Atkinson, D. & Hirst, A.G. (2007). Life histories and body size. In: *Body Size: The Structure and Function of Aquatic Ecosystems*. A.G. Hildrew & D.G. Raffaelli & R. Edmonds-Brown. Cambridge University Press, Cambridge 356.
- Audzijonyte, A., Daneliya, M.E. & Väinölä, R. (2006) Comparative phylogeography of Ponto-Caspian mysid crustaceans: isolation and exchange among dynamic inland sea basins. *Molecular Ecology*, 15, 2969-2984.
- Audzijonyte, A., Wittmann, K.J., Ovcarenko, I. & Väinölä, R. (2009) Invasion phylogeography of the Ponto-Caspian crustacean *Limnomysis benedeni* dispersing across Europe. *Diversity and Distributions*, 15, 346-355.

References

- Audzijonyte, A., Wittmann, K.J. & Väinölä, R. (2008) Tracing recent invasions of the Ponto-Caspian mysid shrimp *Hemimysis anomala* across Europe and to North America with mitochondrial DNA. *Diversity and Distributions*, 14, 179-186.
- Bacescu, M. (1954) Crustacea: Mysidacea. *Fauna Republicii Populare Romine*, 4, 1-126.
- Baltz, C. (1990). Autecology. In: *Methods for Fish Biology*. C.B. Schreck & P.B. Moyle. American Fisheries Society, Bethesda, Maryland, USA. 585-607.
- Basen, T., Martin-Creuzburg, D. & Rothhaupt, K.O. (2011) Role of essential lipids in determining food quality for the invasive freshwater clam *Corbicula fluminea*. *Journal of the North American Benthological Society*, 30, 653-664.
- Bäuerle, E., Ollinger, D. & Ilmberger, J. (1998) Some meteorological, hydrological, and hydrodynamical aspects of Upper Lake Constance. *Archiv für Hydrobiologie Special Issues Advances in Limnology*, 53, 31-83.
- Beckermann, A.P., Wieski, K. & Baird, D.J. (2007) Behavioural versus physiological mediation of life history under predation risk. *Oecologia*, 152, 335-343.
- Begon, M.E., Harper, J.L. & Townsend, C.R. (1998) *Ökologie*, Spektrum, Akademischer Verlag, Heidelberg, Berlin.
- Benard, M.F. (2004) Predator-induced phenotypic plasticity in organisms with complex life histories. *Annual Review of Ecology, Evolution, and Systematics*, 35, 351-373.
- Bennett, W.N. & Boraas, M.E. (1989) An experimental test of the egg-ratio method with instantaneous birth rate as an independent variable. *Limnology & Oceanography*, 34, 1120-1125.
- Bernauer, D. & Jansen, W. (2006) Recent invasions of alien macroinvertebrates and loss of native species in the upper Rhine River, Germany. *Aquatic Invasions*, 1, 55-71.
- Bij de Vaate, A., Jazdzewski, K., Ketelaars, H.A.M., Gollasch, S. & Van der Velde, G. (2002) Geographical patterns in range extension of Ponto-

- Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 1159-1174.
- Bogut, I., Galir, A., Cerba, D. & Vidakovic, J. (2007) The Ponto-Caspian invader, *Limnomysis benedeni* (Czerniavsky, 1882), a new species in the fauna of Croatia. *Crustaceana*, 80, 817-826.
- Borcherding, J., Hermasch, B. & Murawski, P. (2007) Field observations and laboratory experiments on growth and lipid content of young-of-the-year perch. *Ecology of Freshwater Fish*, 16, 198-209.
- Borcherding, J., Murawski, S. & Arndt, H. (2006) Populations ecology, vertical migration and feeding of the Ponto-Caspian invader *Hemimysis anomala* in a gravel-pit lake connected to the River Rhine. *Freshwater Biology*, 51, 2376-2387.
- Boscarino, B.T., Rudstam, L.G., Eillenberger, J.L. & O`Gorman, R. (2009) Importance of light, temperature, zooplankton and fish in predicting the nighttime vertical distribution of *Mysis diluviana*. *Aquatic Biology*, 5, 263-279.
- Bößnek, U. (1997) Verbreitung und Ökologie in Thüringen eingeschleppter oder eingewanderter Süßwassermollusken (Mollusca: Gastropoda, Bivalvia). *Thüringer faunistische Abhandlungen*, IV, 5-32.
- Bowers, J.A., Cooper, W.E. & Hall, D.J. (1990) Midwater and epibenthic behaviors of *Mysis relicta* Loven: observations from the *Johnson-Sea-Link II* submersible in Lake Superior and from a remotely operated vehicle in northern Lake Michigan. *Journal of Plankton Research*, 12, 1279-1286.
- Briski, E., Bailey, S.A. & MacIsaac, H.J. (2011) Invertebrates and their dormant eggs transported in ballast sediments of ships arriving to the Canadian coasts and the Laurentian Great Lakes. *Limnology & Oceanography*, 56, 1929-1939.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, 85, 1771-1789.
- Busacker, G.P. (1990). Growth. In: *Methods for Fish Biology*. C.B. Schreck & P.B. Moyle. American Fisheries Society, Bethesda, Maryland, USA. 363-387.

References

- Carlton, J.T. & Geller, J.B. (1993) Ecological roulette: The global transport of nonindigenous marine organisms. *Science*, 261, 78-82.
- Chandra, S. & Gerhardt, A. (2008) Invasive species in aquatic ecosystems: issue of global concern. *Aquatic Invasions*, 3, 1-2.
- Chapin, F.S., Walker, B.H., Hobbs, R.S., Hooper, D.U., Lawton, J.H., Sala, O.E. & Tilman, D. (1997) Biotic Control over the Functioning of Ecosystems. *Science*, 277, 500-504.
- Chigbu, P. & Sibley, T.H. (1998) Predation by longfin smelt (*Spirinchus thaleichthys*) on the mysid *Neomysis mercedis* in Lake Washington. *Freshwater Biology*, 40, 295-304.
- Chovanec, A., Schindler, M., Pall, K. & Hostettler, K. (2010) *Bewertung des österreichischen Bodenseeufers auf der Grundlage libellenkundlicher Untersuchungen*, Institut für Umwelt und Lebensmittelsicherheit des Landes Vorarlberg & inatura Dornbirn, Bregenz.
- Costantini, M.L. & Rossi, L. (1998) Competition between two aquatic detritivorous isopods – a laboratory study. *Hydrobiologia*, 368, 17-27.
- Crawford, G. I. (1937) An amphipod, *Eucrangonyx gracilis* S. I. Smith, new to Britain. *Nature*, 139, 327.
- Crozet, B., Pedroli, J.-C. & Vaucher, C. (1980) Premières observations de *Potamopyrgus jenkinsi* (Smith) (Mollusca, Hydrobiidae) en Suisse romande. *Revue Suisse de Zoologie*, 87, 807-811.
- Davis, C.C. (1966) A study of the hatching process in aquatic invertebrates, XXII. Multiple membrane shedding in *Mysidium columbiae* (Zimmer) (Crustacea: Mysidacea). *Bulltin of Marine Science*, 16, 124-131.
- Dediu, I.I. (1966) Répartition et caractéristique écologique des Mysides des bassins des rivières Dniestr et Pruth. *Revue roumaine de Biologie / Serie de Zoologie*, 11, 233-239.
- Devin, S., Bollache, L., Noel, P.-Y. & Beisel, J.-N. (2005) Patterns of biological invasions in French freshwater systems by non-indigenous macroinvertebrates. *Hydrobiologia*, 551, 137-146.
- Dick, J.T.A. & Platvoet, D. (2000) Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. *Proceedings of the Royal Society of London, Series B*, 267, 977-983.

