

An underwater photograph showing a dense cluster of blue mussels on a rocky substrate. The mussels are dark blue with some lighter, yellowish-green patches. The water is slightly turbid, and the background is a soft, out-of-focus blue-green. The text is centered over the image.

**Host–parasite co-evolution and co-infection  
of invasive parasitic *Mytilicola* copepods  
in blue mussel hosts**

Marieke Eveline Feis

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Host–parasite co-evolution and co-infection  
of invasive parasitic *Mytilicola* copepods  
in blue mussel hosts

Dissertation

in fulfillment of the requirements for the degree “Dr. rer. nat.”

of the Faculty of Mathematics and Natural Sciences

at Kiel University

submitted by

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Zwolle, 2018

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Date of the oral examination: 25 June 2018

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Dedicated to my late father



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Summary

Zusammenfassung

## Summary

Parasites are ubiquitous in nature and the strong natural selection pressures they impose on their hosts are predicted to elicit rapid evolutionary adaptive responses of hosts towards their parasites, leading to antagonistic host–parasite co-evolution. While most of what we know about these processes stems from laboratory studies with a restricted set of model organisms, much less is known about host–parasite co-evolution in the wild, largely due to logistical challenges of experimental manipulations on an ecosystem scale. Biological invasions represent excellent opportunities to overcome these logistical issues and study host–parasite interactions and co-evolution in non-model species in the wild, as they can be seen as “natural experiments” in which different invasion scenarios lead to different ecological and evolutionary dynamics. This dissertation utilises the invasions of two parasitic copepods *Mytilicola intestinalis* and *Mytilicola orientalis* in the Wadden Sea to address the study of host–parasite co-evolution and co-infection in non-model species in the wild. This conceptual approach and the biological system are introduced in *Chapter 1*.

Validation of the presumed origins and invasion routes of both parasites were still lacking, therefore my first aim was to confirm them. This was done through an extensive literature review, in combination with invasion genetics (*Chapter 2*), which resulted in the validation of Japan as the native and North America and Europe as the invaded ranges of *M. orientalis* (where it was co-introduced with the Pacific oyster *Magallana gigas*), while it remained unclear whether the Mediterranean Sea is really the native range of *M. intestinalis*.

The biological invasion of *M. intestinalis* and later *M. orientalis* created a situation in which two congeneric species co-occur and share the same novel host in their invaded range. The two parasites have different degrees of host specificity in the Wadden Sea, as *M. intestinalis* only infects blue mussels *Mytilus edulis*, while *M. orientalis* also infects Pacific oysters *M. gigas*, and at least two other bivalve species. As generalists and specialists are not expected to occupy the same niche over extended periods of time, my second aim was to investigate potential competitive interactions between the two parasites. In an experiment, I showed that Pacific oysters are not suitable hosts for *M. intestinalis* (*Chapter 3*). Furthermore, from an infection experiment with mussels, there were no indications of direct competition or

superiority of either parasite in co-infections, but the infection rate of *M. orientalis* was lower than that of *M. intestinalis* (Chapter 3). Therefore, the ongoing invasion of *M. orientalis* in the Northern Wadden Sea at locations where *M. intestinalis* is already present is more likely to be facilitated by the other hosts *M. orientalis* can utilise, than by competitive interactions within the shared host.

Moreover, I highlighted the use of biological invasions of parasites to study host–parasite co-evolution in non-model organisms in the wild. By making experimental cross-infections of mussels and *M. intestinalis* from two invasion fronts with similar co-evolutionary time periods (Texel and Sylt) and an uninvaded location (Kiel), I could study evolutionary changes after introduction. Kiel mussels lacked a co-evolved response to parasite infection. Furthermore, invasions of *M. intestinalis* at separate fronts in the Wadden Sea led to different evolutionary trajectories in both hosts and parasites in the mussel–*M. intestinalis* system, with pre-infection traits (infectivity/resistance) evolving on Texel, while post-infection traits (virulence/tolerance) may have evolved on Sylt (Chapter 4). A dual-species transcriptomics approach on Texel and Sylt hosts and parasites of the sympatric, allopatric and control treatments was used next to document the molecular underpinnings of the different evolutionary trajectories. This uncovered a general immune response of mussels towards *M. intestinalis* infections, as well as several candidate genes and processes that mediate the different evolutionary trajectories (Chapter 5). The combination of studying responses on the phenotypic level and the transcriptional level through dual transcriptomics thus promises to be a fruitful approach to unravel the molecular mechanisms behind evolution of host–parasite interactions in many other non-model organisms.

