Mating success and sexual selection in a pelagic copepod, Temora longicornis: Evidence from paternity analyses

Knowledge about mating patterns is essential for understanding and explaining rates of reproduction and genetic potential of copepods populations. The aim of this study was to examine (1) the occurrence of multiple paternity in Temora longicornis, (2) the effect of multiple paternity (if present) on the females reproductive output, and (3) whether mating is random or some individuals have a higher than average chance of fertilizing or being fertilized (super individuals). We show that multiple paternity is common in this copepod species, that females benefit from multiple matings by increased offspring production, and that a relatively small fraction of the males and females in a population account for most of the offspring production. In both males and females, mating is nonrandom. Superior individuals with a higher than average matings success were identified both among females and among males.
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Low fertilization rates in a pelagic copepod caused by sexual selection?

We studied female fertilization status in North Sea summer populations and laboratory cultures of the marine copepod Temora longicornis and found fractions of fertilized females in both field and laboratory populations that were much smaller (<50%) than predicted by a theoretical model that assumes random mating. Such low fertilization rates are normally related to environmental factors such as poor food or low densities, which we could not confirm in our experiment. Male density was negatively related to fertilization rate, and a large fraction of males did not mate in laboratory incubations. We therefore suggest that sexual selection, through mate choice or male–male competition could account for low fertilization rates of females in populations of pelagic copepods during some periods of the year.
Sexual selection in marine plankton

Copepods are among the most abundant metazoans on the planet and play an important role in the marine food web. Many aspects of their ecology have consequently been studied, including details of their reproductive biology and mating behaviour. Sexual selection, the part of evolution which selects for increased mating and fertilization success, is an important evolutionary process, with consequences at individual, population and species level. Yet very little is known about the significance of sexual selection for the evolution and ecology of this key group of animals. The presented thesis used behavioural studies and genetic parentage analyses to examine the fertilization status and occurrence of mate choice and polygamy in the copepod Temora longicornis (Copepoda, Calanoida). The overall objective of my PhD project was to examine the intensity and direction of sexual selection in T. longicornis and elucidate the role of sexual selection for the behaviour of individuals, the dynamics of populations, and the
functioning of the pelagic ecosystem. I wanted to address the following overarching questions: i) What is the fraction of fertilized females in field and laboratory populations? Is it influenced by adult abundance, male mating capacity and the environment? ii) Is mating in T. longicornis random, or do some individuals have a higher-than-average chance of fertilizing or being fertilized? iii) Which traits control mating in T. longicornis? Are body size and age significant factors influencing male fecundity (mating rate and sperm production) and female reproductive fitness? iv) Does multiple mating lead to multiple paternity? What is the effect of multiple mating on the female’s reproductive output as well as the longevity of the individual? The thesis is divided into 5 chapters that report on different efforts to address these objectives. It opens with a general introduction and synopsis that lays out the context for the research, summarizes the main findings and discusses perspective for future research (Chapter 1). In Chapter 2 we studied female fertilization status in North Sea summer populations and in laboratory cultures of T. longicornis. The study showed that the fractions of fertilized females in both field and laboratory populations were much smaller (< 50%) than predicted by a theoretical model that assumes random mating. Such low fertilization rates are normally related to environmental factors such as poor food or low densities, which we could not confirm in our experiment. Male density was negatively related to fertilization rate, and a large fraction of males did not mate in laboratory incubations. This led to Chapter 3, where we investigated age- and size-dependent reproductive performance (egg and sperm production, mating success) in T. longicornis. We found that ageing effects were evident: mortality rate increased with age, and fertility decreased rapidly with age. We also found that several aspects of reproductive performance increased with size in both males and females: large females produced more offspring than small ones, and large males mated more often, produced larger spermatophores containing more sperm cells and sired more offspring. The study also showed that repeated mating was not only potentially advantageous (e.g. in terms of higher genetic variability) for females, but can come at the disadvantage of increased mortality. Chapter 4 describes the identification and characterization of the six microsatellites primers used in Chapter 5 to do paternity testing of the offspring. To investigate if mating was random or under the influence of sexual selection, we tested which males sired the female’s offspring. By establishing paternity, we can precisely quantify the reproductive success of individual males and thus assess how successful particular males have been. Our study clearly demonstrated the occurrence of multiple paternity in T. longicornis. This is the first time that genetic polyandry has been documented in a pelagic copepod. Multiple paternity opens up for the possibility of post-copulatory sexual selection, such as sperm competition and cryptic female choice. We further found that mating was non-random, as we identified superior individuals with a higher than average mating success both among females and among males. Some of the variation between individuals could be explained by variation in size and age. Large males were superior to small males in terms of reproductive success, with the larger males (0.8 mm) mating about 3 times as frequent as the smaller males (0.6 mm). In accordance with the findings in Chapter 2, we found that a fraction of the males (8-14 %) in our study never mated during incubations, despite a plentiful supply of females. Only about half of the females in our experiments were fertilized, even though male availability was high and mate encounters not limiting. The strong size- and age-dependent fertility in this species is conducive to the existence of sexual selection via mate choice for young and large partners, as has been shown in another copepod species. We further suggest that sexual selection, through mate choice or male–male competition could account for low fertilization rates of females in populations of pelagic copepods during some periods of the year.