- Dick, J.T.A., Platvoet, D. & Kelly, D.W. (2002) Predatory impact of the freshwater invader *Dikerogammarus villosus* (Crustacea: Amphipoda). *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 1078-1084.
- Drake, D.A.R. & Mandrak, N.E. (2010) Least-cost transportation networks predict spatial interaction of invasion vectors. *Ecological Applications*, 20, 2286–2299.
- Ebert, D. (2005) *Ecology, Epidemiology, and Evolution of Parasitism in Daphnia*, National Library of Medicine (US), National Center for Biotechnology Information, Bethesda (MD).
- Eckmann, R., Mörtl, M., Baumgärtner, D., Berron, C., Fischer, P., Schleuter, D. & Weber, A. (2008) Consumption of amphipods by littoral fish after the replacement of native *Gammarus roeseli* by invasive *Dikerogammarus villosus* in Lake Constance. *Aquatic Invasions*, 3, 184-188.
- Edmondson, W.T. (1971). Reproductive rate determined indirectly from egg ratio. In: *A Manual of Methods for the Assessment of Secondary Productivity in Freshwaters*. Blackwell Scientific Publications, Oxford and Edinburgh. 165-169.
- Eggers, T.O., Martens, A. & Grabow, K. (1999) *Hemimysis anomala* SARS in the branch-canal Salzgitter, northern Germany (Crustacea: Mysidacea). *Lauterbornia*, 35, 43-47.
- Ellis, B.K., Stanford, J.A., Goodman, D., Stafford, C.P., Gustafson, D.L., Beauchamp, D.A., Chess, D.W., Craft, J.A., Deleray, M.A. & Hansen, B.S. (2011) Long-term effects of a trophic cascade in a large lake ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 1070–1075.
- Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Hülber, K., Jarosík, V., Kleinbauer, I., Krausmann, F., Kühn, I., Nentwig, W., Vilà, M., Genovesi, P., Gherardi, F., Desprez-Loustau, M.-L., Roques, A. & Pysek, P. (2011) Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 203-207.
- Essl, F. & Rabitsch, W. (2002) *Neobiota in Österreich*, Umweltbundesamt, Wien.

References

- Fiedler, W. (1988). Süßwassermollusken der Mettnau und der angrenzenden Seeteile. In: *Jahresbericht 1988 Naturschutzgebiet Halbinsel Mettnau*. Deutscher Bund für Vogelschutz (DBV), Radolfzell. 3.
- Fink, P., Kottsieper, A., Heynen, M. & Borchering, J. (2012) Selective zooplanktivory of an invasive Ponto-Caspian mysid and possible consequences for the zooplankton community structure of invaded habitats. *Aquatic Sciences*, 74, 191-202.
- Flössner, D. (1987) Populationsdynamik und Produktion von *Asellus aquaticus* (L.) und *Proasellus coxalis* (DOLLFUS) in der mittleren Saale. *Limnologica*, 18, 279-295.
- Fockedey, N., Ghekiere, A., Bruwiere, S., Janssen, C.R. & Vinex, M. (2006) Effect of salinity and temperature on the intra-marsupial development of the brackish water mysid *Neomysis integer* (Crustacea: Mysidacea). *Marine Biology*, 148, 1339-1356.
- Fockedey, N. & Mees, J. (1999) Feeding of the hyperbenthic mysid *Neomysis integer* in the maximum turbidity zone of the Elbe, Westerschelde and Gironde estuaries. *Journal of Marine Systems*, 22, 207-228.
- Fockedey, N., Mees, J., Vangheluwe, M., Verslycke, T., Janssen, C.R. & Vincx, M. (2005) Temperature and salinity effects on post-marsupial growth of *Neomysis integer* (Crustacea: Mysidacea). *Journal of experimental marine Biology and Ecology*, 326, 27-47.
- Fritz, B., Nisch, A., Wittkugel, C. & Mörtl, M. (2006) First record of *Limnomysis benedeni* Czerniavsky in Lake Constance (Crustacea: Mysidacea). *Lauterbornia*, 58, 157-160.
- Geissen, H.-P. & Schöll, F. (1998) Erste Nachweise des Fischegels *Caspiobdella fadejewi* (Epshtein 1961) (Hisudinea: Piscicolidae) im Rhein. *Lauterbornia*, 33, 11-12.
- Geiter, O., Homma, S. & Kinzelbach, R. (2002) *Bestandsaufnahme und Bewertung von Neozoen in Deutschland*, Umweltbundesamt, Berlin.
- Gentile, J.H., Gentile, S.M., Hairston, N.G. & Sullivan, B.K. (1982) The use of life-tables for evaluating the chronic toxicity of pollutants to *Mysidopsis bahia*. *Hydrobiologia*, 93, 179-187.
- Gergs, R., Grey, J. & Rothhaupt, K.-O. (2011) Temporal variation in zebra mussel (*Dreissena polymorpha*) density structure the benthic food web

- and community composition on hard substrates in Lake Constance, Germany. *Biological Invasions*, DOI 10.1007/s10530-011-9943-8.
- Gergs, R., Hanselmann, A.J., Eisele, I. & Rothhaupt, K.-O. (2008) Autecology of *Limnomysis benedeni* Czerniavsky, 1882 (Crustacea: Mysida) in Lake Constance, southwestern Germany. *Limnologia*, 38, 139-146.
- Gergs, R., Rinke, K. & Rothhaupt, K.-O. (2009) Zebra mussels mediate benthic–pelagic coupling by biodeposition and changes in detrital stoichiometry. *Freshwater Biology*, 54, 1379-1391.
- Gergs, R. & Rothhaupt, K.-O. (2008a) Effects of zebra mussels on a native amphipod and the invasive *Dikerogammarus villosus*: the influence of biodeposition and structural complexity. *Journal of the North American Benthological Society*, 27, 541-548.
- Gergs, R. & Rothhaupt, K.-O. (2008b) Feeding rates, assimilation efficiencies and growth of two amphipod species on biodeposited material from zebra mussels. *Freshwater Biology*, 53, 2494-2503.
- Gervais, M. (1835) Crevettes des environs de Paris. *Annales des sciences naturelles*, 2, 127-128.
- Ghekiere, A., Fockedey, N., Verslycke, T., Vincx, M. & Janssen, C.R. (2007) Marsupial development in the mysid *Neomysis integer* (Crustacea: Mysidacea) to evaluate the effects of endocrine-disrupting chemicals. *Ecotoxicology and Environmental Safety*, 66, 9-15.
- Gorokhova, E. (2002) Molt cycle and its chronology in *Mysis mixta* and *Neomysis integer* (Crustacea, Mysidacea): implications for growth assessment. *Journal of experimental marine Biology and Ecology*, 278, 179-194.
- Gorokhova, E. & Hansson, S. (2000) Elemental composition of *Mysis mixta* (Crustacea, Mysidacea) and energy costs of reproduction and embryogenesis under laboratory conditions. *Journal of experimental marine Biology and Ecology*, 246, 103-123.
- Guma'a, S.A. (1978) The food and feeding habits of young perch, *Perca fluviatilis*, in Windermere. *Freshwater Biology*, 8, 177-187.
- Hänfling, B. (2011) Invasive alien Crustacea: dispersal, establishment, impact and control. *BioControl*, 56, 573–595.

