The biology and impacts of Oreochromis niloticus and Limnothrissa miodon introduced in Lake Kariba
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BIOLOGY AND IMPACTS OF *OREOCHROMIS NILOTICUS* AND *LIMNOTHRISSA MIODON*


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BIOLOGY AND IMPACTS OF *OREOCHROMIS NILOTICUS* AND *LIMNOTHRISSA MIODON*


The biology and competitive displacement of a native fish, *Oreochromis mortimeri*, by a congeneric species, *Oreochromis niloticus*, and the biology and exploitation of an introduced pelagic sardine, *Limnothrissa miodon* in Lake Kariba were studied in this thesis. *O. niloticus* was introduced from escapees of an aquaculture farm in the early 1990s and displaced an endemic and native fish to the Middle Zambezi River, *O. mortimeri*, from the Sanyati basin of Lake Kariba. To provide insight on the displacement process, the growth, reproductive effort, aggression and diet of the two species were compared.

Kariba dam was constructed for Hydro Electricity generation in 1957, creating a relatively large aquatic lacustrine habitat with conditions that in many ways differed from fluvial conditions of the Zambezi River. The indigenous fish species were able to adapt to living in the inshore area, leaving the pelagic area that constitutes about 70% of the lake, devoid of fish. The pelagic area was hence considered to be a ‘vacant niche’ with plankton that could be used to enhance the fish production of the new lake. A pelagic freshwater sardine, *Limnothrissa miodon* was introduced into Lake Kariba from Lake Tanganyika, to fill this vacant niche, in 1967 and 1968. By 1974, *L. miodon* was considered established in the lake and a pelagic fishery based on the introduced sardine commenced that year. It became the most productive fishery on Lake Kariba and in Zimbabwe. Since 1990, the fishery has declined. In the thesis the causes of the decline were evaluated. How well the two introduced fish species became established in Lake Kariba was assessed by comparing their growth in Kariba to that in other water bodies.

Based on its growth rate ($k$), maximum length ($L_\infty$) and age at maturity, *Oreochromis niloticus* thrives in Lake Kariba. However, the growth rate determined in Lake Kariba in 1997 ($k = 0.25$), 2003 ($k = 0.29$) and 2010 ($k = 0.29$) is in the middle of the range reported for some populations throughout the world ($k = 0.11 – 0.75$). Similarly, the maximum size ($L_\infty$) in Lake Kariba (32.4, 44.6 and 37.8 cm standard length (SL) in 1997, 2003 and 2010, respectively) is in the middle of the range of the same reported populations (10.2 – 57.2 cm SL). The length at first maturity in Kariba is high (17.26 cm SL) compared, for example, to the small size at maturity (11.2 – 13.2 cm SL) of populations in eight reservoirs of varying sizes in Côte d’Ivoire, but it is much lower than that published for a population in Lake Victoria (26 and 29 cm SL for females and males, respectively). The differences in size and age at maturity in the populations of *O. niloticus* in the various water bodies, reflects the plasticity in growth rate and maximum size of this species in relation to environmental conditions. The oldest specimen of *O. niloticus* in Lake Kariba were 10, 6 and 8 years in 1997, 2003 and 2010, respectively. Length frequency data from the artisanal fishery and experimental fishing show that the population has many age groups. Such a population is less vulnerable to some years of recruitment failure than
a population comprising only a few age classes. A population with this age structure, coupled with a high age at maturity, may reflect a moderate fishing pressure. For the sustainability of this fishery, these population attributes need to be monitored.

The introduction of *Oreochromis niloticus* into Lake Kariba, where *O. mortimeri* was already present, brought together two formerly geographically separated congeners with a similar niche. Following the introduction, the catches of *O. niloticus* rose whilst those of *O. mortimeri* declined, resulting in the displacement of the native species from many parts of the lake. The total catches of these two species, however, remained the same since *O. niloticus* first appeared in the catches. The mechanisms that conferred competitive advantage to *O. niloticus* over *O. mortimeri*, were explored in studies comparing growth, aggression, diet and reproductive effort. The mean stomach fullness was 70.9% ± 9.4 for *O. niloticus* and 73.4% ± 9.8 for *O. mortimeri*, and the difference between species was not significant. The two species had a similar diet of plankton and detritus, and a crude protein digestion efficiency that indicates potential competition for food. However, the higher growth rate and maximum size of *O. niloticus* may have conferred this species competitive advantage over *O. mortimeri*.