In general, this dissertation demonstrates the value of using biological invasions to investigate host–parasite co-evolution in the wild, which is especially promising for research on non-model organisms. Future research should, however, further unravel the relative importance of phenotypic plasticity and genetic determinism for the co-evolutionary dynamics between hosts and parasites, but should also investigate the potential effects of other factors, such as, in the case of *Mytilicola*, the roles of the mussel microbiome and the hyperparasite *Unikaryon mytilicolae* (discussed in Chapter 6).

## Zusammenfassung

Parasiten sind in der Natur allgegenwärtig und es wird angenommen, dass der starke Selektionsdruck, den sie auf ihre Wirte ausüben, zu zu schnellen evolutionären Anpassungen der Wirte gegenüber ihren Parasiten führt und damit zu einer antagonistischen Koevolution von Wirt und Parasit. Unser Wissen über diese Prozesse stammt vor allem aus Laboruntersuchungen mit einer beschränkten Anzahl von Modellorganismen. Weit weniger untersucht ist hingegen die Koevolution von Wirten und Parasiten in natürlichen Systemen, vor allem aufgrund der logistischen Herausforderung experimenteller Manipulationen auf Ökosystemebene. Biologische Invasionen bieten ausgezeichnete Möglichkeiten, diese Komplikationen zu umgehen, und Wirt-Parasit-Interaktionen und Koevolution von Nichtmodellorganismen im Freiland zu untersuchen, da sie als "natürliche Experimente" angesehen werden können, in welchen verschiedene Invasionsszenarien zu unterschiedlichen ökologischen und evolutionären Dynamiken führen. Diese Dissertation nutzt die Invasionen der beiden parasitären Ruderfußkrebse *Mytilicola intestinalis* und *Mytilicola orientalis* im Wattenmeer, um die Koevolution von Wirten und Parasiten sowie von Koinfektion in natürlichen System zu untersuchen. Dieser konzeptionelle Ansatz sowie das biologische System werden in Kapitel 1 vorgestellt.

Bisher gab es keine validierten Informationen über die Herkunft und Invasionsrouten beider Parasitenarten. Daher war es mein erstes Ziel, diese Wissenslücke zu füllen. Durch eine umfangreiche Literaturrecherche in Kombination mit Invasionsgenetik (Kapitel 2) konnte ich Japan als das ursprüngliche Verbreitungsgebiet validieren und demonstrieren, dass *M. orientalis* erst später in Nordamerika und Europa mit der Pazifischen Auster *Magallana gigas* eingeführt wurde. Unklar blieb jedoch, ob das Mittelmeer tatsächlich das ursprüngliche Verbreitungsgebiet von *M. intestinalis* ist.

Die biologische Invasion von *M. intestinalis*, und später die von *M. orientalis*, schuf eine Situation, in der zwei nah verwandte Arten zusammen vorkommen und sich den gleichen Wirt in ihrem neuen Verbreitungsgebiet teilen. Allerdings haben die beiden Parasiten im Wattenmeer unterschiedliche Wirtsspezifitäten. *M. intestinalis* infiziert nur Miesmuscheln *Mytilus edulis*, während *M. orientalis* auch Pazifische Austern *M. gigas* und mindestens zwei weitere Muschelarten infiziert. Generell ist zu erwarten, dass Generalisten und Spezialisten nicht über längere Zeiträume dieselbe

Nische besetzen können. Es war daher mein zweites Ziel, eine mögliche Konkurrenz zwischen den beiden Parasitenarten zu untersuchen. In einem ersten Experiment habe ich gezeigt, dass Pazifische Austern kein geeigneter Wirt für *M. intestinalis* sind (Kapitel 3). Mein Infektionsexperiment mit Miesmuscheln erbrachte jedoch keine Hinweise auf direkte Konkurrenz oder Überlegenheit einer der beiden Parasiten bei Koinfektionen. Allerdings war die Infektionsrate von *M. orientalis* geringer als die von *M. intestinalis* (Kapitel 3). Es ist daher wahrscheinlich, dass die fortschreitende Invasion von *M. orientalis* im nördlichen Wattenmeer, an Stellen an denen *M. intestinalis* bereits vorhanden ist, vor allem durch andere von *M. orientalis* genutzte Wirte bestimmt wird und nicht durch Konkurrenz innerhalb des gemeinsamen Wirts.

