

# **ON THE ECOLOGY OF A TROPICAL FISH COMMUNITY**

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CENTRALE LANDBOUWCATALOGUS



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# ON THE ECOLOGY OF A TROPICAL FISH COMMUNITY

G.J. Piet

## Proefschrift

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The research described in this thesis was carried out at the Department of Zoology of the Ruhuna University (RU), Matara, Sri Lanka, the Centre for Limnology (CL) of the Netherlands Institute of Ecology (NIE) and Wageningen Institute of Animal Sciences (WIAS), Department of Fish Culture and Fisheries (DFCF). The investigations were partially supported by grant W84-313 of the Netherlands foundation for the Advancement of Tropical Research (WOTRO) which is subsidized by the Netherlands Organisation for Scientific Research (NWO).

## Stellingen

1. In de ondiepe Sri Lankaanse laagland reservoirs neemt de geïntroduceerde exotische tilapia een voorheen onbezette niche in en derhalve is er geen sprake van competitie met de inheemse soorten.  
**Dit proefschrift**
2. De hoge efficiëntie van biologische visproductie in tropische reservoirs kan grotendeels verklaard worden door de korte voedselketen vanwege het grote aandeel van herbivoren in de visgemeenschap.  
**Dit proefschrift**
3. De overdreven voorstelling van het effect van de introductie van de exotische tilapia op de inheemse vissoorten in de Sri Lankaanse reservoirs is voornamelijk gebaseerd op het feit dat biologische visproductie in de tropen meestal wordt geschat aan de hand van de commerciële vangsten.  
**Dit proefschrift**
4. Het succes van de geïntroduceerde tilapias in Zuid-Oost Aziatische reservoirs komt niet zozeer voort uit een betere aanpassing van deze soorten aan de lacustriene omstandigheden als wel uit een onvoldoende aanpassing van de lokale visserij aan het inheemse visaanbod.  
**Dit proefschrift**
5. De binnenvisserij en de rijstproductie hebben tegenstrijdige belangen bij het beheer van het water in de reservoirs in Sri Lanka. Gezien de overeenkomst tussen de verhouding vis/rijst in een Sri Lankaanse maaltijd en het toekennen van prioriteit bij de allocatie van water is het van belang uit te zoeken wat oorzaak en wat gevolg is.
6. Omdat de waarde van ieder goed bepaald wordt door de relatieve schaarste van dit goed zal de intrinsieke waarde van een mensenleven afnemen met toenemende bevolkingsdichtheid.
7. Culturele verschillen wijzen op menselijke overeenkomsten.
8. Gegeven de huidige problematiek omtrent de bevolkingstoename zou een kinderreffing beter op zijn plaats zijn dan een kinderbijslag.
9. Exotisch sentimentalisme komt voort uit hetzelfde onbegrip als racisme.
10. Gezien de verhouding alcoholverslaafden/drugsverslaafden in de Europese Gemeenschap zou er eerder bezwaar moeten zijn tegen de export van Franse wijn dan tegen de toevoer van drugs uit Nederland.

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## Voorwoord

Na het beëindigen van mijn studie aan de Landbouw Universiteit was ik er van overtuigd dat alle onderzoek dat ik nog zou doen, zich achter de computer zou afspelen. Mijn kennis van vis beperkte zich tot enkele zeevissen waarvan ik wist hoe ze gevangen moesten worden en hoe ze smaakten. Luttele maanden later zat ik in Sri Lanka tot mijn ellebogen in een berg vis waar ik met de grootste moeite vier soorten in kon onderscheiden. Dankzij de niet aflatende hulp van begeleiders en collega's, ben ik er gaandeweg in geslaagd, niet alleen te ontdekken dat er zowaar meer dan vier soorten in die berg vis zaten maar heb ik ook enig idee gekregen welke factoren bepalend zijn voor de grootte en samenstelling van deze berg.

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## Samenvatting

Sri Lanka heeft geen natuurlijke meren maar wel meer dan 12.000 door de mens aangelegde reservoirs met een totaal oppervlak van ongeveer 175.000 ha. Over het algemeen zijn deze reservoirs ondiep, de maximale diepte is vaak minder dan 5 m, en het watermivo vertoont aanzienlijke schommelingen. Verder worden de reservoirs gekenmerkt door een hoge primaire productie. Daarentegen bleef de visproductie, vastgesteld aan de hand van de visserijopbrengsten, ruimschoots achter bij wat verwacht mocht worden aan de hand van deze hoge primaire productie. Een mogelijke verklaring hiervoor zou kunnen zijn dat de inheemse riviervissen die deze reservoirs bevolkten onvoldoende waren aangepast aan de lacustrine omstandigheden. Deze situatie veranderde drastisch toen omstreeks 1952 de Afrikaanse tilapias *O. mossambicus* en *O. niloticus* werden geïntroduceerd. Vanaf dat moment is het aandeel van de binnenvisserij tot de totale visserij gestegen van bijna 0 tot op het ogenblik ongeveer 20%. Het overgrote deel van de vangsten van de binnenvisserij bestaat uit deze geïntroduceerde tilapias. De beschikbaarheid van goedkope zoetwatervis is vooral van belang voor de arme bevolking in de onderontwikkelde droge laaglanden in het noorden, oosten en zuid-oosten van Sri Lanka. De invloed van de introductie van de exotische tilapias op de productie en samenstelling van de inheemse visgemeenschap werd echter nooit vastgesteld.

Het onderzoek werd uitgevoerd aan het Tissawewa reservoir. Tissawewa is een ondiep (gemiddelde diepte = 1.2 m) irrigatie-reservoir van ca. 200 ha, dat representatief is voor het droge laagland van zuid-oost Sri Lanka. In deze studie is de biologische visproductie geschat op 2430 kg/ha/jr waarvan ongeveer 20% voor rekening van de tilapias kwam. Daarentegen bestond ongeveer 80% van de commerciële vangst van 242 kg/ha/jr uit tilapias. Dit laat zien dat het aandeel van tilapias tot de totale biologische visproductie in Sri Lanka en hoogstwaarschijnlijk in de hele Zuid-Oost Aziatische regio altijd overschat is omdat deze schattingen gebaseerd waren op de commerciële vangsten. De bruto primaire productie is geschat op ongeveer 13.000 kg C/ha/jr wat betekent dat 1.9% van de bruto productie wordt omgezet in vis. Deze efficiëntie is hoog vergeleken met de efficiënties tussen de 0.2% en 1.6% waargenomen in andere meren en reservoirs over de gehele wereld en wordt mogelijk gemaakt door de specifieke structuur van de visgemeenschap. Een groot deel van de vis-biomassa (ca. 45%) bestaat uit een kleine inheemse karperachtige vis, *A. melettinus*, die zich voornamelijk voedt met phytoplankton en detritus. Daarnaast voeden ook de tilapias (die ca. 9% van de biomassa uitmaken) zich met plantaardig voedsel. Deze soorten vormen de primaire consumenten die in totaal ca. 64% bijdragen aan de biologische visproductie. De secundaire consumenten dragen ongeveer 36% bij terwijl in totaal maar 0.3% van het voedsel dat door de visgemeenschap gegeten wordt over meer dan drie trofische nivo's gaat. De korte voedselketens, kenmerkend voor de structuur van het Tissawewa voedselweb, zijn dus hoogstwaarschijnlijk verantwoordelijk voor de uitzonderlijk hoge efficiëntie van de visproductie.

De structuur en het functioneren van de visgemeenschap kunnen worden gereguleerd door verschillende mechanismen zoals een deterministische versus stochastische regulatie of, indien deterministisch gereguleerd, door de primaire producenten (bottom-up) dan wel de predatoren (top-down). Een deterministisch



gereguleerde gemeenschap bevindt zich doorgaans in een evenwichtstoestand waarbij de abundantie van de populaties bepaald wordt door een samenspel van de hoeveelheid voedsel aanwezig en competitie om dit voedsel met andere populaties. Mechanismen als niche segregatie zijn hierbij belangrijk voor de coëxistentie van soorten. Ingeval van een stochastische regulatie is de omgeving niet stabiel genoeg, zodat er geen evenwicht bereikt kan worden en wordt de abundantie van een populatie voornamelijk bepaald door onvoorspelbare veranderingen in zijn omgeving in plaats van door interacties met andere populaties. In deze studie is gevonden dat de structuur en het functioneren van de Tissawewa visgemeenschap voornamelijk deterministisch gereguleerd is waarbij extreem lage waterstanden of de droogval van het reservoir een relatief kortstondige periode van stochastische regulatie teweeg kunnen brengen.

Gedurende de monsterperiode is, ten gevolge van een langdurige droogte, het waternivo van het reservoir gestadig gedaald tot het geheel droog stond. Toen het enkele maanden later weer volgelopen was, bleken de omstandigheden aanzienlijk veranderd te zijn. Voor de droogval was phytoplankton de voornaamste primaire producent, was het water troebel ten gevolge van de resuspensie van een dikke laag detritus op de bodem en kwam vegetatie alleen in de ondiepe littorale zone voor. Na de droogval was het water relatief helder omdat de laag detritus op de bodem verdwenen was en kwam vegetatie over het hele reservoir voor. De gemiddelde visbiomassa voor de droogte was 1700 kg/ha, daarna was dit nog maar 770 kg/ha. Toen de gemiddelde waterdiepte daalde beneden de 0.5 m begon de structuur van de visgemeenschap steeds verder af te wijken van de evenwichtstoestand waarin deze zich daarvoor bevond. Ongeveer één jaar nadat het reservoir weer was volgestroomd bevond de visgemeenschap zich weer in een nieuwe evenwichtsstand waarbij echter de structuur van de levensgemeenschap bij deze nieuwe evenwichtsstand, sterk afweek van die van voor de droogte. De voornaamste verschillen konden teruggevoerd worden op de veranderingen in de omgeving, met name die van de voedselbeschikbaarheid. De soort die het meest beïnvloed was door deze veranderingen was *A. melettinus*, waarvan het aandeel in de totale visbiomassa daalde van 45% voor de droogte tot 9% na de droogte. Dit werd veroorzaakt omdat de concentratie van zijn voornaamste voedselbron, die van zwevend detritus, daalde van respectievelijk 7.3 g C/m<sup>3</sup> tot 2.1 C/m<sup>3</sup>. Dit illustreert ook dat de structuur van de visgemeenschap voornamelijk bepaald wordt door bottom-up regulatie terwijl top-down invloeden relatief onbelangrijk zijn.

Het deterministische karakter tesamen met het belang van bottom-up regulatie van de structuur van de Tissawewa visgemeenschap impliceert dat biotische interacties zoals competitie en niche segregatie, bepalend zijn voor de abundantie van de verschillende populaties. Van de tien belangrijkste soorten werd de niche bezetting bepaald langs drie dimensies: de trofische, de spatiële en de temporele. De positie van een populatie langs de trofische dimensie wordt bepaald door het voedsel dat gegeten wordt, de positie langs de spatiële dimensie door de verspreiding over de verschillende habitats in het reservoir en de positie langs de temporele dimensie door het tijdstip van de dag dat de soort aan het foerageren is. Omdat met name bij vissen de lichaamsgrootte aanzienlijk verandert gedurende hun ontwikkeling en dit belangrijke consequenties kan hebben voor de niche bezetting van een individu, is iedere soort onderverdeeld in grootte-klassen waarvoor de niche bezetting afzonderlijk bepaald werd. Verder werd in dit onderzoek niet alleen de

niche bezetting langs iedere dimensie apart bepaald maar werd ook aandacht besteed aan de interactie tussen de verschillende dimensies. Om het belang van de verschillende interacties te doorgronden moet onderscheid gemaakt worden tussen exploitatieve competitie en interferentie competitie. Bij de eerste gaat het om een indirecte interferentie zoals bijvoorbeeld de mate waarin voedsel geëxploiteerd wordt, bij de tweede gaat het om een directe interferentie middels het innemen van ruimte.

Voor exploitatieve competitie is de interactie tussen de trofische en spatiële dimensie van belang. Met andere woorden welk voedsel wordt waar vandaan gehaald, waarbij het tijdstip waarop dit gebeurt onbelangrijk is. Daarentegen is voor interferentie competitie de interactie tussen de spatiële en temporele dimensie bepalend. Of te wel, waar is de soort actief en op welk tijdstip. Voor wat betreft het tijdstip van foerageren is gebleken dat zeven soorten voornamelijk overdag actief zijn, één soort gedurende de schemering, terwijl de twee roofvissen voornamelijk s'nachts actief zijn. Wanneer een soort aan het foerageren is wordt zijn verspreiding over het reservoir vooral bepaald door de verspreidingspatronen van zijn voornaamste voedselorganismen en door het ontwijken van de roofvis. Deze laatste strategie is voor die soorten of grootte-klassen die gevaar lopen gegeten te worden door de roofvissen, bepalend voor hun distributie, zelfs als dit suboptimaal foerageren tot gevolg heeft. Het ontwijken van predatie wordt door de juvenielen van alle soorten gerealiseerd door zich voornamelijk tussen de vegetatie op te houden. De belangrijkste volwassen prooien zijn *A. melettinus*, *H. gaimardi* en *R. daniconius*. Deze soorten proberen aan predatie te ontkomen, door de laag dicht bij bodem, waar de roofvissen zich bevinden, te ontwijken. Zodra een vis niet meer foerageert verandert zijn verspreidingspatroon zodanig dat hij zoveel mogelijk interferentie competitie en predatie ontwijkt. Dit wordt door alle vissen gerealiseerd door omhoog te migreren. Door de perioden voor en na het droogvallen van het reservoir met elkaar te vergelijken, is gevonden dat de vissen zowel de efficiëntie van foerageren als ook het gevaar voor predatie kunnen inschatten afhankelijk van de omstandigheden en daar hun verspreiding op aanpassen. Omdat de interferentie competitie was afgenomen na de droogval ten gevolge van de lagere visdichtheid nam ook de opwaartse migratie af.

Voor de belangrijkste vissoorten in Tissawewa is een korrelatie vastgesteld tussen morfologie en dieet. Hierbij bleek dat een beperkt aantal morfologische kenmerken bepalend is voor de samenstelling van het dieet. De grootte van de bek beperkte de maximale grootte van het voedsel, de lengte van de darm bepaalde in hoeverre plantaardig materiaal als voedselbron gebruikt kon worden en de oriëntatie van de mondopening en de aanwezigheid van barbelen was gekorreleerd met de positie van het voedsel in de waterkolom. De eerste twee relaties tussen morfologische- en voedsel kenmerken bleken voldoende om de potentiële trofische niches van de verschillende populaties vast te stellen en daarmee de trofische structuur als ook de belangrijkste ontogenetische verschillen binnen de soorten. De gerealiseerde trofische niches zoals die waren vastgesteld gedurende de perioden voor- en na de droogval bleken zodanig binnen de potentiële niches te vallen dat een maximale niche segregatie gerealiseerd kon worden.

Voor de bepaling van niche overlap en niche breedte is aangetoond dat een andere manier van berekenen waarbij de ontogenetische veranderingen in de berekende maat verdisconteerd zijn, een aanzienlijke verbetering ten opzichte van conventionele methoden met zich mee brengt. Bijvoorbeeld, niche breedte die gebruikt wordt als een maat voor de

flexibiliteit van een soort om zich aan te passen aan veranderde voedselomstandigheden wordt aanzienlijk beïnvloedt door ontogenetische veranderingen. Soorten die gedurende hun ontwikkeling grote veranderingen ondergaan, wordt een hogere flexibiliteit toegedicht dan in werkelijkheid het geval is. Zo bleken soorten die op grond van hun niche overlap, berekend volgens de conventionele methode, geen potentiële concurrenten zijn, dit tijdens hun juveniele stadia wel te zijn. Bovendien werd ook mogelijke voedselconcurrentie aangetoond tussen de juvenielen in het algemeen en de volwassen zooplanktivore soorten. De abundantie van een soort wordt bepaald door een samenspel van intra-specifieke (binnen de soort) en inter-specifieke (tussen de soorten) competitie. De berekende niche overlap waarden zijn vergeleken: 1) binnen een soort tussen de ontogenetische stadia; 2) tussen de soorten; en 3) voor de gehele visgemeenschap tussen de perioden voor en na de droogte. Hieruit bleek met grote waarschijnlijkheid dat: 1) intra-specifieke competitie lager is voor soorten met grote ontogenetische verschillen; 2) inter-specifieke competitie lager is voor specialisten; en 3) er sprake is van competitie tussen de soorten. Dit laatste werd geïllustreerd doordat gedurende de periode voor de droogval toen de visdichtheid hoger was, de gemiddelde niche overlap lager was en er derhalve sprake was van een hogere mate van niche segregatie. Voor de visgemeenschap in Tissawewa is trofische segregatie belangrijker dan spatiële of temporele segregatie.

Gebaseerd op de niche overlap langs de belangrijkste dimensies is de meest waarschijnlijke inheemse concurrent van de exotische tilapias, de pelagische karperachtige vis, *A. melettinus*. Echter een nauwkeuriger bestudering van het foerageergedrag van de beide potentiële concurrenten leert dat *A. melettinus* voornamelijk fijn detritus en phytoplankton zwevend in de waterkolom eet terwijl de tilapias het grovere detritus van de bodem grazen. Dit betekent dat *A. melettinus* geen concurrent is van de tilapias en mogelijk zelfs profijt kan hebben van het feit dat de tilapias het grovere detritus afbreken tot deeltjes die door *A. melettinus* benut kunnen worden. De succesvolle introductie van de lacustriene tilapias kan dus verklaard worden door het vermogen van de soorten een niche te benutten die voorheen niet bezet was en heeft derhalve hoogstwaarschijnlijk geen nadelige invloed op de inheemse riviervissen in de reservoirs.

De kennis van het ecosysteem met betrekking tot de invloed van, onder andere, competitie, predatie en fluctuaties in het waternivo op de vis gemeenschap, wordt gebruikt om het effect van verschillende beheersmaatregelen te evalueren. Voor Tissawewa geldt dat de additionele exploitatie van kleine pelagische vissoorten zoals onder andere *A. melettinus*, hetzij direct, hetzij middels de introductie van een controleerbare roofvis, hoogstwaarschijnlijk een positieve invloed op de bestaande visserij op tilapias zal hebben. Gebaseerd op de bevindingen in Tissawewa is geconcludeerd dat niet alleen voor Tissawewa maar waarschijnlijk voor alle vergelijkbare tropische wateren een aanzienlijk hogere proportie van de biologische visproductie geoogst kan worden dan de 10% die tot nog toe haalbaar werd geacht.

## Summary

Sri Lanka has more than 12,000 artificial reservoirs and no natural lakes as is true for many other areas in SE Asia. These reservoirs cover a total surface area of around 175,000 ha. They are shallow with maximum depths often less than 5 m and exhibit considerable fluctuations in water level. In general the fish production, estimated from commercial catches, is high in these reservoirs, but lower than would be expected on the basis of the high primary production. This situation changed drastically when around 1952 the exotic tilapias *O. mossambicus* and *O. niloticus* were introduced. From that moment onward the fish yield increased and the proportion of inland fisheries to total commercial fisheries rose from almost 0% up to the current 20%. This freshwater fish yield is dominated by the introduced tilapias. The cause of this successful introduction of the tilapias has long been debated. Two different hypotheses exist. Firstly, it has been suggested that the relatively low fish production (based on the yield) in the reservoirs before the introduction of the tilapias was probably due to the origin of the fish, mainly indigenous riverine carps, which may not be optimally adapted to their new conditions. According to this hypothesis the introduced tilapias were competitively dominant and were able to capture niches formerly occupied by the indigenous fish species. Secondly, the alternative hypothesis assumes that the tilapias are able to occupy an empty niche when introduced in the reservoirs and consequently did not compete with the indigenous fish species. Determination of the correct theory is important, both from a theoretical and applied (fisheries management) point of view. This is attempted by studying, for the first time, the effects of the exotic lacustrine tilapias on the indigenous riverine fish species, within the framework of a tropical fish community.

The present study was conducted at Tissawewa reservoir. Tissawewa is a typical shallow lowland irrigation reservoir (average depth = 1.2 m) with a surface area of about 200 ha in the dry SE corner of Sri Lanka. In this study the total biological fish production was estimated at 2430 kg/ha/yr of which about 20% consisted of the exotic tilapias. In contrast, about 80% of the commercial catches of 242 kg/ha/yr consisted of these species. This strongly suggests that the importance of tilapias in terms of biological fish production was markedly overestimated not only in Sri Lanka but most probably in all of SE Asia because all estimates of fish production were based on commercial catches. The gross primary production was estimated at about 13,000 kg C/ha/yr of which 1.9% is transferred into fish. This efficiency is high compared to efficiencies between 0.2% and 1.6% reported for other lakes and reservoirs. This high transfer efficiency of fish production can be explained by the short food chain. Most of the fish biomass (ca 45%) consists of a small indigenous cyprinid, *A. meletinus*, which feeds predominantly on phytoplankton and detritus. The tilapias (which make up ca. 9% of the fish biomass) are also herbivorous. These primary consumers represent about 64% of the biological fish production in the reservoir. The secondary consumers represent 36% of the biological fish production while only 0.3% of the fish production is made up by the third trophic level, that of the tertiary consumers.

The structure and functioning of the fish community can be regulated according to several mechanisms such as a deterministic versus a stochastic regulation or, when deterministically regulated, by bottom-up (regulated by primary producers) versus top-down (regulated by predators) control. A deterministically regulated community is generally at an equilibrium, with population levels at carrying capacity determined by resource limitations

and coexisting species avoiding competitive exclusion through biotic interactions such as resource partitioning. In contrast, a community is stochastically regulated when the environment is not stable enough to allow an equilibrium to persist. The abundances of species in such a community are determined largely through differential responses to unpredictable environmental changes, rather than through biotic interactions. Based on the disturbances, caused by water level fluctuations, acting on the fish community and community characteristics such as resistance and resilience, the Tissawewa fish community is considered to be deterministically regulated. However, extreme low water levels or the drying up of the reservoir which occur occasionally can cause a relatively brief time of stochastic regulation. Both these phenomena could be studied because during the sampling period, due to a long period of extreme drought, the water level decreased until the reservoir was completely dry. After filling up a different ecosystem had evolved. Before the drought (Period 1) Tissawewa had vegetation only in the shallow, littoral zone and a high turbidity due to resuspension of the thick layer of detritus on the bottom. After the drought (Period 2) vegetation was found all over the reservoir, covering the entire water column, and the water was significantly clearer due to a lower concentration of suspended detritus and phytoplankton. During Period 1 the average fish biomass was about 1700 kg/ha, while during Period 2 this was only 770 kg/ha. The community was at equilibrium at the beginning of the sampling period but as the water level decreased below 1.5 m maximum depth, this equilibrium was disturbed. About one year after the reservoir refilled, a new equilibrium different from the former equilibrium was established. The species mainly affected by these environmental changes was *A. melettinus*. Its share in the total fish biomass decreased from on average 45% during Period 1 to 9% during Period 2. This was mainly caused by a decrease of its main food source, that of suspended detritus, from respectively 7.3 g C/m<sup>3</sup> to 2.1 g C/m<sup>3</sup>. This also illustrates the importance of bottom-up regulation for the structure of the Tissawewa fish community.

The fact that the structure of the Tissawewa fish community is deterministically regulated together with the importance of bottom-up regulation implies that competition and resource partitioning are important mechanisms determining the abundance of the different populations. Therefore the niche occupation of the ten most important fish species was determined along three dimensions: the trophic, the spatial and the temporal dimension. The position along the trophic dimension depends on the diet of the species, the position along the spatial dimension on the distribution over the various habitats in the reservoir and the position along the temporal dimension depends on the time of day the species were actively foraging. Because the body size of fish can increase several orders of magnitude during ontogeny which, in turn, can have considerable consequences for the niche occupation of an individual, each species was subdivided into size-classes for which niche occupation was determined separately. Not only the size-specific niche occupation along each dimension was determined in this study, but also the interaction between the different dimensions. In order to comprehend the impact of these interactions two types of competition should be distinguished: exploitative competition and interference competition. The former describes how species affect each other through the exploitation of the same food sources, the latter deals with a more direct interference through the capturing of space.

Exploitative competition mainly depends on the interaction between the trophic and spatial dimension. In other words: what food is taken from where while the time at which this happens is unimportant. Interference competition depends on the interaction between the spatial and temporal dimension: where and when is a certain species active. With regard to the time of day a species is actively foraging, seven diurnal species were observed, two nocturnal piscivores while one species was mainly active during dusk and dawn. When actively foraging the distribution of a fish is determined by a trade-off between foraging profitability and risk of predation. For those species or size-classes subject to predation, avoidance of predation is the main factor determining their distribution even if this results in suboptimal foraging. The juveniles of all species avoid predation by using the cover provided by the vegetation. The main adult prey, *A. melettinus*, *H. gaimardi* and *R. daniconius* avoid predation by evading the bottom layer of the reservoir where the piscivores reside. For those individuals which are not foraging their distribution is aimed at avoiding interference competition and predation. This is realised by all fish through a migration upward along the vertical plane. Environmental changes affecting the risk of predation and foraging rate are reflected in the distribution patterns of the fish species involved, confirming the ability of species to facultatively respond to these factors. Because fish density and consequently interference competition was lower after the drought, the upward migration also decreased.

For the Tissawewa fish community a correlation was observed between the morphology of a fish and its diet. This diet was apparently determined by only a few morphological characters. The gape width constrained the maximum size of the food particles, the gut length was related to the potential of utilising vegetable matter and the orientation of the mouth and the presence of barbels were correlated with the position of the food along the vertical gradient. Assuming functional relationships, the potential niches of the species were established, and within each species the main ontogenetic differences could be explained. The realised trophic niches of each population both before and after the drought coincided with what could be expected from the relative positions of the potential niches of these populations along the trophic resource dimension assuming niche segregation.

It was observed that size-specific measures of calculating niche breadths and niche overlaps, in which ontogenetic changes can be incorporated, present considerable advantages to the conventional measures when studying intra- and interspecific competition. For example, niche breadth which can be considered an indicator of the flexibility of a species to adjust to changes in food availability is markedly affected by ontogenetic changes; species with large ontogenetic changes would be considered more flexible than they actually are. Species of which the juvenile stages appeared to compete for resources would not be considered potential competitors based on the conventional measures. Also, possible competition for food was observed between the zooplanktivorous juvenile stages of several species with non-zooplanktivorous large adults, and the adult zooplanktivores: the juvenile competitive bottleneck. The abundance of a species is determined by the combination of intra- and interspecific competition. The calculated niche overlap measures were compared: 1) within one species between ontogenetic stages; 2) between species; 3) for the entire fish community between the periods before and after the drought. This strongly suggested that: 1) intra-specific

competition is lower for species with large ontogenetic changes; 2) inter-specific competition is lower for specialists; and 3) competition for resources exists. The latter was concluded because during Period 1 when fish biomass was highest, niche segregation was highest and consequently average niche overlap was lowest. For the Tissawewa fish community segregation along the trophic dimension was more important than along the spatial or temporal dimension.

Based on niche overlap along three resource dimensions, the main potential indigenous competitor of the exotic introduced tilapias is the small pelagic cyprinid, *A. melettinus*. However, a more detailed analysis of the foraging behaviour of these potential competitors shows that *A. melettinus* mainly feeds on the fine particulate detritus and phytoplankton, suspended in the water column, while the tilapias graze the detrital aggregate from the bottom. This implies that *A. melettinus* is not a true competitor of the tilapias and might even benefit from the tilapias breaking down the flocculant material from the bottom into smaller, better suspendable, particles. Therefore, the successful introduction of the lacustrine tilapias can be explained from the ability of these species to occupy a previously unfilled niche, and as a consequence the indigenous fish community was most probably not harmed by this introduction.

The acquired knowledge of the Tissawewa ecosystem pertaining to the effects of, among others, competition, predation and water level fluctuations on the fish community is used to discuss the consequences of various management measures on the fish production and fish yield. It was concluded that an additional exploitation of van the small pelagic fish species, either directly, or through introduction and exploitation of a large (controllable) piscivore, will most probably enhance the existing fishery on tilapias. Based on the Tissawewa case study it is concluded that at least for Tissawewa, but most probably for all similar tropical waterbodies a markedly higher utilisation efficiency (yield/production) can be achieved than the 10% that is currently assumed.

# CHAPTER 1

## GENERAL INTRODUCTION

### Scientific background

The ultimate subject matter of ecology is "the distribution and abundance of organisms" (Krebs 1972). With how many they are, where they are or what they do is for each organism determined by the interaction with its environment. This environment consists of all those factors, whether abiotic (physical and chemical) or biotic (other organisms), outside the organism that influence it. The interaction with the environment varies in its degree of complexity (Evans 1956) and therefore different levels of organisation are distinguished: the individual organism, the population and the community.

The objectives of study at the organismal level relate primarily to the manner in which the various morphological, physiological and behavioural characteristics of organisms determine the fitness under miscellaneous environmental conditions. A population consists of the interacting members of a particular species occupying a defined geographic area. Characteristics such as density, condition, patterns of distribution of individuals in space and rates of natality and mortality are determined at the population level. These characteristics of the population can be explained in terms of the behaviour of the organisms that comprise it which in turn is determined by the interaction with their environment. Competition and predation are among the most important interactions. The community is defined as an assemblage of species populations which occur together in space and time. Because the community is the sum of its constituent species together with the interactions between them, it has emergent properties such as the structure of the food web, biodiversity and community biomass and productivity.

Competition for resources is a major factor determining the coexistence and abundance of species and has therefore been a central focus in ecology. Resource partitioning is an important accommodative mechanism allowing species to avoid competition. Over evolutionary time, avoidance of competition can be facilitated by divergent changes of morphological characteristics (Taper & Case 1985, Wikramanayake 1990, Motta & Kotrschal 1992). This simultaneous morphological and ecological segregation ascertains the close relationship between an organisms morphology and behaviour (Watson & Balon 1984, Winemiller 1991) and shows that a species' potential niche is largely determined by the morphological constraints acting on the individuals whereas its realised niche depends on the interactions among the individual organisms in a particular environment. Establishing the potential niches of the species in the assemblage based on their organisms' morphological characteristics is an important tool in determining possible competitors while comparison of the potential and realised niche of the species reveals whether competition is acting on these species.

According to optimal foraging theory an animal will occupy the habitat where a maximum foraging efficiency can be realised (MacArthur & Pianka 1966, Townsend & Winfield 1985). The actual occupation of an optimal habitat often depends on factors such as the risk of being predated in this habitat or competition for the same resources with



other species (Werner *et al.* 1983, Werner & Hall 1988). Common mechanisms responding to these factors are respectively predator avoidance and resource partitioning (Schoener 1974), each resulting in a suboptimal resource utilisation. Segregation of coexisting species can occur along trophic, spatial or temporal resource dimensions. Ross (1986), who reviewed the work on resource partitioning in fish communities, concluded that for freshwater fishes in a lacustrine environment the trophic dimension is slightly more important than the spatial dimension which in turn is markedly more important than the temporal dimension. When considering resource use, the ecological literature on species interactions stresses the importance of body size (Werner & Gilliam 1984). Differences in body size are a major means by which species avoid direct overlap in resource use (Schoener 1974). In contrast to several other taxa, conspecific individuals of fish vary greatly in body size which often spans several orders of magnitude (Werner & Gilliam 1984). Thus, considering the assumption that competing species must differ in size by a factor of 2 in order for them to coexist (MacArthur 1972, Bowers & Brown 1982), for fish the body dimensions experienced ontogenetically often transcend those limits purported to isolate competing species (Enders 1976, Keast 1977, Maiorana 1978, Polis 1984). Paradoxically, ecologists have virtually ignored the implications of these observations when determining measures of resource use or competition such as niche breadth or niche overlap. Also, body size determines the ability of an animal to avoid predation and thereby harvest resources from different habitat types. Consequently, as body size changes during ontogeny, many species will exhibit size-specific shifts in feeding behaviour or habitat use (Werner & Hall 1988). Fitness of a species often depends on the timing of these shifts which in turn depends on various trade-offs such as between foraging profitability and predation risk. One implication of the relation between body size and feeding behaviour is that smaller ontogenetic stages of one species often have resource use requirements similar to those of older individuals of smaller species (Werner 1986). As a consequence, competition during this stage can cause a significant bottleneck to recruitment to the subsequent ontogenetic stages of the larger species (Persson & Greenberg 1990).

Interactions at the population level such as competition or predation play in concert to determine characteristics such as the structure or functioning of the community. Grossman (1982) and Wiens (1977) developed a theoretical framework for characterising different mechanisms regulating community structure. This framework introduces a continuum with the stochastic and deterministic mechanisms occupying opposite endpoints and the competitive crunch mechanism resting somewhere in between. A deterministically regulated community is generally at an equilibrium, with population levels at carrying capacity determined by resource limitation and coexisting species avoiding extinction through biotic interactions such as resource partitioning (Schoener 1974, Tilman 1982). In contrast, a community is stochastically regulated when the environment is not stable enough to allow an equilibrium to persist. Thus, although some species might be mutually exclusive under stable environmental circumstances, the speed of the process of exclusion, is relatively slow compared to the environmental changes, resulting in different competitive relationships and thereby preventing competitive exclusion.

Another ongoing debate, pertaining to the regulation of community structure and functioning, focusses on whether primary control is by predators (top-down forces) or by

resources (bottom-up forces). The theories propagating top-down control predict that changes in abundance of the top predators will cascade down the foodweb (Shapiro *et al.* 1975, 1982, Carpenter *et al.* 1985, Fretwell 1987, Oksanen 1988, Hairston *et al.* 1960, Wiegert & Owen 1971) whereas the theories propagating bottom up control (Odum and Biever 1984, Vadas 1989) argue that while removal of higher trophic levels leaves lower levels present (if perhaps greatly modified), removal of primary producers leaves no system at all. Recently, these opposing viewpoints have been incorporated in conceptual models in which the effects of ecological factors can cascade up as well as down the trophic system (McQueen *et al.* 1986, 1989, Hunter & Price 1992, Power 1992, Strong 1992).

The discrepancy between high primary production and poor fish yields in some tropical reservoirs, especially in South East Asia, is apparently due to the fact that not all available niches are occupied (Fernando & Holcik 1982). This is probably due to the riverine origin of the fish communities which are not well adapted to lacustrine habitats in such reservoirs (Fernando & Holcik 1982, 1991). For example, riverine fishes are more generalised in their diet than lacustrine fish and consequently specialised herbivores or plankton feeders are very rare in riverine fish. Also, only few riverine fish are preadapted to take advantage of the pelagic zone, especially in large and deep reservoirs. The introduction of exotics, capable of occupying these unfilled niches can markedly increase fish yield (Fernando 1977, Fernando & Furtado 1975) but the effects on the indigenous fish species are not known.

There is a growing awareness of the relevance of community ecology to fisheries management. Although productivity of fish communities is determined by energy inputs, nutrients, edaphic factors and habitat variables it is now recognised that the distribution of the production over the species is strongly influenced by both size- and density-dependent interactions among species. The size-dependence follows from the morphological, physiological and behavioural constraints on predator-prey relationships while density-dependent interactions such as competition or predation influence growth rates, size distributions, age-specific mortality and reproductive rates and vice versa. Fish communities can be managed as relatively discrete functional units, but dependency on whole system dynamics ultimately necessitates an ecosystem perspective (Evans *et al.* 1987).