A large size offers advantages in the form of increased reproductive effort (since the egg number in the ovary is often correlated to female size) and dominance. The largest fish of a pair in an aquarium contest to test aggression, was more aggressive and became dominant most of the time, in both species. Even though in general *Oreochromis mortimeri* was the more aggressive species, being larger in size at a particular age, *O. niloticus* negates this species-specific difference in aggression. *Oreochromis niloticus* may have a reproductive advantage, because the proportion of fish at a high level of gonadal development every month, was always higher than in *O. mortimeri*. A high number of reproducing females may signal a higher breeding effort of *O. niloticus* compared to *O. mortimeri*.

Unlike the unplanned introduction of *Oreochromis niloticus*, the deliberate introduction of *Limnothrissa miodon* into Lake Kariba had no major negative impact. The major difference between these two introductions is that *L. miodon* was introduced in order to occupy a vacant niche. Therefore, interactions with other fish species were rare. The availability of a vacant niche should be an important consideration in all fish introductions, to avoid potential biodiversity loss. The objective of the introduction of *L. miodon* to increase fish production in Lake Kariba was achieved. In order to maximize the social and economic advantages gained, the management of the *L. miodon* fishery needs to be optimized through the acquisition of scientific knowledge on sardine biology and fishery, such as collected in the studies contained in this thesis.

Growth rate and size at maturity were estimated, and what they reveal about the status of the fish population and fishery was discussed. The maximum size (\(L_\infty\)) estimates of *Limnothrissa miodon* obtained from the Gompertz models were: 18.0, 9.6 and 15.2 cm (TL), in 1993 – 1994, 1996 and 2012 – 2013, respectively. These
values, including some annual variation, are comparable to those in Lake Tanganyika. Early studies of *L. midon* concluded that the population in Lake Kariba was stunted. The lack of large fish may be due to the capture of fish before they reach a large size, and to the migration of the large fish into a more inshore area, where they are not captured by the offshore operating fishing fleet. The age at first maturity is lower than in Lake Tanganyika and has declined since the time the species was introduced into Lake Kariba. Maturity occurred at a much smaller size in this study (3.43 and 3.63 cm for females and males, respectively), compared to 5.2 – 5.6 cm for females and 7.1 – 7.3 cm for males in 1970 – 1972, indicating a large temporal decrease in size at maturity. The decline in age at maturity may be an indicator of overfishing, which causes the selective removal of fast-growing fish and favours the survival of those with a shorter life cycle. This change in the life history of the sardine can slow down the recovery of the fish population.

The introduced species in Lake Kariba have provided lessons on the importance of fish introductions to enhance fish production in a reservoir, and lessons on how overfishing and an adverse environment reduce the catches, resulting in an erosion of social and economic benefits. I conclude that management of the fishery should incorporate these two factors in the estimation of productivity, management and monitoring of the fishery. The fish introductions also provided an opportunity to witness the effect of the introduction of a species that shares an ecological niche with a native species. I conclude that an introduction into an occupied niche may not result in higher fish catches and profit. Instead, it may inflict costs in terms of reduced biodiversity through the loss of native and endemic species.
Samenvatting (Dutch summary)
Door de bouw van de Kariba stuwdam, met daarin twee waterkrachtcentrales, ontstond in 1957 een groot stuwmeer (6 000 km²) in de Zambezi rivier op de grens van Zambia en Zimbabwe: het Karibameer. De omstandigheden in het nieuwgevormde lotische ecosysteem verschilden in vele opzichten van die in de rivier. De reeds aanwezige riviervissen konden zich alleen aanpassen aan de omstandigheden in de oeverzone van het nieuwe meer. Daarom bleef het open water, dat ongeveer 70% van de totale oppervlakte beslaat, verstoken van vis. De pelagische zone werd beschouwd als een onbezette niche voor vis, waarin voldoende plankton aanwezig was om de visproductie van het meer te kunnen verhogen.