Des Weiteren hebe ich in dieser Dissertation hervor, wie biologische Invasionen zur Untersuchung von Koevolution von Wirten und Parasiten in Nichtmodellorganismen in freier Wildbahn genutzt werden können. Durch experimentelle Kreuzinfektionen von Miesmuscheln und *M. intestinalis* von zwei Invasionsfronten mit ähnlichen Koevolutionszeiträumen (Texel und Sylt) und von einem bisher nicht besiedelten Gebiet (Kiel) konnte ich evolutionäre Veränderungen seit der Erstansiedlung untersuchen. Kieler Miesmuscheln fehlte eine koevolutionäre Reaktion auf Parasiteninfektionen. Darüber hinaus führte die Invasion von *M. intestinalis* an den verschiedenen Fronten im Wattenmeer zu unterschiedlichen evolutionären Verläufen sowohl auf der Wirts- als auch auf der Parasitenseite. Während sich auf Texel Eigenschaften entwickelt haben, welche die Wirt-Parasit-Interaktion vor der Infektion beeinflussen (Infektiosität / Resistenz), sind auf Sylt wahrscheinlich Eigenschaften entstanden, die nach der Infektion die Wirt-Parasit-Interaktion beeinflussen (Virulenz / Toleranz) (Kapitel 4). Um die molekularen Grundlagen dieser verschiedenen evolutionären Verläufe zu dokumentieren, habe ich einen Zwei-Arten-Transkriptomik-Ansatz verwendet. Dabei wurden Wirte und Parasiten von Texel und Sylt aus den sympatrischen, allopatrischen und Kontrollbehandlungen verwendet. Die Analysen zeigten eine allgemeine Immunantwort von Miesmuscheln auf Infektionen mit *M. intestinalis* sowie mehrere Kandidatengene und Prozesse, welche den verschiedenen evolutionären Verläufen zugrunde liegen (Kapitel 5). Die Kombination von Untersuchungen auf der phänotypischen und der transkriptionellen Ebene durch duale Transkriptomik ist somit ein vielversprechender Ansatz, um die molekularen Mechanismen der

evolutiven Dynamik von Wirt–Parasit-Wechselwirkungen in anderen Arten als den üblichen Modellorganismen zu entschlüsseln.

Insgesamt demonstriert diese Dissertation die Nützlichkeit von biologischen Invasionen als natürliche Experimente, um die Koevolution von Wirten und Parasiten in natürlichen Systemen zu untersuchen, was vor allem im Hinblick auf Nichtmodellorganismen vielversprechend ist. Zukünftige Herausforderungen bei solchen Untersuchungen sind nicht nur die Quantifizierung der relativen Bedeutung von phänotypischer Plastizität und genetischem Determinismus für die koevolutionäre Dynamik zwischen Wirten und Parasiten, sondern auch der mögliche Einfluss anderer Faktoren, wie im Fall von *Mytilicola* die Rolle des Mikrobioms des Wirtes und des Hyperparasiten *Unikaryon mytilicolae* (Kapitel 6).

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## Acknowledgements

The successful completion of this dissertation would not have been possible without the support of many people.

I would like to especially thank my PhD advisor **Dr. Mathias Wegner**. You gave me the opportunity to conduct my doctoral studies at the Alfred Wegener Institute on the beautiful Wadden island of Sylt. You have always supported me, from start to end, and were available for questions and discussions. You also challenged me to think critically, and rethink again. Thank you so much for your valuable insights. I am deeply thankful for your support!

Further, I would like to thank **Prof. Dr. Hinrich Schulenburg**. You were so kind to review my dissertation and to join my examination committee as the second referee. I am also very grateful to **Prof. Dr. Mojib Latif** and **Dr. Frank Melzner** for becoming chair and member of my examination committee.

The **DFG SPP1399** “Host–Parasite Coevolution: Rapid Reciprocal Adaptation and its Genetic Basis” funded my PhD (We4641/1-2 to Dr. Wegner). I am grateful to have been selected to be part of this programme and its wonderful community, and to partake in the annual symposia. They were fun and inspiring.