References

- Hanselmann, A.J. (2008) *Einfluss von Temperatur und Invertebraten-Prädation auf die Population von Limnomysis benedeni im Bodensee*, Diploma thesis, Albert-Ludwigs-University Freiburg.
- Hanselmann, A.J. (2010) *Katamysis warpachowskyi* Sars, 1877 (Crustacea, Mysida) invaded Lake Constance. *Aquatic Invasions*, 5, Supplement 1, S 31-S 34.
- Hanselmann, A.J. (2011a) *Bodenlebende Wirbellose am „Grünen Damm“ (Vorarlberger Ufer, Bodensee)*, Institut für Umwelt und Lebensmittelsicherheit des Landes Vorarlberg, Bregenz.
- Hanselmann, A.J. (2011b) A review of spatio-temporal patterns of the colonisation of Lake Constance with alien Macrozoobenthos. *Lauterbornia*, 72, 131-148.
- Hanselmann, A.J. & Gergs, R. (2008) First record of *Crangonyx pseudogracilis* Bousfield 1958 (Amphipoda, Crustacea) in Lake Constance. *Lauterbornia*, 62, 21-25.
- Hanselmann, A.J., Gergs, R. & Rothhaupt, K.-O. (2011a) Embryonic development time of the freshwater mysid *Limnomysis benedeni* Czerniavsky as a function of water temperature. *Aquatic Ecology*, 45, 539-546.
- Hanselmann, A.J., Gergs, R. & Rothhaupt, K.-O. (2011b) Seasonal shifts in the life-cycle of the ponto-caspian invader *Limnomysis benedeni* (Crustacea: Mysida) - a physiological adaptation. *Hydrobiologia*, 673, 193-204.
- Hempel, M., Grossart, H.-P. & Gross, E.M. (2009) Community composition of bacterial biofilms on two submerged macrophytes and an artificial substrate in a pre-alpine lake. *Aquatic Microbial Biology*, 5, 79-94.
- Hesselschwerdt, J., Necker, J. & Wantzen, K.M. (2008) Gammarids in Lake Constance: habitat segregation between the invasive *Dikerogammarus villosus* and the indigenous *Gammarus roeselii*. *Fundamental and Applied Limnology*, 173, 177-186.
- Hesselschwerdt, J., Tscherner, S., Necker, J. & Wantzen, K.M. (2009) A local gammarid uses kairomines to avoid predation by the invasive crustaceans *Dikerogammarus villosus* and *Orconectes limosus*. *Biological Invasions*, 11, 2133-2140.

- Hilton, C., Walde, S.J. & Leonard, M.L. (2002) Intense episodic predation by shorebirds may influence life history strategy of an intertidal amphipod. *Oikos*, 99, 368-376.
- Hofmann, F. (1970) Über das Vorkommen der Wander- oder Dreikantmuschel *Dreissena polymorpha* im Bodensee- und Hochrheingebiet. *Mitteilungen der Naturforschenden Gesellschaft Schaffhausen*, 29, 63-75.
- Hofmann, H., Lorke, A. & Peeters, F. (2008) The relative importance of wind and ship waves in the littoral zone of a large lake. *Limnology & Oceanography*, 53, 368-380.
- IGKB (2004) *Der Bodensee Zustand - Fakten - Perspektiven*, Internationale Gewässerschutzkommission für den Bodensee (IGKB), Stuttgart.
- Imbrock, F., Appenzeller, A. & Eckmann, R. (1996) Diel and seasonal distribution of perch in Lake Constance: a hydroacoustic study and *in situ* observations. *Journal of Fish Biology*, 49, 1-13.
- Institut für Seenforschung an der Landesanstalt für Umwelt Messungen und Naturschutz B.-W. (LUBW) (2010) *Limnologischer Zustand des Bodensees*, Internationale Gewässerschutzkommission für den Bodensee (IGKB), Langenargen.
- Ishikawa, M. & Oshima, Y. (1951) On the life history of a mysid crustacean *Neomysis japonica* Nakazawa. *Bull. Jap. Soc. scient. Fish.*, 16, 461-472.
- Jacobs, J. (1974) Quantitative Measurement of Food Selection. *Oecologia*, 14, 413-417.
- Johnson, J.B. & Belk, M.C. (2001) Predation environment predicts divergent life-history phenotypes among populations of the livebearing fish *Brachyrhaphis rhabdophora*. *Oecologia*, 126, 142-149.
- Johnston, N.M, Ritz, D.A. & Fenton, G.E. (1997) Larval development in the Tasmanian mysids *Anisomysis mixta australis*, *Tenagomysis tasmaniae* and *Paramesopodopsis rufa* (Crustacea: Mysidacea). *Marine Biology*, 130, 93-99.
- Josens, G., Bij de Vaate, A., Usseglio-Polatera, P., Cammaerts, R., Chérot, F., Grisez, F., Verboonen, P. & Van den Bossche, J.-P. (2005) Native and exotic Amphipoda and other Peracarida in the River Meuse: new assemblages emerge from a fast changing fauna. *Hydrobiologia*, 542, 203-220.

References

- Jungbluth, J.H. & von Knorre, D. (2008) Trivialnamen der Land- und Süßwassermollusken Deutschlands (Gastropoda et Bivalvia). *Mollusca*, 62, 105-156.
- Kaestner, A. (1967) *Lehrbuch der Speziellen Zoologie, Band I: Wirbellose 2. Teil*, Gustav Fischer Verlag, Stuttgart.
- Kelleher, B., van der Velde, G., Wittmann, K.J., Faasse, M.A. & Bij de Vaate, A. (1999) Current status of the freshwater Mysidae in the Netherlands: with records of *Limnomysis benedeni* (Czerniavsky 1882), a pontocaspian species in Dutch Rhine branches. *Bulletin Zoologisch Museum Universiteit van Amsterdam*, 16, 89-94.
- Ketelaars, H.A.M., Lambregts-van de Clundert, F.E., Carpentier, C.J., Wagenvoort, A.J. & Hoogenboezem, W. (1999) Ecological effects of the mass occurrence of the Ponto-Caspian invader, *Hemimysis anomala* G.O. Sars, 1907 (Crustacea: Mysidacea), in a freshwater storage reservoir in the Netherlands, with notes on its autecology and new records. *Hydrobiologia*, 394, 233-248.
- Kiefer, F. (1972) *Naturkunde des Bodensees*, Thorbecke, Sigmaringen.
- Kinzelbach, R. (1972) Einschleppung und Einwanderung von Wirbellosen in Ober- und Mittelrhein. *Mainzer Naturwissenschaftliches Archiv*, 11, 109-150.
- Kinzelbach, R. (1995) Neozoans in European waters - Exemplifying the worldwide process of invasion and species mixing. *Experientia*, 51, 526-538.
- Komarova, T.I. (1989) Ecological and faunistic review of mysidacea (Crustacea, Mysidae) in the sea of azov, USSR. *Vestnik Zoologii*, 4, 3-7.
- Kotta, J., Lauringson, V., Martin, G., Simm, M., Kotta, I., Herkül, K. & Ojaveer, H. (2003). Gulf of Riga and Pärnu Bay. In: *Ecology of Baltic Coastal Waters*. U. Schiewer. Springer-Verlag Berlin Heidelberg. 217-243.
- Krebs, C.J. (2001) *Ecology: The Experimental Analyses of Distribution and Abundance*, Benjamin Cummings, San Francisco.
- Kulhanek, S.A., Riccardy, A. & Leung, B. (2011) Is invasion history a useful tool for predicting the impacts of the world's worst aquatic invasive species? *Ecological Applications*, 21, 189-202.