In tegenstelling tot de introductie van *Limnothrissa miodon*, was de introductie van een andere exoot, de Nijltilapia (*Oreochromis niloticus*), niet bewust. In het begin van de jaren negentig van de vorige eeuw, vestigde deze soort zich in het meer via ontsnappingen vanuit aangrenzende viskwekerijen. In dit geval was geen sprake van een onbezette niche die kon worden opgevuld. De inheemse tilapia *Oreochromis mortimeri*, een endemische soort van de Midden Zambezi, vormde een concurrent voor habitat en voedsel. Beide tilapias verkiezen de oeverzone als leefgebied, hebben een grotendeels overlappend planktvoor dieet, een vergelijkbare vlootplantings-strategie, en zijn genetisch nauw verwant. Na enkele jaren bleek de inheemse tilapia in het onderzoeksgebied (Sanyati basin) al te zijn verdrongen door de Nijltilapia.

De biologie van, en de visserij op, de twee geïntroduceerde soorten, *Oreochromis niloticus* en *Limnothrissa miodon*, vormen samen met de invloed die ze uitoefenen op de visgemeenschap en de visserij, het onderwerp van dit proefschrift. Door de groeiparameters van beide soorten in het Karibameer te vergelijken met die in andere wateren, zijn de habitatgeschiktheid van het meer en de mate van vestiging van de beide exoten in beeld gebracht. Het proces van concurrentie en verdringing binnen het genus *Oreochromis* is onderzocht door het vergelijken van de groeiparameters, de reproductieve inspanning, de agressiviteit en het dieet van *O. niloticus* en *O. mortimeri*. Inzicht in de ontwikkeling van de sardinepopulatie en de effecten hiervan op de visserij is verkregen door onderzoek aan de relatieve groeisnelheid en de gemiddelde lengte bij geslachtsrijpheid.

De relatieve groeisnelheid (*k*), de maximale gemiddelde lengte (*L∞*) en de gemiddelde lengte bij geslachtsrijpheid van *O. niloticus* wijzen op het floreer van de soort in het Karibameer, en daarmee op gunstige milieumondstigheden. De in
het Karibameer gemeten relatieve groeisnelheden in 1997 \((k = 0.25)\), 2003 \((k = 0.29)\) en 2010 \((k = 0.29)\) liggen centraal in het bereik dat voor diverse over de wereld verspreide populaties is gerapporteerd \((k = 0.11 – 0.75)\). Hetzelfde geldt voor de maximale gemiddelde lengte in Kariba \((L_\infty = 32.4, 44.6\) en 37.8 cm standaard lengte \((SL)\) in respectievelijk 1997, 2003 en 2010\) ten opzichte van dezelfde over de wereld verspreide populaties \((L_\infty = 10.2 – 57.2\) cm SL). De gemiddelde lengte bij geslachtsrijpheid in het Karibameer \((17.26\) cm SL) is hoog in vergelijking tot de waarden \((11.2 – 13.2\) cm SL) die in acht reservoirs van verschillende omvang in Ivorkust zijn gevonden, maar veel lager dan de gepubliceerde waarden \((respectievelijk 26\) en \(29\) cm SL voor vrouwtjes en mannetjes) voor een populatie in het Victoriameer. De variatie in de gemiddelde lengte en leeftijd bij geslachtsrijpheid van \textit{Oreochromis niloticus} in verschillende wateren weerspiegelt de plasticiteit in de relatieve groeisnelheid en de maximale lengte van deze soort in relatie tot omgevingsfactoren. In 1997, 2003 en 2010 waren de oudste gevangen exemplaren van de Nijltilapia in het Karibameer respectievelijk 10, 6 en 8 jaar oud. De lengte-frequentiegegevens van de artisanale visserij en de bemonstering laten zien dat de populatie bestaat uit een groot aantal leeftijdsklassen. Een populatie met deze leeftijdsopbouw is minder kwetsbaar voor enkele jaren zonder aanwas dan een populatie die bestaat uit slechts een paar leeftijdsklassen. In combinatie met een hoge gemiddelde leeftijd bij geslachtsrijpheid weerspiegelt een dergelijke populatie waarschijnlijk een bescheiden visserijdruk. Om de duurzaamheid van de tilapiavisserij te waarborgen, is het monitoren van de leeftijdsopbouw van de populatie noodzakelijk.