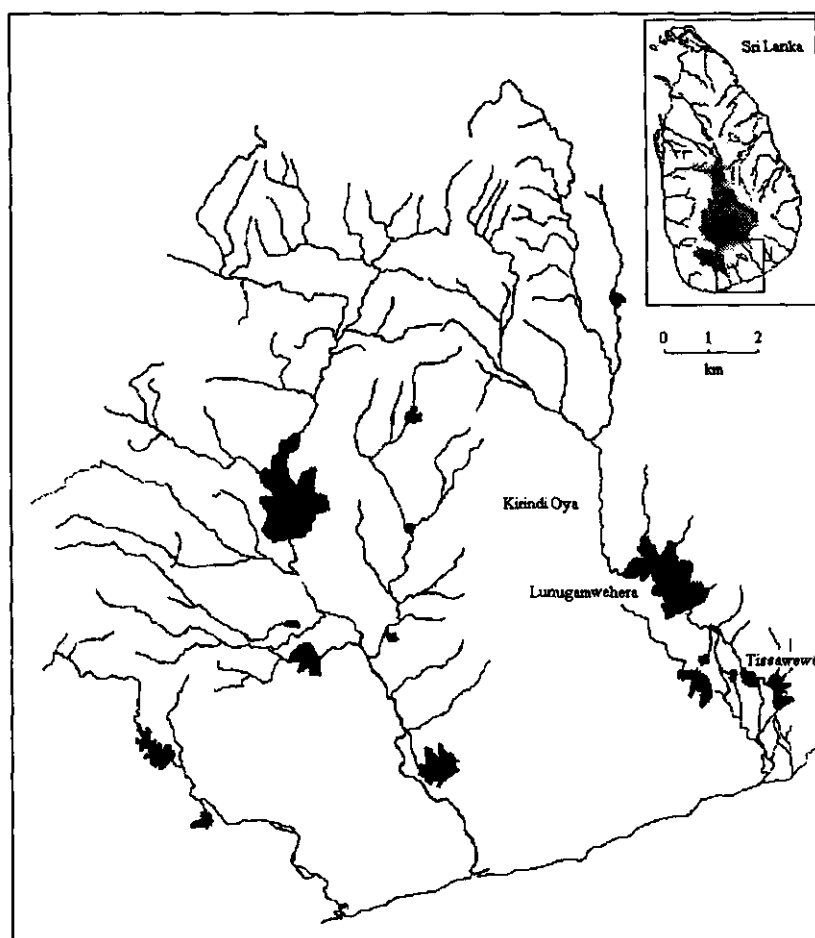
## Study area

Sri Lanka is a tropical continental island of 65,525 km<sup>2</sup> in SE Asia (79°30'-81°35'E; 5°55'-9°50'N). The natural water resources of the island consist of extensive river systems, including the associated flood plains and marshes but no natural lakes. However, Sri Lanka is reputed to possess over 12,000 man-made reservoirs (Baldwin 1991) with a total estimated area of 175,774 ha (De Silva 1988). This density of 3 ha of reservoir for every km<sup>2</sup> of the island is possibly the highest in the world (Fernando 1984). Almost all of the reservoirs are confined to the dry zone, to irrigate rice cultivation. Maximum depth and surface area fluctuations follow the annual patterns in rainfall. Two monsoon periods occur annually in the dry zone: a NE monsoon active from December to February and a SW monsoon active from mid May to September.

Tissawewa is a typical lowland irrigation reservoir, some 2000 years old, situated in the dry SE corner of Sri Lanka. It is shallow (mean depth = 1.2 m), eutrophic and wind exposed. This reservoir is part of the Kirindi Oya irrigation scheme constituting of the

Fig. 1.1

Location of Tissawewa and the Kirindi Oya Irrigation Scheme in SE Sri Lanka



river, Kirindi Oya, feeding the main reservoir Lunugamwehera (3023 ha) from which, through the left bank canal, five reservoirs downstream are fed: Pannegamuwawewa (255 ha), Weerawilawewa (570 ha), Debarawewa (60 ha), Tissawewa (250 ha) and Yodawewa (488 ha). Tissawewa is subject to considerable water level fluctuations and has a mean surface area of 193 ha and a mean maximum depth of 2.5 m since January 1987 (data from the Sri Lankan Irrigation Department). During the study period September 1991 to January 1994 these values were even lower, respectively 171 ha and 2.2 m, due to a long spell without significant rainfall. This spell eventually caused the reservoir to dry up completely. After filling up of the reservoir, a different ecosystem had evolved: Before the drought Tissawewa had macrophytes only in the shallow, inshore zone and turbidity was high (Secchi-depth transparency = 30 cm) due to resuspension of a thick layer of detritus on the bottom. After the drought macrophytes were found all over the reservoir covering

the entire watercolumn and there was relatively clear water (Secchi-depth transparency = 130 cm) because the detritus had vanished. To study the effect of an environmental change, two periods were distinguished: Period 1 covers the sampling occasions before the drought while period 2 covers the sampling occasions after the drought. During period 1 Tissawewa is representative of a typical Sri Lankan lowland reservoir.

### Sampling program

In the reservoir four different habitats were distinguished: Respectively the surface and bottom layer of the deep part of the open water zone, the intermediate zone and the inshore zone. One sampling station was chosen within each of these habitats. Experimental fishing was carried out in each of these stations, on a monthly basis from September 1991 to January 1994 with two interruptions from respectively September 1992 to November 1992 and from August 1993 to November 1993 when physical conditions prevented this. Three types of gear were used: gillnets and two active gears, bottom trawl and cast net (Table 1.1).

Table 1.1 The use of different fishing gears within the stratified sampling program. (Water level: H=High, I=Intermediate, L=Low) (Habitat: A = Surface layer, deep, open water; B = Bottom layer, deep, open water; C = Intermediate zone; D = Shallow, inshore zone). Period: 1= before the drought, 2= After the drought

Sampling	Regular			Diurnal	
Gear	Gillnet		Bottom trawl	Cast net	Gillnet
	Small	Large			
Mesh-size	12.5-37	50-90			12.5-50
Setting time	6,18	6,18	Noon	Noon	6,12,18,24
Duration	2	12			2
Station	A, B, C, D	A, B, C, D	B,C	A/B, C, D	A,B
Period	1, 2	1, 2	1	1	2
Water level	H, I, L	H, I, L	H, I	H, I, L	H,I

Only the gillnets were employed throughout the sampling period; the dense vegetation after the drought prevented the use of the active gears. A total of 480 meters of multi-mesh monofilament gillnets consisted of ten different mesh sizes ranging from 12.5 to 90 mm stretched mesh. Two nets of 60x1.5 m<sup>2</sup> were set simultaneously at each station, one with smaller (12.5 to 37 mm) and one with larger meshes (50 to 90 mm). This was done four times each month, twice at day-time and twice at night. Day-time settings were from 06.00 hours to 08.00 and 06.00 to 18.00 hours, for gillnets with small and large meshes, respectively. Similarly, night-time settings were from 18.00 to 20.00 hours and 18.00 to 06.00, respectively. Gillnets, together with bottom trawl and cast net, efficiently sampled the entire size range (above 3 cm total length) of the available species. The catch-data consisted of length-frequency distributions per species, station and setting time. Size of the fish was incorporated in the data by establishing six size-classes. For analysis of gut contents and gut fullness of the ten most abundant species, each month a maximum of 10 specimens per species, size-class, gear type, station and time of day were pooled. A maximum of twenty-four specimen per 0.5 cm class per month of the six most abundant

species were measured weighed and dissected for data on respectively: body length and body weight, gonad weight and sex.

From November 1993 to January 1994 the diel variations in feeding behaviour and vertical distribution were studied using gillnets dividing the water column in six horizontal layers. These nets were set for approximately two hours on four setting times throughout the day: 12.00, 18.00, 24.00, 06.00 and 12.00. In total 359,920 fish were caught of which 20,492 fish were used for analysis of gut contents and gut fullness and 14,382 fish were dissected and used for determination of the length-weight relationship and gonado-somatic index (Table 1.2).

Table 1.2 For the ten most abundant species of the Tissawewa fish assemblage are presented: the number of fish caught (C), used for gut content analysis (G) and for determination (D) of the length-weight relationship and Gonado-somatic index per species. The species abbreviations are used throughout the thesis.

Species		C		G	D
		Gillnet	Active		
<i>A. melettinus</i>	AM	99429	143437	2912	1667
<i>O. mossambicus</i>	OM	12782	7020	2706	3134
<i>O. niloticus</i>	ON	2048	639	636	823
<i>B. chola</i>	BC	13701	1020	3412	1917
<i>B. dorsalis</i>	BD	14096	230	2586	2922
<i>B. sarana</i>	BS	4971	369	1340	1618
<i>H. gaimardi</i>	HG	2858	20047	1229	152
<i>R. daniconius</i>	RD	12660	10411	2649	1541
<i>G. giuris</i>	GG	1849	1876	1289	243
<i>Mystus spp.</i>	MY	4942	5535	1733	365

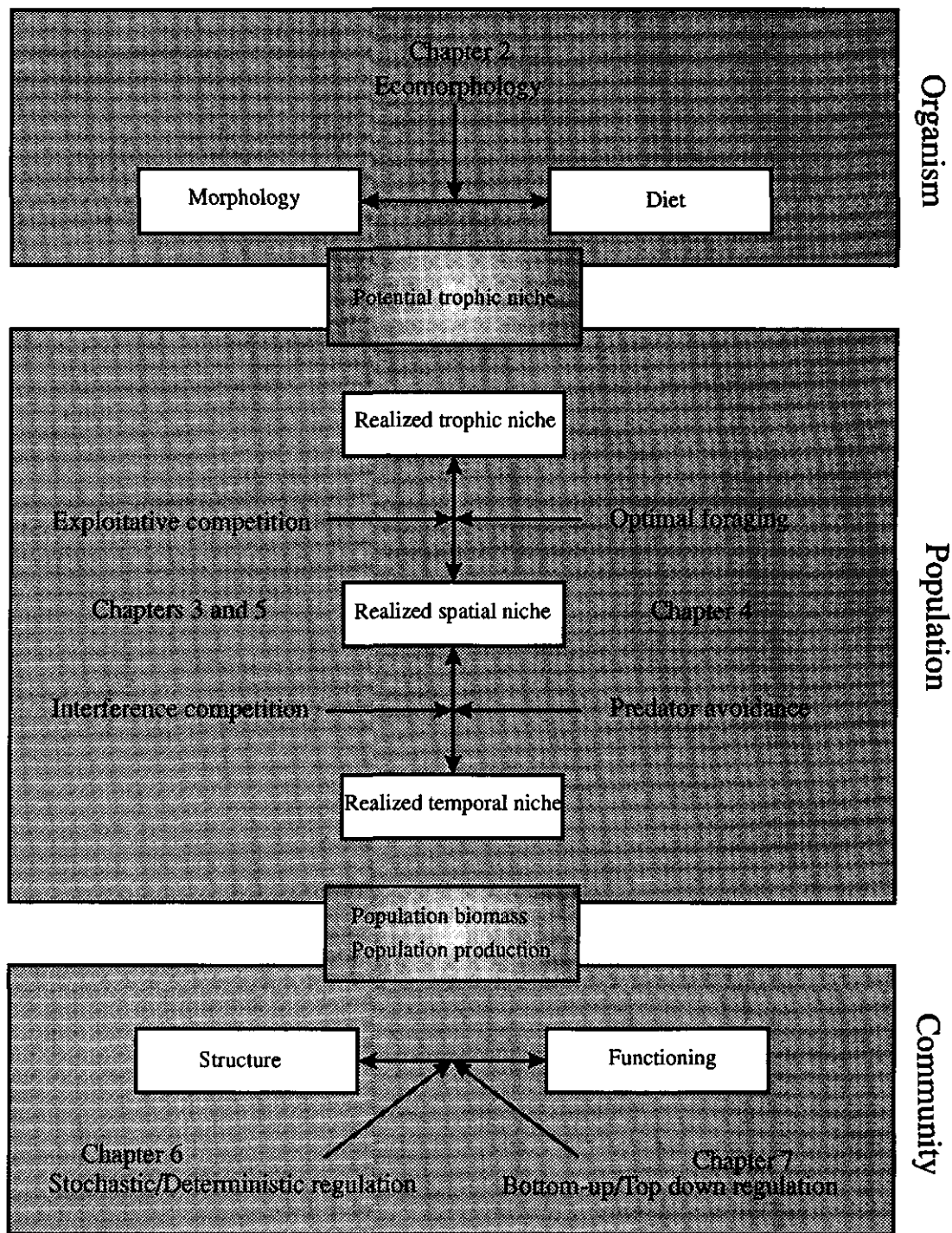
## Outline of the thesis

### Ecomorphology

In Chapter 2 the size-dependent relations between the morphological characteristics and the diet of the major fish species were analysed statistically by means of multivariate methods such as canonical analysis and principal component analysis as well as by means of correlations between the morphological characteristics and three food characteristics. The three food characteristics chosen were the size of the food items, the nature (animal versus vegetable) and the vertical position in the water column. All methods revealed a distinct relationship between morphology and feeding behaviour suggesting that the feeding behaviour of a fish of a particular species and size is largely determined by morphological constraints. The maximum size of the food was constrained by the gape width, a larger mouth allowing the ingestion of larger food items. This also accounts for most of the observed ontogenetic shifts in feeding behaviour. The nature of the food was closely related to the intestine length, where a longer intestine (both relative to the standard length as in absolute sense) allowed the fish to digest vegetable food. The vertical position of the captured food in the watercolumn was mainly determined by the orientation

Fig. 1.2

Scheme indicating how the different concepts, theories or disciplines used in the various chapters interact and how this fits in the hierarchy of three levels of organisation.



of the mouth and the presence of barbels. A ventral orientation of the mouth forces fish to forage on prey below them as opposed to fish with a dorsal orientation. Fish with barbels are better adapted to forage on benthic organisms. Based on the morphological characteristics, the potential niches of the major fish species were determined based on the three food characteristics: particle size, nature and vertical position. The realised niches of the members of the fish assemblage can be predicted by considering what refuges in their potential niche species have, to avoid overlap with potential niches of co-occurring species.

### *Resource partitioning*

Partitioning of resources can occur along three resource dimensions. The importance of these dimensions is often difficult to establish. Firstly, it is unclear what variables determined in the field can be used to characterise the occupation of this resource dimension, and secondly, interrelation between the various resource dimensions can occur. The position on the diel temporal resource dimension and the possible interrelation with the trophic dimension and the vertical component of the spatial resource dimension are described, for the period after the drought, in Chapter 3. The resource use along the diel temporal resource dimension is represented by the time of active feeding and three variables measured throughout the day were selected to determine for each species the time of active feeding. The three variables measured were: gut fullness, proportion of digested matter and relative activity. By means of a two-way Analysis of variance, gut fullness was found to be the most reliable indicator of the time of active feeding and in general there was very little contradiction between the different variables. Based on these variables practically all species showed a significant diel variation in feeding activity: the piscivores *G. giurii* and *Mystus spp.* can be characterised as nocturnal starting to feed around dusk, *R. daniconius* is active during twilight of dusk and dawn, while the remaining species are primarily diurnal. The vertical distribution of all fish species showed significant diel variation and was interrelated with the time the respective species were actively feeding and the position of their main food source(s) in the water column. When actively feeding, the filter-feeding detritivore *A. melettinus* and the piscivores occupy the bottom half of the water column, the benthivorous barbs and the tilapias were found close to the bottom while the zooplanktivores/ insectivores *H. gaimardi* and *R. daniconius* preferred the surface layer. However, when fish were not feeding, the vertical distribution was mainly determined by avoidance of both interference competition and predation by piscivores. Based on the observed diel changes in feeding behaviour and vertical distribution it was concluded that sampling fish twice a day, 12 hours apart, sufficiently prevents bias in these variables from diel variation.

The size-specific and spatial differences in feeding behaviour and distribution of the most abundant fish species are described in Chapter 4 for the periods before and after the drought. By assuming all unrecognisable matter in the guts of the non-detritivorous species was digested matter a size-dependent relationship per period was established for the proportion of digested matter. With these relationships the proportion of unrecognisable matter was divided into a proportion of detritus and a proportion of digested matter. Significant differences in feeding behaviour were observed both between size-classes and between periods. The basic pattern of size-specific feeding behaviour, observed during both periods, was that all juveniles fed mainly on zooplankton and with increasing size the herbivorous/ detritivorous species switched toward consumption of vegetable matter whereas the carnivorous species switched to

either benthic or pelagic prey of increasing size. The main changes in feeding behaviour from period 1 to period 2 were: 1) a shift from fine particulate detritus of algal origin to detritus from macrophytes by the tilapias; 2) from zooplankton to insects by all carnivores in general and the small pelagics *H. gaimardi* and *R. daniconius* in particular; 3) a decrease of the proportion of gastropods in the guts of the benthivores while the proportion of chironomids increased and 4) a decrease in the proportion of fish in the diet of the piscivores while the proportions of chironomids and shrimps increased.

The spatial differences in distribution and feeding behaviour were studied in the vertical (between surface and bottom) and horizontal (between the open water and the shore) plane. The observed size-specific and environment-dependent differences in spatial distribution, were similar for most species and often significant; The size of the fish mainly affected the distribution in the horizontal plane with the smallest size-classes displaying a distinct preference for the shallow parts of the reservoir and the presence of vegetation. During period 1 when all vegetation was restricted to the inshore zone, the ratio for the entire fish assemblage, between numbers of size-class 1 caught in the inshore zone versus the open water, was 4.4 while this was only 2.6 during period 2 when vegetation covered the entire reservoir. An effect of the increased transparency during period 2, was a shift toward the bottom of the deepest part of the reservoir by all species except for the typical pelagics.

The profitability of a food item in a certain habitat depends on the density of this food item and the foraging efficiency by its consumer. Although in a particular habitat, density of most food items can be established by sampling, foraging efficiency is difficult to determine. Employing the fish therefore provides the most straightforward and reliable method to establish habitat profitability. Spatial differences in the gut contents and gut fullness of fish caught in different habitats are assumed to reflect the profitability of one habitat relative to the others. Optimal foraging predicts that a species will prefer the habitat that maximises foraging profitability. Therefore a positive correlation between the distribution of a species and the indicators of foraging profitability implies the species is capable of assessing the profitability of a habitat and adjusting its distribution accordingly. Another factor determining the distribution of a species is predator avoidance. Predation by piscivorous fish increases toward the bottom. The main prey of the piscivores are the adult *A. melettinus*, and to a lesser extent *H. gaimardi* and *R. daniconius* as well as juvenile fish. In Tissawewa, the distribution of those species or size-classes subject to predation is determined by the avoidance of predation, even if foraging profitability is suboptimal; juveniles prefer vegetated habitats while the adults avoid the bottom layer. The distribution of the remaining species/ size-classes is determined by the profitability per habitat. This, and the observation that environmental changes affect the spatial distribution patterns of the fish species, confirms that fish are capable of estimating differences in predation risk and foraging rates between habitats and adapt their distribution accordingly in order to maximise fitness.

Niche overlap and niche breadth are considered measures indicating potential competition for resources between populations and a populations capacity to avoid it. Based on the size-specific differences in niche occupation along the trophic, spatial and temporal dimension, the measures niche breadth and niche overlap were calculated in Chapter 5 per size-class and per species for each dimension, distinguishing the periods before and after the drought. Thus far, niche breadth and niche overlap were generally calculated per species



respectively species-pair. It is shown that these measures are biased by ontogenetic changes in resource use and by interrelation between the respective niche dimensions.

The effect of ontogenetic changes is anticipated by calculating niche breadth per size-class of a particular species and niche overlap between all possible combinations of size-classes of a particular species-pair. For evaluation of species interactions these measures can be transformed by weighting the calculated measures for size-classes with the relative abundance(s) involved. Incorporating size when calculating the size-specific niche breadth or niche overlap has several advantages to the conventional methods which neglect ontogenetic changes and the size-structure of the population. Firstly, the measure of niche breadth is not dependent on possible ontogenetic changes in resource use. Secondly, sampling bias in both measures, which occurs when the size-structure of the population(s) involved differs from that in the sample, is eliminated. In effect, the measures niche breadth and niche overlap calculated according to the conventional method are systematically higher than according to the size-specific method. For the species with the largest ontogenetic changes in resource use this can amount to an overestimation of 72% for the niche breadth and an overestimation by a factor 3 for the niche overlap. According to the overlaps observed between size-classes juvenile competitive bottlenecks (Persson 1986, Werner 1986, Persson and Greenberg 1990) are likely to occur in the Tissawewa fish assemblage.

There are three possible combinations of niche dimensions where interrelation can bias the measures niche breadth and niche overlap. Along the trophic dimension species respond to the level of resource depletion (exploitative competition, Schoener 1983) and although differences in the degree of resource depletion among habitats can be important, the time of day when resources were depleted will not make any difference. However, for Tissawewa spatial differences in feeding behaviour are relatively small and therefore this combination is considered negligible. Contrary to the trophic dimension, interaction between the spatial and temporal dimension can be of relevance, because here species interact directly, by capturing space (interference competition, Park 1962). Thus, only the interrelation between the spatial and temporal dimension was considered a potential source of bias and therefore niche breadth and niche overlap were calculated from the spatial distributions during day- and night-time separately, weighted according to the relative contributions of day-time and night-time to the 24-hour period. Failing to incorporate this interrelation into the calculated measures introduced a bias in niche breadth up to 13% while niche overlap was biased up to a maximum of 31%.

In Tissawewa, the trophic resource dimension is the most important dimension for segregating species. Based on the overlap values between the various species combinations an ecological "key" was created per period indicating how species are segregated along the different dimensions. Although segregation of species differed between periods, resource use along the trophic dimension was in both cases within the boundaries of the potential niche predicted from morphological constraints (Chapter 2). Because of the higher fish density before the drought resources along at least the spatial dimension were more limiting during this period. During period 1 niche overlap along each dimension is lower because of an increased partitioning of resources. Increased partitioning of resources when these are presumed limiting is considered strong circumstantial evidence for the importance of competition. (Zaret and Rand 1971, Gascon

and Legget 1977, Ross 1977, Werner & Hall 1977, Thorman 1982, Greenfield *et al.* 1983, Lammens *et al.* 1985).

### *Community structure and functioning*

In Chapter 6 the effects of two types of disturbances on the fish community were described: A disturbance caused by a progressively decreasing water level, a seasonal effect which occurs each year, and a disturbance caused by a drought, which rarely occurs. The effects of these disturbances were measured at different levels of organisation: the organism, the population and the community. At the level of the organism the effect on the feeding behaviour was studied by monitoring gut contents and gut fullness, for the population condition and abundance were determined while at the level of the fish community the structure of the community was considered as an indicator of the possible effect of the disturbances. Each level responded differently: at the level of the organism an instantaneous response to a relatively small disturbance was observed while the higher levels only responded to bigger disturbances, with a certain time-lag. The community was at equilibrium at the beginning of the sampling period but extreme low water levels disturbed this equilibrium. Although immediately after the drought, the community was not at equilibrium, after some time a new equilibrium was established, different from the former equilibrium. Based on the knowledge of the effect of water level-dependent disturbances on the community structure, and data (Sri Lanka Irrigation Department) on the water level of the past seven years, the community is considered to be deterministically regulated.

The Tissawewa ecosystem is described for both periods in Chapter 7 from the perspective of the total fish community production and the contributions of the respective forage base groups to this production together with its utilisation by birds. Also, the primary production was estimated. For the period before the drought, when Tissawewa was representative of a typical Sri Lankan lowland reservoir, production of the small detritivorous pelagic, *A. melettinus*, almost equals that of all other fish species combined. Compared to other waterbodies, both in the tropics and in the temperate zone, fish production and -yield are relatively high as is the gross primary production. In contrast, the efficiencies of energy transfer between trophic levels in Tissawewa are comparable to those in the temperate zone, suggesting the high fish production and -yield follow from the high gross primary production and the short food chains. Compared to the period before the drought, primary production by phytoplankton was markedly lower in the second period while primary production by macrophytes was higher. The main differences between periods, with regard to the fish community, is that during period 2 the species with the highest biomass and production during period 1, *A. melettinus*, almost disappeared. This was accounted for by both bottom-up (availability of its main food source, suspended detritus, decreased) and top-down (piscivore predation increased) processes. Overall the community is regulated by bottom-up processes confirming the importance of resource partitioning for species, to coexist.

### *Exotics versus indigenous species*

The two most important exotics in Sri Lanka, *O. mossambicus* and *O. niloticus*, also co-occur in Tissawewa. Because no significant differences were observed in the morphological features presented in Chapter 2 only *O. mossambicus* was used for the ecomorphological study. The observations on feeding behaviour and distribution, described in Chapter 3 and Chapter 4 emphasise the similarities between these species. Both are herbivorous and detritivorous, grazing the benthic detrital aggregate from the bottom (Bowen 1979, 1980, 1981, Schiemer & Duncan 1987). Furthermore both species are diurnal feeders and move toward the surface at night. From the niche overlaps described in Chapter 5, one potential indigenous competitor emerged: *A. melettinus*. This species showed the highest overlap values along the trophic and spatial niche dimensions and among the highest along the less important temporal dimension. However, this first impression appeared misleading. After studying the vertical distribution of the species in more detail (Chapter 3) together with the conclusion drawn based on its morphological characteristics (Chapter 2) and taking into consideration the different effect the environmental changes had on *A. melettinus* and the tilapias (Chapter 6), I concluded that *A. melettinus* is predominantly a filter-feeder relying on suspended detritus. This confirms with findings of Bitterlich (1985), that stomachless fish, such as *A. melettinus*, are not able digest phytoplankton. Also, it implies that *A. melettinus* is not a true competitor of the tilapias and might even benefit from the tilapias breaking down the flocculant material from the bottom into smaller, better suspendable, particles.

The production estimates described in Chapter 7 show that the tilapias account for only 20% of the total fish production while their contribution to the commercial fisheries of around 80% (Pet *et al.* 1995c), is markedly higher. In Tissawewa about 90% of the fish production is realised by fish smaller than the gillnet selection range of the commercial fishery. This strongly suggests that the presumed importance of the exotic tilapias in Sri Lanka and probably South East Asia is markedly overestimated because this presumption is based on commercial catches only. The argument of Fernando (1981, 1991) that fish yield in reservoirs depends on the nature of the fish community, i.e. origin with regard to lacustrine or riverine habitat, contradicts with the findings in this study. Although fish yield of the indigenous riverine species in Tissawewa is almost negligible, comparison of the productivity of indigenous and exotic species shows the indigenous species are capable of sustaining a much higher yield than the current yield of exotic species.

### *Fisheries management*

There is a growing awareness that variation in abundance of fishes in a population depends on parental stock size and structure, intra- and interspecific interactions and abiotic environmental factors. This ecosystem perspective is applied to the fish community in Tissawewa. In Chapter 8 the impact on the fish community of competition, predation, water level management and species introductions are discussed as well as their consequences for management of the commercial fisheries. Besides, the impact of the estimates on fish yield, fish production and their ratio, for the case study of Tissawewa are put in a world-wide perspective by comparing them to those of a similar ecosystem in the temporal zone.

## CHAPTER 2

### ECOMORPHOLOGY OF A SIZE-STRUCTURED TROPICAL FISH ASSEMBLAGE

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#### Abstract

Among nine species of a tropical assemblage ecomorphological correlates were sought throughout ontogeny. Ontogenetic changes were distinguished by establishing six pre-defined size-classes. Morphometric data associated with feeding were compared by canonical correspondence analysis to dietary data. This analysis revealed seven significant relationships, showing 71% of the morphological variance explained 77% of the variance in diet. Based on functional ecomorphological relationships established in other studies and results of the canonical correspondence analysis, three food characters were selected: the size of the food particles, the type of food (vegetable versus animal) and the vertical position in the water column. The morphometric data were reduced using principal component analysis into three axis explaining 83% of the variation. The morphological characters with the highest loadings were: mouth gape on the first principal component axis, length of the intestine tract on the second and the orientation of the mouth together with the presence of barbels on the third. These axis were significantly correlated with respectively the size, the type and the vertical position of the food. The importance of morphological changes during ontogeny in explaining dietary changes was shown because 75% of the variation in the first, and most important, morphological principal component was accounted for by differences between size-classes. Assuming functional relationships, the potential niches of the species/size-classes were established, distinguishing herbivorous, omnivorous/molluscivorous and carnivorous species which, in turn, were segregated by their potential to feed on larger prey.

## Introduction

The structure of a community of coexisting species may be described by the positions of these species along different resource dimensions of an ecological space. These positions depend on the availability of resources and on ecological processes such as interspecific competition. Whenever interspecific competition predominates, evolution produced nonrandom assemblages of interacting species, specialised on exploitation of specific resources according to their morphological, behavioural and physiological characters (Sibbing *et al.* 1994, Motta *et al.* 1995). Resource partitioning is an important mechanism for competing species to coexist (Schoener 1974). Over evolutionary time, resource partitioning of competing species can be facilitated by divergent changes of morphological characters (Taper & Case 1985, Wikramanayake 1990, Motta & Kotrschal 1992, Nagelkerke *et al.* 1994, 1995). This simultaneous morphological and ecological segregation illustrates the close relationship between morphology and ecology (Watson & Balon 1984, Winemiller 1991). There have been various attempts to conceptualise the interactions between morphology and ecology (e.g. Bock & von Wahlert 1965, Bock 1980, 1990, Barel 1983, Balon 1985, Liem 1991, 1993, Motta & Kotrschal 1992, Reilly & Wainwright 1994, Motta *et al.* 1995, Smirnov *et al.* 1995). A first approach was to compare morphological variation with variation in ecological characters, either at the intra- or interspecific levels. Together with this inductive, comparative approach, functional studies were needed to provide a plausible mechanism for an observed ecomorphological correlation, and thereby generate predictions on the role of morphological variation in determining the potential niche (Barel 1983, Norton & Brainerd 1993, Motta *et al.* 1995). According to Norton *et al.* (1995), the realised niche is a product of the complex interaction between the organism and its environment (Bock & von Wahlert 1965, Bock 1980, Motta & Kotrschal 1992, Reilly & Wainwright 1994). Internal constraints of the organism, determining the actual resource use, are factors such as behaviour or physiology (Motta *et al.* 1995). Environmental constraints determining the actual resource use, are factors such as resource abundance, predator distribution, intra- and interspecific competition.

Resource partitioning in a community can occur along different resource dimensions of an ecological space. Ross (1986) who reviewed the work on resource partitioning in fish communities distinguished three resource dimensions: the trophic, spatial and temporal dimension, of which the trophic dimension was found to be the most important dimension for segregating fish in lakes. Assuming the position of a member of an assemblage along the trophic dimension is related to its morphology, then 1) the morphological constraints acting on this member should determine its fundamental trophic niche and 2) its realised niche depends on the relative positions of the assemblage members in morphological space and possible restrictions the environment places on the availability of resources along the trophic dimension. In a specific environment the trophic structure of an assemblage depends on the realised niches of its members.

The selected morphological and ecological variables may often obscure ecomorphological relationships because of the confounding influence of evolutionary history, or because these variables are not relevant to important functional relationships (Norton *et al.* 1995). This can be, at least partly, obviated by selecting a suite of

morphological characters which demonstrated some functional relevance, or were found important in other studies (Miles & Ricklefs 1994, Norton 1995). Also the selection of functional ecological characters instead of those derived from phylogeny (e.g. prey types by taxa) can help to detect meaningful ecomorphological correlations (Norton *et al.* 1995). Relationships which have been demonstrated between morphology and the main ecological dimension are between the type of food (vegetable versus animal) and gut length (e.g. De Groot 1969, Montgomery 1977, Horn 1989, Zihler 1982, Stoner & Livingston, 1984, Motta 1988, Vergina 1991, Eggold & Motta 1992, Sturmbauer *et al.* 1992) and between prey size and mouth gape (Wainwright & Richard 1995).

When explaining the trophic structure of a fish assemblage from the relationship between morphology and feeding ecology it should be realised that, compared to other vertebrates for which the correlation between morphology and ecology was studied such as bats (Fenton 1972, Findley 1976, Findley & Black 1983) or birds (Karr & James 1975, Herrera 1978, Ricklefs & Travis 1980, Miles & Ricklefs 1984), fish take up a unique position for two reasons. 1) The diversity of food resources available to fish is larger than for any other group of vertebrates (Nikolsky 1963) thus expecting considerable specialisations in architecture, functioning and food-handling behaviour of fish species in order to optimise feeding on specific food types while unavoidably limiting the use of others (Sibbing 1991). 2) In contrast to bats or birds where juveniles resemble adults both morphologically and ecologically and are nearly as large by the time they are old enough to forage for themselves, conspecific individuals of fish or reptiles vary greatly in body size and often undergo drastic changes in morphology and ecology as they grow (Werner 1986). For fish or reptiles ontogenetic body sizes often transcend the limits purported to isolate competing species (Maiorana 1978, Polis 1984, Werner & Gilliam 1984). However, in spite of the recognition of body size as an important factor influencing ecological relationships (Wilson 1975, Ricklefs *et al.* 1981, Miller 1984, Douglas 1987), both ecologists and morphologists have virtually ignored its implications when analysing covariation of ecology and morphology on a community-wide scale.

The effect of management practices on the aquatic ecosystem cannot be predicted without qualitative and quantitative knowledge of the trophic community structure. For example, it is important to predict the effect of an exotic species on the trophic structure of a community before its introduction, or the effect of selective fishing activities and overexploitation of specific species (Schiemer & Duncan 1987, Sibbing *et al.* 1994). Ecomorphology can be an important tool in providing part of this knowledge, by deducing the specific abilities and limitations of various fish species to exploit the available resources from their feeding structures. Since deducing the trophic structure of an assemblage from intestinal contents can be subject to environmental changes, a considerable improvement could be achieved if this does not apply to a trophic structure based on ecomorphological principles (Sibbing *et al.* 1994).

In Sri Lankan reservoirs most of the fish yield is sustained by the exotic tilapia, introduced in the 1950's (Fernando & Indrasena 1969, De Silva 1988). This species is hypothesised to be able to occupy unfilled spatial and trophic niches in reservoirs, because it is better adapted to the lacustrine conditions than the indigenous riverine species are (Fernando & Holcik 1982, Fernando 1984). If morphology determines the niche occupation of the reservoir fish assemblage, then it is possible to test this hypotheses on

morphological grounds, while at the same time providing an example of the alleged predictive power of ecomorphology (Karr & James 1975, Miles & Ricklefs 1984, Grossman 1986, Douglas 1987) with regard to the position of an introduced exotic species in the trophic structure of an assemblage, and consequently the success of this introduction.

In this paper the diets and a selection of feeding-related morphological characters of a size-structured fish assemblage in a Sri Lankan reservoir were studied addressing the following questions. 1) Is there a correlation between morphology and diet; 2) Do intraspecific morphological changes during ontogeny affect the diet; 3) Can a trophic structure of the fish community be created, based on morphological- and food characters and is this structure dependent on the environment; 4) Could the success of the introduction of the exotic tilapia be predicted from its morphological characters and those of the indigenous species?

## Material and methods

Gut content analyses and morphological measurements were made on fish caught in Tissawewa, a shallow (mean depth = 1.2 m, average maximum depth = 2.6 m), lowland reservoir of ca. 200 ha in the SE corner of Sri Lanka. The most abundant species of the Tissawewa assemblage are: the cyprinids *Amblypharyngodon melettinus* (Valenciennes), *Barbus chola* (Hamilton), *Barbus dorsalis* (Jerdon), *Barbus sarana* (Hamilton) and *Rasbora daniconius* (Hamilton), one gobiid *Glossogobius giurus* (Hamilton), one halfbeak *Hyporhamphus gaimardi* (Valenciennes), the clariids *Mystus gulio* (Hamilton) and *Mystus vittatus* (Bloch) which were not distinguished for the gut content analysis and are therefore treated as *Mystus spp.* and finally the introduced exotic cichlid *Oreochromis mossambicus* (Peters). These species together make up more than 95% of the fish biomass as determined from experimental gillnet catches and bottom trawl surveys.

From September 1991 until September 1992 fish were collected monthly for gut content analysis while fish for morphological measurements were collected until June 1993. The fish were sampled using multimesh gillnets set during day-time and night-time at different habitats as well as two active gears, bottom trawl and cast net, which were employed only during day-time. These combined gears ensured the entire size range (above 3 cm total length) of the most abundant species was sampled. In order to determine changes in diet and morphology throughout ontogeny the total size range was divided into six size-classes (Table 2.1).

Table 2.1 Total length ranges of each size-class of fish

Size-class	1	2	3	4	5	6
Total length (cm)	3.0-4.4	4.5-6.9	7.0-9.9	10.0-13.9	14.0-18.9	≥ 19.0

## Gut content analyses

To study the feeding ecology, each month the contents of the stomach or anterior 1/3 part of the gut were analysed per species and per size-class for a maximum of 16 pooled samples of ten specimens each. Per pooled sample the relative biovolumes of food items in gut/ stomach were estimated according to the point's method (Hynes, 1950) using

a microscope. The following categories of contents were distinguished: Fish, insects (both aquatic and terrestrial but not benthic), microcrustacean zooplankton (cladocerans, cyclopoid and calanoid copepods), gastropods, shrimps, fish eggs, chironomids, microbenthos (mainly ostracods and some benthic cladocerans), porifera, macrophytes, epiphytic filamentous algae, phytoplankton and unrecognisable matter (digested matter and/or fine particulate detritus). To distinguish between ingested detritus and digested matter the proportion of digested matter per size-class was calculated per period according to Piet *et al.* (Chapter 4). The proportion of detritus was calculated by subtracting the calculated proportion of digested matter from the observed proportion of unrecognisable matter.