- Laman, T.G., Daniell, D.L. & Blankespoor, H.D. (1984) The role of *Gyraulus parvus* as an intermediate host for avian schistosomes. *Proceedings of the Helminthological society of Washington*, 51, 267-269.
- Lampert, W. (1988) The relative importance of food limitation and predation in the seasonal cycle of two *Daphnia* species. *Verhandlungen der internationalen Vereinigung für Limnologie*, 23, 713-718.
- Lampert, W. & Sommer, U. (2007) *Limnoecology*, Oxford University Press, New York Oxford.
- Langeland, A., Koksvik, J.I. & Nydal, J. (1991) Impact of the Introduction of *Mysis relicta* on the Zooplankton and Fish Populations in a Norwegian Lake. *American Fisheries Society Symposium*, 9, 98-114.
- Lasenby, D.C., Northcote, T.G. & Fürst, M. (1986) Theory, Practice, and Effects of *Mysis relicta* Introductions to North American and Scandinavian Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 43, 1277-1284.
- Lehtiniemi, M., Kiljunen, M. & Jones, R.I. (2009) Winter food utilisation by sympatric mysids in the Baltic Sea, studied by combined gut content and stable isotope analyses. *Marine Biology*, 156, 619-628.
- Leighton, B. J., Zervos, S. & Webster, J. M. (2000) Ecological factors in schistosome transmission, and an environmentally benign method for controlling. *Parasitology international*, 49, 9-17.
- Lesutiene, J., Gasiunaite, Z.R. & Griniene, E. (2005) Habitat-induces heterogeneity in the Curonian Lagoon littoral assemblages: mysids, juvenile fish and plankton Crustaceans. *Acta Zoologica Lituanica*, 15, 312-323.
- Lesutiene, J., Gorokhova, E., Gasiunaite, Z.R. & Razinkovas, A. (2008) Role of mysid seasonal migrations in the organic matter transfer in the Curonian Lagoon, south-eastern Baltic Sea. *Estuarine, Coastal and Shelf Science*, 80, 225-234.
- Leuven, R.S.E.W., van der Velde, G., Baijens, I., Snijders, J., van der Zwart, C., Lenders, H.J.R. & bij de Vaate, A. (2009) The river Rhine: a global highway for dispersal of aquatic invasive species. *Biological Invasions*, 11, 1989-2008.

References

- Lindén, E. & Kuosa, H. (2004) Effects of grazing and excretion by pelagic mysids (*Mysis* spp.) on the size structure and biomass of the phytoplankton community. *Hydrobiologia*, 514, 73-78.
- Lindén, E., Lehtiniemi, M. & Viitasalo, M. (2003) Predator avoidance behavior of Baltic littoral mysids *Neomysis integer* and *Praunus flexuosus*. *Marine Biology*, 143, 845-850.
- Lindström, M. & Sandberg-Kilpi, E. (2008) Breaking the boundary — The key to bottom recovery? The role of mysid crustaceans in oxygenizing bottom sediments. *Journal of experimental marine Biology and Ecology*, 354, 161-168.
- LUBW (Ed.) (2008) *FIREBO - Fischfreundliche Renaturierung am Bodensee*, Landesamt für Umwelt, Messungen und Naturschutz B.-W. (LUBW), Langenargen.
- Manton, S.M. (1928) On the embryology of a mysid Crustacean, *Hemimysis Lamornae*. *Philosophical transactions of the Royal Society of London / B*, 216, 363-463.
- Margalef, R. (1955) Temperature and morphology in freshwater organisms. *Verhandlungen der internationalen Vereinigung für Limnologie*, 12, 507-514.
- Martens, A. & Grabow, K. (2006) *Crangonyx pseudogracilis* am Oberrhein (Crustacea: Amphipoda): ein Neozoe besiedelt erfolgreich Gewässer abseits der ausgebauten Fahrwinne. *Lauterbornia*, 58, 131-137.
- Martens, A. & Grabow, K. (2008) Das Risiko der Verschleppung neozoischer Amphipoda beim Überlandtransport von Yachten. *Lauterbornia*, 62, 41-44.
- Martin-Creuzburg, D., Wacker, A., Ziese, C. & Kainz, M.J. (2011) Dietary lipid quality affects temperature-mediated reaction norms of a freshwater key herbivore. *Oecologia*, DOI 10.1007/s00442-011-2155-1.
- Masclaux, H., Bec, A., Kainz, M.J., Desvillettes, C., Jouve, L. & Bourdier, G. (2009) Combined effects of food quality and temperature on somatic growth and reproduction of two freshwater cladocerans. *Limnology & Oceanography*, 54, 1323-1332.
- Mauchline, J. (1973) The broods of British Mysidacea (Crustacea). *Journal of the Biological Association of the UK*, 53, 801-817.

- Mauchline, J. (1980) The biology of mysids and euphausiids. *Advances in Marine Biology*, 18, 1-681.
- Mauchline, J. (1982) The predation of mysids by fish on the Rockall Trough, northeastern Atlantic ocean. *Hydrobiologia*, 93, 85-99.
- McFeeters, B.J. & Frost, P.C. (2011) Temperature and the effects of elemental food quality on *Daphnia*. *Freshwater Biology*, 56, 1447-1455.
- McLaren, I.A. (1963) Effects of Temperature on Growth of Zooplankton, and the Adaptive Value of Vertical Migration. *Journal Fisheries Research Board of Canada*, 20, 685-727.
- Mees, J., Abdulkerim, Z. & Hamerlynck, O. (1994) Life history, growth and production of *Neomysis integer* in the Westerschelde estuary (SW Netherlands). *Marine Ecology Progress Series*, 109, 43-47.
- Modlin, R.F. (1979) Development of *Mysis stenolepis* (Crustacea:Mysidacea). *The American Midland Naturalist*, 101, 250-254.
- Moog, O., Graf, W., Ofenböck, T. & Schmidt-Kloiber, A. (2008) Benthic invertebrate neozoa in Austrian rivers. *Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie*, 16, 113-116.
- Morgan, M.D. (1980) Life history characteristics of two introduced populations of *Mysis relicta*. *Ecology*, 61, 551-561.
- Mörrtl, M. (2004) *Biotic interactions in the infralittoral of Lake Constance*, PhD dissertation, University of Konstanz, Germany.
- Mörrtl, M. & Rothhaupt, K.-O. (2003) Effects of adult *Dreissena polymorpha* on settling juveniles and associated macroinvertebrates. *International Review of Hydrobiology*, 88, 561-569.
- Müller, E.-D. & Falkner, G. (1984) *Potamopyrgus jenskyi* (E. A. Smith) in Bayern (Prosobranchia: Hydrobiidae). *Heldia*, 1, 22-24.
- Murano, M. (1964) Fisheries biology of a marine relict mysid *Neomysis intermedia* Czerniavsky. IV. Life cycle, with special reference to growth. *Aquiculture (Jpn)*, 12, 109-117.
- Mürle, U., Becker, A. & Rey, P. (2004) *Dikerogammarus villosus* (Amphipoda) in Lake Constance. *Lauterbornia*, 49, 77-79.
- Nalepa, T. F. & Schloesser, D.W. (1993) *Zebra mussels: biology, impacts, and control*, Lewis Publisher, Boca Raton.