De introductie van Nijltilapia in het Karibameer, waar \textit{Oreochromis mortimeri} al aanwezig was, bracht twee nauw verwante soorten met dezelfde ecologische niche samen die voorheen geografisch gescheiden voorkwamen. Hierna begonnen de vangsten van \textit{O. niloticus} te stijgen en die van \textit{O. mortimeri} af te nemen totdat de inheemse soort op de meeste plaatsen in het meer verdrongen was. De totale hoeveelheid tilapia in de vangsten is echter gelijk gebleven sinds \textit{O. niloticus} voor het eerst in de vangsten verscheen. Uit vergelijkend onderzoek aan groei, agressie, dieet en reproduceertieve inspanning is gebleken dat de mechanismen af te leiden die \textit{O. niloticus} een concurrentievoordeel op kunnen leveren. De gemiddelde maagvulling van \textit{O. niloticus} was \(70.9\% \pm 9.4\) en die van \textit{O. mortimeri} \(73.4\% \pm 9.8\), een niet significant verschil. Het dieet van beide soorten overlapte grotendeels en bestond hoofdzakelijk uit plankton en detritus. Omdat beide tilapias daarnaast een vergelijkbare verteringsefficiëntie bleken te hebben, is de conclusie dat met de introductie van \textit{O. niloticus} in het Karibameer een grote kans op het voorkomen van voedselconcurrentie is ontstaan. Hierbij hebben de relatief hoge groeisnelheid en maximale grootte van de Nijltilapia deze exoot waarschijnlijk een concurrentievoordeel gegeven ten opzichte van zijn inheemse verwant.

Een grote lichaamslengte levert een vis voordelen op in de vorm van 1) een hogere reproduceertieve inspanning, omdat per broedpoging het aantal eieren in het ovarium
Samenvatting (Dutch summary)

in het algemeen sterk positief gecorreleerd is met de grootte van het vrouwtje, en 2) dominantie bij conflicten. De mate van agressie van beide tilapiasoorten is getest in aquarium-experimenten. Hierbij bleek dat het grootste exemplaar van een paar in een testsituatie, onafhankelijk van de soort, het meest agressief was en meestal in de loop van het experiment dominant werd. Hoewel *O. mortimeri* in het algemeen als de agressievere soort kan worden beschouwd, wordt dit soortspecifieke verschil in agressie tenietgedaan door het feit dat voor elke leeftijdsklasse geldt dat *O. niloticus* groter is dan *O. mortimeri*. Het maandelijkse percentage vissen met een hoog niveau van gonadenontwikkeling was altijd het hoogst voor *O. niloticus*. Dit vormt een aanwijzing voor een reproductief concurrentievoordeel voor de exoot, want een continu groter aantal rijpe vrouwtjes wijst op een relatief grote reproductieve inspanning ten opzichte van de inheemse tilapia.

In tegenstelling tot de onbewuste introductie van de Nijltilapia, heeft het bewust uitzetten van de sardine *Limnothrissa miodon* geen negatieve invloed op het ecosysteem gehad. Het grote verschil tussen beide introducties is het feit dat de sardine een onbezette niche kon opvullen, waardoor interacties met andere vissoorten vrijwel niet voorkwamen. De beschikbaarheid van een onbezette niche zou een belangrijke standaardafweging moeten zijn bij het plannen van visintroducties, om een potentiële biodiversiteitsverlies te voorkomen. Het doel van de introductie van *L. miodon* in het Karibameer, het verhogen van de visproductie, is gehaald. Maar om de verkregen sociaaleconomische voordelen te maximaliseren, dient de sardinevisserij te worden geoptimaliseerd via het vergaren van wetenschappelijke kennis over de biologie van en de visserij op de sardine, zoals gedaan in het in dit proefschrift beschreven onderzoek.