### *Morphometry*

Of the ten most abundant species eight mensural, and five coded morphometric variables were chosen for study. Measurements less than 150 mm were made with callipers to the nearest 0.01 mm and measurements longer than this were made with a millimetre rule. Each of these morphological characters are listed below with the method of measurement (cf. Nagelkerke *et al.* 1994). 1) Standard length: Straight line distance from the most anterior part of the head to the terminus of the vertebral column. 2) Head length: Straight line distance from the most anterior point of the upper lip to the most posterior margin of the opercular membrane. 3) Maximum body depth: Maximum vertical distance perpendicular to body axis. 4) Diameter eye: diameter between fleshy orbits along an anterior/posterior axis. 5) Snout length: Straight line distance from the pupil of the eye to the anterior margin of the upper jaw at its midpoint. 6) Width of mouth: Interior lateral dimension of the opening when the mouth is fully opened. 7) Height of the mouth: Interior dorso/ventral dimension of the opening when the mouth is fully opened. 8) Gut length: distance from beginning of oesophagus to anus; fully extended without stretching. 9) Presence or absence of barbels. 10) Orientation of the mouth was coded according to the orientation of an imaginary plane perpendicular to the longitudinal axis of the body and tangential to both lips of the open mouth: ventral oriented if the plane faced downward, terminal if the plane was vertical and dorsal oriented if the plane faced upward. These characters were measured per species over the entire size range whereas additionally three morphological characters of the feeding apparatus were examined for only a few adult specimen of all species except for *H. gaimardi*. These morphological characters were: the shape of jaw teeth and pharyngeal teeth and the number of branchiostegal rays. First the presence or absence of jaw teeth was established and, in case present, two shapes were distinguished: unicuspid and bi- or multicuspid. For the pharyngeal teeth the distinction was made between teeth with flattened grinding surfaces, short and pointed or small and slightly hooked. Also, the number of branchiostegal rays were counted.

Because the size of the body and of several structures of the feeding apparatus are known to be an important factor influencing ecological and evolutionary relationships (Ricklefs *et al.* 1981, Douglas 1987, Wikramanayake 1990, Winemiller 1991), absolute measurements of the morphological characters were used for the multivariate morphological analysis. The body length per size-class was entered as the mid-range standard length of the size-class or, in case the maximum standard length of a species was below the upper boundary of the size-class, between the lower boundary of the size-class



and the maximum standard length of the species. The area of the mouth opening is determined by assuming an ellipsoid shape and calculating the area of this ellipse from the multiplication of the width and height measurements with  $\pi$ . On the other hand, the shape of the body or relevant structures have often proven to be a better indicator of a specific type of feeding behaviour (Gatz 1979, Winemiller 1991). Shape is indicated by converting the linear measures to ratios (Winemiller 1991). Relative measures of mouth opening, gut length, body depth and head length were calculated by using the standard length as denominator, for the relative measures of snout length and diameter of the eye the head length was used.

Table 2.2 Scores of three food characters per food item. Two types are distinguished: Plant (0) and animal (100). The vertical position in the water-column varied between bottom (0), water-column (50) and water surface (100).

Food item	Size (mm)	Type (%)	Position (%)
Fish Size-class 4	17	100	50
Fish Size-class 3	13	100	50
Fish Size-class 2	10	100	50
Fish Size-class 1	7	100	50
Fish Size-class 0	6	100	50
Aquatic Insects	4	100	50
Terrestrial Insects	4	100	100
Cladocerans	1	100	50
Calanoid copepods	1	100	50
Cyclopoid copepods	0.7	100	50
Gastropods	8	100	0
Shrimps	6	100	0
Chironomids	2	100	0
Microbenthos	1	100	0
Porifera	2	100	0
Macrophytes	0.5	0	50
Epiphytic Algae	0.1	0	50
Phytoplankton	0.01	0	50
Detritus	0.01	0	25

#### *Data analysis*

For the analysis of the ecomorphological relationships two approaches were used. For the first approach, food categories were used in the analysis because there were no a priori assumptions pertaining to the functionality of the ecological characters. In contrast, the second approach assumed three functional food characters based on the proven relevance of these characters by other studies, as well as results of the first approach. Multivariate statistics were used for both approaches. For the first approach Canonical correspondence analysis was used to determine associations between the morphological characters and the food categories while for the second approach the number of morphological variables were reduced using principal component analysis after which Pearson correlations were used to detect any relationships between the principal components and the food characters. For the second approach food categories were characterised according to three criteria: Size, type and position in the water-column (Table 2.2). Size of each food item was determined by estimating the size of each specimen found in the gut of the fish. When possible, species and size-class (Table 2.1) of

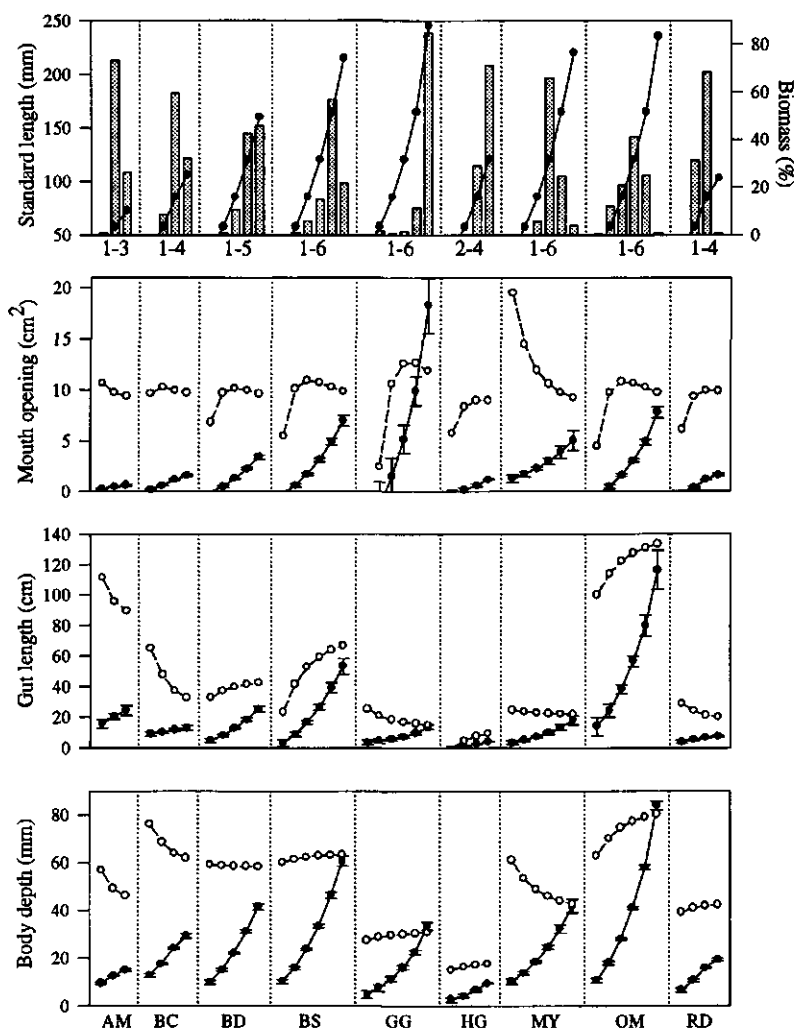
the ingested prey fish were determined. The size of prey fish, relevant for ingestion by predators, was assumed to be equal to the body depth of a fish of the mid-range length of its size-class. The size of gastropods which were crushed before they were swallowed was assumed to be equal to the average size of gastropods available in the environment. For the type of the food only two scores were assigned: 0 for vegetable matter, 100 for animal matter. The scores depending on the vertical position in the water-column varied from 0 for the bottom to 50 for the water column to 100 for the water surface. Per species, per size-class a value per criteria was calculated depending on its diet.

## Results

### *Morphological characters*

For each species the absolute dimensions of their morphological characters increased with increasing size (Fig. 2.1). The species in the assemblage with a relatively large adult size were *G. giuris*, *B. sarana*, *Mystus spp.* and *O. mossambicus*, while *A. melettinus*, *R. daniconius* and *H. gaimardi* were relatively small. Consequently, the absolute dimensions of the morphological characters of the largest size-classes were in general larger than those of the species with smaller adult sizes. However, for most species the increase of most of their morphological characters was not proportional to the increase in length. For most species the mouth height and -width of the larger size-classes increased proportional to the length while for the smallest size-class(es) the mouth opening was disproportionally small. In contrast, *Mystus spp.* and to a lesser extent *A. melettinus* showed a relative decrease of the mouth opening with increasing size. There were two species with a relatively long gut length, *A. melettinus* and *O. mossambicus*, while the barbs, *B. chola*, *B. dorsalis* and *B. sarana* have an intermediate relative gut length. Longest in absolute sense were the mid-range gut length of all size-classes above 4.5 cm of *O. mossambicus* and *A. melettinus* as well as size-class 5 of *B. dorsalis* and size-classes 4, 5 and 6 of *B. sarana*, each longer than 20 cm. Throughout ontogeny relative body depth of each species appears to be related to the relative gut length. Between species this pattern was disturbed by the high relative body depth of the barbs and *Mystus spp.*. For all species except for *G. giuris* the increase in head length was small relative to the increase in standard length. Throughout ontogeny the snout length remains more or less proportional to the head length for the smaller species such as *A. melettinus*, *H. gaimardi* and *R. daniconius* whereas the increase was larger for the remaining species with a larger maximum length. For all species the increase of the diameter of the eye was small relative to the increase in head length. Striking is the large relative eye diameter for *H. gaimardi* and *R. daniconius*. Morphological characters which differed between species but did not change during ontogeny were the orientation of the mouth and the presence of barbels. The mouth of the barbs *B. chola* and *B. dorsalis* was ventrally oriented, that of the other barb, *B. sarana*, as well as *O. mossambicus*, *A. melettinus* and *Mystus spp.* was terminally while the mouth of *G. giuris*, *H. gaimardi* and *R. daniconius* was dorsally oriented. The only species with barbels were the *Mystus spp.* and the barbs.

Other morphological characters which were determined for only a few adult specimen of all species except for *H. gaimardi*, and were therefore not included in the principal component analysis are: the shape of jaw teeth and pharyngeal teeth and the



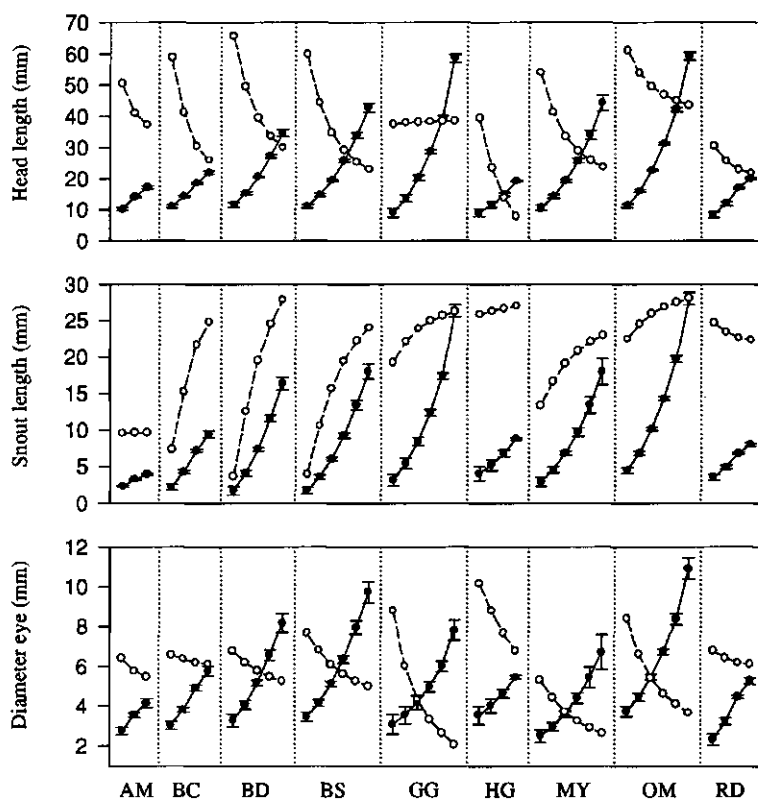


Fig. 2.1

Absolute (closed dot) and relative (open dot) size-specific measurements of morphological characters for the most abundant species. Bars show the biomass distribution (%) per species. Left y-axis shows the values of the absolute measurements, the right y-axis those of the relative measurements. The error bars around the absolute measurements indicate 95% confidence limits. Indicated are the range of size-classes used per species. For species abbreviations see table 1.2.

Species	Food item	Size-class					
		1	2	3	4	5	6
MY	Fish size-class 4		0	0	0	0	5
	Fish size-class 3		0	0	0	9	27
	Fish size-class 2		0	0	17	21	40
	Fish size-class 1		1	4	29	28	10
	Fish size-class 0		5	8	6	6	0
	Insects		21	21	11	13	6
	Zooplankton		73	55	30	15	2
	Chironomids		1	10	6	3	0
OM	Insects	6	5	2	0	0	0
	Zooplankton	30	7	6	5	2	1
	Chironomids	0	3	0	0	0	0
	Macrophytes	4	3	7	9	6	0
	Epiphytic algae	0	4	4	1	3	0
	Phytoplankton	18	41	34	25	21	8
	Detritus	37	33	42	54	65	91
RD	Calanoid copepods	7	16	21	10		
	Cyclopoid copepods	45	30	23	5		
	Cladocerans	45	33	25	23		
	Aquatic insects	0	10	9	43		
	Terrestrial insects	0	6	14	12		
	Chironomids	0	2	4	6		
	Macrophytes	3	1	2	0		
	Epiphytic algae	1	0	0	1		

#### Diet composition

The species of the Tissawewa fish assemblage can be divided into four trophic groups: A herbivorous/ detritivorous trophic group consisting of *A. melettinus* and *O. mossambicus*, a benthivorous trophic group consisting of the barbs *B. chola*, *B. dorsalis* and *B. sarana*, a zooplanktivorous group consisting of *H. gaimardi* and *R. daniconius* and a piscivorous group consisting of *G. giuris* and *Mystus spp.* For the herbivorous/ detritivorous species, detritus and to a lesser extent phytoplankton and macrophytes were the main food items. For *O. mossambicus* the proportion of zooplankton decreased with increasing size whereas the proportion of detritus increased. The diet of the barbs *B. chola*, *B. dorsalis* and *B. sarana* consisted mainly of benthic food items such as chironomids, gastropods and microbenthos. Although the diets of the benthivorous barbs were qualitatively similar the quantities of the different food items differed considerably. Comparison of the most important size-classes, in terms of biomass, of the barbs showed *B. chola* fed mainly on chironomids, microbenthos and detritus, *B. dorsalis* fed on chironomids, gastropods and microbenthos whereas for *B. sarana* the principal food items were gastropods and macrophytes. With increasing size the proportion of zooplankton decreased for all barbs while the proportions of chironomids, gastropods and fish increased for respectively *B. chola*, *B. dorsalis* and *B. sarana*. Remarkable is the decrease of plant matter with increasing size in the diet of *B. chola* while that of *B. sarana* increased. The zooplanktivorous species fed almost entirely on zooplankton. However, with increasing size, especially *R. daniconius* showed an increased proportion of insects in its diet. The piscivores exhibited some distinct size-related changes in their diet. With increasing size both species switched from zooplankton to macro-invertebrates to fish of increasing size. For both

predators the main prey species was *A. melettinus*. From the size-specific diet composition of each species (Table 2.4) and the quantitative characterisation of the food items with regard to the size, type and vertical position in the watercolumn, an average value for each of these characters was calculated per species per size-class.

### *Morphology and diet*

Canonical correspondence analysis was used to compare the positions of species and ontogenetic stages in morphological and ecological space. This analysis revealed seven significant relationships ( $R^2 > 0.75$  and  $p < 0.01$ ) and showed that 71% of the variance in morphological characters explains 77% of the variance in diet. For morphology the canonical axis 1 and 5 were the most important explaining respectively 14% and 20% while for the feeding ecology the main canonical axis were 1, 3 and 4 explaining respectively 18%, 16% and 15% of the variance. The correlations between the respective morphological and ecological axis revealed several interpretable relationships. The first correlation showed how the relative gut length distinguishes between a vegetable and an animal diet; A high relative gut length is associated with a vegetable diet. The second correlation indicates that fish with a large mouth opening and a small body depth are mainly piscivorous. The relative size of the mouth opening and the relative eye diameter occupy opposite endpoints of the third morphological axis which corresponds to the proportion of benthic food items in the diet. The fourth morphological axis has inverse loadings for the presence of barbels and the orientation of the mouth opening and was correlated with an ecological axis with inverse loadings on zooplankton and benthic food items; Fish with barbels prefer benthic food while fish with a dorsal oriented mouth prefer zooplankton. The fifth morphological axis indicated large fish have a high proportion of fish in their diet. The sixth correlation showed species with an upward oriented, relatively small, mouth fed mainly on zooplankton and terrestrial insects. Finally, the seventh correlation showed how a long gut length was associated with a high proportion of detritus in the diet.

The possible relationship between morphological features and a species' foraging efficiency follows from correlations between the morphological variables and food characters or, between the morphological principal components and the food characters (Table 2.5). Size of the food was mainly determined by principal component 1 but also correlates with principal component 2: size increases with principal component 1 increasing (Fig. 2.2a) and principal component 2 decreasing. This coincides with the significant positive correlations ( $p < 0.01$ ) between the size of the food and the size of the mouth opening (both absolute and relative), head length, standard length and relative gut length. The only significant ( $p < 0.01$ ) negative correlation was with the relative diameter of the eye. The proportion of plant material increases with principal component 2 increasing (Fig. 2.2b). The variables with the highest loadings on principal component 2, gut length (both absolute and relative) and relative body depth, were also the only variables which correlated significantly ( $p < 0.01$ ) with the food type. Fish with a longer gut or with a higher relative gut length and consequently higher relative body depth had a higher proportion of plant material in their diet. Although for some species (*A. melettinus* and *B. sarana*) during ontogeny the food type was better correlated with the absolute gut length,

Table 2.5 Correlation coefficients ( $R^2$ ) between three food characters and both morphological characters and principal components. Significant ( $p \leq 0.05$ ) relationships are in bold.

Morphology		Food	
Characteristics	Size	Type	Position
Standard length	<b>0.40</b>	0.00	0.00
Head length	<b>0.35</b>	0.02	0.01
Diameter eye	<b>0.14</b>	0.04	<b>0.09</b>
Mouth gape	<b>0.50</b>	0.00	0.01
Relative head length	0.08	<b>0.14</b>	0.02
Relative body depth	0.07	<b>0.29</b>	<b>0.30</b>
Relative diameter eye	<b>0.38</b>	0.00	0.01
Relative gape width	<b>0.27</b>	0.00	0.01
Relative gut length	<b>0.15</b>	<b>0.86</b>	<b>0.10</b>
Presence barbels	0.04	0.14	<b>0.25</b>
Orientation mouth	0.04	0.04	<b>0.53</b>
Principal components			
PC1	<b>0.52</b>	0.00	0.01
PC2	<b>0.17</b>	<b>0.66</b>	<b>0.17</b>
PC3	0.00	0.05	<b>0.38</b>

for the assemblage as a whole, the correlation coefficient of food type with the relative gut length ( $R^2=0.86$ ) was markedly higher than that with the absolute gut length ( $R^2=0.41$ ).

The preference for food items depending on their vertical position in the watercolumn was mainly determined by principal component 3 (Fig. 2.2c) and to a lesser extent by principal component 2. The morphological characters with the highest loadings were also significantly ( $p < 0.01$ ) correlated with the position of the food items: possession of barbels, orientation of the mouth and relative body depth. Fish with barbels and a ventrally oriented mouth will forage closer to the bottom while fish without barbels will forage in the watercolumn or on the surface depending whether their mouth was oriented terminally respectively dorsally. Other morphological characters without high loadings on the principal component but also significantly correlated ( $p < 0.05$ ) were the absolute diameter of the eye and two variables correlated with the relative body depth: relative gut length and absolute body depth.

## Discussion

The initial goal of an ecomorphological study is to identify which features of an organism's form are correlated with particular features of its ecology (Motta *et al.* 1995). This approach however, provides predictability, but no causal explanation. The causal mechanism can be provided by a functional analysis which can be used to generate predictions on the role of morphological variation in determining the potential niche. For fish communities, resource partitioning occurs mainly along the trophic dimension (Ross 1986). Therefore, when determining the potential niches of fish species from their morphology, the morphological characters related to feeding ecology can be expected to be decisive. Based on the morphological characters correlated with the feeding ecology, both species and ontogenetic stages are segregated in morphological space. The canonical analysis as well as correlations between morphological principal components and food

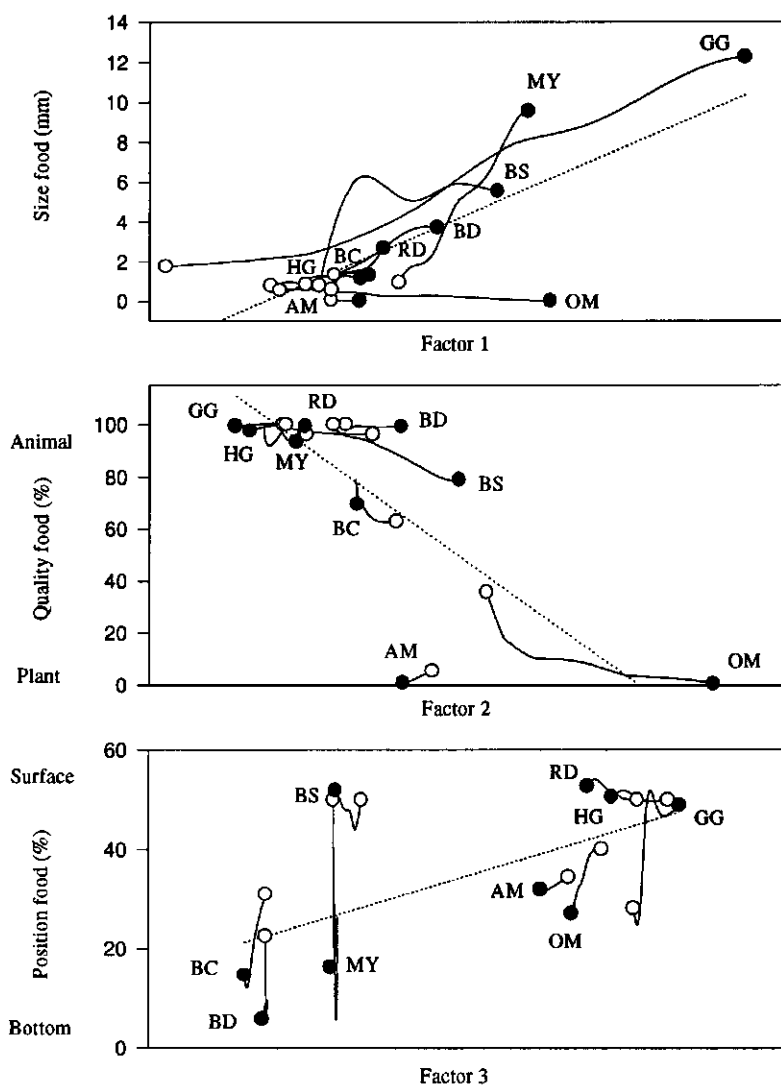


Fig. 2.2 abc

Relationship between food characters and morphological principal components. The dotted line indicates the linear regression, the solid lines indicate the observed positions of the entire size ranges of the species. Size increases from open towards closed dots. For species abbreviations see table 1.2.



characters indicate which morphological attributes probably determine the feeding ecology. Since the ecomorphological correlations established through canonical analysis never contradicted those revealed by the correlations between the morphological variables and food characters it suffices to discuss only the latter. Of the morphological variables which based on these correlations are considered important, a causal relationship has been established for size of the food particles and the mouth gape (Wainwright & Richard 1995) while for the length of the intestinal tract clear correlations with the digestive demands have been established (De Silva *et al.* 1980, Zihler 1982, Vergina 1991, Sturmbauer *et al.* 1992).

Because the morphological variables used for the multivariate analysis consisted of measurements, ratios of measurements and codes, the derived axes will have complex units. Miles & Ricklefs (1984) caution about interpreting axes with complex units because they may reflect spurious correlations among variables (Atchley *et al.* 1976). However, repetition of these analyses using only variables with the same scales or units showed the same correlations.

### *Ecological characters*

The characterisation of a food item with regard to its size, type or vertical position in the water-column is not always as clear cut as the values suggest. Detritus, for instance, is characterised as 100% vegetable matter but not all detritus is from plant origin and aquatic detritus is associated with heterotrophic and autotrophic micro-organisms which can increase the nutritional value markedly (Bowen 1979, 1981, Mann 1988). Also, detritus is difficult to quantify because of its heterogeneous composition (Bowen 1979, 1981, Mann 1988). This is partly related to the difficulty to characterise the detritus with regard to its vertical position in the water-column. In Tissawewa basically two types of detritus can be distinguished: suspended, or in the form of flocculant material on the bottom. Obviously the latter contains larger particles than the former. This also explains the characterisation of detritus with regard to its vertical position, as in between the watercolumn (50) and the bottom (0).

The size of most food items could be easily measured from the contents of the fish intestines but for some food items this proved difficult. Gastropods are crushed before ingestion so only small fragments could be found in the gut. Bottom samples from the reservoir showed they varied in size between about 5 and 12 mm (pers. observations) with an average of 8 mm. The assumption that all gastropods have a fixed size, equal to that observed in the environment, neglects the probability of size-specific selection and suggests the average food size of species with a large proportion of gastropods in their diet hardly changes during ontogeny. Other food items difficult to measure were the macrophytes and Porifera because fish bite or tear of parts, and in case of the Porifera only the spines are found in the gut.

Finally, the ecological characters selected in the present study only present a subset of possible ecological characters. For example, mechanical attributes, or evasibility of the prey, were not considered.

### *Mouth gape*

The most important morphological principal component, accounting for 49% of the total variance consists of a size- and a shape component. Fish with a larger mouth opening can consume larger prey. This large mouth gape can be realised through allometric growth (size component), an ontogenetic change in head shape to a more than proportional increase of the mouth gape which in turn can inhibit the size of structures with a different function such as the eye (Barel *et al.* 1989). Since variation in this principal component is mainly related to the large within species variation depending on differences between the ontogenetic stages, the importance of this principal component might be biased because of the relatively high proportion of ontogenetic stages relative to species (9 species in a dataset of 44 cases). However, other studies in which ontogenetic stages of the species were not considered, confirmed the importance of mouth gape, with regard to food selection (Gatz 1979, Wikramanayake 1990, Winemiller 1991, Nagelkerke *et al.* 1994, Wainwright & Richard 1995). The argument that prey size is primarily constrained by the pharyngeal gape instead of the mouth gape, is contradicted by laboratory studies which showed that fish do eat prey as wide as their mouth diameter, even if pharyngeal gape is actually narrower than the prey (Werner 1974, Kislalioglu & Gibson 1976, Osenberg & Mittelbach 1989).

The high loadings of other absolute mensural variables follow from their allometric relationship with the mouth gape. The advantages gained from a larger mouth opening apply mainly to the carnivorous species since their prey cover the largest size range. All species, except for the herbivorous *A. melettinus* and *O. mossambicus* display an increase in the average size of their prey throughout ontogeny, the maximum size of prey depending on the size of the mouth opening. Similar observations among carnivorous species with different adult sizes were reported by other studies (e.g. Randall 1967, Starck & Schroeder 1971, Gladfelter & Johnson 1983, Keast 1985, Wainwright 1987, Osenberg & Mittelbach 1989).

### *Length of the intestine tract*

The second important principal component, with high loadings on the morphological characters gut length and body depth, distinguishes between herbivory and carnivory. The increased digestive efficiency for fish with a longer gut length and consequently slower elimination rate is widely accepted as an explanation for the possibility to utilise relatively energy-poor food resources (Hofer 1991). Although at least for some species the absolute gut length appeared to be decisive for the switch towards utilisation of vegetable matter during ontogeny, overall the relative gut length was found to be a better indicator of adaptation to vegetable diets than the absolute measure, confirming findings in other studies (Gatz 1979, Hofer 1991, Winemiller 1991). The correlation between body depth and food type is probably of a constructional nature since longer intestines require more space in the body of the fish.

### *Possession of barbels and the orientation of the mouth*

The possession of barbels and the orientation of the mouth, the two main variables correlated with principal component 3, were found to be related to the vertical position in the watercolumn of the prey species. The possession of barbels indicates the importance of

non-optic senses in feeding (Gilbert & Bailey 1972) and the benthic habit of the fish (Gosline 1973, Aleev 1969, Gatz 1979, Nagelkerke *et al.* 1994). This is confirmed by the large proportion of benthic food items such as chironomids, ostracods and gastropods in the diet of the barbs and to a lesser extent in that of *Mystus spp.* as well as the observed preference for the bottom layer of the reservoir (Pet & Piet 1993). For *B. sarana* and *Mystus spp.* which often feed on non-benthic food items the possession of barbels allows the species to forage nocturnally (Pet & Piet 1993, Piet *et al.* Chapter 3). The orientation of the mouth is considered an indicator of the location of the prey relative to the predator (Gatz 1979) or of the relative water-column depth at which feeding generally occurs, with a ventral orientation associated with benthic feeding and a dorsal orientation with foraging in the upper water-column (Wikramanayake 1990, Winemiller 1991). For the Tissawewa fish assemblage the latter interpretation does not hold because the piscivore *G. giuris* with its dorsal oriented mouth, prefers the bottom layer (Pet & Piet 1993) from which it attacks its prime target species, *A. melettinus*, which prefers the lower part of the water-column (Pet & Piet 1993, Piet *et al.* Chapter 3). The negative correlation between the absolute size of the eyes and the vertical position suggests species with larger eyes are better equipped to forage closer to the bottom, where light conditions are poorer. Because of their small eyes and dorsal oriented mouth *R. daniconius* and *H. gaimardi* are therefore expected to forage most efficiently in the surface layer. This corresponds with their spatial distribution: both species occur almost exclusively in the surface layer (Pet & Piet 1993, Piet *et al.* Chapter 3). The only body shape characteristic significantly correlated with the vertical position of the food was the relative body depth; species with a higher relative body depth foraged on benthic food items. The species with the highest relative body depth are the three barbs *B. chola*, *B. dorsalis* and *B. sarana* as well as the tilapia *O. mossambicus*. For the barbs this corresponds to Sibbing *et al.* (1994) who found the typical benthic molluscivore to have a deep body shape, thereby improving its manoeuvrability.

#### *Ontogenetic impact*

Differences in resource use are not only observed between species but within species between ontogenetic stages as well (Werner & Gilliam 1984, Werner 1986). Therefore it is important to ascertain ontogenetic changes in ecomorphology (Motta & Kotrschal 1992). Nevertheless, thus far several studies have focused on the interaction between morphology and ecology for species assemblages considering only adults, but to our knowledge only few studies (Galis 1993, Nagelkerke *et al.* 1995) have incorporated ontogenetic stages into their analysis. In this study the importance of incorporating ontogenetic stages in the analysis results from the observation that 75% of the variation in the most important morphological principal component is accounted for by the differences between the various size-classes leaving only 25% for differences between species. This implies that several absolute measures of morphological characters which were considered species-specific were in fact size-specific and therefore dependent on the size of that species in the samples. Also, fish populations which contain a wide range of sizes may be represented differently at certain times of the year simply because of demographic characters (Miller 1984). Part of this bias can be eliminated by using relative measures but for several morphological characters this relative measure changes during ontogeny or it is

the absolute measure that determines the feeding behaviour and hence the diet. For example the absolute measure of the mouth gape determines the maximum size of the potential prey and the absolute size of the eye can determine the importance of sight in the feeding of the fish, thereby affecting feeding position and microhabitat depth (Gatz 1979, Barel *et al.* 1989, Wikramanayake 1990, Wainwright & Richard 1995). Like differences between species in size and shape can account for differences in feeding behaviour, the changes in size and shape of the fish during ontogeny can explain observed ontogenetic changes in feeding behaviour. For example, the shift from carnivory to partial or complete herbivory during ontogeny might well be explained by the increase in either relative or absolute gut length and the shift toward increasingly larger prey during ontogeny, common for piscivores (Gilliam 1982) follows from the increase in size of the mouth opening (Wainwright & Richard 1995). From the observed differences in morphology between size-classes compared to between species it can be expected that for several species intraspecific competition between specific ontogenetic stages will be smaller than interspecific competition. Based on their morphological characters competition can be expected between the juveniles of *Mystus spp.* and *G. giuris* and the adults of *H. gaimardi* and *R. daniconius*. This also applies for size-classes of the omnivorous fish species.

#### *Potential and realised niche*

Feeding performance is assumed to provide the link between morphology and diet (Norton 1991, Wainwright 1991, Motta & Kotrschal 1992, Wainwright & Richard 1995). The morphological characters of a species determine its potential niche from the constraints they put on foraging efficiency on the available food resources. The realised niche of a species is determined by the foraging efficiency of this species relative to the other members of the assemblage. In the present study, foraging efficiency on each food resource is assumed to depend on three food characters, namely the size of the food, the type and the vertical position in the water-column. Per population the potential niche will be established based on its size-specific constraints and size-distribution and compared to the realised niche with special emphasis on differences in the realised niche depending on the environment. This is attempted by considering the realised niches of the species involved, in as many different environments as possible. For some species their diets were studied in either lacustrine or riverine environments while the diets of all species were studied in the same reservoir when environmental conditions were markedly different due to water level fluctuations and a drought (Piet Chapter 6).

In Tissawewa primary production exceeds by far the consumption of it by herbivorous species (Piet Chapter 7). Therefore, animals capable of eating plants are exposed to far less competition than carnivorous species. Thus, a species potential of avoiding competition is directly related to its potential of utilising vegetable food resources. Based on the morphological constraints determining the utilisation of vegetable food resources the community can be divided roughly into two herbivorous species, *A. melettinus* and *O. mossambicus*, three omnivorous species, the barbs *B. chola*, *B. dorsalis* and *B. sarana* and four remaining carnivores: *H. gaimardi*, *R. daniconius*, *Mystus spp.* and *G. giuris*. For the herbivores and omnivores a switch from a predominantly animal diet to a diet containing various proportions of vegetable matter can be expected during ontogeny. With regard to their intestinal tract there is one considerable difference between

the herbivores: the tilapia *O. mossambicus* has a stomach while the cyprinid *A. melettinus* does not. As a consequence the secretion of pepsin and hydrochloric acid, realising a pH in the stomach between 1.5 and 2.0 (Moriarty 1973), can markedly increase the denaturation and subsequent lysis of bacterial or plant cells (Bowen 1976) thereby increasing the utilisation of plant, algal or detrital matter by *O. mossambicus* (Moriarty & Moriarty 1973, Bowen 1979). According to Bitterlich (1985) the stomachless *A. melettinus* is not capable of digesting phytoplankton. However, cyprinids such as grasscarp or rudd are known to break down the vegetable material mechanically by their pharyngeal jaws (Sibbing 1991). This may also apply to *A. melettinus* considering the grinding shape of its pharyngeal jaws. The shape of the pharyngeal teeth makes the barbs capable of crushing hard prey such as gastropods. Morphological measurements on the feeding apparatus of the same cyprinid species in another Sri Lankan reservoir (Adamicka 1983) showed *B. sarana* has the most powerful pharyngeal musculature making it the species best equipped to exploit gastropods as a food source. Several studies established a clear association between dentition and diet (Lauder 1983, Kotschal & Goldschmid 1983, Stoner & Livingston 1984, Norton 1988, Motta 1989). Based on the shape of the jaw teeth, *Mystus spp.* and *G. giuris* are best adapted for piscivory (Gatz 1979, Winemiller 1991) and the lack of jaw teeth of the cyprinids can impose considerable constraints on the handling of struggling prey (Sibbing 1988).