References

- Ooms-Wilms, A.L., Postema, G. & Gulati, R.D. (1999) Population dynamics of planktonic rotifers in Lake Loosdrecht, the Netherlands, in relation to their potential food and predators. *Freshwater Biology*, 42, 77-97.
- Ovcarenko, I., Audzijonyte, A. & Gasiunaite, Z.R. (2006) Tolerance of *Paramysis lacustris* and *Limnomysis benedeni* to sudden salinity changes: implications for ballast water treatment. *Oceanologia*, 48, 231-242.
- Paloheimo, J.E. (1974) Calculation of instantaneous birth rate. *Limnology & Oceanography*, 19, 692-694.
- Paunovic, M., Miljanovic, B., Simic, V., Cakic, P., Djikanovic, V., Jakovcev-Todorovic, D., Stojanovic, B. & Veljkovic, A. (2005) Distribution of non-indigenous tubificid worm *Branchiura sowerbyi* (Beddard, 1892) in Serbia. *Biotechnology and Biotechnological Equipment*, 19, 91-97.
- Peeler, E.J., Oidtmann, B.C., Midtlyng, P.J., Miossec, L. & Gozlan, R.E. (2011) Non-native aquatic animals introductions have driven disease emergence in Europe. *Biological Invasions*, 13, 1291-1303.
- Peters, L. & Traunspurger, W. (2005) Species distribution of free-living nematodes and other meiofauna in littoral periphyton communities of lakes. *Nematology*, 7, 267-280.
- Pöckl, M. (2007) Strategies of a successful new invader in European freshwaters: fecundity and reproductive potential of the Ponto-Caspian amphipod *Dikerogammarus villosus* in Austrian Danube, compared with the indigenous *Gammarus fossarum* and *G. roeseli*. *Freshwater Biology*, 52, 50-63.
- Pollux, B., Minchin, D., van der Velde, G., van Alen, T., Moon-van der Staay, S.Y. & Hackstein, J. (2003) Zebra mussels (*Dreissena polymorpha*) in Ireland, AFLP-fingerprinting and boat traffic both indicate an origin from Britain. *Freshwater Biology*, 48, 1127-1139.
- Porter, M.L., Meland, K. & Price, W. (2008) Global diversity of mysids (Crustacea-Mysida) in freshwater. *Hydrobiologia*, 595, 213-218.
- Poulin, R., Paterson, R.A., Townsend, C.R., Tompkins, D.M. & Kelly, D.W. (2011) Biological invasions and the dynamics of endemic diseases in freshwater ecosystems. *Freshwater Biology*, 56, 676-688.

- R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria.
- Rasmussen, J.B., Rowan, D.J., Lean, D.R.S. & Carey, J.H. (1990) Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 47, 2030-2038.
- Reinhardt, F., Herle, M., Dastiansen, F. & Streit, B. (2003) *Ökonomische Folgen der Ausbreitung von Neobiota*, Umweltbundesamt, Berlin.
- Reinhold, M. & Tittizer, T. (1998) *Limnomysis benedeni* Czerniavsky 1882 (Crustacea: Mysidacea): a further alien species of pontocaspian origin in the Main-Danube-Canal. *Lauterbornia*, 33, 37-40.
- Rey, P., Mürle, U., Ortlepp, J., Mörtl, M., Scheifhacken, N., Werner, S., Ostendorp, W. & Ostendorp, J. (2005a) *Wirbellose Neozoen im Bodensee*, Landesanstalt für Umweltschutz Baden-Württemberg, Karlsruhe.
- Rey, P., Ortlepp, J. & Küry, D. (2005b) *Wirbellose Neozoen im Hochrhein. Ausbreitung und ökologische Bedeutung*, Bundesamt für Umwelt, Wald und Landschaft, Bern.
- Rey, P., Teiber, P. & Huber, M. (2009) *Renaturierungsleitfaden Bodenseeufer*, Internationale Gewässerschutzkommission für den Bodensee (IGKB), Bregenz.
- Ricciardi, A. (2001) Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 2513–2525.
- Richardson, D.M. & Pysek, P. (2008) Fifty years of invasion ecology – the legacy of Charles Elton. *Diversity and Distributions*, 14, 161-168.
- Rinke, K., Huber, A.M.R., Kempke, S., Eder, M., Wolf, T., Probst, W.N. & Rothhaupt, K.-O. (2009) Lake-wide distributions of temperature, phytoplankton, zooplankton, and fish in the pelagic zone of a large lake. *Limnology & Oceanography*, 54, 1306–1322.
- Rinke, K., Hülsmann, S. & Mooij, W. (2008) Energetic costs, underlying resource allocation patterns, and adaptive value of predator-induced life-history shifts. *Oikos*, 117, 237-285.

References

- Roth, G. (1987) Zur Verbreitung und Biologie von *Potamopyrgus jenkinsi* (E.A. SMITH, 1889) im Rhein-Einzugsgebiet (Prosobranchia: Hydrobiidas). *Archiv für Hydrobiologie*, Supplement 79, 49-68.
- Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, 287, 1770-1774.
- Saltzmann, J. (1996) Ecology and life history traits of the benthopelagic mysid *Boreomysis oparva* from the eastern tropical Pacific oxygen minimum zone. *Marine Ecology Progress Series*, 139, 95-103.
- Sato, M. & Jumars, P.A. (2008) Seasonal and vertical variations in emergence behaviors of *Neomysis americana*. *Limnology & Oceanography*, 53, 1665–1677.
- Scharf, J. & Koschel, R. (2004) Distribution, abundance and life history of *Mysis relicta* (LOVÉN) in the Feldberg Lake District, Germany. *Limnologica*, 34, 199-212.
- Schleuter, A., Geissen, H.-P. & Wittmann, K.J. (1998) *Hemimysis anomala* G. O. SARS 1907 (Crustacea: Mysidacea), an euryhaline Pontocaspian mysid in the rivers Rhine and Neckar. First report for Germany. *Lauterbornia*, 32, 67-71.
- Schleuter, D. & Eckmann, R. (2006) Competition between perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*): the advantage of turning night into day. *Freshwater Biology*, 51, 287-297.
- Schleuter, D. & Eckmann, R. (2008) Generalist versus specialist: the performances of perch and ruffe in a lake of low productivity. *Ecology of Freshwater Fish*, 17, 86-99.
- Schmid, G. (1977) Eine neue Schnecke im Bodensee (*Potamopyrgus jenkinsi*). *Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Wuerttemberg*, 44/45, 358-368.
- Schmid, G. (1983). Mollusken vom Mindelsee. In: *Der Mindelsee bei Radolfzell*. J. Aufdermauer & U. Einsle. Landesanstalt für Umweltschutz Baden-Württemberg, Karlsruhe. 796.