In dit proefschrift zijn de relatieve groeisnelheid en de gemiddelde lengte bij geslachtsslijpheid van *L. miodon* geschat en is besproken wat deze tekenden voor de status van de populatie en de visserij. De maximale gemiddelde lengte (*L∞*) van *L. miodon*, zoals geschat met behulp van het Gompertz model, bedroeg in 1993 – 1994, 1996 en 2012 – 2013 respectievelijk 18.0, 9.6 en 15.2 cm (TL). Deze waarden en de bijbehorende jaarlijkse variatie, zijn vergelijkbaar met die in het meer van oorsprong van de soort, het Tanganyikameer. Mijn resultaten wijken af van die van eerdere studies, waarin de conclusie werd getrokken dat de sardinepopulatie in het Karibameer dwerggroei vertoont. Het ontbreken van grote exemplaren in de vangsten van de sardinevisseren kan echter worden verklaard door de grote hoeveelheid onvolgroeide vis die wordt weggevangen, in combinatie met de voorkeur van grote sardines voor de oeverzone, waar ze onbereikbaar zijn voor de in het open water opererende vissersvloot. De gemiddelde leeftijd bij geslachtsslijpheid in het Karibameer is lager dan die in het Tanganyikameer en is sinds de introductie steeds verder afgenomen. Ook de gemiddelde lengte bij geslachtsslijpheid is sterk afgenomen in de loop der jaren. Dit wordt geïllustreerd door een vergelijking van de waarden die in deze studie zijn gevonden (vrouwtjes: 3.43 cm; mannetjes: 3.63 cm) met geraapteerde waarden voor de periode 1970 – 1972 (vrouwtjes: 5.2 – 5.6 cm; mannetjes: 7.1 – 7.3 cm).
De afname in de gemiddelde leeftijd bij geslachtsrijpheid kan worden toegeschreven aan overbevissing, waarbij een selectieve visserijdruk op snelgroeiende vis de relatieve overleving van exemplaren met een kortere generatietijd bevordert. Deze verandering in de ontwikkelingscyclus van de sardine vertraagt het herstel van de populatie.

De introducties in het Karibameer leverden ons lessen op met betrekking tot het belang van het uitzetten van vis in een reservoir om de visproductie te verhogen. Het uitzetten van de sardine *Limnothrissa miodon* leerde ons hoe overbevissing en ongunstige milieuomstandigheden de vangsten kunnen reduceren en vervolgens leiden tot een erosie van sociaaleconomische baten. Voor een duurzaam visserijbeheer dienen deze twee factoren te worden geïntegreerd in de productiviteitsschatting, het beheer en de monitoring van de visserij. De introductie van de Nijltilapia bood de mogelijkheid tot het volgen van de effecten van de introductie van een exotische soort met dezelfde ecologische niche als een reeds aanwezige inheemse soort. Ik laat zien dat de introductie van een vissoort in een bezette niche niet tot hogere vangsten (baten) hoeft te leiden maar integendeel, kosten kan veroorzaken met betrekking tot een afname van de biodiversiteit ten gevolge van het verlies van inheemse en endemische soorten.
Curriculum Vitae
According to my passport I am Chiyedza Portia Chifamba but somehow, I was registered at school as Portia Chifamba. Hence, my school certificates are by that name and I have used it thereafter. I was born on the 2nd of August 1963 in Zimbabwe. I am married to Jan Wanink, who is from the Netherlands, and we have three children: Marjo, Nyasha and Paula. I obtained a BSc General degree with a major in Biological Sciences at the University of Zimbabwe (UZ) in 1985.

I am employed as a Senior Lecturer in the Department of Biological Sciences (DBS), of the UZ, in Harare. In 2006, I joined the DBS as a lecturer on a Fish Biologist post. I teach ichthyology, fisheries biology, tetrapod biology and environmental impact assessment to students enrolled in the BSc Honours in Biological Sciences degree programme. I also teach fish communities, fish stock assessment, aquaculture, conservation and management of biodiversity in the MSc in Tropical Hydrobiology and Fisheries. I have taught ecology and biodiversity in the MSc Integrated Water Resource Management offered in the Department of Civil Engineering. Through this degree programme, I was once invited to teach a module on Environmental Flows Legislation at the University of Malawi, Chancellor College. I have supervised eight MSc and at least seven undergraduate research projects and I currently have two undergraduate students. I was the Chair of DBS from 2009 to 2012. I was an external examiner at Bindura University, Zimbabwe. Completing my PhD means that I will finally have more time for this part of my teaching duties.

Before going to Harare, I worked at the University Lake Kariba Research Station (ULKRS) as a Research Fellow from 1995 to 2006. My duties were to research, teach and supervise student researchers. I participated in the development and delivery of short courses on water resources, fisheries management, environmental impact assessment and integrated coastal zones management. I was Project Manager of the Water Group of the SANTREN (Southern African Training on the Environment Network) project run by the Institute of Environmental Studies (IES) of UZ. Within this project I developed and delivered a short training course on Integrated Coastal Zones Management in 2000. I also carried out a training need assessment in Zambia, Zimbabwe and Malawi. I participated in the Water Resources in the Lake Kariba Environs (DARMA) project, where I contributed a chapter in a book. I also participated in the Global International Water Assessment (GIWA).