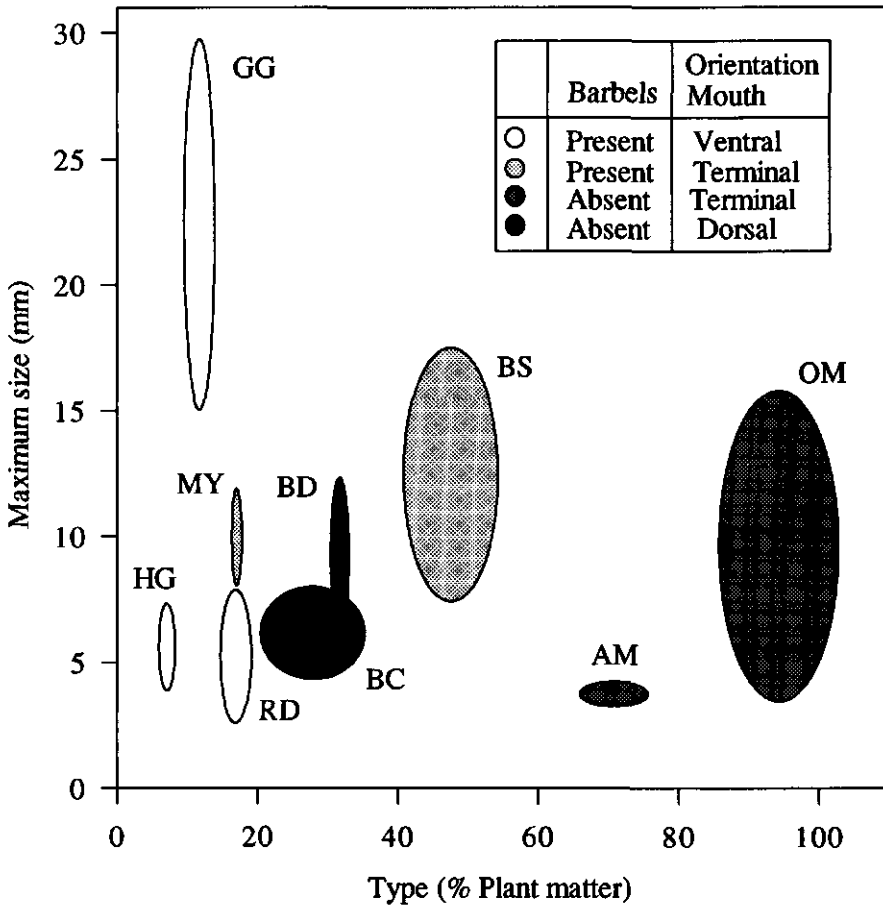
Because of the relatively high competition between non-herbivorous species in Tissawewa (Piet *et al.* Chapter 5), and the larger variation in size of animal prey compared to vegetable food sources, trophic segregation based on food size is expected to be especially important for these species. Avoidance of competition can be achieved by the potential to exploit larger food items than the competitors. This potential is constrained by the mouth gape. For the obligate carnivores this implies *G. giuris* can exploit the largest food particles, not available to any of the other species while *Mystus spp.* can exploit food items of intermediate size, larger than the small food items which can be ingested by *H. gaimardi* and *R. daniconius*. For the omnivores the maximum mouth gape increases from *B. chola* to *B. dorsalis* to *B. sarana* but remains below that of *G. giuris* and in case of *B. dorsalis* and *B. chola* even below that of *Mystus spp.*. This implies that in order to avoid competition the omnivores will have to apply themselves to a food source not available to the carnivores such as gastropods, which can only be exploited by those cyprinids with a sufficiently large mouth gape and powerful crushing pharyngeal jaws.

The orientation of the mouth divides the assemblage into two typical benthivores, *B. chola* and *B. dorsalis*, and three species, *G. giuris*, *H. gaimardi* and *R. daniconius* adapted to feed on prey from the water surface or at least higher up in the water-column relative to the position of the fish. Species with a dorsal orientation of the mouth are not able to exploit benthic food sources whereas a ventral orientation of the mouth prevents species from feeding on organisms occurring on the water surface. Because of the position of *G. giuris* below its prey and its preference for large prey (mostly fish) induced by its morphological characters, *G. giuris* can be expected to occupy the bottom layer attacking its prey upwards. This reasoning is confirmed by the observed preference of *G. giuris* for the bottom layer (Pet & Piet 1993). In the Tissawewa fish assemblage there are four species with barbels, *B. chola*, *B. dorsalis*, *B. sarana* and *Mystus spp.*, which can be

expected to have an advantage when foraging during conditions of poor visibility such as the benthic layer or at night.

The realised niches of the species of the Tissawewa fish assemblage in the same reservoir under markedly different environmental conditions (Piet *et al.* Chapter 5) as well as in other waterbodies, either lacustrine (Schiemer & Hofer 1983, Trewavas 1983, Kumar 1987) or riverine (Schut *et al.* 1984, De Silva *et al.* 1984, Kortmulder 1987) corroborated the established potential niches.

Fig. 2.3 Ecological "key" of the Tissawewa fish assemblage based on morphological characters of its members. Indicated are the potential niches of the respective size-structured populations, showing segregation according to food type and food size as well as the variation caused by ontogenetic differences within each population. The indicated ontogenetic effect is a relative measure calculated by weighting the values per size-class with the relative contribution of that size-class to the biomass of the species and determining the variation. For species abbreviations see table 1.2.



### *Trophic structure*

From the potential niches of the species and size-classes, a trophic structure can be created for the Tissawewa fish assemblage describing how the different size-structured populations are expected to be segregated trophically based on their morphological characters (Fig. 2.3). The type of the food distinguishes three groups: herbivores, omnivores and carnivores. Within the herbivores, the relatively large mouth gape of the tilapia *O. mossambicus* suggests this species can ingest larger food particles than *A. melettinus* but considering the size distribution of their main food source this hardly seems relevant. The potential of *O. mossambicus* to utilise the primary producers at least as efficient as *A. melettinus* confirms the success of the introduction of this exotic species. The omnivores *B. chola* and *B. dorsalis* are better adapted than *B. sarana* to forage on benthic food items because of the ventral orientation of their mouths. On the other hand *B. sarana* can exploit larger food items, such as gastropods, better than *B. dorsalis*, which in turn can consume larger food items than *B. chola*. The carnivores are mainly segregated by the constraint the mouth gape puts on the maximum size of their prey, and the orientation of their mouth puts on the vertical position of the predator relative to their prey.

Thus, the variation in relatively few morphological characters accounts for most of the, inter- and intraspecific, ecological variation. Further development of explicit cause-and-effect hypotheses between the most relevant morphological and ecological characters, can make ecomorphology a powerful tool to predict resource use and trophic structure of a fish assemblage and thereby predict the success of fisheries management measures, like the introduction of exotics, with regard to natural conservation or the endangerment of indigenous species.

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## CHAPTER 3

### **DIEL VARIATION IN FEEDING AND VERTICAL DISTRIBUTION OF TEN CO-OCCURRING FISH SPECIES: CONSEQUENCES FOR RESOURCE PARTITIONING**

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#### **Abstract**

The diel variations in feeding behaviour and vertical distribution were determined for ten species of a tropical fish community in a shallow SE Sri Lankan reservoir. The fish assemblage consisted of two introduced exotic tilapias and eight indigenous riverine species including five cyprinids, one catfish, one halfbeak and one gobus. Multi-mesh gillnets dividing the water column in six depth-strata, were set with a six-hour interval throughout four 24-hour periods. The study of the diel variation in feeding behaviour was based on analysis of catch data, gut contents and gut fullness per setting time. The diel variation in vertical distribution was determined per species, from the diurnal changes in length-frequency distribution for each of the six depth-strata. Feeding behaviour and vertical distribution differed significantly among species and for most species throughout the 24-hour period. Feeding behaviour and vertical distribution were correlated. The status of whether or not a fish is feeding, determines if the trophic and spatial resource dimensions are interrelated. Resource partitioning along the spatial dimension is mainly aimed at avoiding exploitative competition at the time of feeding, whereas it is governed by avoidance of interference competition or predation when feeding is not taking place.



## Introduction

Resource partitioning is an important mechanism allowing species in an assemblage to coexist. Segregation of coexisting species can occur along trophic, spatial, or temporal resource dimensions. Ross (1986), who reviewed the work on resource partitioning in fish communities, concluded that trophic and spatial dimensions are generally more important than the temporal dimension. An important parameter of the spatial dimension in lakes is the vertical distribution in the water column. For the temporal dimension, diel and seasonal components are distinguished. With regard to segregation based on feeding behaviour, the diel component is probably the most important (Keast & Welsh 1968, Baker & Ross 1981, Rask 1986, Jansen & Mackay 1992). When considering the importance of resource dimensions it is important to distinguish between exploitative competition (Schoener 1983) which deals with the depletion of resources and interference competition (Park 1962) which is determined by direct interactions between organisms capturing space. Exploitative competition can be avoided by partitioning along the trophic or spatial resource dimension. Temporal partitioning will not reduce exploitative competition between fish species since the life span of most prey is much greater than the diel period. In contrast, avoidance of interference competition depends on resource partitioning along the spatial and temporal resource dimension.

Diurnal cycles of vertical migration are commonly observed phenomena in many freshwater species. Changes in vertical distribution may be related to factors such as temperature, dissolved oxygen, light, interactions with other species and prey availability (Alabaster & Robertson 1961, Crowder *et al.*, 1981; Rudstam & Magnuson 1985). Hence, diurnal variations in vertical distribution and feeding behaviour are expected to be interrelated (Wurtsbaugh & Li 1985, Clark & Levy 1988, Levy 1990). The feeding behaviour of a species is described by the time at which active feeding takes place as well as the quality and quantity of the food items consumed during that time. The diet of a species depends on factors which change throughout the 24-hour period, like prey availability and light intensity (Hall *et al.* 1979, Diehl 1988, Dervo *et al.* 1991). Therefore, when studying resource partitioning, diel changes in diet should be taken into account. Although in the temperate regions diel vertical distribution and feeding behaviour of freshwater fishes are reasonably well documented, these aspects have rarely been studied in tropical freshwater fishes (Dunn 1975, Goldschmidt *et al.* 1990).

We studied the interrelationships between the diurnal variations in feeding behaviour and the vertical distribution of ten common species belonging to the fish community of Tissawewa, a tropical lowland reservoir in SE Sri Lanka. Because Tissawewa is a shallow, well-mixed reservoir there is no apparent gradient of temperature or dissolved oxygen leaving only light and the biotic interactions as possible factors influencing the diel vertical distribution of the fish assemblage. Piscivorous fish are the main potential predators that can determine the vertical distribution.

In this study we focus on the significance for resource partitioning of the diurnal variation in vertical distribution and associated feeding behaviour. We addressed the following five questions. 1) Are there diel changes in feeding behaviour or vertical distribution; 2) Are feeding behaviour and the vertical distribution interrelated; 3) What are the main factors explaining the observed patterns in feeding behaviour and vertical

distribution; 4) Do species differ in time of active feeding and how can this parameter best be determined; 5) What are the consequences for resource partitioning?

## Material and methods

Tissawewa is a shallow (mean depth = 1.2 m; average maximum depth = 2.6 m) lowland reservoir of ca. 200 ha in SE Sri Lanka. Secchi-depth transparency (mean  $\pm$  95% c.l.) was  $130 \pm 18$  cm and vegetation was abundant, covering the entire water column. The dissolved oxygen concentrations varied between 6.8 and 7.7 mg.l<sup>-1</sup> throughout the 24-hour period with a maximum difference of less than 0.4 mg.l<sup>-1</sup> between bottom and surface. The maximum temperature difference between bottom and surface was less than 1 °C. The most abundant species were the cyprinids *Amblypharyngodon melettinus* (Valenciennes), *Barbus chola* (Hamilton), *Barbus dorsalis* (Jerdon), *Barbus sarana* (Hamilton) and *Rasbora daniconius* (Hamilton), one goby *Glossogobius giuris* (Hamilton), one halfbeak *Hyporhamphus gaimardi* (Valenciennes), two catfishes *Mystus gulio* (Hamilton) and *Mystus vittatus* (Bloch) which for practical reasons were treated as *Mystus spp.* and two introduced tilapias *Oreochromis mossambicus* (Peters) and *Oreochromis niloticus* (Linnaeus). These species together made up more than 98% of the biomass as determined from experimental gillnet catches.

From November 1993 to January 1994 on four different occasions, at least one week apart, the diel variation in feeding behaviour and vertical distribution of these species were measured using two multi-mesh gillnets consisting of seven panels each of mesh sizes 12.5, 16, 20, 25, 33, 37 and 50 mm stretched mesh. Each net was 75 m long and 1.5 m high: one covered the upper 1.5 m of the water column, the other the lower 1.5 m. Each net was subdivided into 3 horizontal layers of 0.5 m each by a string woven through the meshes. Nets were always set at the deepest part of the reservoir. Because of the low water level in November (ca. 1.5 m at the deepest point), both nets were placed at 1.5 m depth so that each net covered the entire water column. On the other three occasions the nets were placed at three meter depth with the surface net on top of the bottom net. To ensure sufficient fish were caught while preventing saturation of some of the panels and deterioration of the gut contents the setting times of the nets were varied depending on the time of day but never exceeded two and a half hours. On each occasion the nets were set five times at six-hour intervals, each time recording the effort (time the nets were in the water). Because Catch per Unit of Effort (CpUE) was lowest during the noon setting, the sampling was started at noon and finished after the second noon setting, thus including two noon periods for the CpUE. Sunrise and sunset were at 06.00 and 18.00, respectively.

Table 3.1 Gut fullness categories and estimated fullness (slightly modified according to Haram & Jones 1971)

Gut fullness category	Fullness (%)
Completely filled and swollen	90-100
Just filled over full length, not swollen	70-89
Contents divided in different patches	30-69
Very few food particles	10-29
Completely empty	0-9

On each sampling date, from a maximum of 10 specimens per species, per setting time, gut fullness was determined, and gut contents collected and pooled into a single sample independent of the depth-stratum in which they were caught. Per specimen the fullness of the stomach or anterior one-third part of the gut was estimated according to five categories (Table 3.1). Per pooled sample the relative biovolumes of food items in gut/stomach were estimated according to the points method (Hynes 1950, Hyslop 1980) using a microscope to distinguish the categories of contents. The following categories were distinguished: Fish, insects (both aquatic and terrestrial but not benthic), zooplankton (mainly cyclopoid copepods and cladocerans), gastropods, shrimps, fish eggs, chironomids, microbenthos (mainly ostracods and some benthic cladocerans), porifera, macrophytes, epiphytic filamentous algae, phytoplankton and unrecognisable matter (digested matter and/or detritus). Per species the diel effect on the diet was tested using a one-way MANOVA on all food items whose distribution of proportions in the gut, did not differ from normal (Shapiro-Wilks W-test,  $p < 0.05$ ).

In detritivores, detritus could not be distinguished from digested matter causing the proportion of digested (unrecognisable) matter to be overestimated. Species with a significantly higher proportion of unrecognisable matter in their diets were considered to feed on detritus. Differences among species for the proportion of unrecognisable matter were tested using a *t*-test.

Data on vertical distribution were based on three dates when the reservoir was at least 3 m deep. Per species the relative vertical distribution of each setting time was compared to an even distribution among the six depth-strata (16.67% per stratum) using the chi-square test of goodness of fit. The effect of species and sampling time on the vertical distribution were tested using a two-way ANOVA.

For each sampling date the relative activity per setting time (defined as the CpUE at that setting time divided by the summated CpUE on that sampling date) was calculated for each species. Contrary to the vertical distribution where only three sampling dates were used, the variables indicating the time of active feeding: gut contents, gut fullness and relative activity, were determined using all four sampling dates. Differences in time of active feeding between species were tested using a two-way MANOVA on the three indicators of active feeding.

Suitability of the variables gut fullness, proportion of digested matter and relative activity as indicators for the time of active feeding was determined per variable and per species, using a two-way ANOVA to compare the variance within one setting time to the variance among setting times.

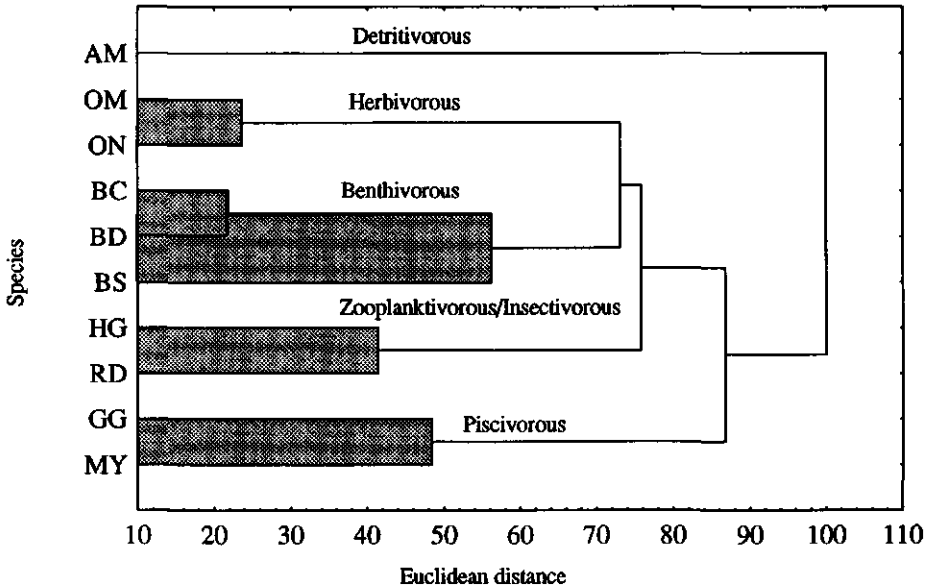
## Results

### *Diel variation in diet*

Based on the gut content analysis five trophic groups were distinguished: the detritivorous *A. melettinus*, the herbivorous tilapias *O. mossambicus* and *O. niloticus*, the benthivorous barbs *B. chola*, *B. dorsalis* and *B. sarana*, the small pelagics *R. daniconius* and *H. gaimardi* feeding on insects, and the piscivores *G. giuris* and *Mystus spp.* (Fig. 3.1).

Fig. 3.1

Dendrogram indicating the similarity of diets of ten species based on the Euclidean distances of each of the food items in the diet. For species abbreviations see table 1.2



Significant ( $p < 0.01$ ) diel changes in diet were observed for five species belonging to three trophic groups (Table 3.2). *O. mossambicus* was the only herbivorous species that exhibited significant (one-way MANOVA,  $p < 0.05$ ) diel variation in feeding. The two main food items that caused this variation, macrophytes and phytoplankton, showed inverse diel variations in their proportion in the diet. Although the proportion of epiphytic algae in the gut of *O. niloticus* was significantly higher at midnight than during the rest of the day, there was no significant diel variation in the gut contents of *O. niloticus*.

Within the benthivorous trophic group the diel feeding behaviour varied significantly for *B. chola* and *B. sarana*. The proportion of zooplankton in the gut of *B. chola* was significantly higher at night than during the day-time while for the proportion of fish eggs an opposite pattern was observed. In the gut of *B. sarana* only insects and gastropods showed significant diel changes. The proportion of insects in the gut of *B. sarana* was highest at noon and the proportion of gastropods was highest at dusk.

Table 3.2      Diel variation in diet expressed as the proportion of the most important food items per species at different times of day. \* and \*\* indicate significant ( $p < 0.05$  resp.  $p < 0.01$ ) diel variation.

Species	Food item	Setting time (hr)			
		6	12	18	24
<i>A. melettinus</i>	Zooplankton	0	0	1	2
	Phytoplankton*	18	13	13	15
	Detritus	82	87	84	81
<i>B. chola</i> **	Insects	2	0	8	7
	Zooplankton**	13	3	8	15
	Gastropods	23	11	9	0
	Chironomids	17	12	5	25
	Fish eggs**	28	54	43	23
	Microbenthos	12	20	27	25
<i>B. dorsalis</i>	Insects	0	20	0	0
	Gastropods**	15	3	31	16
	Chironomids	42	18	38	22
	Fish eggs	27	36	20	30
	Microbenthos	12	8	7	21
	Macrophytes*	4	6	1	11
<i>B. sarana</i> **	Fish	0	14	3	0
	Insects**	20	0	2	12
	Gastropods**	72	53	78	63
	Chironomids	0	4	0	6
	Microbenthos	0	9	12	0
	Macrophytes*	7	13	5	14
<i>G. giuris</i>	Fish	68	63	82	69
	Insects*	5	26	0	3
	Shrimp	25	2	8	26
	Chironomids	0	1	10	1
<i>H. gaimardi</i> **	Insects**	75	21	50	80
	Zooplankton	2	19	13	20
	Macrophytes**	19	58	0	0
<i>Mystus spp.</i>	Fish			64	0
	Insects			0	35
	Zooplankton			10	13
	Shrimp			14	0
	Chironomids			0	50
<i>O. mossambicus</i> **	Insects	14	0	8	0
	Macrophytes**	34	23	58	18
	Epiphytic algae	32	31	12	0
	Phytoplankton**	9	29	12	49
	Porifera	7	1	6	33

Species	Food item	Setting time (hr)			
		6	12	18	24
<i>O. niloticus</i>	Insects	16	0	0	2
	Macrophytes	61	51	76	62
	Epiphytic algae**	4	2	4	14
	Phytoplankton*	11	24	14	18
	Porifera	2	15	5	0
<i>R. daniconius**</i>	Insects	72	73	94	69
	Zooplankton	0	8	0	3
	Chironomids	14	0	0	0
	Macrophytes	7	13	6	20

Although the insectivorous small pelagic fish had significant diel changes in feeding behaviour, only the proportions of insects and macrophytes in the gut of *H. gaimardi* varied significantly. No macrophytes were found in the guts of fish collected at night. At noon the proportion of macrophytes was significantly higher while the proportion of insects was lower than during the rest of the day. Notable for *R. daniconius* was the high proportion of insects at dusk and chironomids at dawn.

Neither the piscivores nor the detritivorous *A. melettinus* showed significant diel changes in feeding behaviour. Important with regard to species interactions was the observation that *A. melettinus* was the main prey species for the piscivores. *A. melettinus* is the only species with a significantly ( $p \leq 0.05$ ) higher proportion of unrecognisable matter than the other species, indicating *A. melettinus* consumes detritus.

#### *Time of active feeding*

The diel variation in feeding behaviour of a species was described by the changes in its diet throughout the 24-hour period, as described above. Also important was the time at which active feeding occurred, which was established from three independently determined variables: gut fullness, proportion of digested matter and relative activity (Fig. 3.2). During active feeding relative activity was expected to be high, gut fullness was expected to increase and the proportion of digested matter to decrease. For the entire fish assemblage gut fullness and proportion of digested matter were negatively (Pearson  $r$ ,  $p \leq 0.05$ ) correlated while the relative activity was not correlated with any of the other variables. In general, variables with relatively large differences among and small differences within the different setting times were considered to be the best indicators of the time at which active feeding took place. Results of the two-way ANOVA showed gut fullness to be the best indicator for most of the species, except for *B. sarana*, *H. gaimardi*,

Fig. 3.2

Mean gut fullness, proportion of digested matter and relative activity of the ten most abundant fish species, at four setting times. Numbers of fish per variable per species are indicated in table 3.3. For species abbreviations see table 1.2.

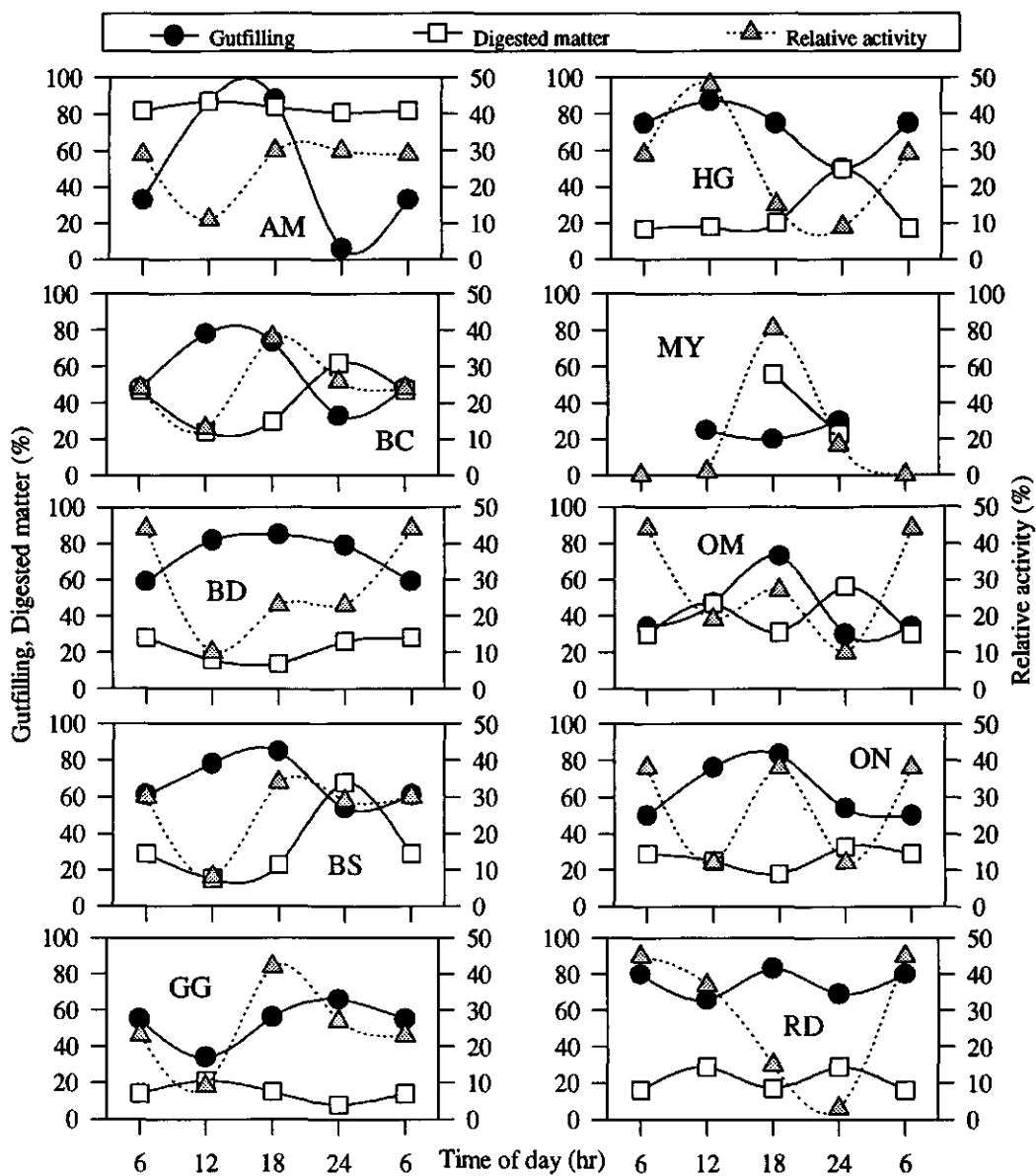
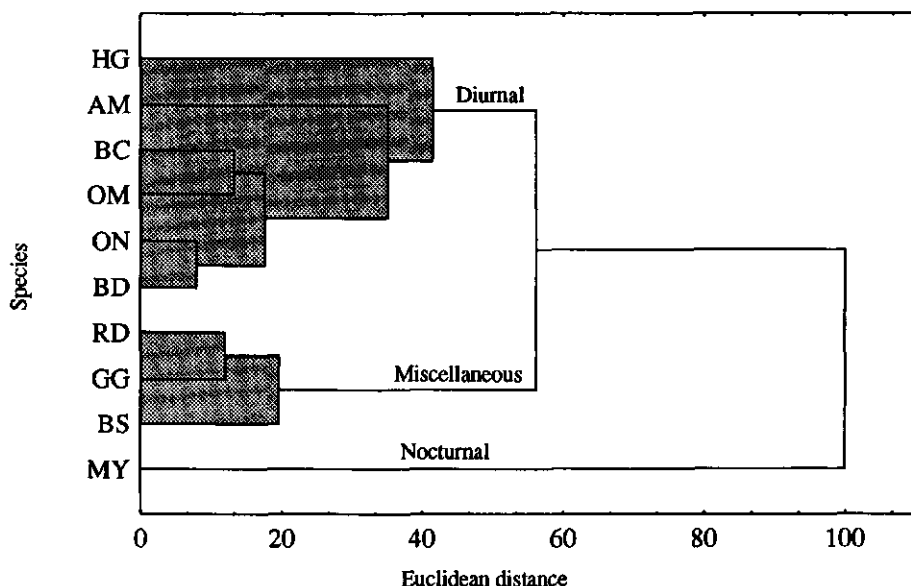


Table 3.3 The p-values indicating an effect of the setting time on the vertical distribution and three variables indicating the time of active feeding. Significant p-values are in bold. N represents the total number of fish examined per variable over respectively three (active feeding) and four (vertical distribution) sampling dates. For the three variables indicating the time of active feeding a two-way ANOVA was used, testing the effects of the setting time and sampling date, for the vertical distribution a one-way ANOVA was used. For species abbreviations see table 1.2

Species	Gut fullness		Digested matter		Relative activity		Vertical distribution	
	p	N	p	N	p	N	p	N
AM	<b>0.02</b>	105	0.38	105	0.12	202	<b>0.00</b>	85
BC	<b>0.00</b>	382	<b>0.03</b>	382	0.03	2247	<b>0.00</b>	371
BD	0.06	191	0.54	191	0.18	298	<b>0.00</b>	107
BS	0.17	89	0.35	89	0.10	110	<b>0.00</b>	69
GG	<b>0.05</b>	169	0.38	169	0.22	199	<b>0.01</b>	144
HG	0.19	32	0.94	32	<b>0.00</b>	32	0.96	23
MY	0.26	21	0.38	21	<b>0.00</b>	23	0.16	16
OM	<b>0.01</b>	203	0.06	203	0.56	330	<b>0.00</b>	125
ON	<b>0.00</b>	226	0.90	226	0.16	376	<b>0.00</b>	190
RD	0.65	118	0.52	118	0.93	409	0.16	23

*Mystus spp.* and *R. daniconius*, in which gut fullness did not differ significantly between the times of day (Table 3.3). Of these four species the relative activity differed significantly between the times of day for *H. gaimardi* and *Mystus spp.* leaving only *B. sarana* and *R. daniconius* for which none of the variables differed significantly between the times of day.

Fig. 3.3 Dendrogram indicating the similarity of time of active feeding of ten species based on the Euclidean distances of the variables: Gut fullness, proportion of digested matter and relative activity. For species abbreviations see table 1.2.





The two-way MANOVA testing for a species- and diel effect on the three above mentioned variables showed both effects as well as their interaction to be significant ( $p < 0.01$ ). Six species namely *A. melettinus*, *B. chola*, *B. sarana*, *H. gaimardi*, *Mystus spp.* and *O. mossambicus* showed a significant diel variation in their feeding activity. Cluster analysis (Fig. 3.3) distinguished between three major clusters: The largest cluster consisted of *H. gaimardi*, *A. melettinus*, two barbs and the tilapias which were diurnal species. *Mystus spp.* was an exclusively nocturnal taxon while the third cluster consisted of species which, although mainly diurnal (*B. sarana*), nocturnal (*Mystus spp.*) or crepuscular (*R. daniconius*), showed a feeding activity which was more evenly distributed over the 24-hour period.

The typical diurnal feeders are active from dawn until dusk. For most of the diurnal feeders their activity was based on their gut fullness and inversely related proportion of digested matter. Only for the detritivorous *A. melettinus*, the proportion of unrecognisable matter did not correlate with the gut fullness because the ingested food could not be distinguished from digested matter. For *B. dorsalis* the diel pattern of the relative activity differed from the patterns of gut fullness and proportion of digested matter (Fig. 3.2). The two feeding behaviour variables suggested *B. dorsalis* was more active at noon while the relative activity suggested the fish was more active at dawn. However, all variables were consistent in characterising *B. dorsalis* as a diurnal feeder. *O. mossambicus* and *O. niloticus* displayed a similar period of active feeding during day-time. As with the benthivorous barbs the patterns of the variables differed but the significant differences between the times of day (Table 3.4) did not contradict each other. Although the relative activity appears to be a better indicator of the time of active feeding of *H. gaimardi*, there is no contradiction between three variables confirming *H. gaimardi* is a typical diurnal feeder.

Table 3.4 Significant ( $p < 0.05$ ,  $p < 0.01$ ) differences between the different times of day for the variables indicating time of active feeding. For species abbreviations see table 1.2

Species	Gut Fullness	Digested matter	Relative activity
AM	18>6, 18>24, 6>24		
BC	12>6, 12>24, 18>24	12>24, 18>24	18>6, 18>12
BD	12>6	12>6	6>12, 24>12
BS	18>24	12>24, 18>24	18>6, 18>12
GG	6>12, 18>12, 24>12		
HG	12>24		6>18, 6>24, 12>6, 12>18, 12>24
MY			18>6, 18>12, 18>24
OM	18>6, 18>12		
ON	18>6, 18>24		6>24, 18>24
RD			

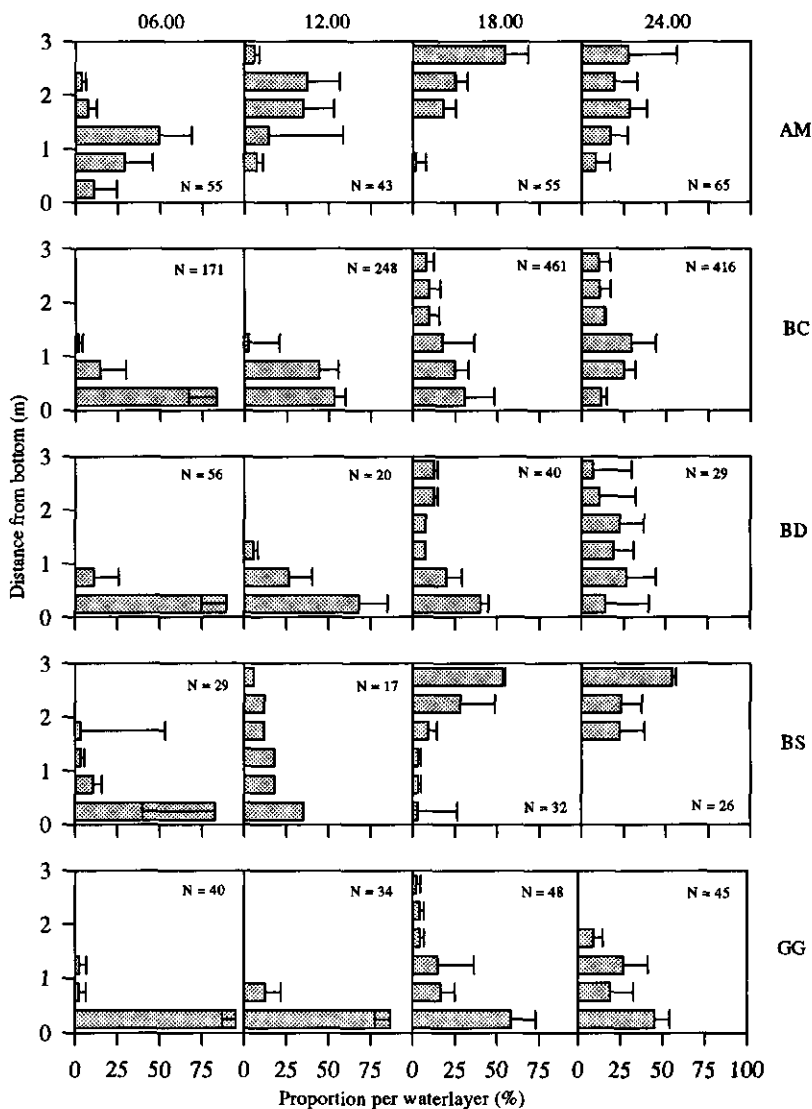
None of the variables exhibited a distinct diel pattern for *B. sarana*, *G. giuris* and *R. daniconius* suggesting these species were more or less evenly active throughout the 24-hour period. However, from the patterns of the different variables it was concluded that *B. sarana* was a diurnal species showing a relatively longer period of feeding activity as it appeared to be active from dawn until after dusk, *G. giuris* was a nocturnal species while *R. daniconius* was mainly crepuscular. *Mystus spp.* was the only exclusively nocturnal taxon with the highest activity around dusk.