Further, I am grateful for receiving two travel grants from the **POLMAR graduate school** that allowed me to present a poster at the 15<sup>th</sup> biennial conference of the European Society for Evolutionary Biology in Lausanne and to participate in the Eu-SPRI 2017 winterschool at the University of Sussex. I am grateful for receiving the **MARS Travel Award 2016**, which allowed me to visit the CNRS-IMBE in Marseille for collaboration.

Additionally, I would like to thank the members of the Coastal Ecology group at AWI Sylt and the Ecological Chemistry group at AWI Bremerhaven. In this context, I would like to especially mention **Christian Buschbaum, Dario Fiorentino, Jonas Geburzi, Lars Harms, Uwe John, Nancy Kühne, Dagmar Lackschewitz, Ana Lokmer, Lisa Shama, Rebekka Wolfensberger**, and students **Leo Gottschalek** and **Florian Schmidt**. My experiments would not have been as successful without the support and assistance from **Kaibil Escobar Wolf** and **Sonja Anslinger**. A big thanks

also to the **AWI librarians**, who were able to provide the full text of nearly any reference that I was interested in, no matter how old or in what language.

Similarly, I would like to thank my colleagues at NIOZ, whose discussions, shared insights and support were very valuable to me: thank you **Dr. Pieternella Luttkhuizen** for inspiring me to take this career path, and for your unwavering support and positivity, **Dr. David Thieltges** for your enthusiasm about parasites, which sparked my own interest in parasites during my MSc. Thank you **Anouk Goedknecht** for being an excellent partner in crime in studying biological invasions in general and invasive *Mytilicola* spp. in particular.

Special thanks are due to **Prof. Dr. Susumu Ohtsuka** and **Yusuke Kondo**. Thank you for the warm welcome in your lab in Takehara, your care and support, and the many interesting discussions we had. My time in Japan was very special to me. I am also grateful to all other colleagues at the Takehara Marine Science Station of the Hiroshima University for their hospitality and support.

Furthermore, my thanks go to all people who have helped collect mussels for experiments and dissections, and to those people who sent parasite samples. In this context I would like to thank **Isabelle Arzul, Camille de la Vega, Xavier de Montaudouin, Onno den Boon, Shuichiro Hashimoto, Sadaharu Iwasaki, Benoit Lebreton, Chiara Manfrin, Frank Melzner, Hiroshi Miyake, Ole Müller, Reinier Nauta, Martin Paar, Andreas Pansch, Trystan Sanders, H. Uchiumi, Makoto Urata, Ellen van Veenendaal** and the **AWI Helgoland diving team**. Moreover, I am grateful to **Dr. Fred Batista** and **Dr. Anne Chenuil** who welcomed me in their labs in Tavira and Marseille for short stays to collect parasites. I enjoyed these visits immensely.

Last but not least, I would like to thank my closest friends **Sabine** and **Alexa** who have been constant sources of support during the last years. **Rik**, lief, I thank you for being my sounding board on everything I have ever wanted to discuss. Thank you for keeping me grounded and for being my biggest supporter from the start of my PhD until the end. My warmest thanks.



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## About the author

Marieke Eveline Feis was born on 29 August 1989 in 's-Gravenhage, the Netherlands. Her father, who taught biology at a high school and who loved explaining all things nature, opened her mind to the natural world. The decision what to study was therefore not difficult, and she subsequently moved to Groningen to study biology at the University of Groningen with a major in Marine Biology and a minor in Arctic and Antarctic Studies. After finishing her bachelor degree in 2010, she continued with the master Marine Biology at the same university. Her first research project on the dispersal of marine trematodes at the Royal Netherlands Institute for Sea Research was supervised by Dr. Pieterella Luttkhuizen and Dr. David Thieltges. The international collaboration within this project meant short stays in France, Denmark, Ireland and Morocco for parasite collection. The successful completion of the project furthermore led to her first peer-reviewed publication. After that, she did her second research project abroad with Marco Polo funding, to study climate change-induced evolution in mummichogs, which she did under the supervision of Dr. Erik Sotka and Prof. Dr. Allan Strand at the College of Charleston and Grice Marine Lab. These research projects were so far mainly lab-oriented, and she also wanted to do a project that had a heavier focus on fieldwork and ecology. She found an opportunity to do a 3.5-month research project led by PhD student Thomas Oudman (now Dr.), which included 2 months of fieldwork in Mauritania. In this project, she looked at the available food resources during winter for red knots on the tidal flats in the Parc Nationale du Banc d'Arguin. She graduated as a marine biologist in 2013 and started as a PhD candidate a month later in Dr. Mathias Wegner's group at the Alfred Wegener Institute in Germany. In 2018 she will defend her thesis entitled "*Host-parasite co-evolution and co-infection of invasive parasitic Mytilicola copepods in blue mussel hosts*". She is looking forward to her next step in science!