- Schmid, G. (2002) In Baden-Württemberg eingeschleppte oder ausgesetzte Mollusken. *Jahreshefte der Gesellschaft für Naturkunde in Württemberg*, 158, 253-302.
- Schmidlin, S. & Baur, B. (2007) Distribution and substrate preference of the invasive clam *Corbicula fluminea* in the river Rhine in the region of Basel (Switzerland, Germany, France). *Aquatic Sciences*, 69, 153-161.
- Schoener, T. (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*, 51, 408-418.
- Schöll, F. (2000) Die Wassertemperatur als verbreitungsregulierender Faktor von *Corbicula fluminea* (O.F. Müller 1774). *Hydrologie und Wasserbewirtschaftung*, 44, 318-321.
- Schröder, H.G. (2008) *Schlußbericht Projekt 107: "ANeBo - Aquatische Neozoen im Bodensee"*, Interreg IIIA, <http://www.interreg.org/>, Langenargen.
- Shaw, R.F. & Bercaw, B.L. (1962) Temperature and life-span in poikilothermous animals. *Nature*, 196, 454-457.
- Shirley, S.M. & Kark, S. (2006) Amassing efforts against alien invasive species in Europe. *PLoS Biology*, 4, 1311-1313.
- Siessegger, B (1969) Vorkommen und Verbreitung von "*Dreissena polymorpha* PALLAS" im Bodensee. *Gas- u. Wasserfach (gwf), Wasser u. Abwasser*, 110, 813-814.
- Simberloff, D. (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters*, 9, 912-919.
- Sluys, R., Kawakatsu, M. & Yamamoto, K. (2010) Exotic freshwater planarians currently known from Japan. *Belgian Journal of Zoology*, 140 (Suppl.), 103-109.
- Sousa, R., Gutiérrez, J.L. & Aldridge, D.C. (2009) Non-indigenous invasive bivalves as ecosystem engineers. *Biological Invasions*, 11, 2367-2385.
- Specziár, A. (2005) First year ontogenetic diet patterns in two coexisting *Sander* species, *S. lucioperca* and *S. volgensis* in Lake Balaton. *Hydrobiologia*, 549, 115-130.

References

- Staub, R. & Ribi, G. (1995) Size-assortative mating in a natural population of *Viviparus ater* (Gastropoda: Prosobranchia) in Lake Zurich, Switzerland. *Journal of Molluscan Studies*, 61, 237-247.
- Stearns, S.C. (1989) Trade-offs in life-history evolution. *Functional Ecology*, 3, 259-268.
- Steinmann, P. (2006) *Dikerogammarus villosus* im Zürcher-Obersee, Finanzdepartement des Kantons St. Gallen, Amt für Jagd und Fischerei, Zürich.
- Stich, H.-B. & Brinker, A. (2010) Oligotrophication outweighs effects of global warming in a large, deep, stratified lake ecosystem. *Global Change Biology*, 16, 877-888.
- Stich, H.-B. & Lampert, W. (1981) Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature*, 293, 396-398.
- Stockwell, J.D. & Johannsson, O.E. (1997) Temperature-dependent allometric models to estimate zooplankton production in temperate freshwater lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 2350–2360.
- Stojaspal, F. (1975) *Potamopyrgus jenkinsi* (E.A. SMITH 1889) in Österreich. *Mitteilungen der Deutschen Malakozoologischen Gesellschaft*, 3 (28/29), 243.
- Stoll, S., Probst, W.N., Eckmann, R. & Fischer, P. (2010) A mesocosm experiment investigating the effects of substratum quality and wave exposure on the survival of fish eggs. *Aquatic Sciences*, 72, 509-517.
- Straile, D. & Hälbig, A. (2000) Life history and multiple antipredator defences of an invertebrate pelagic predator, *Bythotrephes longimanus*. *Ecology*, 81, 150-163.
- Straile, D., Jöhnk, K. & Rossknecht, H. (2003) Complex effects of winter warming on the physicochemical characteristics of a deep lake. *Limnology & Oceanography*, 48, 1432-1438.
- Strayer, D. & Dudgeon, D. (2010) Freshwater biodiversity conservation: recent programs and future challenges. *Journal of the North American Benthological Society*, 29, 344-358.
- Streble, H. & Krauter, D. (2008) *Das Leben im Wassertropfen*, Franckh-Kosmos Verlags-GmbH & Co. KG, Stuttgart.

- Sudo, H., Kajihara, T. & Noguchi, M. (2011) Life history and production of the mysid *Orientomysis robusta*: high P/B ratio in a shallow warm-temperate habitat of the Sea of Japan. *Marine Biology*, 158, 1537–1549.
- Thorpe, J.E. (1977) Morphology, physiology, behavior, and ecology of *Perca fluviatilis* L. and *P. flavescens* Mitchill. *Journal of the Fisheries Research Board of Canada*, 34, 1504-1514.
- Tittizer, T., Schöll, F., Banning, M., Haybach, A. & Schleuter, M. (2000) Aquatische Neozoen im Makrozoobenthos der Binnenwasserstraßen Deutschlands. *Lauterbornia*, 39, 1-72.
- van der Velde, G., Leuven, R.S.E.W., Platvoet, D., Bacela, K., Huijbregts, M.A.J., Hendriks, H.W.M. & Kruijt, D. (2009) Environmental and morphological factors influencing predatory behaviour by invasive non-indigenous gammaridean species. *Biological Invasions*, 11, 2043-2054.
- van Kleef, H., van der Velde, G., Leuven, R.S.E.W. & Esselink, E. (2006) *Pumpkinseed sunfish* (*Lepomis gibbosus*) invasions facilitated by introductions and nature management strongly reduce macroinvertebrate abundance in isolated water bodies. *Biological Invasions*, 10, 1481-1490.
- Vaughn, C.C. & Hakenkamp, C.C. (2001) The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology*, 46, 1431-1446.
- Vermonden, K., Leuven, R.S.E.W. & Van der Velde, G. (2010) Environmental factors determining invasibility of urban waters for exotic macroinvertebrates. *Diversity and Distributions*, 16, 1009-1021.
- Verslycke, T., Ghekiere, A., Raimondo, S. & Janssen, C. (2007) Mysid crustaceans as standard models for the screening and testing of endocrine-disrupting chemicals. *Ecotoxicology*, 16, 205-219.
- Viherluoto, M., Kuosa, H., Flinkman, J. & Viitasalo, M. (2000) Food utilisation of pelagic mysids, *Mysis mixta* and *M. relicta*, during their growing season in the northern Baltic Sea. *Marine Biology*, 136, 553-559.
- Viherluoto, M. & Viitasalo, M. (2001) Effect of light on the feeding rates of pelagic and littoral mysid shrimps: a trade-off between feeding success and predation avoidance. *Journal of experimental marine Biology and Ecology*, 261, 237-244.
- Wallace Jr., R.K. (1981) An assessment of diet-overlap indexes. *Transactions of the American Fisheries Society*, 110, 72-76.