#### *Diel variation in vertical distribution*

The vertical distribution of all species except for *Mystus spp.*, *H. gaimardi* and *R. daniconius* varied significantly throughout the 24-hour period (Table 3.3), and for all species at least one setting time differed significantly ( $p < 0.01$ ) from the even distribution (Fig. 3.4). Size-related diel differences in vertical distribution were not observed for any of the species. The two-way ANOVA testing for a species and diel effect on the vertical distribution showed both effects as well as their interaction to be significant ( $p < 0.01$ ). To test to what extent the feeding behaviour determines this diel variation in vertical distribution, the clusters of species with similar diets (Fig. 3.1) were used to pool the vertical distributions of species together in feeding guilds and the setting times were pooled together depending on whether or not a species was actively feeding at that time (Fig. 3.3). In spite of these alterations, a significant ( $p < 0.01$ ) effect on the vertical distribution was observed for both the feeding guild and feeding status, as well as their interaction. In contrast, when applied per feeding guild, the two-way ANOVA showed no significant species effect nor interaction on the vertical distribution but the effect of the feeding status remained significant ( $p < 0.01$ ). A one-way ANOVA showed a significant ( $p < 0.01$ ) feeding status effect on the vertical distribution for all species except for the insectivores *H. gaimardi* and *R. daniconius* which occupy the upper layers of the water column throughout the 24-hour period. Contrary to *H. gaimardi*, *R. daniconius* did exhibit a slight, not significant, diel variation in its vertical distribution. Especially at dawn when both species were actively feeding, *R. daniconius* was found just below the upper layer which was occupied by *H. gaimardi*. When feeding, the typical benthivores *B. chola* and *B. dorsalis* occupy the bottom layer as do the herbivorous grazers *O. mossambicus* and *O. niloticus*. *B. sarana* was found in the bottom layers at dawn and moved strongly toward the surface when it became dark. *A. melettinus* was mainly found in the lower half of the water column avoiding the bottom layer. Because of the low numbers of *Mystus spp.* caught, and because the fish was only active at night, the vertical distribution during day-time could not be measured. When actively feeding, the piscivores *G. giuris* and *Mystus spp.* were found throughout the water column. In contrast, when the species were not actively feeding all species except for the piscivores moved upward away from the bottom layer whereas the piscivores exhibited the inverse pattern. This is confirmed by comparing the vertical distributions, using a two-way ANOVA, of piscivorous and non-piscivorous species at the time of feeding and when feeding is not taking place. This shows a significant ( $p < 0.01$ ) difference in vertical distribution between piscivores and non-piscivores as well as a significant ( $p < 0.01$ ) interaction with the time of active feeding. The fact that no significant effect on the vertical distribution was observed for the time of

Fig. 3.4

Vertical distribution, expressed as the proportion of the total number of fish per depth stratum, for the ten most abundant fish species, at four setting times. N is the total number of fish per species per setting time over three occasions. Variance bars indicate 95% confidence limits.



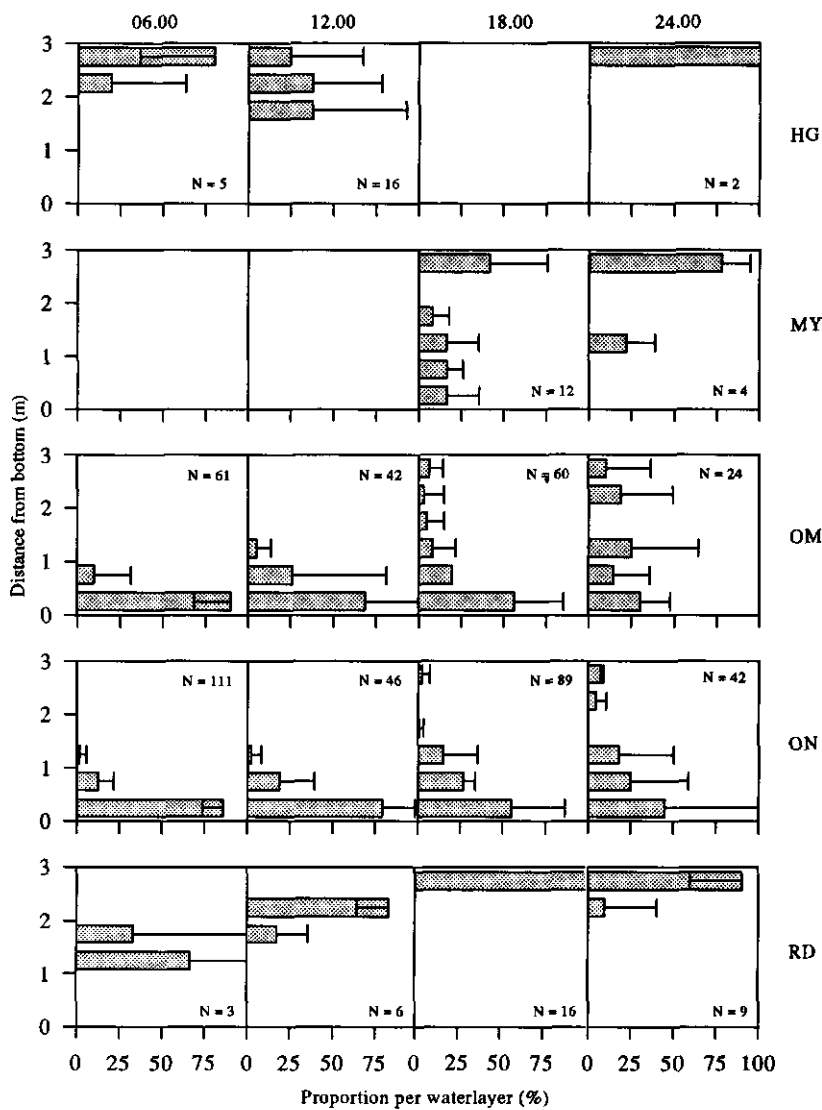
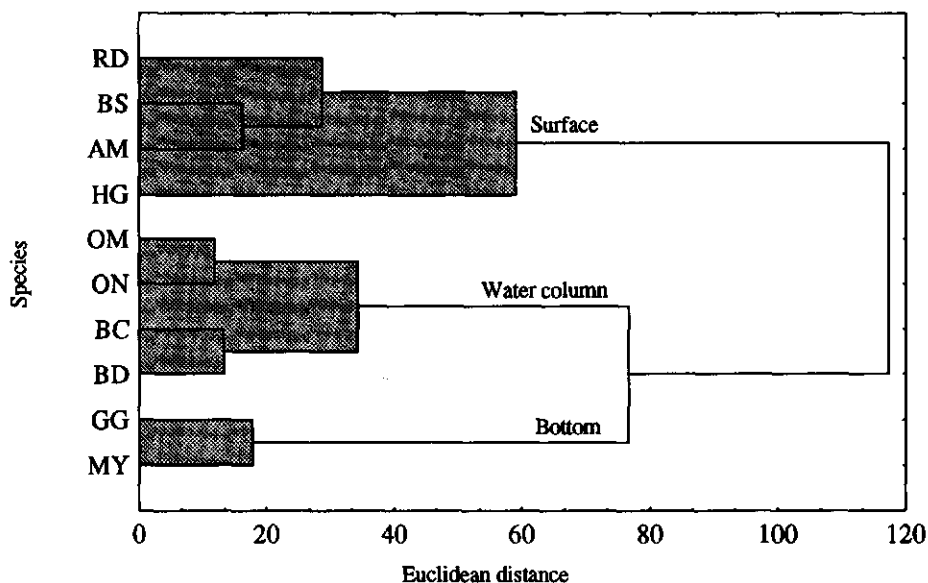
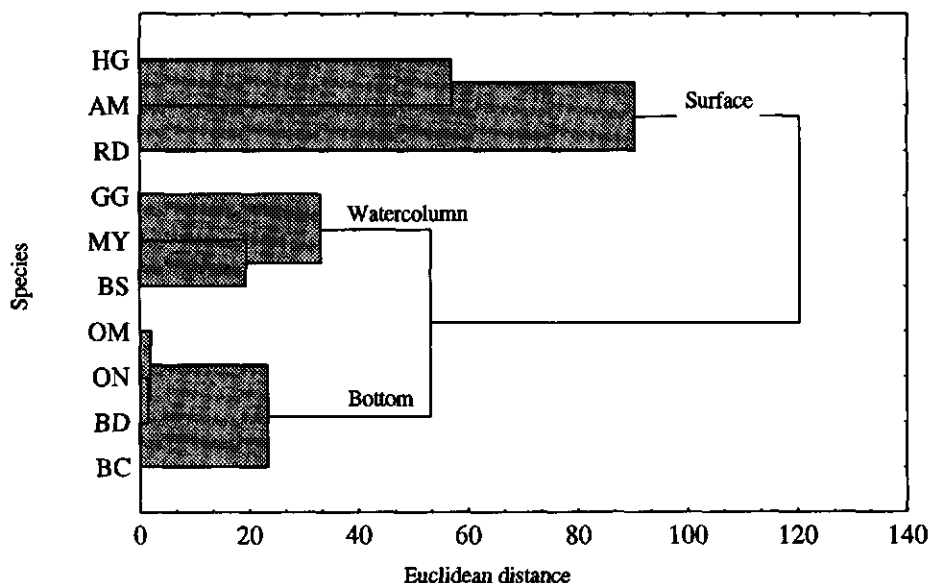


Fig. 3.5

Dendrograms indicating the similarity of vertical distribution of ten species when active feeding is (top), respectively is not (bottom), taking place. Similarity is based on the Euclidean distances of the number of fish per horizontal layer. For species abbreviations see table 1.2.



active feeding shows that the vertical distribution of the piscivores when feeding is similar to that of the non-piscivores when not feeding.

Cluster analysis was used to indicate the similarity in diel vertical distribution patterns between species. This similarity was determined from the vertical distribution per setting time of each species and showed how species were segregated based on their diel position in the water column. Because of the significant effect on the vertical distribution of whether or not a species is feeding, two clusters were distinguished (Fig. 3.5). The cluster based on the vertical distribution of species when they are actively feeding distinguishes three major clusters. One cluster consists of species avoiding the bottom layer consisting of *A. melettinus*, *H. gaimardi* and *R. daniconius*. One cluster of species occupying the entire water column such as *B. sarana* and the piscivores *G. giuris* and *Mystus spp.* The third cluster consists of species which were observed almost exclusively in the bottom layer. When species were not feeding only the piscivores occupied the bottom layer. The relationship between feeding behaviour and vertical distribution was confirmed by the significant ( $p < 0.01$ ) correlation between the calculated Euclidean distances among species pairs based on diet (Fig. 3.1), and those based on the vertical distribution when actively feeding (Fig. 3.5) whereas this was not observed with those based on the vertical distribution when feeding was not taking place (Fig. 3.5).

## Discussion

### *Feeding behaviour and vertical distribution*

Diel variation in the vertical distribution of the fish may be either caused by abiotic or biotic factors, or both. Dissolved oxygen and temperature in Tissawewa do not show variations during 24 hours that could have caused the observed patterns of vertical distribution of the fish. Light intensity will manifest itself indirectly through predator avoidance or efficiency of particulate feeding (Clark & Levy 1988). An important biotic interaction is between fish species and their prey; zooplanktivorous fish species often exhibit a diel vertical distribution pattern similar to zooplankton (Begg 1976, Gliwicz 1986, Janssen & Brandt 1980). In Tissawewa zooplankton is not known to exhibit any diel changes in vertical distribution (Amarasinghe personal communications) thus leaving only biotic interactions such as avoidance of potential competitors or predators to explain the observed diel patterns. Avoidance of potential competitors can be realised by partitioning of resources along different dimensions. Because these resource dimensions can be interrelated, resource partitioning should only be discussed as a factor explaining the observed patterns in vertical distribution when the other resource dimensions, both temporal and trophic, are considered as well. When a fish is feeding, the vertical distribution of the fish corresponds with that expected on the basis of occurrence of their food items along the vertical gradient. Species feeding on benthic food items are active in the bottom layers, species feeding on surface-related food items are active in the surface layers and filter-feeders are active in the water column. For those species exploiting the same food resources, the interrelated positions along the trophic and spatial dimensions are predominantly determined by avoidance of exploitative competition. However, when the fish is not feeding the vertical distribution is determined mostly by avoidance of interference competition or predation.

The proportion of benthic food items in the gut of the barbs corresponds to the vertical distribution at the time of active feeding: *B. chola* and *B. dorsalis*, feeding almost exclusively on benthic food items, are found close to the bottom at the time of active feeding while *B. sarana* also occupies the water column which is reflected in the higher proportion of fish and insects in the gut of this fish. When the barbs are not feeding they move away from the bottom layer; *B. chola* and *B. dorsalis* occupy the entire watercolumn, *B. sarana* only the upper half.

Like the barbs, the tilapias are found close to the bottom at the time of active feeding and occupy the entire watercolumn when this is not the case. This pattern and the day-time feeding activity of *O. mossambicus* and *O. niloticus* is confirmed by observations on tilapia feeding behaviour, reported by Trewavas (1983). *O. mossambicus* (Hofer & Schiemer 1983) and *O. niloticus* (Moriarty & Moriarty 1973) have a higher gut fullness around dusk corresponding with findings in this paper. Schiemer & Hofer (1983) consider *O. mossambicus* to show "a more or less continuous diel feeding pattern" because they found only slight diel variation in gut fullness. This confirms the difficulty of determining diel patterns in feeding activity from only one variable rather than the absence of diel variation. No segregation was observed between the two tilapia species.

*Mystus spp.* lie on the bottom during day-time and occupy the entire water column when feeding at night (Pet & Piet 1993) confirming that *G. giuris* and *Mystus spp.* display a similar vertical distribution and are therefore not spatially segregated. Temporal segregation however, is important because whereas *G. giuris* is not strictly nocturnal, *Mystus spp.* are. When both species are active, *Mystus spp.* is found higher up in the water column while *G. giuris* occupies the bottom layers. This is reflected in the relatively high proportion of food items like insects and zooplankton in the gut of *Mystus spp.*

The species feeding on insects, *H. gaimardi* and *R. daniconius*, are both temporally and spatially segregated. *R. daniconius* is active during crepuscular periods, as is confirmed by Kumar (1985) who found a higher gut fullness for *R. daniconius* at these times. *H. gaimardi* is mainly active during day-time with a peak around noon. Spatial segregation is most conspicuous around dawn: *R. daniconius* avoids the upper layer, which is occupied by *H. gaimardi*. Both species remain in the surface layers when they are not feeding.

In the present study, *A. melettinus* deserves special attention. Not only because it is the only filter-feeding detritivorous species, but also because it is the main prey of the piscivores (Piet *et al.* Chapter 4). Because of its filter-feeding habit it is segregated from all other species, along the trophic and spatial dimension. The importance of detritus as a food source for this stomachless fish is explained by Bitterlich (1985) who states that stomachless fish cannot utilise the major part of the ingested algae. Aquarium observations confirmed that *A. melettinus* actively feeds in the water column (Pethiyagoda 1991). *A. melettinus* occupies the surface layers when it is not actively feeding. The observation that, in spite of a higher concentration of suspended detritus near the bottom (Piet *et al.* Chapter 4), *A. melettinus* avoids the bottom layer when it is feeding, emphasises the importance of predator avoidance and is a common phenomenon explained by the trade-off between food intake and predation risk (Clark & Levy 1988).

Thus, knowledge of the time of active feeding is crucial for an explanation of the diel variation in the vertical distribution of the species of the Tissawewa fish assemblage.

When a fish is feeding, the vertical distribution is interrelated with the food source the fish is exploiting. Therefore partitioning of resources in order to avoid exploitative competition involves the position of a species along both the spatial and the trophic resource dimension. When feeding is not taking place, all species except for the piscivores display the same trend of avoiding the bottom layer, confirming that avoidance of both interference competition and predation are important factors explaining the vertical distribution.

#### *Time of active feeding*

The time of active feeding, representing the temporal dimension, can be established from three independently determined variables: gut fullness, proportion of digested matter and relative activity of which only the first two are significantly correlated. This discrepancy necessitates the examination of the reliability of the observed patterns as indicators of the feeding activity. In this study two strategies are used: 1) the most reliable variable is used as an indicator of the pattern of feeding activity or 2) per variable, only those times of day are used which are significantly different from each other. For each species both strategies yield the same pattern of feeding activity, suggesting the apparent disparity between the relative activity and the other two variables arises mainly because the variables are difficult to determine precisely, thereby causing the considerable variation around the calculated averages to obscure the true diel pattern. None of the variables on its own could have provided the patterns of feeding activity of each of the species of the fish assemblage with the accuracy obtained by combining these variables. The results of the cluster analysis based on the time of active feeding correspond to the "temporal ratios" of Helfman (1978) who found that about half to two-thirds of the species in an assemblage are diurnal, one quarter to one third are nocturnal and the remaining ten percent or so are primarily crepuscular.

#### *Consequences for sampling*

Significant diel variations in diet were observed for most species, suggesting that the time of the day fish are caught for gut content analysis might introduce a bias when determining a species' diet. With regard to differences per food item per species the gut contents of fish differ the most at noon and at midnight. Only on one occasion did the proportion of a food item in the gut of a fish caught at one time significantly differ from all other diurnal sampling times (insects in the gut of *G. giuris* caught at noon). Thus if fish are caught at two different times of day, 12 hours apart, for example noon and midnight or dawn and dusk, practically any chance on bias caused by the time of sampling in a diet determined from gut content analysis, will be eliminated.

#### *Consequences for resource partitioning*

Diel changes in feeding behaviour or vertical distribution are observed for most species of the Tissawewa fish community and can have a considerable impact when determining the position of a species along the trophic, spatial or temporal resource axis. Because for each species the positions on each of the three resource axes are clearly interrelated, caution should be exercised when comparing the importance of the different resource dimensions. Although partitioning along the temporal dimension appears



relatively unimportant, the status of whether or not a fish is feeding determines if the position along the spatial resource dimension is dependent, respectively independent, of the position along the trophic resource dimension. At the time of feeding, resource partitioning is mainly aimed at avoiding exploitative competition, whereas avoidance of interference competition or predation govern the partitioning of resources when feeding is not taking place.

### **Acknowledgements**

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## CHAPTER 4

### OPTIMAL FORAGING VERSUS PREDATOR AVOIDANCE IN A SIZE-STRUCTURED TROPICAL FISH ASSEMBLAGE

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#### Abstract

In Tissawewa, a tropical reservoir, the size-specific and spatial differences in feeding behaviour and distribution of the ten most abundant species of the fish assemblage were determined. The effect of the environment on these variables was studied by distinguishing two periods separated by a term during which the reservoir was completely dry. Before the drought, the reservoir had macrophytes only in the shallow, inshore zone and turbidity was high due to suspension of a thick layer of detritus on the bottom. After the drought macrophytes covered the entire watercolumn throughout the reservoir and water was relatively clear because the detritus had disappeared. The spatial effect on the feeding behaviour and distribution of the fish assemblage was determined from four habitats differing in either the vertical plane (surface to bottom), or the horizontal plane (open water to shore), or both. Any size-specific effect was examined from differences between six predefined size-classes. For each species significant spatial effects, size-specific effects and/ or environmental effects were observed. In general, the juveniles were mainly found in the vegetation feeding on zooplankton while during ontogeny the diet changed and distribution was altered according to their choice of prey.

Profitability per food item and predation risk, were estimated per habitat. Also, the species or size-classes subject to predation, were determined. Comparison of the spatial and size-specific distributions of the fish species, to the spatial trends in profitability of their main food sources, showed that the distribution of all the fish in Tissawewa is determined by foraging profitability except for those species or size-classes subject to predation, for which the distribution is determined by the avoidance of predation. Environmental changes affecting the risk of predation and foraging rate are reflected in the distribution patterns of the fish species involved confirming the ability of species to facultatively respond to these factors.

Fig. 4.1

Position of the sampling stations. Station A = Surface layer offshore zone, Station B = Bottom layer offshore zone, Station C = Intermediate zone, Station D = Inshore zone. The vegetation indicated applies only for period 1.

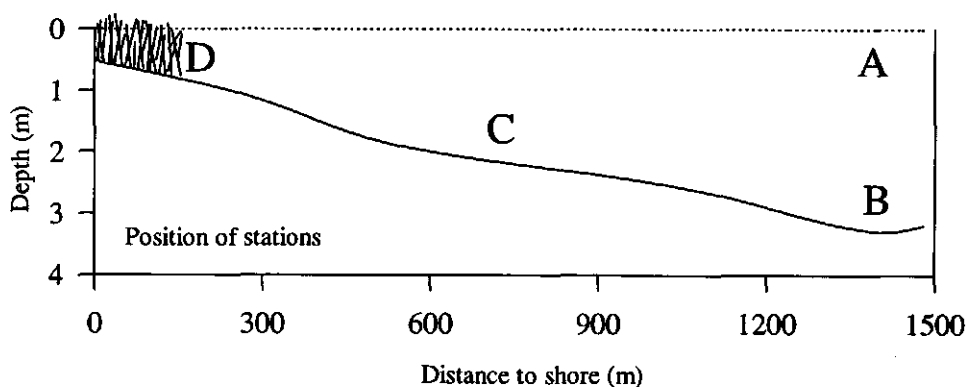
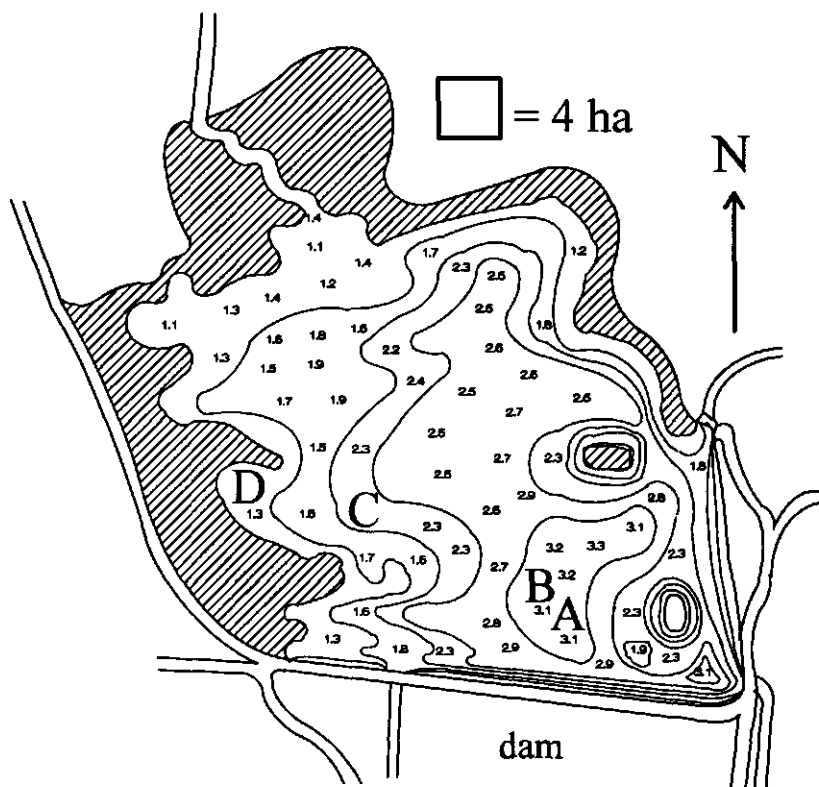


Fig. 4.2

Morphometric map of Tissawewa during period 1 when vegetation was confined to the inshore zone (shaded). Positions of the stations are indicated (see figure 4.1).



During each monthly sampling session the four sampling stations were sampled with multi-mesh monofilament gillnets: twice during day-time and twice during the night. In addition to the gillnets, two active gears, bottom trawl and cast net, were used. These gears ensured the entire size range ( $\geq 3$  cm total length) of the available species was sampled. To distinguish size-related differences, the total size range was divided into six predefined size-classes (Table 4.1).

Table 4.1 Total length ranges of each size-class

Size-class	1	2	3	4	5	6
Total length (cm)	3.0-4.4	4.5-6.9	7.0-9.9	10.0-13.9	14.0-18.9	$\geq 19.0$

To study the feeding behaviour each monthly sampling session twice, a maximum of 10 specimens per species, size-class, gear type, station and time of day were selected for determination of gut fullness after which the gut contents of the selected fish were pooled for further analysis. The fullness of the stomach or anterior one-third part of the gut was estimated according to five gut fullness categories (Table 4.2).

Table 4.2 Gut fullness categories and estimated percentage of fullness (slightly modified according to Haram & Jones 1971).

Gut fullness category	Fullness (%)
Completely filled and swollen	90-100
Just filled over full length, not swollen	70-89
Contents divided in different patches	30-69
Very few food particles	10-29
Completely empty	0-9

The contents of the stomach or anterior 1/3 part of the gut were analysed for each pooled sample. The relative biovolumes of food items in gut/ stomach were estimated according to the points method (Hynes, 1950) using a microscope. The following categories of contents were distinguished: Fish, insects (both aquatic and terrestrial but not benthic), microcrustacean zooplankton (cladocerans, cyclopoid and calanoid copepods), gastropods, shrimps, fish eggs, chironomids, microbenthos (mainly ostracods and some benthic cladocerans), porifera, macrophytes, epiphytic filamentous algae, phytoplankton and unrecognisable matter (digested matter and/or detritus).

In stations A and B the concentration of suspended particulate organic matter, or seston (Golterman *et al.* 1978), and phytoplankton (Moed & Hallegraeff 1978) were measured. The concentration of detritus was calculated by subtracting the phytoplankton concentration from the seston concentration.

#### Data Analysis

Differences in feeding behaviour were determined using a three-way MANOVA with which the effects of species, environment (before and after drought) and size-class on the gut contents were tested. Species were categorised into feeding guilds by cluster analysis on the average gut contents of each species independent of environment, size or station. The effect of size on the contents in the gut was tested per species using a two-

way MANOVA in which the effect of two environments (represented by the periods) and, depending on the species, as many size-classes as possible, were analysed. Also, two-way ANOVA was used to test for these effects on each of the main food items separately. In case size-related differences were observed for a food item, linear regression was used to determine if the proportion of that food item was significantly correlated to the mid-range length of the size-classes involved. Spatial differences in feeding behaviour were examined per species using a two-way MANOVA in which the effects of two environments and four stations on the gut contents were analysed. For the statistical tests only food items were used whose distribution of proportions did not differ significantly from normal (Shapiro-Wilks W-test,  $p \leq 0.05$ ).

For each species, habitat profitability was indicated by the availability of the species' major food items and the fullness of its gut in this habitat, relative to the other habitats. The relative availability of a food item was determined per period from the spatial differences of all major consumers combined. The major consumers of a food item were those species which had a proportion of this food item in their gut, higher than the average proportion of the entire fish assemblage. A Students t-test was used to examine whether the trends in availability observed along the vertical and horizontal gradients were significant. The trend along the vertical gradient was tested based on differences between stations A and B and the trend along the horizontal gradient was tested by combining data from stations A and B in the deep, offshore zone and comparing this to data from station D in the inshore zone. Spatial differences in gut fullness per species were determined along the same gradients as the availability of the food items but differences along each of the gradients were examined using a 2-way ANOVA testing for an effect of environment or station.

Habitat occupation of species during one period was based on the number of fish caught per species, per size-class and per station. The position along the vertical gradient (VG) and horizontal gradient (HG) were calculated using the following equations:

$$VG = \frac{\# A}{(\# A + \# B)} * 100\%$$

$$HG = \frac{(\# A + \# B)}{(\# A + \# B + \# D)} * 100\%$$

where #A, #B and #D are the number of fish caught at the respective stations. A two-way ANOVA was used to test for spatial or size-specific effects on the distribution of the different species during each of the periods.

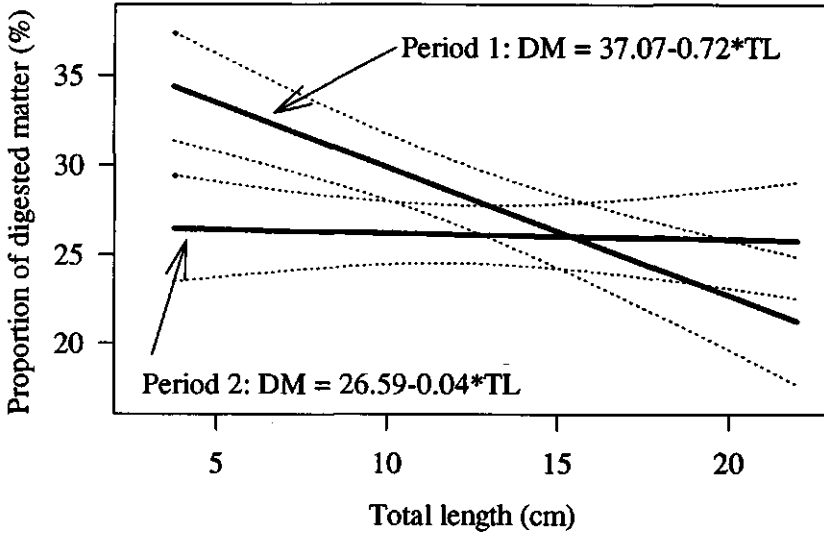
## Results

### *Detritus versus digested matter*

For many species the proportion of unrecognisable matter consisting of digested matter and ingested detritus occupied a considerable part of the gut contents. Therefore, when determining the diet of a species it is important to distinguish between species that

Fig. 4.3

Regression relationships of the proportion of digested matter (DM) as a function of the Total Length (TL) for periods 1 and 2. Indicated are 95% confidence limits.



ingest detritus and those that did not. Assuming the rate of digestion did not differ between species, the species ingesting detritus would have a higher proportion of unrecognisable matter than the species that do not ingest detritus. A three-way ANOVA in which the effects of ten species, two environments and two size-classes (2, 3) were measured on the proportion of unrecognisable matter, showed a significant effect of species ( $p < 0.01$ ), environment ( $p < 0.01$ ) and their interaction ( $p = 0.02$ ). When the smallest species (*A. melettinus*) was excluded and one more size-class (4) was included, an additional significant ( $p = 0.02$ ) interaction between all three effects was observed. To distinguish between species that ingested detritus and those that did not, the species with the highest proportion of unrecognisable matter was excluded until no significant ( $p > 0.05$ ) species effect was observed. The excluded species were in the following order: *A. melettinus*, *O. mossambicus*, *O. niloticus* and *B. chola*. For the remaining species it was assumed that all the unrecognisable matter was digested matter. Thus, the proportion of digested matter per size-class could be determined from the linear regression between the proportion of digested matter and the mid-range length per size-class for each environment separately (Fig. 4.3). With this regression the proportion of unrecognisable matter can be divided, for each species and size-class, into a calculated proportion of digested matter and a remaining proportion of ingested detritus.

Fig. 4.4

Hierarchical tree diagram with results of the cluster analysis on the gut contents of ten most abundant species. For species abbreviations see table 1.2

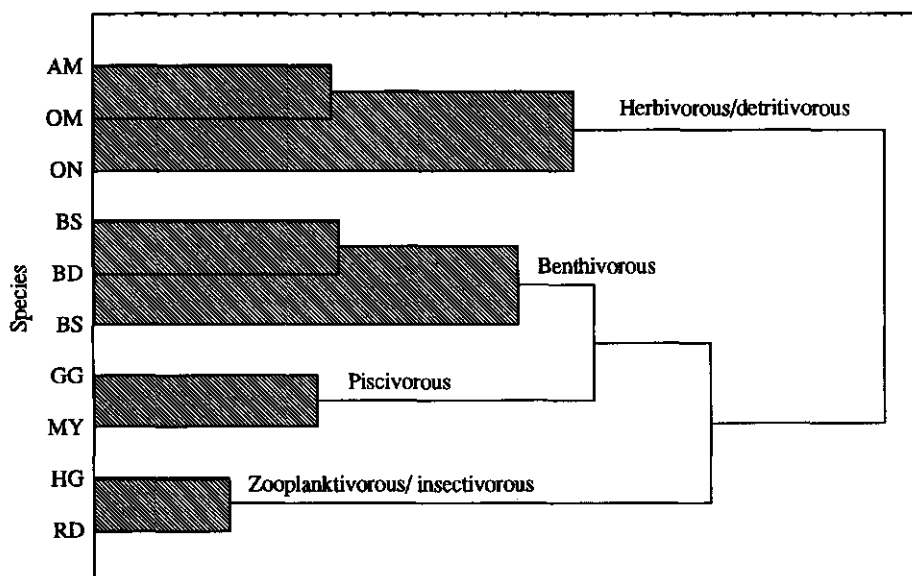


Table 4.3

p-values of two-way MANOVA testing for an environmental and a size-specific effect as well as an interaction on the gut contents of the fish species. Significant p-values are in bold. For species abbreviations see table 1.2

Species	Period	Size	Interaction
AM	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
OM	<b>0.00</b>	<b>0.03</b>	<b>0.00</b>
ON	<b>0.00</b>	0.39	0.36
BC	<b>0.00</b>	<b>0.00</b>	<b>0.05</b>
BD	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
BS	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
GG	<b>0.00</b>	<b>0.00</b>	0.06
MY	<b>0.00</b>	<b>0.00</b>	<b>0.05</b>
HG	<b>0.00</b>	0.29	0.12
RD	<b>0.00</b>	<b>0.00</b>	0.75

#### Establishing feeding guilds

A three-way ANOVA testing the effects of species, environment and size on the gut contents showed all effects and their interactions were significant. Cluster analysis first distinguishes a herbivorous guild (consisting of *A. melettinus*, *O. mossambicus* and *O. niloticus*) and a carnivorous guild. The latter can be subdivided into three guilds: a benthivorous guild consisting of the barbs *B. chola*, *B. dorsalis* and *B. sarana*; a piscivorous guild consisting of *G. giuris* and *Mystus spp.*; and a zooplanktivorous/ insectivorous guild consisting of *H. gaimardi* and *R. daniconius*.

### Size-related differences in feeding behaviour

Size-related and environmental effects on the gut contents of each species, tested using a two-way MANOVA, showed for all species the environmental effect to be significant ( $p < 0.01$ ) and for most species a significant size-related effect which also interacted significantly with the environmental effect (Table 4.3). Similar tests were performed on each food item separately, results are presented per feeding guild.

For all herbivorous species comparison between the two environments showed a higher proportion of phytoplankton and detritus during period 1, and a higher proportion of insects, chironomids, zooplankton, epiphytic algae and macrophytes during period 2 (Table 4.4). Although significant differences between the size-classes of *A. melettinus* were observed for most food items, none of them were significantly correlated with fish

Table 4.4 Gut contents (%) of the herbivorous/ detritivorous species per size-class per period. Indicated are the significant ( $p \leq 0.05$ ) differences per food item between periods (P), between size-classes (L) and the interaction between period and size-class (P\*L). For species abbreviations see table 1.2, size-classes as given in table 4.1.

Food item	Period 1						Period 2						
	1	2	3	4	5	6	1	2	3	4	5	6	
AM Zooplankton	7	2	2				51	7	5				P,L,P*L
Chironomids	0	0	0				8	2	1				P,L,P*L
Phytoplankton	34	29	28				13	23	22				P
Detritus	59	69	71				28	66	67				P,L,P*L
OM Insects	6	5	2	0	0	0	4	11	4	6			P
Zooplankton	30	7	6	5	2	1	4	11	4	6			
Chironomids	0	3	0	0	0	0	6	10	13	1			P
Macrophytes	4	3	7	9	6	0	24	17	17	30			P,L,P*L
Epiphytic algae	0	4	4	1	3	0	23	9	21	27			P
Phytoplankton	18	41	34	25	21	8	13	27	26	15			P,P*L
Detritus	37	33	42	54	65	91	23	12	10	12			P,P*L
ON Fish		0	0	0	0	16		0	0	0	4		
Insects		0	0	0	0	0		12	9	4	14		P
Zooplankton		0	12	1	0	1		4	7	3	1		
Macrophytes		11	21	22	21	13		38	44	49	50		P
Epiphytic algae		4	1	1	1	0		4	6	16	1		P
Phytoplankton		39	16	16	20	14		15	19	20	14		
Porifera		5	5	5	4	7		2	3	5	7		
Detritus		41	45	55	54	50		24	8	0	0		P,P*L



size. In contrast, a significant correlation with size was observed for several food items in the gut of *O. mossambicus*. The proportions of insects, zooplankton and phytoplankton decreased while the proportion of detritus increased with increasing fish size during period 1. During period 2 the proportions of zooplankton and detritus decreased with increasing size. The latter was also the only size-related difference observed for *O. niloticus*.

Table 4.5 Gut contents (%) of the benthivorous species per size-class per period. Indicated are the significant ( $p \leq 0.05$ ) differences per food item between periods (P), between size-classes (L) and the interaction between period and size-class (P\*L). For species abbreviations see table 1.2, size-classes as given in table 4.1.