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## List of publications

### Peer reviewed publications

**Feis M. E.**, John U., Lokmer A., Luttikhuizen P. C., Wegner K. M. (2018) Dual transcriptomics reveals co-evolutionary mechanisms of intestinal parasite infections in blue mussels *Mytilus edulis*. *Molecular Ecology* 27: 1505-1519.

**Feis M. E.**, Goedknecht M. A., Thieltges D. W., Buschbaum C., Wegner K. M. (2016) Biological invasions and host–parasite co-evolution: different coevolutionary trajectories along separate parasite invasion fronts. *Zoology* 119: 366-374.

Goedknecht M. A., **Feis M. E.**, Wegner K. M., Luttikhuizen P. C., Buschbaum C., Camphuysen K. (C. J.), van der Meer J., Thieltges D. W. (2016) Parasites and marine invasions: Ecological and evolutionary perspectives. *Journal of Sea Research* 113: 11-27.

**Feis M. E.**, Thieltges D. W., Olsen J. L., de Montaudouin X., Jensen K. T., Bazairi H., Culloty S. C., Luttikhuizen P. C. (2015) The most vagile host as the main determinant of population connectivity in marine macroparasites. *Marine Ecology Progress Series* 520: 85-99.

### Submitted manuscripts

Oudman T., Ahmedou Salem M. V., **Feis M. E.**, Dekinga A., Holthuijsen S., van Gils J. A., Piersma T., Bijleveld A. I. From grouping nomads to solitary residents in one species: the resource environment sets the compromise between aggregation and site fidelity in red knots.

### Manuscripts in preparation

**Feis M. E.**, Goedknecht M. A., Arzul I., Chenuil A., den Boon O., Gottschalck L., Kondo Y., Ohtsuka S., Shama L. N. S., Thieltges D. W., Wegner K. M., Luttikhuizen P. C. Global invasion genetics of two parasitic copepods infecting marine bivalves.

**Feis M. E.**, Wegner K. M. Do invasions create competitors? Co-infections of specialist *Mytilicola intestinalis* vs. generalist *Mytilicola orientalis* in blue mussels.

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## Affidavit

I hereby confirm that the content and design of my thesis entitled:

**“Host–parasite co-evolution and co-infection of invasive parasitic *Mytilicola* copepods in blue mussel hosts”**

are the result of my own work apart from my supervisor’s guidance and co-operation with my co-authors. I prepared this thesis following the Rules of Good Scientific Practise of the German Research Foundation.

Furthermore, I confirm that this thesis has not been submitted as a part of another examination process neither in identical nor in similar form.

Parts of this thesis have been published or submitted to scientific journals:

- Chapter 3 has been published as: Feis M. E., Goedknecht M. A., Thieltges D. W., Buschbaum C., Wegner K. M. (2016) Biological invasions and host–parasite co-evolution: different coevolutionary trajectories along separate parasite invasion fronts. *Zoology* **119**, 366-374
- Chapter 4 has been published as: Feis M. E., John U., Lokmer A., Luttikhuizen P. C., Wegner K. M. (2018) Dual transcriptomics reveals co-evolutionary mechanisms of intestinal parasite infections in blue mussels *Mytilus edulis*. *Molecular Ecology* **27**, 1505-1519
- Chapter 1 is in preparation for submission with M. A. Goedknecht, I. Arzul, A. Chenuil, O. den Boon, L. Gottschalck, Y. Kondo, S. Ohtsuka, L. N. S. Shama, D. W. Thieltges, K. M. Wegner and P. C. Luttikhuizen
- Chapter 2 is in preparation for submission with K. M. Wegner

Kiel, May 2018

Marieke Eveline Feis