From 1986 to 1994, I worked at the Lake Kariba Fisheries Research Institute (LKFRI) of the Department of National Parks and Wildlife Management (Ministry of Environment and Tourism) as a Research Officer. My duties were to carry out research, extension and to assist in administration. While on this job, I obtained in 1991 an MSc in Fisheries Biology and Management from then the University of Wales, Bangor (now the University of Bangor) in the UK. I won the Jeremy Jones Memorial Prize for being the best student of my class. After that, I did a Diploma in...
Management for Sustainable Fisheries at the University of Tromsø (Norway) in 1992.

I taught on the US Pitzer College programme, that was based in Harare at UZ. In 2008, at the request of the National Parks and Wildlife Management Authority, I reviewed part of the curriculum of the Diploma offered by the Natural Resources College and assisted the students of this college in undertaking research on Lake Chivero.

I have published research in the field of fisheries biology and water pollution. For the research I did on the displacement of the Kariba tilapia (*Oreochromis mortimeri*) by the Nile tilapia (*Oreochromis niloticus*) I won the Ibaraki Kasumigaura Prize for outstanding content of a paper on Lake Conservation by the International Lake Environment Commission (ILEC) in 2005.

I have interest in integrated management and the environment in general. In line with this, I have coordinated the Lake Chivero Integrated Lake Basin Management program that was sponsored by (ILEC). I was a member of the Zimbabwe National Steering Committee for Integrated Water Resource Management and the Pollution Monitoring of the Zambezi River. I am a member of Wildlife and Environment Zimbabwe.

Basically, I love to work with fish, how they are harvested, where they live and so on.
Acknowledgements
The thesis celebrates the end of a long journey. It’s an accumulation of ideas originating from many people associated with collection and processing of samples in the field, analysis of samples in the laboratory, and the writing of manuscripts and thesis chapters. I see it as a magnificent quilt made up of these grand patches. The first definite steps on the journey must have been taken in 1994, when I registered for a PhD with the Aberdeen University in the UK. Then I was working at the Lake Kariba Fisheries Research Institute (LKFRI). Prof Christopher Magadza, then Director of the University Lake Kariba Research Station (ULKRS) and Prof George Turner, then at Aberdeen University, shaped my research project into a PhD project, for which I am most grateful. Thank you, George and Rosanna Robinson, for your hospitality when I came to Aberdeen. My research project was on growth and factors affecting exploitation of sardine is contained in Chapters 6 and 7. Unfortunately, my funding for the PhD stopped and I was also stopped from working on the research project, having moved from LKFRI to work at ULKRS.

Later, with assistance from Chris and Prof Ngoni Moyo, I came up with a new research project and in 2002 registered for a PhD at the University of Zimbabwe with the two as my supervisors. I am grateful for their help and encouragement. This time my project was on the impact of the Nile tilapia introduced into Lake Kariba. Sadly, for me, Ngoni left for the University of Limpopo in South Africa and a new supervisor had to be found. Prof Brian Marshall took me under his wings and set about redirecting the research to be focused sharply on the biology. Prof Marshall could not tolerate any socio blah blah, insisting that sociology has no place in science. He gave me encouraging remarks on the aggression experiment in Chapter 5. Too soon, an opportunity arose for Brian to work in Uganda on an EU project on Lake Victoria. After he left, there was no suitable supervisor for me. To make matters worse, the adverse socio-economic situation forced me to stop my fieldwork. Fuel, needed for sampling, became scarce around 2002 and was virtually unavailable thereafter. The situation worsened and was at its worst in 2008, when basic survival was difficult and most of my time was spend in queues for whatever became available.

Despite these setbacks I still wanted to pursue my PhD and explored other avenues. Jan Wanink and the late Dr Frans Witte (Leiden University) assisted in arranging my study at the University of Groningen under the supervision of Prof John Videler. Thank you, Frans, for inviting me twice to spend my contact leave at Leiden University, for the help in setting up my experiments in the basement and letting me use your fish. Your hospitality and generosity knew no bounds. Thank you and Els for opening your house to my family during my stay in Leiden. I fondly remember the evening you brought toys down from the attic for Paula to play with
and everyone spent the whole evening enjoying them. What fun we had. You will always be missed.

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Those who know me well understand that my memory of names is very poor indeed. That is a lame excuse, I know. I apologise profusely to those I failed to name but have contributed to the process. I am indebted to you all, for without your help the thesis and PhD would not have been attained.

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