Food item		Period 1						Period 2						
		1	2	3	4	5	6	1	2	3	4	5	6	
BC	Insects	0	5	2	2			1	13	6	6			P,L
	Zooplankton	40	19	12	10			5	9	7	6			P,L,P*L
	Gastropods	0	4	4	3			0	3	5	10			L,P*L
	Chironomids	0	12	30	29			36	28	36	36			P,L,P*L
	Fish eggs	1	4	5	5			16	15	10	15			P
	Microbenthos	21	22	24	19			26	23	25	24			
	Macrophytes	6	4	2	3			2	1	2	3			P
	Detritus	31	29	18	27			14	8	8	0			P
BD	Insects		5	4	6	4		0	9	10	13	12		P
	Zooplankton		11	14	10	6		6	2	2	3	1		P,L,P*L
	Gastropods		2	12	27	31		0	6	0	5	9		P,L,P*L
	Chironomids		39	38	35	42		86	53	64	55	43		P
	Fish eggs		10	9	3	2		0	6	2	8	14		P*L
	Microbenthos		33	22	17	14		9	22	20	13	14		L
BS	Fish		0	0	0	7	10		0	2	0	0	16	L
	Insects		10	4	29	8	0		29	26	26	25	8	P
	Zooplankton		19	8	3	1	2		5	2	1	4	0	P,L,P*L
	Gastropods		59	69	45	59	54		11	18	17	24	58	P
	Chironomids		2	8	8	2	3		42	29	19	6	0	P,L,P*L
	Microbenthos		4	1	2	0	0		9	12	6	2	4	P,L,P*L
	Macrophytes		3	4	5	15	20		3	3	12	17	11	L
	Epiphytic algae		0	1	4	2	1		0	2	13	19	1	L,P*L

For all species belonging to the benthivorous feeding guild, the proportions of zooplankton and gastropods were lower during period 2 but those of insects and chironomids higher (Table 4.5). In period 1 all species showed a significant decrease of zooplankton in their diet, with increasing fish size. Besides that, significant trends were observed with increasing fish size for each of the benthivorous species separately. The proportion of chironomids increased for *B. chola*. So did the proportion of gastropods for *B. dorsalis* while the proportions of fish eggs and microbenthos decreased. *B. sarana* showed increasing proportions of fish and macrophytes while the proportion of microbenthos decreased. During period 2 all species showed a significant increase of the proportion of gastropods in their diet, with increasing size. Other food items showed similar correlations with fish size as observed for period 1, only the proportions of chironomids and epiphytic algae in the diet of *B. sarana* displayed a significant decrease with increasing fish size during period 2, which was not observed during period 1.

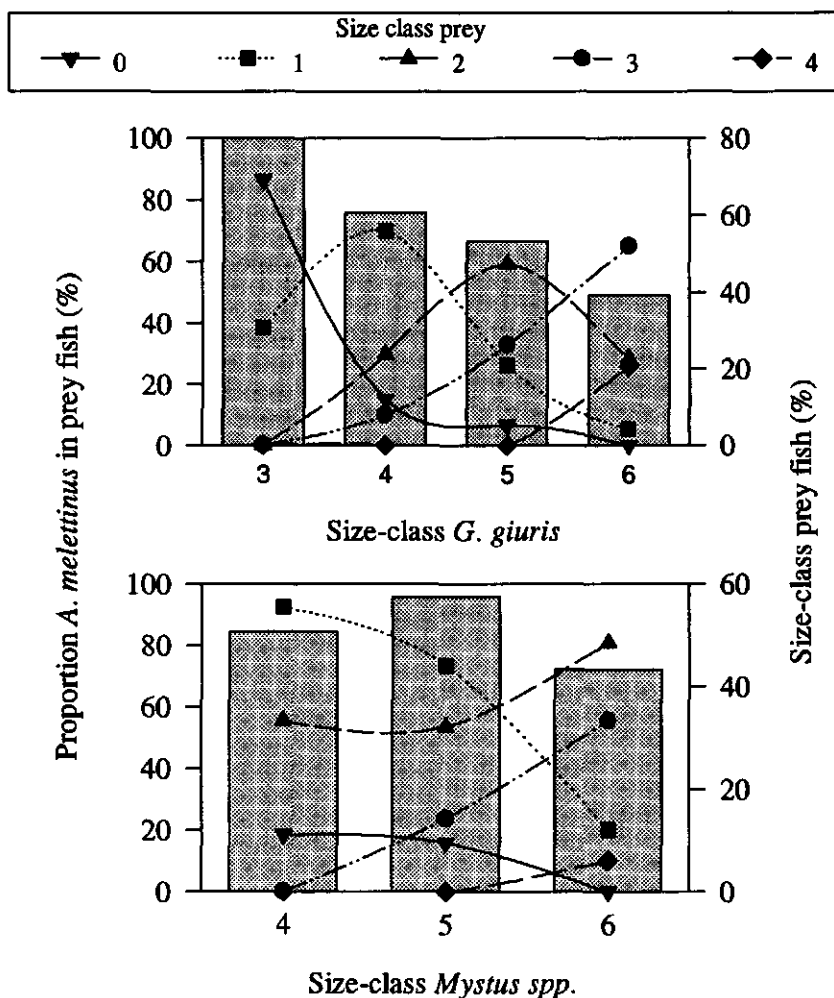
For the piscivores the environmental change resulted in a lower proportion of fish and zooplankton after the drought, which was compensated by an increased proportion of insects and chironomids (Table 4.6). Size of the piscivores correlated significantly with the proportion of most food items in their diet. This applied especially for the main food item, fish. With increasing size of the predator, the average size of prey fish increased, which in turn affected the choice of prey species (Fig. 4.5). The proportion of *A. melettinus* decreased with increasing size of the predator, in favour of other species like *H. gaimardi*, *G. giuris*, *R. daniconius* and to a lesser extent *O. mossambicus* and *B. chola*. Other food items like insects and shrimps for *G. giuris*, and during period 1, chironomids for *Mystus spp.* were significantly preferred by intermediate size-classes (respectively size-classes 3 and 5 for *G. giuris* and 3 for *Mystus spp.*).

Table 4.6 Gut contents (%) of the piscivorous species per size-class per period. Indicated are the significant ( $p \leq 0.05$ ) differences per food item between periods (P), between size-classes (L) and the interaction between period and size-class (P\*L). For species abbreviations see table 1.2, size-classes as given in table 4.1.

Food item		Period 1						Period 2					
		1	2	3	4	5	6	1	2	3	4	5	6
GG	Fish	0	7	53	98	90	93	0	32	26	48	47	89 L
	Insects	11	11	24	0	0	3	32	29	40	23	23	7 P,L
	Zooplankton	30	30	9	2	3	1	9	4	2	1	0	0 P,L,P*L
	Shrimps	0	0	0	0	3	0	0	6	9	13	22	2 P
	Chironomids	52	44	11	0	3	0	59	23	18	12	7	1 L
MY	Fish	5	11	52	64	82		0	0	3	2	25	P,L
	Insects	21	21	11	13	6		0	20	25	32	22	
	Zooplankton	73	55	30	15	2		20	13	24	17	14	P,L,P*L
	Chironomids	1	10	6	3	0		53	54	41	42	33	P

Fig. 4.5

Proportion *Amblypharyngodon melettinus* and size-classes of the total number of consumed prey fish in the gut of the piscivores *Glossogobius giuris* and *Mystus spp.*



The food items in the diet of the zooplanktivores/ insectivores which were mainly affected by the environment were the three zooplankton groups (cladocerans, cyclopoid and calanoid copepods), insects and macrophytes (Table 4.7). Before the drought zooplankton was the main prey item but thereafter it was replaced for the greater part by insects and macrophytes. Considerable, and often significant, size-related changes were observed for each of the zooplankton groups during period 1. After the drought a significant decrease of the proportion of zooplankton and a significant increase of insects with increasing size of *R. daniconius* was observed.

Table 4.7 Gut contents (%) of the zooplanktivorous species per size-class per period. Indicated are the significant ( $p \leq 0.05$ ) differences per food item between periods (P), between size-classes (L) and the interaction between period and size-class (P\*L). For species abbreviations see table 1.2, size-classes as given in table 4. 1.

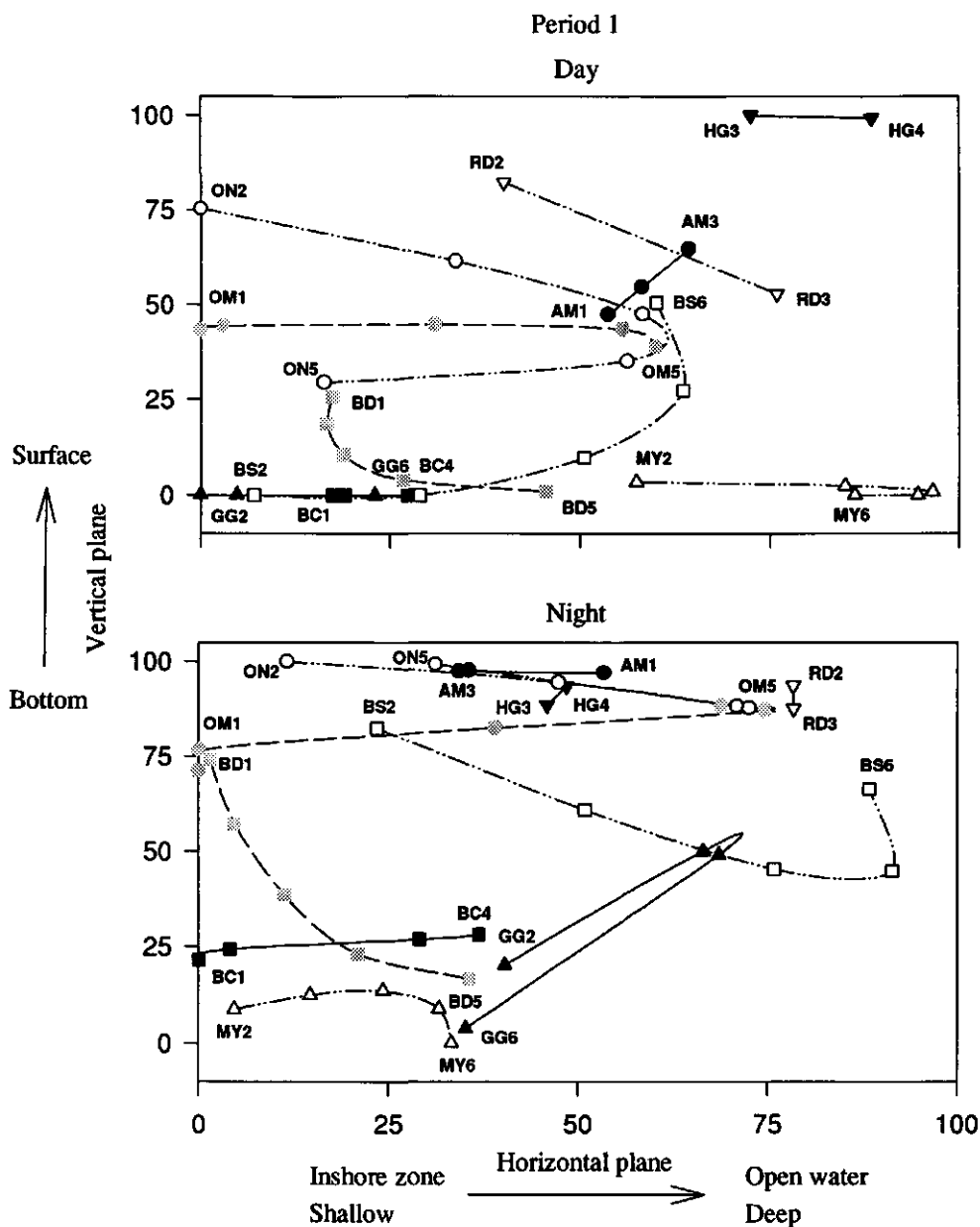
Food item		Period 1						Period 2					
		1	2	3	4	5	6	1	2	3	4	5	6
HG	Calanoid cop.	0	21	25	33					0	0	0	0 P
	Cyclopoid cop.	70	41	29	27					0	1	0	0 P
	Cladocerans	30	37	31	26					0	10	7	0 P
	Insects	0	0	11	8					6	40	37	49 P
	Chironomids	0	0	2	3					7	10	8	14
	Macrophytes	0	1	2	2					86	33	43	34 P,L,P*L
RD	Calanoid cop.	7	16	21	10			0	1	0	0		P
	Cyclopoid cop.	45	30	23	5			20	8	3	1		P,L
	Cladocerans	45	33	25	23			67	26	15	3		L
	Insects	0	16	23	55			5	42	52	72		P,L
	Chironomids	0	2	4	6			0	6	9	6		
	Macrophytes	3	1	2	0			0	7	11	12		P
	Epiphytic algae	1	0	0	1			0	9	6	3		

### Abundance

The relative abundance of the species showed that the herbivorous guild was, by virtue of the abundance of *A. melettinus*, the most important guild, both in terms of numbers as well as biomass (Table 4.8). The distribution among size-classes showed *A. melettinus* with size-class 2 as its most abundant size-class, is much smaller than *O. mossambicus* and *O. niloticus* with respectively size-classes 4 and 6 as their most important size-classes in terms of biomass. The benthivorous guild was, both in terms of biomass and numbers, the second most important guild with *B. dorsalis* as its most important species, in terms of biomass. In this guild *B. chola* was the smallest species with 62% of the species biomass in size-class 3, *B. dorsalis* somewhat larger with more than 90% of its biomass in size-classes 4 and 5 and *B. sarana* the largest species with over 80% of its biomass in size-classes 5 and 6. The piscivorous feeding guild was the least important guild with *Mystus spp.* slightly more abundant than *G. giuris*. *G. giuris* was larger than *Mystus spp.* with most of its biomass in size-class 6 while size-classes 4 and 5 were the main size-classes for *Mystus spp.*. Within the zooplanktivorous guild, *R. daniconius* was the most important species with about twice the biomass of the slightly larger *H. gaimardi*.

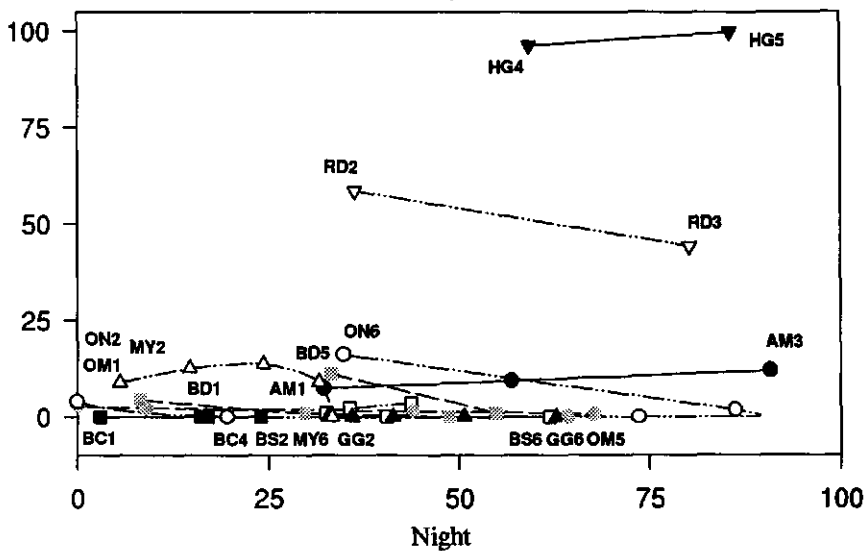
Fig. 4.6

Size-specific distribution of the ten most abundant species in a two-dimensional plane, during day-time and night-time for the periods before and after drought. The horizontal plane ranges from the inshore zone (0) to the open water (100) and a vertical plane from the bottom (0) to the surface (100). Indicated are the species abbreviations with the smallest or largest size-class. For species abbreviations see table 1.2, size-classes as given in table 4.1.



# Period 2

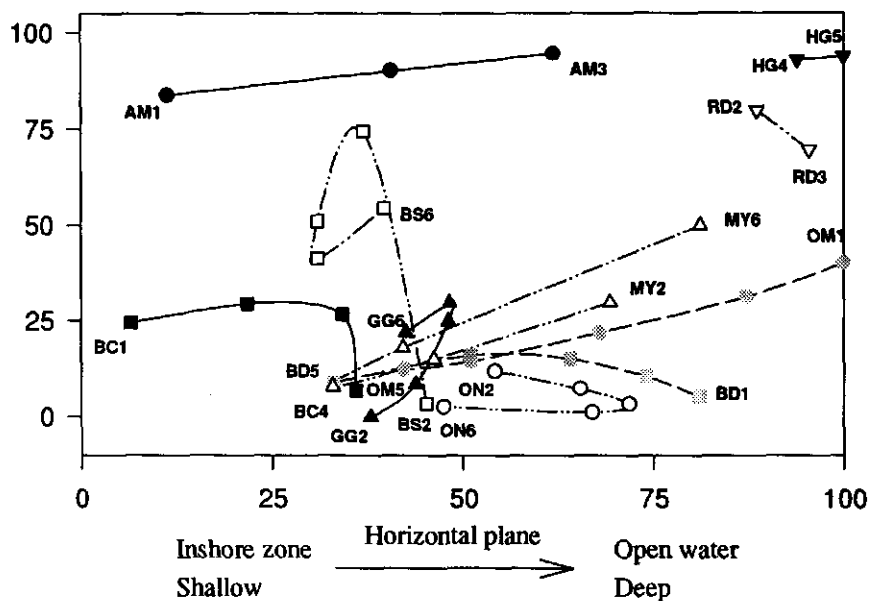
Day



Surface

Vertical plane

Bottom



Inshore zone  
Shallow

Horizontal plane

Open water  
Deep

Table 4.8 Percent biomass and (numbers) per size-class per period. The total abundance of each species is relative to the abundance of the total fish assemblage for the entire sampling period, the abundance of each size-class relative to the species abundance per period. For species abbreviations see table 1.2, size-classes as given in table 4.1.

Species	Total	Period 1						Period 2					
		1	2	3	4	5	6	1	2	3	4	5	6
AM	37(74)	0(1)	64(79)	35(20)				0(1)	53(67)	47(32)			
OM	8(2)	0(2)	7(33)	19(29)	51(28)	23(7)		0(1)	1(7)	11(26)	54(54)	29(12)	5(1)
ON	1(0)	0(2)	3(29)	7(25)	24(29)	19(11)	47(5)		0(3)	4(19)	23(44)	32(24)	40(10)
BC	10(5)		8(21)	62(62)	30(16)			1(6)	21(39)	55(47)	23(7)	1(0)	
BD	20(4)		0(2)	7(19)	42(51)	50(27)		0(3)	1(7)	11(24)	68(58)	20(8)	
BS	6(1)		0(4)	3(16)	13(22)	68(53)	15(6)	0(1)	5(24)	12(28)	46(34)	35(12)	3(0)
GG	3(1)		1(35)	0(5)	1(4)	13(17)	84(40)		1(9)	6(18)	41(51)	34(18)	18(4)
MY	5(1)			0(3)	21(78)	34(57)			1(3)	15(31)	67(57)	17(8)	
HG	3(3)			30(35)	70(65)					1(2)	38(56)	60(41)	1(0)
RD	7(10)		33(57)	66(43)	1(0)			15(30)	81(68)	4(2)			

## Distribution

Distribution of species and size-classes differed considerably for the fish assemblage (Fig. 4.6, Table 4.9). Since water transparency and vegetation differed markedly between two periods, the size-specific distributions of each species during day-time and night-time respectively, are presented per period. The increased transparency during period 2 affected the day-time distribution of the entire fish assemblage, causing a shift toward the bottom of the deepest part of the reservoir. During period 1, small size-classes of almost every species preferred the vegetated inshore zone significantly, something which was not observed during period 2. This is illustrated by the observed ratio for the entire fish assemblage between numbers of size-class 1 caught in the inshore zone versus the open water zone which was 4.4 for period 1 and only 2.6 for period 2.

Table 4.9 Spatial effect per period on the abundance and size of the ten most important fish species in the vertical (V) and horizontal (H) planes. For species abbreviations see table 1.2. Indicated are the change in abundance and size toward respectively the bottom and the shore.

Species	Abundance				Size			
	Period 1		Period 2		Period 1		Period 2	
	V	H	V	H	V	H	V	H
AM								
OM	-		+			-	-	-
ON	-		+	-		-	+	
BC		+	+		-			
BD	+	+	+		+		-	
BS		-	+			-		
GG	+	+	+		+	-	-	
MY	+		+		+	-	-	
HG	-	-	-					
RD	-			-		-		

During period 1 all herbivorous/ detritivorous species occupied similar positions along both the vertical and horizontal gradient. During day-time the species were found in the water column and in the surface layer at night. No preference for either the open water or the inshore zone was observed (Fig. 4.6). Contrary to *A. melettinus*, the tilapias displayed a distinct shift between periods 1 and 2 in their vertical position resulting in a significant preference for the bottom half of the watercolumn during period 2. During both periods the benthivores *B. chola* and *B. dorsalis* were found close to the bottom and displayed a distinct preference for the inshore zone, while *B. sarana* preferred the water column of the open water. A significant size-specific effect along the vertical gradient was observed during period 1 for all benthivorous species; smaller fish avoided the bottom layer. During both periods the piscivorous species occupied mainly the bottom layer. Day-time segregation occurred during period 1 along the horizontal gradient: *G. giuris* occupying the inshore zone and *Mystus spp.* the offshore zone. The zooplanktivorous/ insectivorous species were found in the pelagic zone indifferent of the time of day.

## Habitat profitability based on spatial differences in feeding behaviour

Indicators used to examine habitat profitability of the major fish species are: 1) the availability of the food items and 2) gut fullness of the fish. Significant spatial differences in the proportion of several food items in the guts of its major consumers were observed



along the vertical and horizontal gradients. They are assumed to reveal spatial trends in availability of this food item to the fish assemblage. The general trend along the vertical gradient, observed for both periods separately, was an increased availability of gastropods, microbenthos and detritus toward the bottom while the availability of zooplankton decreased (Table 4.10).

Table 4.10 Trends of food availability in the vertical (V) and horizontal (H) planes based on the proportions of occurrence of each food item in the guts of the major consumers of this item. The indicated direction of change in the vertical plane is toward the bottom, in the horizontal plane toward the shore. Only significant ( $p < 0.05$ ) trends are indicated. For species abbreviations see table 1.2

Food item	Major Consumers	Period 1		Period 2	
		V	H	V	H
Fish	GG, MY				-
Insects	BS, GG, HG, MY, RD		+		+
Zooplankton	HG, MY, RD		-	-	
Gastropods	BD, BS	+			-
Chironomids	BC, BD, GG, MY				+
Fish eggs	BC, BD		+		-
Microbenthos	BC, BD	+			
Macrophytes	BS, HG, OM, ON		+		-
Epiphytic algae	BS, OM, ON, RD		+		+
Phytoplankton	AM, OM, ON				
Detritus	AM, OM, ON			+	

Along the horizontal gradient the availability of insects, chironomids and epiphytic algae were observed to increase toward the inshore zone while the availability of fish and gastropods decreased. The trends of the two periods only contradicted for the availability of the food items macrophytes and fish eggs, along the horizontal gradient. During period 1 the availability of these food items increased toward the inshore zone whereas during period 2 an opposite trend was observed and both items appeared to be more available in deeper water. Phytoplankton- and detritus concentrations (mg C/l) along the vertical gradient were inversely related. Compared with the surface layer, the concentrations were respectively 14% lower (t-test,  $p = 0.06$ ) and 25% higher (t-test,  $p = 0.02$ ) in the bottom layer.

The three-way MANOVA testing for species-, environmental or spatial effects on the gut contents of the entire fish assemblage, showed each of the effects and their interactions were significant ( $p < 0.01$ ). The two-way MANOVA testing the separate species for environmental or spatial effects on their diet displayed a significant

environmental effect for all species and a significant interaction for *A. melettinus*, *B. chola*, *B. dorsalis* and *H. gaimardi* but the spatial effect was only significant for *B. sarana* and *R. daniconius*. For each of the fish species the observed trends of the proportion of a food item in their gut coincided with the trends of availability except for *G. giuris* in period 1 when the proportion of fish in the gut decreased toward the inshore zone.

Table 4.11 Gut fullness per species per period along the vertical and horizontal gradient. N= Number of fish dissected, S=Surface, B=Bottom, O=Open water, I=Inshore zone. Indicated are significant ( $p<0.05$ ) environmental effects (P) and spatial effects in the vertical (V) or horizontal (H) planes as well as their interactions. For species abbreviations see table 1.2.

Horizontal (H) planes as well as their interactions. For species abbreviations see table 1.2.										
Species	N	Period 1				Period 2				Effect
		Vertical		Horizontal		Vertical		Horizontal		
		S	B	O	I	S	B	O	I	
AM	799	75	74	75	64	52	48	50	42	P,H
OM	329	77	45	64	60	60	47	49	57	P,V
ON	45	63			53	53	55	54	52	
BC	694	63	85	80	74	45	56	53	54	P,V
BD	840	63	78	75	75	63	59	60	58	P
BS	237	88	83	85	66	78	57	72	58	P,H,P*H
GG	315	25	21	22	55	46	46	46	40	V,P*V,P*H
MY	373	39	62	55	38	32	35	34	33	P
HG	289	45	46	45	30	50	94	62	60	P,V
RD	710	63	56	61	78	40	46	42	53	P,H

Fullness of the gut was considered another indicator of habitat profitability (Table 4.11). All herbivorous/ detritivorous species showed the same trends of gut fullness both in the horizontal and vertical plane: an increased fullness toward the bottom and toward the open water. The benthivorous species however differed in the trends in gut fullness in the vertical plane. The gut fullness of *B. chola* and *B. dorsalis* increased towards the bottom while that of *B. sarana* decreased. Also, *B. sarana* was the only benthivore to exhibit a significant trend of gut fullness in the horizontal plane; gut fullness increased toward the open water during period 1 and decreased during period 2. The piscivore *G. giuris* showed along both gradients a significant interaction between the environment and the gut fullness: During period 1 gut fullness decreased toward the bottom and toward the inshore zone, while during period 2 the opposite pattern was observed. In contrast, the spatial pattern of gut fullness of *Mystus spp.* did not differ between periods. The spatial differences in gut fullness of the zooplanktivorous species depended for each species on the direction of the gradient; the gut fullness of *H. gaimardi* was mainly determined by the position along the vertical gradient, increasing downwards but the gut fullness of *R. daniconius* depended on the position along the horizontal gradient, increasing shorewards.

## Discussion

### Detritivory

According to Love (1980), who summarised the data on diets of about 600 fish species, only 3% of fish are detritivorous. This low percentage might explain why, until recently, no attention was paid to the distinction between ingested detritus and digested

matter, resulting in a classification of all unrecognisable matter as being ingested detritus (Maiti & de Silva 1985, Khoo & Tay 1992) or ignoring the ingested detritus and thereby overestimating the proportion of digested matter. Distinction between detritus and digested matter in this study is based on the assumption that digestion rates between species do not differ. However, Fänge *et al.* (1979) reviewed digestion rates of fish species and found that herbivores have a higher rate of digestion, than non-herbivorous species. This implies that although the correction for digested matter is a considerable improvement, the proportion of detritus in the gut is probably still overestimated.

#### *Feeding behaviour*

The feeding behaviour of the fish species in Tissawewa reservoir is consistent with that reported in literature for other, lacustrine or riverine, waterbodies. *A. melettinus* is a filter feeder (Pethiyagoda 1991) feeding almost exclusively on phytoplankton and detritus. Also, Schiemer & Hofer (1983) report a similar diet for this species in another Sri Lankan reservoir (Parakrama Samudra). The importance of detritus as a food source for *A. melettinus* is explained by the experimental results of Bitterlich (1985) who concluded that the stomachless *A. melettinus* cannot utilise the major part of the ingested algae. The tilapias display an ontogenetic shift from feeding on zooplankton to feeding on detritus, phytoplankton and macrophytes. A similar feeding behaviour was reported by Trewavas (1983) who also discussed the opportunism in feeding of these species, illustrated by the shift between periods from detritus to macrophytes. However, probably this apparent change in consumption by the tilapias represents a change in composition of their food source, the benthic detrital aggregate (Bowen 1979, 1980, 1981, Schiemer & Duncan 1987), rather than a change in feeding behaviour of the fish (Piet *et al.* Chapter 7).

The main food items of the benthivorous barbs *B. dorsalis* and *B. chola* were zooplankton and benthic invertebrates which agrees with the characterisation as zoobenthivorous species, by Schiemer & Hofer (1983). The diet in their original riverine habitat did not differ qualitatively from the observed diet in this study. *B. dorsalis* feeds mainly on crustaceans and higher plant leaves (Schut *et al.* 1984) while the main components in the gut of *B. sarana* were molluscs, insects and plant material (Kortmulder 1987). The latter also corresponds to observations by Schiemer & Hofer (1983) on the diet of this species in Parakrama Samudra. The observed piscivory of *B. sarana* was also reported by Menon & Chacko (1958) for southern India.

Within the taxon *Mystus spp.* all specimen containing fish in their gut belonged to the species *Mystus gulio* implying that this species is a piscivore and *Mystus vittatus* is not a piscivore. The latter is confirmed by several workers who found mainly zooplankton and chironomids in the guts of *Mystus vittatus* (Bhatt 1971, Schiemer & Hofer 1983). The ontogenetic shifts from zooplankton to invertebrates to fish of increasing size, are common for piscivores from the temperate region such as the largemouth bass (Gilliam 1982). The differences in size of the prey fish between the piscivores *G. giuris* and *Mystus gulio* and for each of these species between size-classes, is probably determined by the gape width of these species: not only does *G. giuris* grow to a bigger size than *Mystus gulio* but the gape width of a fish of the same size is bigger for *G. giuris* (Piet Chapter 2).

The zooplanktivorous/ insectivorous species show a shift in diet from cladocerans and cyclopoid copepods to calanoid copepods and insects. The major food item in the diet

of *R. daniconius* changes from zooplankton during period 1 to insects during period 2. Other studies found the major part of the diet of *R. daniconius* consisted of insects (mainly from terrestrial origin) both in a river (Schut *et al.* 1984), a eutrophic pond (Kumar & John 1987) and a reservoir (Schiemer & Hofer 1983).

### *Habitat profitability*

The profitability of a food item in a certain habitat depends on the density of this food item and the foraging efficiency. Although in a particular habitat, density of most food items can be established by sampling, foraging efficiency is difficult to determine. Employing the fish therefore provides the most straightforward and reliable method to establish habitat profitability. Spatial differences in the gut contents of fish caught in different habitats are assumed to reflect the profitability of one habitat relative to the others.

All fish display similar spatial trends of the main food items in their guts. However, for each species separately, hardly any of these trends are discernible as can be expected in a relatively small waterbody where food items are homogeneously distributed because the different habitats are not far apart. In contrast, combination of the data on the spatial trends for all major consumers of a food item does reveal significant spatial differences thus indicating spatial trends in availability of this food item. The selection of only the major consumers of a food item instead of the entire fish assemblage, as done by Wallace (1981) and Winemiller (1989), has two main advantages: 1) elimination of species with a relatively low proportion of the food item, thus improving statistical resolution and 2) a decrease of the chance of bias from differences in habitat occupation between species. The latter is exemplified by comparing for detritus the contrasting trends of availability in the vertical plane based on gut contents of the main consumers and based on that of the entire assemblage, to the measured concentrations in that plane. Only the trend of availability based on gut contents of the main consumers shows a trend corresponding to the actual trend. This is because most of the assemblage consists of species that prefer the bottom layer and do not consume detritus, thereby obscuring the trend.

Other significant trends in habitat profitability involve all the major food items and in all cases correspond to what can be expected based on results of other studies, personal observations or common knowledge. The increasing availability towards the inshore zone of insects corresponds to the fact that aquatic insects are often associated with vegetation (Kalk *et al.* 1979, Dvorak & Best 1982, Rabe & Gibson 1984) and availability of insects from terrestrial origin decreases with increasing distance from the shore. Food items like ostracods which make up the major part of the microbenthos and gastropods occur exclusively on the bottom (personal observations). The higher availability to the fish assemblage of zooplankton in the pelagic zone compared with the inshore zone, confirms with findings of Werner & Hall (1988). Since zooplankton density does not change along the vertical gradient (Amarasinghe, personal communication), the decreasing availability towards the bottom might well be caused by a decreasing foraging efficiency of the fish due to a lower visibility (O'Brien 1979, Townsend & Winfield 1985). Because it is known that the species spawning in the reservoir tend to concentrate in the littoral zone during spawning (De Silva & Chandrasoma 1980, De Silva & Sirisena 1988, Pet & Piet 1993), probably fish eggs were most available in the inshore zone during period 1. The shift

during period 2 of the availability of fish eggs and macrophytes toward the open water and the apparent association of fish eggs and macrophytes along the horizontal gradient during the two periods suggests that the presence of vegetation is an important factor determining the spawning sites. The trends of habitat profitability established for the main food items of the herbivorous species (detritus, phytoplankton, macrophytes and epiphytic algae) differ considerably among periods but correspond with the measured or observed changes in availability.

#### *Predator avoidance versus foraging profitability*

The fitness of a species can be increased by maximising foraging profitability or minimising predation risk. As foraging profitability can vary between habitats so can the risk of predation, forcing each species to balance the trade-off between these strategies. Because many species are known to exhibit ontogenetic shifts in diet or habitat use which affect both foraging efficiency and predation risk (Werner & Gilliam 1984), and because the maximisation of foraging profitability is only of consequence at the time of foraging, the possibility of a trade-off will only be considered for those species or size-classes subject to predation and at the time of foraging.

Size-classes 1 and 2 are the favoured prey sizes of the piscivores while predation by *G. giuris* or *Mystus spp.* on species above size-class 4 was not observed. The main prey species are *A. melettinus*, *H. gaimardi* and *R. daniconius*. Predation can be expected to increase toward the bottom because of the distribution of the major predators *G. giuris* and *Mystus spp.* while predation risk is low in habitats where vegetation is abundant (Werner *et al.* 1983, Anderson 1984, Hershey 1985, Werner & Hall 1988). Therefore, species subject to predation will avoid the bottom layer or restrict themselves to the vegetated areas, or both. Avoidance of the bottom layer is observed for all smaller species like *A. melettinus*, *H. gaimardi* or *R. daniconius* during both periods. Also, the smallest size-classes of the fish assemblage preferred the vegetated area in period 1 when vegetation was confined to the inshore zone. Besides, distribution of the smallest size-classes changes when the distribution of vegetation in the reservoir changes after the drought. Thus, predator avoidance is a major factor influencing habitat occupation.

Optimal foraging theory predicts that during feeding, species will prefer the habitat which maximises foraging profitability. Assuming spatial differences in gut fullness and gut contents are appropriate indicators of habitat profitability, then a positive correlation between the trends of habitat profitability and distribution indicates the species can assess foraging profitability in the different habitats and adjust its distribution accordingly. The sampling strategy in which a fixed number of samples at every habitat was taken for gut content analysis ensured the indicators of habitat profitability are independent of fish distribution.

Pertaining to foraging activity the fish assemblage can be divided into two groups: the nocturnal piscivores and diurnal non-piscivores (Pet & Piet 1993, Piet *et al.* Chapter 3). At the time of feeding most species are distributed according to the trends in profitability of their main food sources: the zooplanktivores/ insectivores occupy the upper part of the water column, the herbivorous tilapias and omnivorous *B. sarana* occupy the lower part of the water column and the piscivores and typical benthivores were found close to the bottom. Only the position of *A. melettinus* in the vertical plane is

contradictory to the trend in profitability of its main food source, that of suspended detritus. When foraging is not taking place, all species, except for the piscivores were found higher up in the water column. The distribution among species varies mainly in the vertical plane but for the distribution among size-classes the horizontal plane is determinative. The preference of the juveniles for the inshore zone contradicts with the profitability in this habitat of their main food source, zooplankton.

For the Tissawewa fish assemblage, predator avoidance and habitat profitability are probably the two most important factors to explain the spatial distribution of species. Because of the size and relative homogeneity of the reservoir, differences in profitability between habitats are expected to be small. Therefore, for those species or size-classes subject to predation, predator avoidance will be the decisive factor in determining their distribution. The distribution of the remaining species/ size-classes is determined by the profitability per habitat. This, and the observation that environmental changes affect the spatial distribution patterns of the fish species, confirms that fish are capable of estimating differences in predation risk and foraging rates between habitats and adapt their distribution accordingly in order to maximise fitness. (Werner *et al.* 1983, Werner & Hall 1988).

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## CHAPTER 5

### COMPETITION AND RESOURCE PARTITIONING ALONG THREE NICHE DIMENSIONS IN A SIZE-STRUCTURED TROPICAL FISH ASSEMBLAGE

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#### Abstract

In Tissawewa, a tropical reservoir, the size-specific resource use of the ten most important fish species was determined along three dimensions: the trophic-, spatial- and temporal dimension. During this study a drought occurred distinguishing periods before and after the drought which differed markedly in availability of resources and fish density. In this study size-specific differences in resource use are incorporated in the calculated niche breadth and niche overlap resulting in systematically lower measures of niche breadth, and niche overlap. Contrary to conventional methods of calculating niche breadth, the size-specific niche breadth of a species is not dependent on ontogenetic changes in resource use, thereby improving the potential to distinguish between specialists and generalists. It is shown that species avoid sharing resources with a specialist. Niche overlaps between size-classes showed the juvenile competitive bottleneck can restrain the development of species in this assemblage. Condition and abundance were used as indicators of a species fitness and it is shown that fitness of most species is governed by the availability of resources. When resources are scarce, partitioning of these resources is an important mechanism for potential competitors to coexist. Resource partitioning along the trophic dimension is most important. When fish density is relatively low and resources are not limiting, abundance of a species depends on its potential for niche expansion. Species with large ontogenetic changes appear to have a higher potential for niche expansion, thereby releasing themselves partially from intraspecific competition and allowing a stronger increase in fitness.