This thesis suggests that the processes and mechanisms of sexual selection have to be considered when studying reproductive rates in copepod populations.
Age- and size-dependent mating performance and fertility in a pelagic copepod, Temora longicornis

Prepress abstract: In many species, size and age have been shown to be strong determinants of the reproductive success for both sexes. Here we examine age- and size dependent reproductive performance (egg- and sperm production, mating success) in a pelagic copepod. Compared to smaller males, larger males produce larger spermatophores containing more spermatozoa, and fertilize a larger fraction of available females. Females mating with large males produce more offspring than those mating with small males. Similarly, large females have higher egg production rates as well as a higher life-time egg production than small females. Ageing effects are evident in this species: Mortality rate increases and fertility decreases rapidly with age. The average adult longevity under optimal laboratory conditions was 30 days in both males and females, but females produce eggs for only 18 days, and males can fertilize females for only about eight days after they mature. The strong size- and age-dependent fertility observed in this species is conducive to the development of sexual selection via mate choice for young and large partners, as has been shown in one other copepod species.
Distribution and mortality of diapause eggs from calanoid copepods in relation to sedimentation regimes

Distribution, abundance and age of diapause eggs from three species of calanoid copepods (in particular from Acartia spp. most likely Acartia tonsa, and Centropages hamatus and less numerous from Temora longicornis) were recorded in sediment profiles by enumerating hatched nauplii from incubated sediment samples. Phytoplankton pigments and 210Pb and 137Cs analyses indicated that the sedimentation regimes were different between two southern and two northern stations of the island Funen, Denmark. Significant variations in vertical distribution, abundance and mortality of diapause eggs were found between the stations. Dating of the sediment cores suggested a ~70-year maximum age of viable eggs on the northernmost stations, and ~28 year at the southernmost stations. The eggs exhibited a significantly higher mortality rate at the southernmost stations compared with the northernmost, 0.35–0.53 year−1 vs. 0.07–0.08 year−1 with no systematic pattern among species. The differences in abundance, mortality and age of the diapause eggs are suggested to be due to the sediment characteristics in which they are buried.

General information
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Copepods are important crustaceans studied because of their key role in ecology, trophic biology, fisheries management, in modeling the flow of energy and matter, ecotoxicology, aquaculture and aquarium trade. This paper discusses various aspects of the state of knowledge of copepod culture at large scales and provides the scientific community with ideas and concepts that could improve and quicken the development of copepod mass cultures. As a framework for discussion, we use a conceptual scheme from Teece (1988) and adapted it to our goal: ‘how to capture value from a copepod product’. The suggestions include: 1) optimize cultures by automation and implement recirculation technology for improving water quality; 2) use harpacticoid and cyclopoid copepods in industries that can produce large amounts of these prey on site at any given time; but use calanoid copepods for industries limited in production time and those that export copepod products (e.g. eggs); 3) select preferentially local copepod species and if possible species with lipid conversion capabilities; 4) optimize sex ratio and selection/cross-breeding to develop suitable copepod strains for aquaculture; 5) explore the use of probiotics for improving the fitness of copepod cultures; and 6) encourage copepod producers/retailers to use/develop an efficient sales and marketing strategy.