References

- Wang, N. & Eckmann, R. (1994) Distribution of perch (*Perca fluviatilis* L.) during their first year of life in Lake Constance. *Hydrobiologia*, 277, 135-143.
- Weitere, M., Vohmann, A., Schulz, N., Linn, C., Dietrich, D. & Arndt, H. (2009) Linking environmental warming to the fitness of the invasive clam *Corbicula fluminea*. *Global Change Biology*, 15, 2838–2851.
- Werner, S. & Mörtl, M. (2004) Erstnachweis der Fluss-Körbchenmuschel *Corbicula fluminea* im Bodensee. *Lauterbornia*, 49, 93-97.
- Werner, S., Mörtl, M., Bauer, H.G. & Rothhaupt, K.-O. (2005) Strong impact of wintering waterbirds on zebra mussel (*Dreissena polymorpha*) populations at Lake Constance, Germany. *Freshwater Biology*, 50, 1412-1426.
- Werner, S. & Rothhaupt, K.-O. (2007) Effects of the invasive bivalve *Corbicula fluminea* on settling juveniles and other benthic taxa. *Journal of the North American Benthological Society*, 26, 673-6800.
- Werner, S. & Rothhaupt, K.-O. (2008) Mass mortality of the invasive bivalve *Corbicula fluminea* induced by a severe low-water event and associated low water temperatures. *Hydrobiologia*, 613, 143-150.
- Westheide, W. & Rieger, R. (1996) *Spezielle Zoologie, Erster Teil: Einzeller und Wirbellose Tiere*, Gustav Fischer Verlag, Stuttgart.
- Wiens, J.J. & Graham, C.H. (2005) Nich Conservatism: Integrating Evolution, Ecology, and Conservation Biology. *The Annual Review of Ecology, Evolution, and Systematics*, 36, 519-539.
- Wikström, S.A. & Hillebrand, H. (2012) Invasion by mobile aquatic consumers enhances secondary production and increases top-down control of lower trophic levels. *Oecologia*, 168, 175-186.
- Wittmann, K.J. (1977). Modification of Association and Swarming in North Adriatic Mysidacea in Relation to Habitat and Interacting Species. In: *Biology of Benthic Organisms*. B.F. Keegan & P. O'Ceidigh & P.J.S. Boaden. Pergamon Press, Oxford. 493-502.
- Wittmann, K.J. (1978) Adoption, replacement, and identification of young in marine Mysidacea (Crustacea). *Journal of experimental marine Biology and Ecology*, 32, 259-274.
- Wittmann, K.J. (1981a) Comparative biology and morphology of marsupial development in *Leptomysis* and other mediterranean Mysidacea

- (Crustacea). *Journal of experimental marine Biology and Ecology*, 52, 243-270.
- Wittmann, K.J. (1981b) On the breeding biology and physiology of marsupial development in mediterranean *Leptomysis* (Mysidacea: Crustacea) with special reference to the effects of temperature and egg size. *Journal of experimental marine Biology and Ecology*, 53, 261-279.
- Wittmann, K.J. (1982) Untersuchungen zur Sexualbiologie einer mediterranen Mysidacee (Crustacea), *Leptomysis lingvura* G.O Sars. *Zoologischer Anzeiger Jena*, 209, 362-375.
- Wittmann, K.J. (1984) Ecophysiology of marsupial development and reproduction in Mysidacea (Crustacea). *Oceanography and Marine Biology: Annual Review*, 22, 393-428.
- Wittmann, K.J. (1995) Zur Einwanderung potamophiler Malacostraca in die obere Donau: *Limnomysis benedeni* (Mysidacea), *Corophium curvispinum* (Amphipoda), und *Atyaephyra desmaresti* (Decapoda). *Lauterbornia*, 20, 77-85.
- Wittmann, K.J. (2002a) Further expansion of Pontocaspian Mysidacea (Crustacea) into the middle and upper Danube: first records of *Katamysis warpachowskyi* for Hungary, Slovakia and Austria with notes on the biology and ecological risk potential. *Lauterbornia*, 44, 49-63.
- Wittmann, K.J. (2002b). Krebstiere: "Schwebegarnelen" und Süßwassergarnelen (Crustacea: Mysidacea: Mysidae, Decapoda: Atyidae). In: *Neobiota in Österreich*. F. Essl & W. Rabitsch. Umweltbundesamt, Wien. 269-272.
- Wittmann, K.J. (2007) Continued massive invasion of Mysidae in the Rhine and Danube river systems, with first records of the order Mysidacea (Crustacea: Malacostraca: Peracarida) for Switzerland. *Revue Suisse de Zoologie*, 114, 65-86.
- Wittmann, K.J. (2008) Weitere Ausbreitung der pontocaspischen Schwebgarnele (Crustacea: Mysida: Mysidae) *Katamysis warpachowskyi* in der oberen Donau: Erstnachweis für Deutschland. *Lauterbornia*, 63, 83-86.

References

- Wittmann, K.J. & Ariani, A.P. (2000) *Limnomysis benedeni*: Mysidacé Ponto-Caspien nouveau pour les eaux douces de France (Crustacea, Mysidacea). *Vie et Milieu*, 50, 117-122.
- Wittmann, K.J. & Ariani, A.P. (2008) Reappraisal and range extension of non-indigenous Mysidae (Crustacea, Mysida) in continental and coastal waters of eastern France. *Biological Invasions*, 11, 401-407.
- Wittmann, K.J., Theiss, J. & Banning, M. (1999) The drift of Mysidacea and Decapoda and its significance for the dispersion in the Main-Danube system. *Lauterbornia*, 35, 53-66.
- Wolfenbarger, W.C. (1999) Influences of biotic and abiotic factors on seasonal succession of zooplankton in Hugo Reservoir, Oklahoma, U.S.A. *Hydrobiologia*, 400, 13-31.
- Wonyárovich, E. (1955) Vorkommen der *Limnomysis benedeni* Czern. im ungarischen Donauabschnitt. *Acta zoologica Academiae Scientiarum Hungaricae*, 1, 177-185.
- Woodward, G. & Warren, P. (2007). Body size and predatory interactions in freshwater: scaling from individuals to communities. In: *Body Size: The Structure and Function of Aquatic Ecosystems*. A.G. Hildrew & D.G. Raffaelli & R. Edmonds-Brown. Cambridge University Press, Cambridge 356.

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- Monika Friedel for her courage to work on her Diploma thesis under my supervision
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- all my colleges from the Limnological Institute (scientists, students, technicians,...) for the help in the field, the lab, with data analysing, manuscript correction or just for the nice coffee breaks and barbeques

- my family for all her love, criticism and support
- P for the happiness to join his life, his love, and for ZiB and our future

and all the rest I unfortunately forgot to list.

Record of achievement / Abgrenzung der Eigenleistung

Manuscripts

All Chapters were exclusively written by myself and contribution of the co-authors is mainly based on improvements and amendment statements with regard of content.

Data

Chapter II

Literature and References were exclusively collected and analysed by myself.

Chapter III & IV

Design, field sampling, sample processing and laboratory experiments were exclusively performed by me with support by René Gergs in the beginning and I exclusively analysed the collected data.

Chapter V

Design, field sampling and sample processing was exclusively performed by me except of counting the mysids, which was done by Christian Fiek. Calculations and statistical analyses were exclusively performed by myself.

Chapter IV Design and laboratory experiments were exclusively performed by me. Field sampling and stomach analyses were performed by Bettina Hodapp within the context of her Bachelor thesis under my supervision. Data analyses were exclusively performed by myself.