## Introduction

Competition is a major factor determining the coexistence and abundance of species, which in turn determine community structure. Resource partitioning describes the limits that interspecific competition imposes on the number of species that may stably coexist (MacArthur 1965, Schoener 1974, Roughgarden 1976, Roughgarden 1983). Ross (1986), who reviewed the work on resource partitioning in fish communities, distinguished three resource dimensions along which segregation was observed: a trophic, spatial and temporal. Because the ability to exploit resources varies with body size, extensive ontogenetic shifts in resource use have been reported along several dimensions (Werner & Gilliam 1984, Werner 1986). As resource partitioning is a mechanism to avoid interspecific competition (Schoener 1974), ontogenetic niche shifts reduce intraspecific competition (Tonn *et al.* 1986). Because of these ontogenetic niche shifts, interactions in size-structured populations are difficult to quantify (Mittelbach 1981).

Niche breadth of a population is the length of that part of the niche axis that includes all the points defining viable values of the variable that was measured along the axis (Hutchinson 1978), and is considered an indicator of that populations potential to avoid inter- or intraspecific competition. For a population having different phenotypes, Roughgarden (1972) distinguished two components in niche breadth: the within-phenotype component, which is due to the variety of resources used by each phenotype, and the between-phenotype component, which is due to the population having a variety of phenotypes. Because for fish the body weights of conspecific individuals commonly span up to four orders of magnitude, ontogenetic stages make up most of the phenotypic variation (Werner 1986). Substituting phenotypes for ontogenetic stages it follows that because in general the number of ontogenetic stages per species is restricted, a species' flexibility in resource use will depend almost entirely on the within-ontogenetic stage component. Nevertheless, niche breadth was calculated thus far from a sampling dependent subset of the population thereby introducing an unknown between-ontogenetic stage component to the calculated niche breadth.

Niche overlap is the joint use of a resource or resources by two or more species (Colwell & Futuyma 1971), and is used as a measure of interspecific competition thereby ignoring the fact that intraspecific competition exists and can be calculated in the same manner from interactions between ontogenetic stages. Determining resource use based on ontogenetic stages instead of species not only affects intraspecific interactions but can affect interspecific interactions as well. For example, the juvenile stages of a species with a large adult size might compete for resources with a species which, based on the calculated overall niche overlap, would not be considered a competitor. Consequently, interspecific competition on the juvenile stages of the species with the large adult size may reduce recruitment to adult stages, thus affecting the whole population of this species although overall overlap in resource use is low. This was previously observed for young-of-the-year perch and is referred to as a juvenile competitive bottleneck (Persson 1986, Persson & Greenberg 1990).

Thus far the measures of competition along a certain dimension and the species' potential to avoid it, respectively niche overlap and niche breadth, were based on overall resource use of the species, determined without considering possible ontogenetic



differences in resource use and the abundance of these ontogenetic stages in the sample or the population. Therefore a considerable improvement in quantifying these measures can be obtained by determining resource use along the entire size range of a species and incorporating this into size-structure-dependent measures by weighting the measures per size-class with the abundance of that size-class.

In the same manner ontogenetic shifts in resource use can bias the calculated niche overlap and niche breadth along each dimension, so can niche overlap and niche breadth along one dimension depend on interactions with the other dimensions. Interrelation between two dimensions is a common phenomenon when determining resource use but has never been taken into account when calculating the indicators of resource use in a community. Interrelation between the trophic- and spatial dimension is described by optimal foraging theory (MacArthur & Pianka 1966, Townsend & Winfield 1985) while interrelation between the temporal dimension and the trophic or spatial dimension was observed in studies of diel changes in respectively feeding behaviour and vertical distribution (e.g. Rudstam & Magnuson 1985, Wurtsbaugh & Li 1985, Clark & Levy 1988, Levy 1990, Dervo *et al.* 1991, Piet *et al.* Chapter 3). When studying the importance of these interactions the following arguments should be considered. Along the trophic dimension species respond to the level of resource depletion (exploitative competition: Schoener 1983) and although differences in resource depletion between habitats can be important, the time of day resources are depleted will not make any difference. Contrary to the trophic dimension, interaction between the spatial and temporal dimension can be of relevance because here species interact directly along the spatial dimension by capturing space (interference competition: Park 1962). Thus, niche occupation studies of a species along one dimension, ignoring niche shifts along any other dimension (including ontogenetic shifts) will be biased.

Interspecific competition is observed in field experiments involving species in freshwater, marine and terrestrial systems (Schoener 1983, Connell 1983). Even though most of these studies were done in temperate regions, they present an overview of the importance of this phenomenon in explaining resource use and abundance of species in various natural communities. In most of these field experiments, the degree of resource competition is experimentally manipulated by changing the population densities of one possible competitor after which the response of one or more other possible competitors is measured in order to detect competition. Responses usually measured are: 1) a change in density; 2) a change in some rate that could affect density e.g., growth, condition, mortality, fecundity; and 3) a niche shift, e.g. a change in type of resource used or micro habitat occupied (Connell 1983). In fish ecology, condition is believed to be a good indicator of the general "well-being" or "fitness" of the population under consideration (Adams & Mclean 1985, Booth & Keast 1986, Bolger & Connolly 1989). When studying coexistence of competing species, it is not sufficient to measure only interspecific competition. Often intraspecific competition can be the major factor in realising coexistence of possible competitors by keeping the stronger competitor below the density necessary to eliminate the weaker competitor. For each species the relative roles of intraspecific and interspecific competition in determining the density of this species, should be studied. This is also important when studying resource partitioning because the two types of competition act in opposing directions. In theory, increasing intraspecific

competition should expand a species' niche whereas increased interspecific competition should reduce it (Connell 1983). Expansion or reduction of a species niche can be realised, among others, by respectively increasing or decreasing differences in resource use between ontogenetic stages.

Sri Lanka has a large number of artificial reservoirs and no natural lakes as is true for many other areas in SE Asia. In most of the tropical reservoirs in SE Asia fish yield is lower than would be expected on the basis of the high primary production (Henderson 1979, FAO 1972), probably because most indigenous fishes are riverine, which may not be optimally adapted to the lacustrine conditions and are unable to utilise every niche of the lacustrine habitat (Fernando & Holcik 1982). It is hypothesised that the success of the introduced exotic tilapia in increasing fish yields in the South East Asian tropical lakes and reservoirs may be because these fish are much better adapted to the lacustrine environment and are capable of utilising previously unfilled niches.

Resource partitioning studies serve an important practical need in providing information on habitat requirements of fishes. Therefore studies dealing with problems of sampling bias, temporal and spatial variability or a more complete representation of life history stages are considered important (Ross 1986). In this study three resource dimensions are distinguished: a trophic, spatial and temporal dimension. A drought, markedly decreasing fish density, provided the opportunity to study the occurrence of niche shifts when competition for resources was less severe. For each species the size-specific resource use along each of the dimensions was determined before and after the drought, taking the effect of possible interrelation with the other two dimensions into account. We addressed the following questions. 1) Are the measures of niche overlap and niche breadth along one dimension influenced by ontogenetic shifts or shifts along other dimensions; 2) Does resource partitioning occur and if so, what is the relative importance of the different dimensions in segregating species?

## Material and methods

Tissawewa is a shallow (mean depth = 1.2 m, average maximum depth = 2.6 m), lowland reservoir of ca. 200 ha in Sri Lanka. The most abundant fish species were: the cyprinids *Amblypharyngodon melettinus* (Valenciennes), *Barbus chola* (Hamilton), *Barbus dorsalis* (Jerdon), *Barbus sarana* (Hamilton) and *Rasbora daniconius* (Hamilton), one goby *Glossogobius giuris* (Hamilton), one halfbeak *Hyporhamphus gaimardi* (Valenciennes), two catfishes *Mystus gulio* (Hamilton) and *Mystus vittatus* (Bloch), which for practical reason were treated as *Mystus spp.* and two introduced exotic tilapias *Oreochromis mossambicus* (Peters) and *Oreochromis niloticus* (Linnaeus). These species together made up more than 98% of the biomass as determined from experimental gillnet catches and bottom trawl surveys.

The sampling programme started in September 1991 and continued until January 1994. During this sampling program the reservoir dried up for two months (September/October 1992) due to a long spell of extreme drought. On filling up again a different ecosystem evolved: before the drought (Period 1) vegetation only occurred in the inshore zone and turbidity was high (mean Secchi-depth transparency  $\pm 95\%$  c.l. =  $30 \pm 2$  cm) due

to resuspension of a thick layer of detritus on the bottom. After the drought (Period 2) vegetation was found all over the reservoir covering the entire watercolumn and there was relatively clear water (mean Secchi-depth transparency  $\pm$  95% c.l.=  $127 \pm 18$  cm) because the detritus had vanished.

Table 5.1 Total length ranges of each size-class and the size distribution of the ten most common species, with their abbreviations.

Size-class		1	2	3	4	5	6
Total length (cm)		3.0 - 4.4	4.5 - 6.9	7.0 - 9.9	10.0 - 13.9	14.0 - 18.9	$\geq 19.0$
Species		Relative abundance size-class (%)					
<i>A. meletinus</i>	AM	0.6	72.4	27.0	0.0	0.0	0.0
<i>B. chola</i>	BC	0.2	10.8	58.7	30.2	0.2	0.0
<i>B. dorsalis</i>	BD	0.1	0.9	10.8	51.1	37.0	0.2
<i>B. sarana</i>	BS	0.0	2.5	8.4	27.3	47.7	14.0
<i>G. giuris</i>	GG	0.0	1.3	4.3	27.4	26.2	40.8
<i>H. gaimardi</i>	HG	0.0	0.0	14.4	52.8	32.5	0.3
<i>Mystus spp.</i>	MY	0.0	0.4	12.6	64.7	20.8	1.5
<i>O. mossambicus</i>	OM	0.2	8.7	18.1	44.7	26.3	2.0
<i>O. niloticus</i>	ON	0.0	1.9	5.3	19.5	25.7	47.6
<i>R. daniconius</i>	RD	0.0	25.7	72.6	1.7	0.0	0.0

A stratified sampling program was designed to determine the size-specific niche occupation per species along the three major resource dimensions: the trophic, spatial and temporal dimension. Four different types of habitat were available in the reservoir, and one sampling station was chosen within each of these four habitats (Fig. 4.2). Station A represents the surface layer of the offshore zone, station B the bottom layer of the offshore zone, station C the intermediate zone and station D the inshore zone. Each month the four habitats were sampled simultaneously with monofilament multi-mesh gillnets on four occasions; twice during day-time and twice during the night. Because the relative positions of the stations were water level dependent and resolution of the gradients increased with increasing water level, only data of sampling occasions when the water level was above 2.5 m maximum depth were used when determining the habitat occupation. Additional to the gillnets, use of two active gears, bottom trawl and cast net, ensured that the entire size range (above 3 cm total length) of the available species was sampled. The entire size range was divided into six size-classes to study size-specific differences (Table 5.1). On each sampling occasion the size-specific diet and gut fullness of the different species were determined from pooled samples of a maximum of 10 specimens per species, size-class, gear type, station and time of day. Of each specimen the fullness of the stomach or anterior one-third part of the gut was estimated according to five gut fullness categories (Table 5.2). The contents of the stomach or anterior 1/3 part of the gut were analysed for each pooled sample. The relative biovolumes of food items in gut/ stomach were estimated according to the points method (Hynes, 1950) using a microscope. The following categories of contents were distinguished: fish, insects (both aquatic and terrestrial but not benthic), microcrustacean zooplankton (cladocerans, cyclopoid and calanoid copepods), gastropods, shrimps, fish eggs, chironomid larvae, microbenthos (mainly ostracods and some benthic cladocerans), porifera, macrophytes, epiphytic filamentous algae,

phytoplankton and unrecognisable matter (digested matter and detritus). To distinguish between ingested detritus and digested matter the proportion of digested matter per size-class was determined per period according to Piet *et al.* (Chapter 4). The proportion of detritus was calculated by subtracting the determined proportion of digested matter from the observed proportion of unrecognisable matter.

Table 5.2 Gut fullness categories and estimated percentage of fullness (slightly modified according to Haram & Jones 1971)

Gut fullness category	Fullness (%)
Completely filled and swollen	90-100
Just filled over full length, not swollen	70-89
Contents divided in different patches	30-69
Very few food particles	10-29
Completely empty	0-9

From the relative biovolumes of the different categories of contents, the niche occupation along the trophic dimension was established. Niche occupation along the spatial dimension was determined from the relative biomass distribution among the four habitats during day-time and night-time separately. The relative Catch per Unit of Effort (CpUE) and gut fullness per time of day were chosen as indicators of the diel patterns along the temporal dimension. The relative CpUE is the ratio between the CpUE at one time of the day and the summated CpUE over both times of the day. If possible, resource use along each of the dimensions was determined for all size-classes of the main species.

Niche breadth per size-class  $B$  was calculated using the formula of Levins (1968):

$$B = -\sum_j P_j * \log P_j$$

where  $P_j$  is the proportion associated with resource state  $j$ . To take into account possible size-specific differences in resource use, the niche breadth of a species  $B_s$  was calculated from the niche breadth of different size-classes  $B_c$  according to the following formula:

$$B_s = \frac{\sum_{c=1}^{c=6} (B_c * W_c)}{\sum_{c=1}^{c=6} W_c}$$

where  $W_c$  is a weighting factor depending on the relative abundance of the  $c^{\text{th}}$  size-class. For classifying a species as a specialist or generalist, based on the measurement of niche breadth, the problem of the definition of categories was recognised by Ricklefs (1966), Cody (1968) and Maguire (1967). They all classified a species based on its niche breadth relative to a scale constructed by using as upper and lower bounds the extreme values found for all species combined (Colwell & Futuyma 1971). In this study categorisation of

species and correlations between niche breadth and other variables are based on a niche breadth relative to a scale between extreme values of all species combined.

Niche overlap among members of the size-structured assemblage were calculated using Schoener's (1970) formula:

$$S = 1 - 0.5 * D$$

where  $S$  is an index of similarity ranging from 0 to 1 and  $D$  is a measure of distance in multi-dimensional space between the proportions  $P$  of the resource state  $j$  along one resource dimension for assemblage members  $x$  and  $y$ .

$$D = \sum_{i=1}^a |P_{x_i} - P_{y_i}|$$

For ease of representation the similarities were presented as dendrograms grouping members of the assemblage together in clusters of decreasing similarity. To reduce the number of members represented, while at the same time maintaining information on the size-specific niche overlap between species, the size-classes of which the intraspecific distances were smaller than the interspecific distances, were combined into classes covering a larger size range. The distance shown is between the most distant members of each cluster. As niche breadth of a species was calculated from the niche breadths of its different size-classes, niche overlap  $S_s$  of a species  $x$  with species  $y$  was calculated from the niche overlaps between the different size-classes  $S_{cx,cy}$  using the following formula:

$$S_{s_{x,y}} = \frac{\sum_{cy=1}^{cy=6} \sum_{cx=1}^{cx=6} S_{cx,cy} * W_{cx} * W_{cy}}{(\sum_{cx=1}^{cx=6} W_{cx} + \sum_{cy=1}^{cy=6} W_{cy})}$$

where  $W_{cx}$  and  $W_{cy}$  are the weighting factors depending on the relative abundances of size-classes  $cx$  and  $cy$  of species  $x$  and  $y$ , respectively.

The calculated overlap values appeared to depend on the number of resource categories selected; Lowering the number of food categories from the original thirteen to eight and subsequently to four by combining similar food categories resulted in an increased average overlap for the species matrix. To determine potential competitors, Moyle & Senanayake (1984) introduced a subjective measure dividing overlap values in three categories: "high" ( $>0.67$ ), "intermediate" ( $\leq 0.67$  and  $\geq 0.33$ ) and "low" ( $<0.33$ ) overlap. However, since calculated overlap values were dependent on the resource dimension, resource use along different dimensions cannot be studied using fixed values to distinguish these overlap categories. Therefore, categorisation of species as potential competitors, based on their overlap values, was done similar to the categorisation of species as specialists or generalist based on their niche breadth. The overlap categories were defined relative to the extreme overlap values of the total assemblage instead of the theoretical extreme overlap values (0 and 100) used by Moyle & Senanayake (1984). Two

threshold values were calculated dividing the range of overlap values in three equal parts. Distance measures below the lowest threshold value indicated "high" overlap, distance measures above the highest threshold value indicated "low" overlap. The opposite applies for similarity values. Members of a cluster with distances below, or similarities above the "high" overlap were considered potential competitors.

## Results

### *Fish density and condition*

Between periods before and after the drought, both fish density and condition differed markedly (Table 5.3): absolute density before the drought (Period 1) was more than twice that after the drought (Period 2). The species mainly affected by the changes was *A. melettinus* of which both density and condition were significantly lower during period 2. Most species (*B. dorsalis*, *B. sarana*, *O. mossambicus* and *R. daniconius*) showed a moderate decrease in density and an, often significant, increase in condition while for *O. niloticus* both density and condition increased. Notable were the strong increases in density of the piscivores *G. giuris* and *Mystus spp.*. The changes between periods in density and condition appeared to be related, but because of the extreme increase in condition of *B. sarana* this was not significant ( $p=0.09$ ). Without *B. sarana*, changes in density and condition were significantly correlated ( $p<0.01$ ). The changes in density, together with food availability and water transparency markedly affected the feeding behaviour, spatial distribution and diel activity patterns.

Table 5.3 Biomass, expressed as Catch per Unit of Effort (CpUE) and the calculated average weight per individual based on length weight measurements and population size structure as presented in table 5.1. The average values of these variable are presented for the time before the drought (Period 1) and after the drought (Period 2). The calculated change per variable is relative to the average value of the two periods. For species abbreviations see table 5.1.

Species	CpUE (g.m <sup>-2</sup> .hr <sup>-1</sup> )			Weight per individual (g)		
	Average per period		Change (%)	Average per period		Change (%)
	1	2		1	2	
AM	36.3	2.4	-174.7	3.1	2.9	-7.1
BC	8.7	2.6	-108.7	13.6	13.6	-0.5
BD	10.9	6.9	-44.5	34.4	35.6	3.5
BS	2.8	2.3	-19.8	49.2	60.3	20.2
GG	1.5	3.7	84.7			
HG	2.2	3.1	35.7			
MY	2.8	5.4	65.1			
OM	6.0	3.0	-66.1	40.6	41.6	2.5
ON	1.1	1.7	37.0	105.9	112.6	6.1
RD	7.9	5.3	-39.8	4.9	5.0	1.9

### *Trophic dimension*

For period 1 the threshold distance between "medium" and "high" overlap of 79 distinguished seven clusters of which the members were considered potential competitors along the trophic dimension (Fig. 5.1a and Table 5.4a). The cluster most dissimilar of the

other clusters was that of the herbivorous species *O. mossambicus*, *O. niloticus* and *A. melettinus*. Within the remaining non-herbivorous species, the two clusters least similar to the other clusters were one that contained the adults of *G. giuris* and *Mystus spp.* which fed predominantly on fish and another consisting of only *B. sarana*, which had gastropods as main food item. The juveniles of *O. mossambicus* and *B. chola* that fed mainly on zooplankton and detritus formed one cluster with feeding behaviour slightly similar to the cluster consisting of *R. daniconius*, *H. gaimardi* and the smallest size-classes of *Mystus spp.* which fed mainly on zooplankton and insects. The other two clusters with some similarity consisted of the smallest size-classes of *G. giuris* and *B. dorsalis*, feeding predominantly on chironomids and zooplankton, and the cluster formed by the larger size-classes of *B. chola* and *B. dorsalis* having chironomids and microbenthos as their main food. The threshold distance for period 2 was slightly higher than for period 1. Based on this threshold distance the assemblage can be divided into eleven clusters with "high" overlap (Fig. 5.2b and Table 5.4b) markedly different from the clusters of period 1. One species' feeding behaviour is separated from that of all other species; *A. melettinus* for which detritus and phytoplankton were the main food sources. This leaves two distinct groups of five clusters each. One group consists of two clusters consisting of respectively the tilapias and size-class 3 of *H. gaimardi* feeding mainly on macrophytes, two single-species clusters, namely *B. sarana* feeding mainly on gastropods and the largest size-classes of *G. giuris* feeding predominantly on fish and the fifth cluster was formed by the largest size-classes of *R. daniconius*, *H. gaimardi* and *B. sarana* for which the main food items were insects and macrophytes. The second group involved five clusters. Firstly, a cluster consisting of the largest size-classes of *Mystus spp.* and the smallest size-class of *G. giuris* feeding on chironomids and insects; secondly, a cluster formed by the smallest size-classes of *Mystus spp.* and *B. dorsalis* feeding mainly on chironomids; thirdly, *B. chola* and all except for the smallest size-class of *B. dorsalis*, feeding on chironomids and microbenthos and finally clusters four and five formed by only the smallest size-class of *R. daniconius* and *A. melettinus* feeding mainly on zooplankton, respectively zooplankton and detritus.

Considerable diet shifts occurred between the two periods. In period 2, the smallest size-class of *A. melettinus* shifted from detritus to zooplankton as its main food. In contrast, the smallest size-classes of *B. chola*, *B. dorsalis* and *Mystus spp.* shifted from zooplankton to chironomids, and the smallest size-class of *G. giuris* from zooplankton to insects. For the larger size-classes of *B. dorsalis* and *B. sarana*, gastropods were partially replaced by insects and for the latter, also by chironomids. The larger size-classes of *G. giuris* and *Mystus spp.* partially replaced their main prey, fish, with insects and chironomids, respectively. The tilapias shifted from detritus to macrophytes and *H. gaimardi* shifted from zooplankton to insects and macrophytes. Lastly, for the larger size-classes of *R. daniconius*, zooplankton was replaced by insects, as their main food item.

The threshold similarity values did not differ much but the overlap values in period 1 were lower than in period 2 indicating a higher degree of resource partitioning in period 1. This was confirmed by the markedly higher percentage of species pairs with "low" overlap during period 1 (Table 5.8). Going from period 1 to period 2, niche breadths of species increased resulting in a higher average interspecific niche overlap but lower average intraspecific niche overlap. Species with larger ontogenetic changes (*G. giuris*, *B.*

Fig. 5.2 Dendrograms showing clusters with increasing similarity from top to bottom, for all the size-specific interactions along the spatial dimension during respectively period 1 (top) and 2 (bottom). The calculated threshold distances are displayed near the right y-axis. For explanation size-classes and species abbreviations, see table 5.1.

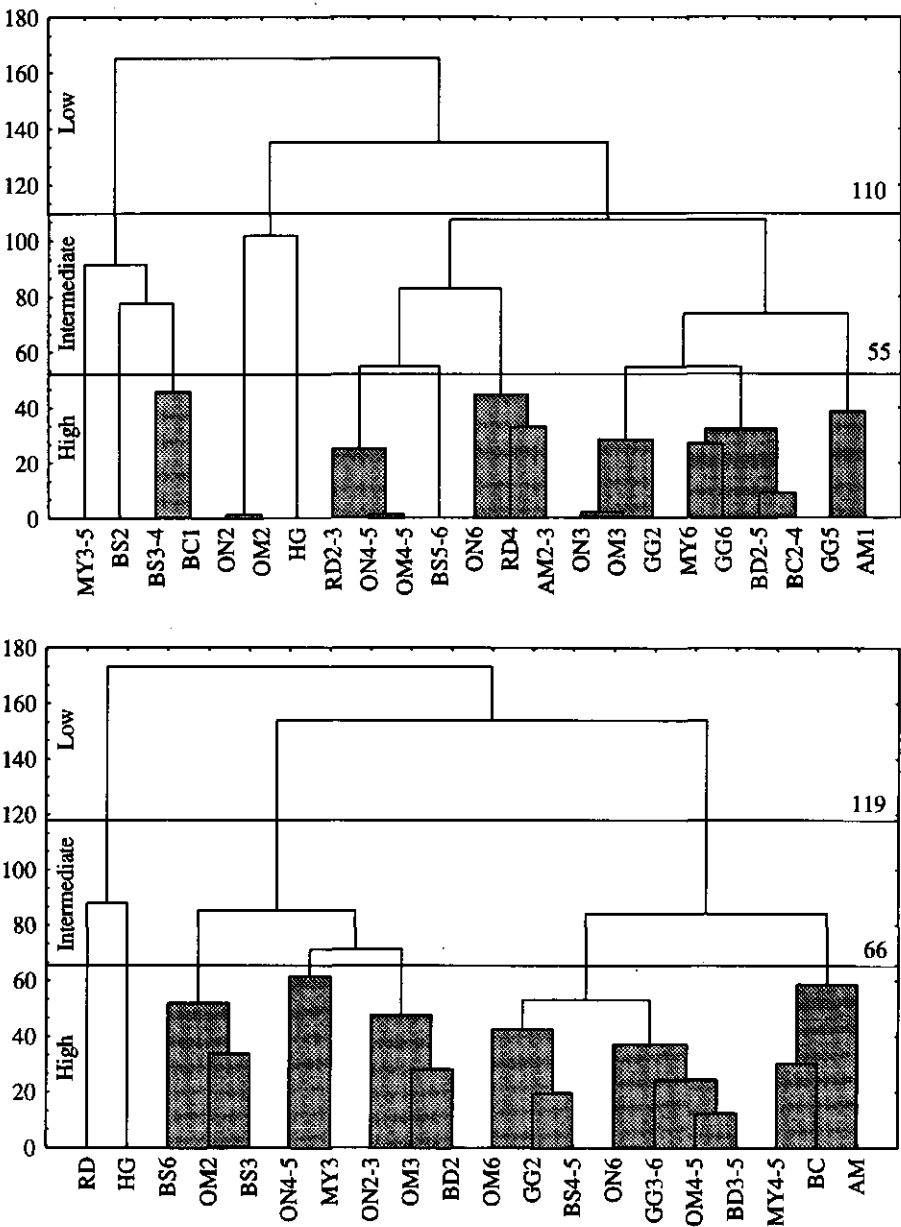




Table 5.5 a,b The proportions of the members of a size-structured assemblage occupying the different stations (A,B,C,D) during day- (D) and nighttime (N) during respectively period 1 and 2. Each combination of station and time of day is considered a resource state along the spatial dimension and was used to calculate the similarities presented in Figures 2 a and b. For explanation size classes or species abbreviations see table 5.1.

	MY	BS	BS	BC	ON	OM	HG	RD	ON	OM	BS	ON	RD	AM	ON	OM	GG	MY	GG	BD	BC	GG	AM
	3-5	2	3-4	1	2	2		2-3	4-5	4-5	5-6	6	4	2-3	3	3	2	6	6	2-5	2-4	5	1
AD	39	7	9	13	0	0	0	10	13	13	15	3	3	7	1	1	0	13	9	8	6	0	3
BD	0	0	1	0	1	1	36	12	9	10	7	0	10	10	0	0	0	0	0	0	0	0	2
CD	8	4	21	20	7	7	2	16	12	11	16	26	24	17	21	20	22	22	16	26	26	32	31
DD	3	39	19	17	42	42	11	12	16	16	11	22	13	16	28	28	28	16	25	16	18	18	14
AN	5	4	7	21	0	0	2	4	4	4	16	0	0	0	2	2	0	14	10	6	6	13	0
BN	1	0	12	0	8	8	20	32	27	28	15	19	11	12	4	4	0	0	0	2	2	10	14
CN	31	41	26	29	2	2	2	4	6	6	16	8	4	12	14	14	27	17	20	24	22	22	20
DN	14	5	5	0	39	39	26	10	13	12	3	23	35	25	30	30	23	19	20	19	20	5	15

	RD	HG	BS	OM	BS	ON	MY	ON	OM	BD	OM	GG	BS	ON	GG	OM	BD	MY	BC	AM
	6	2	3	4-5	3	2-3	3	2-3	3	2	6	2	4-5	6	3-6	4-5	3-5	4-5		
AD	9	1	32	41	36	29	50	45	32	41	15	11	12	8	15	21	16	0	5	17
BD	8	33	0	0	2	0	0	0	1	0	0	0	0	2	0	0	1	0	0	2
CD	26	1	5	3	4	16	0	1	7	3	13	17	16	23	23	20	22	37	31	24
DD	6	15	13	6	8	5	0	4	10	6	22	22	22	17	12	9	12	13	14	7
AN	12	3	12	17	5	24	14	38	29	29	24	14	6	16	16	12	13	10	8	1
BN	32	41	12	21	27	1	1	4	5	5	0	0	5	0	4	2	2	1	1	11
CN	3	6	3	3	8	16	17	3	8	3	9	16	16	17	16	22	19	19	22	20
DN	3	1	23	8	9	10	17	5	8	12	18	20	23	16	14	14	16	20	18	18

Fig. 5.3 Dendrograms showing clusters with increasing similarity from top to bottom, for all the size-specific interactions along the temporal dimension during respectively period 1 (top) and 2 (bottom). The calculated threshold distances are displayed near the right y-axis. For explanation size-classes and species abbreviations, see Table 5.1.

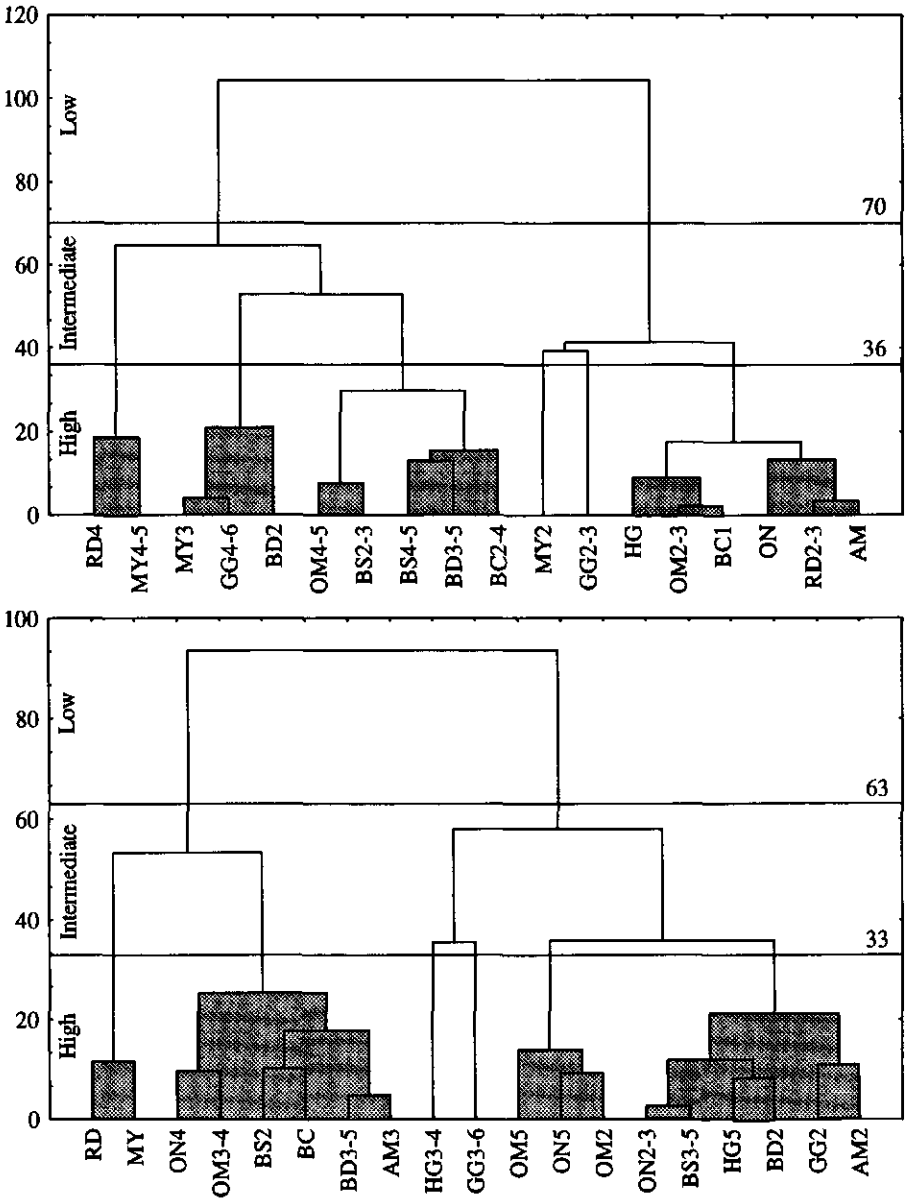


Table 5.6 a,b Day- and nighttime proportions of the activity and gut fullness for the members of a size-structured assemblage during respectively period 1 and 2. These proportions per variable represent resource states along the temporal dimension and were used to calculate the similarities presented in Figures 2 a and b. For explanation size classes or species abbreviations see table 5.1.

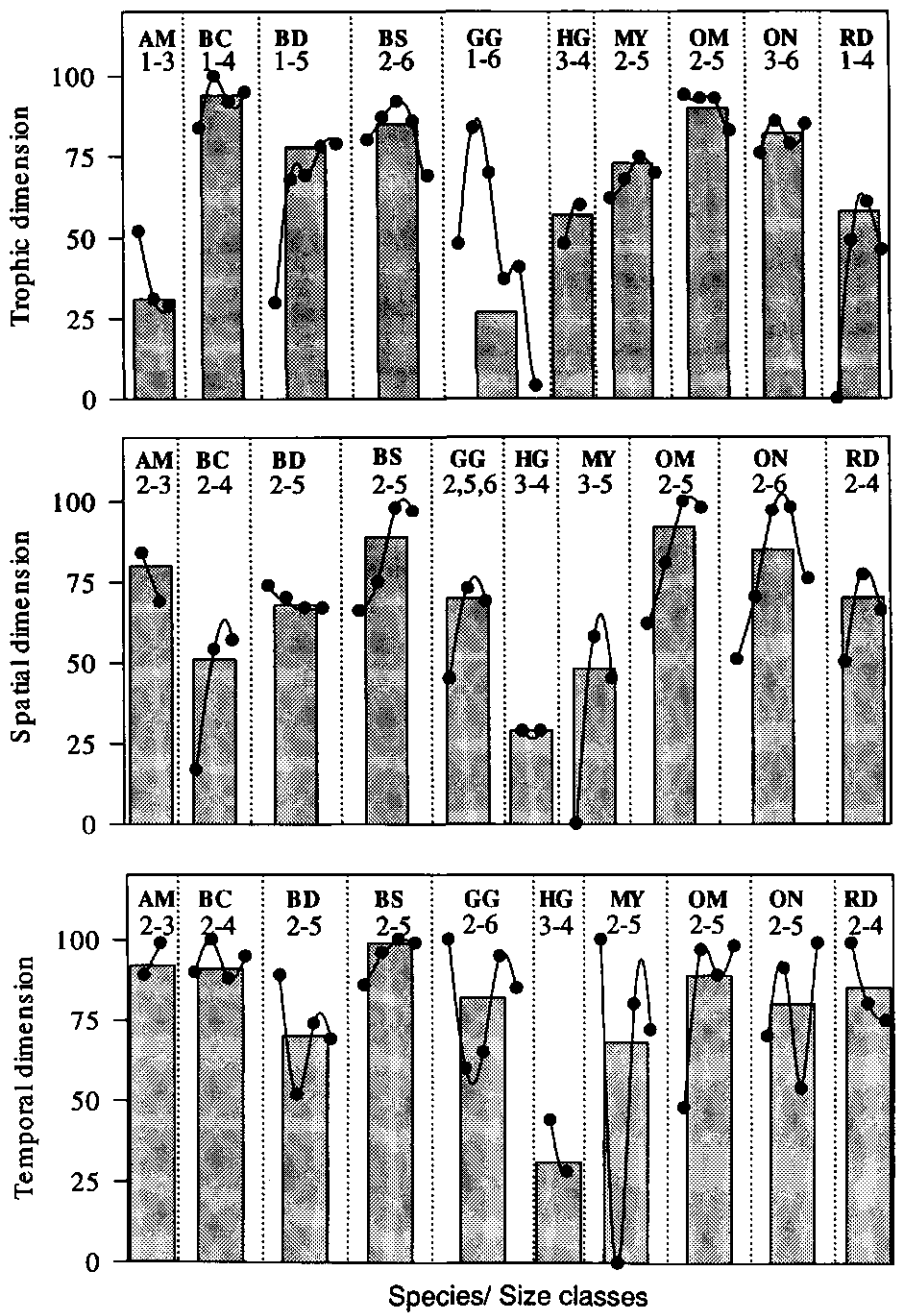
	RD	MY	MY	GG	BD	OM	BS	BS	BS	BD	BC	MY	GG	HG	OM	BC	ON	RD	AM
	4	4-5	3	4-6	2	4-5	2-3	4-5	3-5	2-4	2	2-3	2-3	1	2-3	1	2-3	2-3	
Activity day	31	33	14	14	10	22	27	20	19	24	50	43	42	41	42	39	34	37	
Activity night	19	17	36	36	40	28	23	30	31	26	0	7	8	9	8	11	16	13	
Gut fullness day	29	36	33	29	26	18	18	21	26	24	17	15	25	21	22	19	23	22	
Gut fullness night	21	14	17	21	24	32	32	29	24	26	33	35	25	29	28	31	27	28	

	RD	MY	ON	OM	BS	BC	BD	AM	HG	GG	OM	ON	OM	ON	BS	HG	BD	GG	AM
	4	4	12	16	15	16	11	12	39	3-4	3-6	5	5	2	2-3	3-5	5	2	2
Activity day	2	0	12	16	15	16	11	12	39	22	23	27	29	26	30	30	27	30	25
Activity night	48	50	38	34	35	34	39	38	11	28	27	23	21	24	20	20	23	20	25
Gut fullness day	26	32	18	19	26	25	24	23	25	30	13	14	12	20	21	24	25	18	18
Gut fullness night	24	18	32	31	24	25	26	27	25	20	37	36	38	30	29	26	25	32	32

Fig. 5.4

Niche breadth per species and per size-class along three dimensions. Niche breadth is calculated based on the resource use averaged between periods 1 and 2. For each species the indicated size-classes increase from left to right. For explanation size-classes and species abbreviations, see table 5.1.



herbivorous diet. In contrast, the smallest size-classes of the carnivorous species were more specialised than the larger size-classes because the food items consumed early in their development remain part of the diet during the further course of their development even though the range of food items consumed was expanded. The most specialised species along the trophic axis were the piscivore *G. giuris* and the detritivorous/herbivorous *A. melettinus* while the benthivorous cyprinid *B. chola* and the tilapia *O. mossambicus* can be considered as generalists. For each species the average interspecific niche overlap along the trophic dimension increased with increasing niche breadth. Apparently, species avoid sharing resources with a specialist.