**Status and recommendations on marine copepod cultivation for use as live feed**

Copepods are important crustaceans studied because of their key role in ecology, trophic biology, fisheries management, in modeling the flow of energy and matter, ecotoxicology, aquaculture and aquarium trade. This paper discusses various aspects of the state of knowledge of copepod culture at large scales and provides the scientific community with ideas and concepts that could improve and quicken the development of copepod mass cultures. As a framework for discussion, we use a conceptual scheme from Teece (1988) and adapted it to our goal: ‘how to capture value from a copepod product’. The suggestions include: 1) optimize cultures by automation and implement recirculation technology for improving water quality; 2) use harpacticoid and cyclopoid copepods in industries that can produce large amounts of these prey on site at any given time; but use calanoid copepods for industries limited in production time and those that export copepod products (e.g. eggs); 3) select preferentially local copepod species and if possible species with lipid conversion capabilities; 4) optimize sex ratio and selection/cross-breeding to develop suitable copepod strains for aquaculture; 5) explore the use of probiotics for improving the fitness of copepod cultures; and 6) encourage copepod producers/retailers to use/develop an efficient sales and marketing strategy.
**Projects:**

**Sexual selection in marine plankton**
National Institute of Aquatic Resources  
Period: 01/07/2009 → 02/07/2014  
Number of participants: 6  
PhD Student: Sichlau, Mie Hylstofte (Intern)  
Supervisor: Koski, Marja (Intern)  
Main Supervisor: Kiørboe, Thomas (Intern)  
Examiner: Bekkevold, Dorte (Intern)  
Jonsson, Per (Ekstern)  
Kimmerer, William J. (Ekstern)

**Financing sources**  
Source: Internal funding (public)  
Name of research programme: 1/3 DTU-stip, 2/3 FUR/andet  
Project: PhD

**Scaling from individuals to populations (SLIP) (38726)**
The research school SLIP (Scaling from Individuals to Populations) focuses on how individual behavior and mutual interactions generate the dynamics observed at the population level. This topic forms the link between the basic and applied marine ecological research environments in Denmark and requires input from biology, mathematics and statistics. SLIP is one of the five research networks and research schools under the Danish Network for Aquaculture and Fisheries Research (Fishnet). SLIP has arranged a number of national and international PhD courses and workshops and has served to focus the interest on size and trait-based modeling, as well as on improved understanding of the physiology, genetics and behavior of marine organisms, in particular fish.

The project is coordinated by DTU Aqua.

DTU Data Analysis  
National Institute of Aquatic Resources  
Section for Marine Living Resources  
Roskilde University  
Royal Veterinary and Agricultural University
Aarhus University

University of Copenhagen
Period: 01/01/2000 → 31/12/2008
Number of participants: 9
Research area: Marine Populations and Ecosystem Dynamics
Project participant:
Höffle, Hannes (Intern)
Gürkan, Zeren (Intern)
Therkildsen, Nina Overgaard (Intern)
Sichlau, Mie Hylstofte (Intern)
Mosgaard, Thomas (Intern)
Frisk, Christina (Intern)
Project Manager, academic:
Gislason, Henrik (Intern)
Kiørboe, Thomas (Intern)
Eg Nielsen, Einar (Intern)

Activities:

ASLO 2013 Aquatic Sciences Meeting
Period: 2013 → …
Mie Hylstofte Sichlau (Participant)
National Institute of Aquatic Resources
Centre for Ocean Life

Related event

ASLO 2013 Aquatic Sciences Meeting: Learning for the future
17/02/2013 → 22/02/2013
New Orleans, United States
Activity: Attending an event › Participating in or organising a conference

ASLO 2013 Aquatic Sciences Meeting
Period: 2013 → …
Mie Hylstofte Sichlau (Participant)
National Institute of Aquatic Resources
Centre for Ocean Life

Related event

ASLO 2013 Aquatic Sciences Meeting: Learning for the future
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