Curriculum vitae & Publications

Almut Johanna Hanselmann *Name*
28.11.1982 *Date of birth*
Breisach am Rhein, Germany *Place of birth*
German *Nationality*

Curriculum Vitae

Scientific career

Limnological Institute University of Konstanz Since 10/2008
Workgroup Prof. Rothhaupt

Dissertation
„Life-cycle and population ecology of the freshwater mysid
Limnomysis benedeni“

Education

Limnological Institute University of Konstanz 01/2009 – 04/2009
Workgroup Scientific diving

European Scientific Diver (ECD)

Limnological Institute University of Konstanz 11/2007 – 09/2008

Diploma thesis: „Influence of temperature and invertebrate
predation on the population of *Limnomysis*
benedeni in Lake Constance“

Albert-Ludwigs-University Freiburg 10/2002 – 09/2008

Graduation in Biology (Diploma)
Grade: excellent (1,5)

Main subject:

Limnology

Minor subjects:

Evolution biology and Ecology of Animals

Neurobiology and Physiology of Animals

French (Literature)

Merian-Schule Freiburg 09/1999 – 06/2002
Graduation: Abitur (1,7)

Martin-Schongauer-Gymnasium Breisach 09/1994 – 07/1999

Alemannen-Grundschule Schallstadt-Mengen 09/1989 – 07/1994

Curriculum vitae & Publications

Student trainees

Limnological Institute University of Konstanz 08/2008 and 11-12/2007
Counting of Macrozoobenthos as
student research assistant

IFM-Geomar Kiel 04/2005
Cruise (17 days on the Baltic Sea) with the
research ship „Alkor“

Teaching (Co-Supervisor)

Bachelor thesis Katharina Greiner-Perth (Prof. Rothhaupt)	4 months	07 – 10/2011
Research internship Nicole Ernst (Prof. Rothhaupt)	6 weeks	03 – 04/2011
Diploma thesis Monika Friedel (Prof. Rothhaupt & Prof. Eckmann)	12 months	10/2009 – 10/2010
Bachelor thesis Stephan Rimmele (Prof. Rothhaupt)	4 months	05 – 08/2010
Bachelor thesis Bettina Hodapp (Prof. Rothhaupt)	4 months	05 – 08/2010
Research assistant Cornelia Welte	40 h/month	04 – 06/2010
Research assistant Bettina Hodapp	40 h/month	09 – 10/2009
Research internship Philipp Menzel (Prof. Rothhaupt)	3 months	07 – 09/2009
Advanced course Monika Friedel und Thomas Wanke (Prof. Eckmann)	6 weeks	06 – 07/2008
Research assistant Christine Aßmann	20 h/month	02 – 03/2008
Second examiner in oral examinations by Prof. Rothhaupt (5 times)		2008 – 2011

**Scientific work and
publications**

Peer-reviewed articles

- Hanselmann A.J.**, Rothhaupt, K.-O. (2011): Embryonic development time of the freshwater mysid *Limnomysis benedeni* Czerniavsky as a function of water temperature. *Aquatic Ecology* 45: 539-546
- Hanselmann, A.J.** (2011). A review of spatio-temporal patterns of the colonisation of Lake Constance with alien Makrozoobenthos. *Lauterbornia* 72:131-148.
- Hanselmann A.J.**, Gergs R., Rothhaupt, K.-O. (2011): Seasonal shifts in the life-cycle of the ponto-caspian invader *Limnomysis benedeni* (Crustacea: Mysida): a physiological adaptation? *Hydrobiologia* 673:193-204
- Hanselmann A.J.** (2010) *Katamysis warpachowskyi* Sars, 1877 (Crustacea, Mysida) invaded Lake Constance. *Aquatic Invasions* 5, Supplement 1: S31-S34
- Hanselmann, A.J.** & Gergs, R. (2008): First record of *Crangonyx pseudogracilis* Bousfield 1958 (Amphipoda, Crustacea) in Lake Constance. *Lauterbornia* 62: 21-25
- Gergs, R., **Hanselmann, A.J.**, Eisele, I., Rothhaupt, K.O. (2008): Autecology of *Limnomysis benedeni* Czerniavsky, 1882 (Crustacea: Mysida) in Lake Constance, southwestern Germany. *Limnologica* 38: 139-146

*Non peer-reviewed articles and
symposia contributions*

Hanselmann, A.J., Rothhaupt, K.-O. (*in press*): Mysida, Amphipoda und Fische im Nahrungsnetz des Bodensees – das Beispiel „Grüner Damm“
DGL-Tagungsbericht 2011 (Weihenstephan)

Hanselmann A.J. (2011): Bodenlebende Wirbellose am „Grünen Damm“.- *Schriftenreihe Lebensraum Vorarlberg Band 61*. Institut für Umwelt und Lebensmittelsicherheit des Landes Vorarlberg, Bregenz.

Matuszak, A., **Hanselmann, A.J.**, Voigt, C.C., Gergs, R., Bauer, H.-G., Quillfeldt, P. (2011): Establishing the baseline: Are stable isotope analyses useful for assessing waterbird diets at Lake Constance?
Poster on the meeting of the DZG 2011 (Saarbrücken)

Hanselmann, A.J., Hodapp, B., Rothhaupt, K.-O. (2011): Welche Ressourcen nutzt *Limnomysis benedeni* im Bodensee?
DGL-Tagungsbericht 2010 (Bayreuth), 273-276

Friedel, M., **Hanselmann, A.J.**, Rothhaupt, K.-O., Eckmann, R. (2011): *Limnomysis benedeni* als Futterorganismus für Flussbarsche.
DGL-Tagungsbericht 2010 (Bayreuth), 300-302

Hanselmann, A.J., Gergs, R., Rothhaupt, K.-O. (2010): Life-cycle shifts of *Limnomysis benedeni* - caused by fish?
Poster at the Symposium "The Role of Littoral Processes in Lake Ecology" in Hegne (Bodensee)

Hanselmann, A.J., Rothhaupt, K.-O. (2010): Mögliche Auslöser der saisonal unterschiedlichen Lebenszyklus-Strategien von *Limnomysis benedeni*. *DGL - Tagungsbericht 2009 (Oldenburg)*, 430-432

Hanselmann, A.J., Gergs, R., Rothhaupt, K.-O. (2009): Saisonale Änderungen des Life-Cycle von *Limnomysis benedeni* im Bodensee. *DGL - Tagungsbericht 2008 (Konstanz)*: 390-392

Gergs, R., **Hanselmann, A.J.**, Aßmann, C., Rothhaupt, K.-O. (2009): Syn- und autökologische Untersuchungen von *Limnomysis benedeni* im Bodensee. *DGL - Tagungsbericht 2008 (Konstanz)*, 382-385

Invited talks and interviews

- Colloquium at the Institut für Seenforschung Langenargen (D):** 7/2011
talk on:
"Limnomysis benedeni - Erkenntnisse aus 4 Jahren
Forschung an der Donau-Schwebgarnele im Bodensee"
- Workshop of the Academy for Nature Preservation and Environmental Protection (B.-W.) in Langenargen (D):** 9/2010
"Neozoen im Bodensee – Wege zur ökonomisch-
ökologischen Schadensbegrenzung"
talk on:
"Neozoen im Bodensee - eine aktuelle Bestandsaufnahme"
- Interview partner for** 9/2010
"Abenteuer Wissen – Der Bodensee", a ZDF production
broadcasted on 29.9.2010
- Symposium "Natural Sciences in Vorarlberg (Austria)"** 4/2008
talk on:
"Crangonyx pseudogracilis: Ein weiterer Neozoe im
Bodensee"

*Submitted manuscripts and
Manuscripts in preparation*

- Hanselmann, A. J.**, Hodapp, B., Rothhaupt, K.-O. (major revisions): Nutritional ecology of the invasive freshwater mysid *Limnomysis benedeni* - field data and laboratory experiments on food choice and juvenile growth. *Hydrobiologia*
- Hanselmann, A. J.**, Rothhaupt, K.-O. (submitted): Estimating instantaneous birth and mortality rates of the invasive freshwater mysid *Limnomysis benedeni* in the field *Oecologia*
- Matuszak, A., **Hanselmann, A. J.**, Gergs, R., Voigt, C. C., Storch, I., Bauer, H.-G. & Quillfeldt, P. (submitted): Influence of depth, space and season on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of benthic invertebrates within the littoral of Lake Constance – implications for inferring the diets of waterbirds. *Journal of Zoology*