### *Spatial dimension*

The threshold distance for period 1 distinguished eleven clusters with a "high" overlap. Spatial segregation between clusters was considerable and depended often on the time of the day. *H. gaimardi* was segregated from all other species because it occupied the pelagic zone during day-time. Other clusters had an equal distribution among the different habitats during day-time in common but differed in their preference during night-time: some occupied the pelagic zone (e.g. size-classes 2 and 3 of *R. daniconius*, 4 and 5 of the tilapias and 5 and 6 of *B. sarana*) others the intermediate zone (e.g. size-classes 3 to 5 of *Mystus spp.*, size-classes 2 to 4 of *B. sarana* and the smallest size-class of *B. chola*). Other distribution patterns involved fish occupying the bottom layer of the inshore zone, independent of the time of day (e.g. the largest size-classes of *Mystus spp.*, *G. giuris*, *B. dorsalis* and *B. chola*).

As for the trophic dimension, resource use along the spatial dimension differed considerably between the periods. From the calculated threshold distance seven spatially segregated clusters could be distinguished (Fig. 5.3b and Table 5.5b). Two single-species clusters (*H. gaimardi* and *R. daniconius*) were maximally segregated from all other clusters. These species occupied the pelagic zone at night but in the day-time they either remained in the pelagic zone (*H. gaimardi*) or moved to the intermediate zone (*R. daniconius*). Other specific distribution patterns involved fish occupying the bottom layer during day-time and shifting to a more or lesser degree towards the surface at night (e.g. clusters consisting of size-classes 6 and 3 of *B. sarana*, size-classes 2 and 3 of *O. mossambicus*, 2 to 5 of *O. niloticus*, size-class 3 of *Mystus spp.* and size-class 2 of *B. dorsalis*) or fish displaying varying degrees of preference for the inshore zone (e.g. clusters consisting of the remaining species/ size-classes).

A common change between periods, in the distribution of several species/ size-classes (e.g. *A. melettinus* and *B. sarana* as well as the smallest size-classes of *O. mossambicus*, *O. niloticus* and *B. dorsalis*), was a shift from the shallow part of the reservoir in period 1 to the bottom layer of the deepest part of the reservoir during period 2. Common diel shifts observed along the spatial axis were from: 1) the inshore zone toward the pelagic zone exhibited by size-classes 3 and 4 of *B. sarana* and size-classes 2 and 4 of respectively *O. mossambicus* and *R. daniconius*; 2) the inshore zone towards the bottom layer of the deep water, displayed by size-class 3 of *O. mossambicus*; 3) the pelagic zone toward the bottom layer of the open water, exhibited by the largest size-classes of the tilapias; and 4) the pelagic zone toward the inshore zone by the largest size-classes of *B. sarana*.

Table 5.7 abc:

Niche overlap values for species interactions during periods 1 (lower left) and 2 (upper right) along respectively the trophic- (a), spatial- (b) and temporal (c) dimension. Indicated are the calculated interspecific niche overlap per species pair as well as, between brackets, for each species pair the minimum and maximum niche overlaps of all size class interactions. Across each table (upper left to lower right), intraspecific niche overlap per species and (between brackets) the minimum overlap between size classes for period 1 (left) and period 2 (right). For species abbreviations see table 5.1.

AM	BC	BD	BS	GG	HG	MY	OM	ON	RD
AM 99(88)\99(48)	15(7-27)	6(4-14)	7(0-15)	3(1-11)	11(2-22)	12(7-32)	40(32-46)	22(16-47)	12(5-51)
BC 24(20-38)	95(55)\95(81)	74(43-84)	35(9-69)	15(2-46)	25(9-34)	52(41-63)	29(17-42)	19(9-31)	26(13-34)
BD 2(2-7)	63(21-76)	94(55)\93(53)	41(4-78)	19(1-45)	27(7-35)	58(39-82)	23(8-30)	23(4-28)	28(10-30)
BS 2(1-7)	20(9-39)	41(4-52)	86(60)\81(27)	24(8-61)	46(16-56)	42(12-78)	42(16-53)	35(13-44)	48(9-57)
GG 2(1-7)	7(2-51)	7(2-74)	10(2-39)	93(9)\82(37)	22(7-57)	33(8-76)	12(6-26)	15(6-23)	24(6-53)
HG 2(2-7)	19(16-42)	17(12-48)	15(6-32)	6(2-44)	99(97)\89(46)	47(13-59)	42(30-54)	57(40-68)	64(6-77)
MY 2(2-7)	21(7-43)	20(2-56)	20(8-35)	56(8-88)	42(10-84)	89(14)\93(66)	26(14-38)	23(10-27)	58(19-64)
OM 80(57-88)	32(19-67)	7(1-32)	15(1-32)	4(1-39)	8(1-39)	7(1-39)	90(42)\88(67)	53(44-74)	37(9-51)
ON 69(62-75)	28(23-49)	2(0-13)	18(6-31)	8(0-17)	4(2-14)	9(0-23)	77(49-90)	92(71)\94(67)	31(7-40)
RD 2(2-7)	22(13-44)	19(6-50)	19(5-40)	7(2-49)	84(49-94)	47(5-91)	8(1-40)	3(1-16)	97(39)\95(10)

AM	BC	BD	BS	GG	HG	MY	OM	ON	RD
AM 99(88)\99(48)	15(7-27)	6(4-14)	7(0-15)	3(1-11)	11(2-22)	12(7-32)	40(32-46)	22(16-47)	12(5-51)
BC 24(20-38)	95(55)\95(81)	74(43-84)	35(9-69)	15(2-46)	25(9-34)	52(41-63)	29(17-42)	19(9-31)	26(13-34)
BD 2(2-7)	63(21-76)	94(55)\93(53)	41(4-78)	19(1-45)	27(7-35)	58(39-82)	23(8-30)	23(4-28)	28(10-30)
BS 2(1-7)	20(9-39)	41(4-52)	86(60)\81(27)	24(8-61)	46(16-56)	42(12-78)	42(16-53)	35(13-44)	48(9-57)
GG 2(1-7)	7(2-51)	7(2-74)	10(2-39)	93(9)\82(37)	22(7-57)	33(8-76)	12(6-26)	15(6-23)	24(6-53)
HG 2(2-7)	19(16-42)	17(12-48)	15(6-32)	6(2-44)	99(97)\89(46)	47(13-59)	42(30-54)	57(40-68)	64(6-77)
MY 2(2-7)	21(7-43)	20(2-56)	20(8-35)	56(8-88)	42(10-84)	89(14)\93(66)	26(14-38)	23(10-27)	58(19-64)
OM 80(57-88)	32(19-67)	7(1-32)	15(1-32)	4(1-39)	8(1-39)	7(1-39)	90(42)\88(67)	53(44-74)	37(9-51)
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RD 2(2-7)	22(13-44)	19(6-50)	19(5-40)	7(2-49)	84(49-94)	47(5-91)	8(1-40)	3(1-16)	97(39)\95(10)

AM	BC	BD	BS	GG	HG	MY	OM	ON	RD
AM 99(88)\99(48)	15(7-27)	6(4-14)	7(0-15)	3(1-11)	11(2-22)	12(7-32)	40(32-46)	22(16-47)	12(5-51)
BC 24(20-38)	95(55)\95(81)	74(43-84)	35(9-69)	15(2-46)	25(9-34)	52(41-63)	29(17-42)	19(9-31)	26(13-34)
BD 2(2-7)	63(21-76)	94(55)\93(53)	41(4-78)	19(1-45)	27(7-35)	58(39-82)	23(8-30)	23(4-28)	28(10-30)
BS 2(1-7)	20(9-39)	41(4-52)	86(60)\81(27)	24(8-61)	46(16-56)	42(12-78)	42(16-53)	35(13-44)	48(9-57)
GG 2(1-7)	7(2-51)	7(2-74)	10(2-39)	93(9)\82(37)	22(7-57)	33(8-76)	12(6-26)	15(6-23)	24(6-53)
HG 2(2-7)	19(16-42)	17(12-48)	15(6-32)	6(2-44)	99(97)\89(46)	47(13-59)	42(30-54)	57(40-68)	64(6-77)
MY 2(2-7)	21(7-43)	20(2-56)	20(8-35)	56(8-88)	42(10-84)	89(14)\93(66)	26(14-38)	23(10-27)	58(19-64)
OM 80(57-88)	32(19-67)	7(1-32)	15(1-32)	4(1-39)	8(1-39)	7(1-39)	90(42)\88(67)	53(44-74)	37(9-51)
ON 69(62-75)	28(23-49)	2(0-13)	18(6-31)	8(0-17)	4(2-14)	9(0-23)	77(49-90)	92(71)\94(67)	31(7-40)
RD 2(2-7)	22(13-44)	19(6-50)	19(5-40)	7(2-49)	84(49-94)	47(5-91)	8(1-40)	3(1-16)	97(39)\95(10)

From the species-pairs distribution over the three overlap categories for both periods overlap was found to be higher during period 2 (Table 5.8). According to the calculated niche breadths, *H. gaimardi* and *Mystus spp.* were considered specialists along the spatial dimension and *O. mossambicus* and *O. niloticus* were characterised as generalists (Fig. 5.4). As for the trophic dimension, average interspecific niche overlap increased with increasing niche breadth.

#### Temporal dimension

Resource use along the temporal axis was determined from two variables, gut fullness and relative CpUE, both at day-time and at night. During both periods six clusters with "high" overlap were distinguished (Fig. 5.3 and Table 5.6a). The clusters differed in that: 1) gut fullness was distinctly higher during either day-time (e.g. the cluster consisting of the largest size-classes of *R. daniconius* and *Mystus spp.* during period 1 and during period 2, all size-classes of the same species) or during night-time (e.g. the cluster consisting of size-classes 4 and 5 respectively 2 and 3 of *O. mossambicus* and *B. sarana* during period 1 and during period 2, size-classes 2 and 5 of *O. mossambicus* and size-class 5 of *O. niloticus*); 2) relative CpUE was distinctly higher during day-time (the cluster of *H. gaimardi*, size-classes 2 and 3 of *O. mossambicus* and the smallest size-class of *B. chola* during period 1 and during period 2 size-class 5 of *H. gaimardi* and size-class 2 of *B. dorsalis*) or night-time (e.g. the cluster consisting of size-class 3 of *Mystus spp.* and size-classes 4 to 6 of *G. giuris* during period 1 and during period 2 the cluster consisting of *R. daniconius* and *Mystus spp.*).

As for both the trophic and spatial dimension, the average niche overlap along the temporal dimension was higher during period 2 (Table 5.8). During period 2 twenty-six species-pairs had a "high" overlap while during period 1 this was only fourteen. Niche breadth along the temporal dimension was calculated for the relative CpUE only. According to their relative activity *H. gaimardi*, *Mystus spp.* and *B. dorsalis* were considered specialists, while *B. sarana*, *B. chola* and *A. melettinus* were classified as generalists. The average overlap values of the specialists *H. gaimardi* (51.0) and *Mystus spp.* (37.4) with the other species of the assemblage, were lower than those of the generalists *B. sarana* (63.3), *B. chola* (70.2) and *A. melettinus* (67.9).

Table 5.8 Threshold similarity values and relative occurrence of high, medium or low overlap along three dimensions and during two periods. These values correspond to the species interactions in Tables 5.7abc

Niche dimension Period	Trophic		Spatial		Temporal	
	1	2	1	2	1	2
Threshold value						
Low/ Medium	29	26	47	43	76	69
Medium/ High	57	50	69	66	85	81
Occurrence (%)						
Low overlap	78	49	20	18	24	13
Medium overlap	11	36	56	27	44	36
High overlap	11	16	24	56	31	51



## Discussion

### *Measurement of niche breadth and niche overlap*

Measures of niche overlap or niche breadth should be independent of the number of resource states considered and availability as well as the degree of distinctness of the resource states from the organisms viewpoint should be taken into account (Colwell & Futuyma 1971, Petraitis 1979). For determining niche occupation along three dimensions it is almost impossible to control the number of resource states but the way sampling was conducted ensured that resource states along the spatial and temporal dimension were equally available. Only availability of resource states along the trophic dimension could not be controlled and because none of the known niche overlap indices (Colwell & Futuyma 1971, Petraitis 1979, Smith & Zaret 1981) could prevent bias arising from the number, availability and degree of distinctness of resource states (Loreau 1990), the most straightforward measures of niche overlap (Schoener 1970) and niche breadth (Levins 1968) were chosen which at least have the advantage of compatibility with other published works. The increase of niche overlap with decreasing number of resource states shown for the trophic dimension indicates that niche overlap in field studies generally depends on the number of resource states that can be distinguished along a specific dimension. Thus, unless along each resource dimension the same number of meaningful resource states are distinguished, studies of the importance of different dimensions in segregating competing species will always be biased and will underestimate the importance of the dimension with least resource states.

Resource use along one dimension, expressed by niche breadth and niche overlap, can only be compared for populations within one ecosystem, when sampling bias, which occurs if the size-structure of the population(s) involved differ from that in the sample, is eliminated and if ontogenetic shifts are taken into account. This can be realised by calculating the niche breadth and niche overlap according to the method introduced in this study: size-specific resource use per species is determined for a number of size-classes per species after which standardised measures of niche overlap and niche breadth for a population can be calculated from respectively the weighted niche overlaps and niche breadths of the size-classes. Weighting per size-class is according to their relative abundance. Theoretically the accuracy will improve with increasing number of classes. Comparison of the values of the size-specific niche breadth and niche overlap with those derived by the conventional methods illustrates the improvement achieved using the size-specific measures. Compared with the size-specific niche breadth and niche overlap, the conventional measures are higher along each dimension (Tables 5.9 and 5.10). Thus, ignoring the ontogenetic changes in resource use will bias niche breadth and consequently the distinction between generalists and specialists and will overestimate potential competition. The observed differences between the two methods depend on the magnitude of the ontogenetic changes. For *G. giuris*, the species which exhibited the largest ontogenetic changes along the trophic dimension, the conventional methods overestimated niche breadth with 72% during period 1 and niche overlap was almost three times higher than with the size-specific methods.

Table 5.9 Average niche breadth of the entire assemblage according to the methods used in this study (Current) compared to the conventional method for calculating niche breadth. The indicated change is relative to the current value. The current value is according to the methods used in this study in which size dependent resource use and size structure are incorporated for three dimensions as well as diel changes in resource use along the spatial dimension.

Dimension	Current	Conventional	(%)
Size-specific			
Trophic	62	67	7
Spatial	79	85	7
Temporal	27	28	3
Spatial-temporal interaction			
Spatial	75	79	5

#### Interaction between resource dimensions

In determining niche breadth and niche overlap along a particular dimension, the interaction between the trophic and spatial resource dimensions and between the spatial and temporal resource dimensions can bias results. Because spatial differences in feeding behaviour were relatively small for the Tissawewa fish assemblage (Piet *et al.* Chapter 4), the former interaction was not considered for calculating these measures along the trophic dimension. The latter interaction, however, was incorporated by calculating these measures from the spatial distributions of species during day- and night-time. Failing to do this, causes niche breadth to be overestimated (Table 5.9), the ranked order of species based on their niche breadth to change (Spearman  $R$ ,  $p=0.80$ ) and the average overlap of the entire assemblage to be overestimated (Table 5.10). Despite the small bias for the entire assemblage, for species that exhibit an inverse diel spatial pattern, e.g. *B. sarana* and *Mystus spp.* during period 1, ignoring the interaction with the temporal dimension overestimated niche overlap along the spatial dimension, with 31%. In contrast, for species which exhibited a similar diel spatial pattern, such as *A. melettinus* and *O. mossambicus*, this would cause niche overlap to be underestimated with 15%.

For the species of the Tissawewa assemblage, size-specific differences in resource use were observed along each resource dimension. The impact these ontogenetic shifts can have on competition between species, follows from the observation that for a particular ontogenetic stage often interspecific competition (with ontogenetic stages of other species) was larger than intraspecific competition (with other ontogenetic stages of the same species). Juvenile stages which exhibit a feeding behaviour different from the adult stages, often take up only a minor part of the biomass of a fish population and therefore have a relatively small impact on the calculated niche overlap between species. However, interspecific competition during the juvenile stage of a larger species may reduce recruitment to larger size-classes although resources for these larger size-classes may not be limited, resulting in the so called juvenile competitive bottleneck (Persson 1986, Werner 1986, Persson & Greenberg 1990). Several species-pairs which had only a minor overall overlap, exhibited markedly higher overlaps between the juvenile stages of both species (e.g. *B. dorsalis* and *G. giuris* during both periods) or between the juvenile stage of one species and the entire size-range of an other species (e.g. the juvenile stages of *B. chola*, *O. mossambicus* and *Mystus spp.* with *H. gaimardi* or *R. daniconius*, during period

Table 5.10 Average niche overlap of the entire assemblage per period according to the methods used in this study (Current) compared to the conventional method for calculating niche breadth. For further explanation see table 5.8.

Dimension	Period	Current	Conventional	(%)
Size-specific				
Trophic	1	22	27	25
	2	31	35	13
Spatial	1	60	70	16
	2	61	70	15
Temporal	1	82	89	8
	2	79	87	9
Spatial-temporal interaction				
Spatial	1	58	60	-3
	2	56	61	-7

1). Besides these striking examples, almost all species display at a certain stage a higher overlap with other species, or ontogenetic stages of other species, than follows from the calculated overall niche overlap between species. Therefore, the impact other species might have on the development of a certain species is often underestimated.

#### *Importance resource dimensions*

Determination of the importance of different resource dimensions in segregating potential competitors is difficult because 1) the number of resource states varies between dimensions and 2) subdivision of resources into different categories is subjective and differs between dimensions. This can be partially overcome by introducing a measure of overlap between two species relative to the entire assemblage (Colwell & Futuyma 1971). Instead of an overlap value between the theoretical extremes of the overlap range (0-100), the overlap value is adjusted relative to the minimum and maximum overlap value of all species pairs of the entire assemblage per dimension and per period. Comparison of niche overlaps along three dimensions of one species pair during one period displays the main dimension along which this species pair is segregated. During period 1, 80% of the species pairs was segregated along the trophic dimension, 9% along the spatial dimension and 11% along the temporal dimension. During period 2 this was 62%, 20% and 18%, respectively. These findings correspond to Ross (1986), who reviewed resource partitioning, in that the trophic dimension is the most important dimension for segregating species, but contradict in the relative importance of the three dimensions. Ross (1986) found the trophic dimension to be slightly more important than the spatial dimension while these two dimensions were considerably more important than the diel temporal dimension. In this study, the spatial and diel temporal dimensions are equally important but markedly less important than the trophic dimension. The relatively higher importance during period 2 of the spatial and temporal dimensions in segregating species is caused solely by the fact that resource partitioning along the, most important, trophic dimension was lower during this period.

## Competition

The general consensus that emerges from most recent studies is that the best approach to understanding resource partitioning and the way competition shapes community structure lies in manipulative field experiments (Schoener 1983, Connell 1983, Ross 1986). This study of the Tissawewa fish community can be considered a manipulative field experiment where, although unintentionally, not only resource availability but also the density of the fish species was markedly influenced by the changes induced by the drought. Comparison of resource use between periods showed several species exhibiting shifts in resource use resulting in different overlap values along several dimensions, both between species-pairs and for the entire assemblage. The major shifts, where one food item was almost entirely replaced by another, were observed for all consumers of this food item suggesting that these shifts were caused by a change in availability of this food item rather than a change in food preference. However, during period 1, when fish density was higher, average niche overlap along the trophic dimension was lower, and along all three dimensions a lower proportion of "high" overlap values was observed indicating minor shifts toward utilisation of food items for which competition is less severe. Increased partitioning of resources when these are presumed limiting was also observed in other studies (Zaret & Rand 1971, Gascon & Legget 1977, Ross 1977, Werner & Hall 1977, Thorman 1982, Greenfield *et al.* 1983) and is strong circumstantial evidence for the importance of exploitative competition.

The importance of exploitative competition in structuring the Tissawewa fish community is based on: 1) the condition of most fish species which was highest during period 2 when fish density was lowest and 2) the correlation between changes in condition and changes in abundance. The only species with a significantly lower condition during period 2 was the detritivorous specialist *A. melettinus*. This is because during these periods not only fish density changed but food availability as well. In fact the main food source of *A. melettinus*, suspended detritus (Bitterlich 1985, Pethiyagoda 1991), decreased from  $7 \text{ mgC.l}^{-1}$  to  $2 \text{ mgC.l}^{-1}$  (Piet Chapter 6), a relatively larger decrease than that of the total fish density. Furthermore, changes in density of other species will hardly affect *A. melettinus*; because of its specialistic resource use combined with high density during period 1, its density is expected to be mainly regulated through intraspecific competition. This is confirmed by the expansion of its niche, as indicated by a decrease in minimum overlap between size-classes from period 1 to period 2, when its main resource became scarce. The other species of which condition was not higher during period 2, was the benthivorous generalist *B. chola* feeding mainly on detritus and chironomids. Benthic detritus was almost negligible after the drought (Pers. observations) and competition for chironomids had increased considerably since more species were utilising this food source. The importance of increased interspecific competition on this generalist during period 2, is demonstrated by the reduction of its niche. All species of which interspecific competition decreased while food availability remained constant showed an increase in condition and abundance was relatively high. In contrast, species for which intra- or interspecific competition increased, displayed a decrease in condition and abundance.

The inverse correlation between the average intraspecific niche overlap of a species and the change in condition between periods, indicates that species which are more capable of reducing intraspecific competition through niche expansion have an advantage

in a situation with little interspecific competition such as in period 2. The importance of a high potential for niche expansion is emphasised by the relatively high increases in abundance of species having large ontogenetic shifts such as the piscivores *G. giuris* and *Mystus spp.* even though availability of their preferred food source, fish, is lower. The relatively high fitness during period 2 of species with large ontogenetic changes and, therefore, a large between-ontogenetic stage component of niche breadth confirms the claim of Roughgarden (1972) that species with a greater potency for ecological release in the between-ontogenetic stage component of niche breadth, have a higher colonising ability.

#### *Generalists versus specialists*

The observation of Colwell & Fuentes (1975), that if interference competition occurred between a generalist and a specialist, it was the specialist that successfully interfered with the generalist, is confirmed by several studies (Hixon 1980, Larson 1980, Baltz *et al.* 1982). This probably explains the observation that species seem to avoid sharing resources with a specialist along the spatial or temporal dimension. However, the fact that this was also observed along the trophic dimension strongly suggests that this principle not only applies to interference competition but also to exploitative competition.

#### *Exotics versus indigenous species*

The theory that the apparent success of the introduction of the exotic tilapias, *Oreochromis mossambicus* and *Oreochromis niloticus*, is because these species are, contrary to indigenous riverine species, better adapted to the lacustrine conditions and therefore able to occupy previously unfilled niches (Fernando & Holcik 1982, Fernando 1984, Fernando & Holcik 1991), seems to be contradicted by findings in this study. Tissawewa can be considered representative of a typical lowland reservoir during period 1, and in these conditions the exotic tilapias display "high" overlaps with at least one indigenous species, *A. melettinus*, along the trophic and spatial dimension, and judging from its abundance, *A. melettinus* is even better adapted to the conditions in the reservoir than the tilapias are. However, *A. melettinus* is a filter feeder, feeding on phytoplankton and suspended detritus in the watercolumn (Bitterlich 1985, Pethiyagoda 1991) whereas the tilapias prefer grazing the bottom deposits (Bowen 1979, Schierner & Duncan 1987, Dempster *et al.* 1993). Thus, although these species utilise the same resources they are not true competitors and in effect *A. melettinus* might even benefit from the tilapias breaking down the flocculant material from the bottom into smaller, better suspendable, particles. The difference in feeding behaviour between the indigenous *A. melettinus* and the exotic tilapias implies that the exotic tilapia does occupy an unfilled niche in correspondence with the theory (Fernando & Holcik 1982, Fernando 1984, Fernando & Holcik 1991). A similar study in a deeper waterbody would confirm this finding since there the concentration of suspended detritus would never be high enough to sustain a species like *A. melettinus* and consequently the detritus resource would be even less exploited.

The preference of the tilapias seems to shift from fine particulate detritus during period 1 to macrophytes during period 2 but this apparent change probably represents a change in composition of their food source rather than a change in feeding behaviour of the fish. Before the drought phytoplankton was the main primary producer whereas after

the drought a considerable part of the primary production was realised by macrophytes (Chapter 7) and therefore it is probable that a considerable part of the detritus formed during period 2 comes from macrophyte origin. The reason the other detritivore *A. melettinus* does not show a similar shift is because this species feeds in the watercolumn and the particles from macrophyte origin are too large to be easily suspendable.

### Conclusion

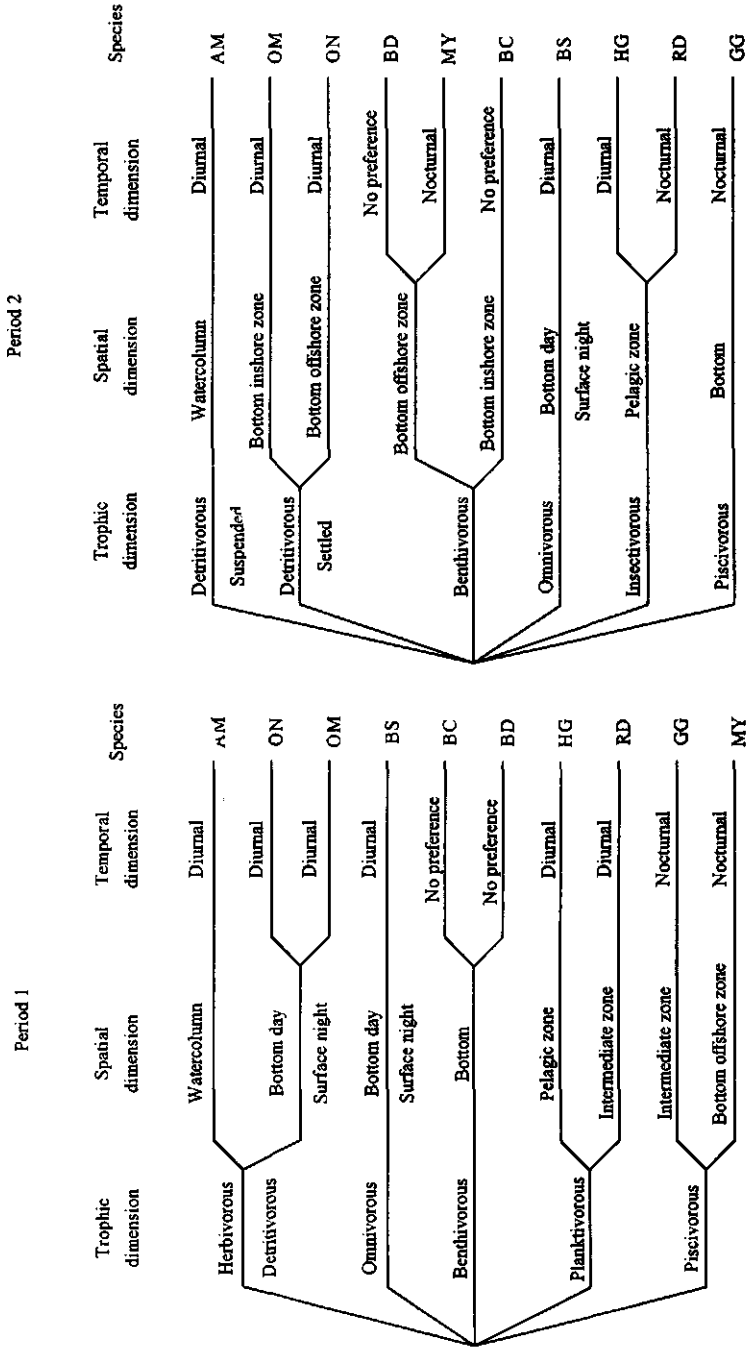
Based on the data on resource use along the trophic, spatial and temporal dimensions an ecological "key" to the Tissawewa fish species is developed (Fig. 5.5a and b). This key shows how the available resources are subdivided between species along three dimensions and how this can be influenced by environmental changes. For the temporal dimension gut fullness is assumed to be the best indicator of resource use for all species except for *H. gaimardi* and *Mystus spp.* (Chapter 3). A species is only characterised as either diurnal or nocturnal in case a distinct difference between day-time or night-time was observed for the best indicator or in case a less distinct difference was corroborated by a distinct difference for the other variable. Because most sampling was conducted at the onset of day-time and night-time period it is assumed a high gut fullness at night-time indicates diurnal activity and a high gut fullness during day-time nocturnal activity. During both periods, *B. sarana* is characterised as omnivorous despite the fact that niche breadth is slightly lower than species such as *B. chola* and *O. mossambicus*, which are not considered omnivorous. The rationale behind this is that while *B. chola* and *O. mossambicus* consume mainly various benthic and plant items, respectively, *B. sarana* feeds on different benthic-, plant- and invertebrate items as well as fish.

Ontogenetic niche shifts can have a considerable impact on intra- and interspecific competition and therefore should be considered when calculating niche overlap or niche breadth. Although the calculated values remain dependent on the number of resource states or their availability, it will at least remove or decrease sampling bias and provide insight into the actual potential of a species to adjust to perturbations or avoid competition. For the fish assemblage in Tissawewa, ontogenetic niche shifts are common phenomena and juvenile bottlenecks can occur because juveniles of several larger species share zooplankton as an important resource with each other as well as two adult zooplanktivores. However, spatial segregation can play an important role because the juveniles occupy the inshore zone while the zooplanktivores are mainly found in the pelagic or intermediate zone (Pet & Piet 1993).

The used indicators of a species' fitness, condition and abundance, together with their correlation with changes in resource use along the trophic dimension, showed that the well-being of the species comprising the Tissawewa fish assemblage was mainly governed by exploitative competition. With increasing niche breadth, interspecific competition becomes more important whereas the importance of intraspecific competition decreases. If such an assemblage is introduced into an environment where interspecific competition is relatively low, those species which are most capable of expanding their niche, thereby reducing intraspecific competition, will have an advantage, which will be expressed in a higher increase in abundance than other species. As the total fish density increases, interspecific competition will increase and niches will be reduced thereby

Fig. 5.5

Ecological “key” to the Tissawewa fish assemblage indicating how species are segregated along the different dimensions during periods 1 (left) and 2 (right). For each species habitat occupation is determined at the time the species is mainly active. For species abbreviations see table 5.1.



increasing intraspecific competition until a steady state is reached where abundance of each species depends on a balanced outcome of intra- and interspecific competition.

Under the conditions prevailing before the drought Tissawewa can be considered a typical shallow lowland reservoir. The change in fish density after the drought and subsequent niche shifts and changes in fitness of most fish species showed that in these shallow lowland reservoirs, resources are limiting and resource partitioning is an important mechanism for potential competitors to coexist. Resource partitioning will occur mainly along the trophic dimension in order to avoid exploitative competition.

### **Acknowledgements**

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## Chapter 6

### THE IMPACT OF ENVIRONMENTAL PERTURBATION ON A TROPICAL FISH COMMUNITY

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#### Abstract

Tissawewa is a tropical reservoir in which water level fluctuations are the main source of environmental variation. From September 1991 to January 1994 the fish assemblage, consisting of 10 species that make up more than 98% of the fish biomass in the reservoir, was monitored. Feeding behaviour inferred from gut content analysis, condition and relative abundance per species were estimated on a monthly basis. During this sampling period different types of disturbances were observed: a disturbance caused by a progressively decreasing water level which occurs every year and a disturbance caused by a drought which rarely occurs. After the drought, a different ecosystem evolved: Before the drought Tissawewa was dominated by detritus and phytoplankton, whereas following the refilling of the reservoir it was dominated by macrophytes. The effects of these disturbances differed at different levels of organisation: the organism, the population and the community. At the level of the organism an instantaneous response to a relatively small disturbance was observed, whereas higher levels only responded to bigger disturbances. The community was at equilibrium at the beginning of the sampling period but extreme low water levels disturbed this equilibrium. After the drought a new equilibrium different from the former equilibrium was established. The structures of the equilibria before and after drought reflected the respective environmental conditions. Based on the disturbances, caused by water level fluctuations, acting on the community and community characteristics such as resistance and resilience, the community is considered to be deterministically regulated.

## Introduction

The impact of environmental perturbations on community structure is of major relevance to our understanding of the influence that resource availability has on biotic interactions such as competition or resource partitioning. Studying the effect of an environmental perturbation at different levels of organisation can show how the reaction of the community depends on the response at lower levels (organism, population) to these factors. The ratio of a variable before and after the change is regarded as a measure of the resistance at that level (Pimm 1991). When discussing the effect of environmental perturbations on community structure, it is important to distinguish between two categories of disturbance. Transient disturbances are repeated variations occurring against a background of a continuing "normal" environment whereas persistent disturbances involve the occurrence of a "new" environment (Begon *et al.* 1987). Depending on the magnitude of the transient disturbance and the resistance of the community, the community structure can change or remain at an equilibrium fitting the "normal" environment. In case of change, the structure of the community depends on the frequency of the disturbance and can vary between a "transient" steady state and a "normal" steady state or seem at equilibrium in the "transient" steady state. A persistent disturbance will force the community structure to adjust to the "new" environment, eventually reaching equilibrium. The rate at which this process takes place is defined as the resilience of the community (Harrison 1979, Pimm 1991).

Most of the ecological research on environmental perturbation in an aquatic environment considers the effects at the level of the community (Kushlan 1976, Osman 1978, Grossman *et al.* 1982, Sale & Douglas 1984, Ross *et al.* 1985, Capone & Kushlan 1991). In spite of the fact that changes at lower levels are more direct indicators of a possible effect of environmental disturbances on the community, little attention is paid to effects at the level of the organism or population. Response variables at the level of the organism, reflecting the status of the environment, are those dealing with the availability of resources such as food and space, both in terms of quality as well as quantity. As resource availability decreases competition is expected to increase (Schoener 1971, Charnov *et al.* 1976, Pianka 1976). Any environmental change altering resource availability will initiate changes at the level of the organism, which in turn can affect higher levels. Two indicators of the health or well-being of a population are the condition of its organisms (Cone 1989) and the abundance of that population, the latter directly influencing community structure.

Grossman *et al.* (1982) and Wiens (1977) developed a theoretical framework for characterising different mechanisms regulating community structure. This framework introduces a continuum with the stochastic and deterministic mechanisms occupying opposite endpoints and the competitive crunch mechanism resting somewhere in between. A deterministically regulated community is generally at an equilibrium, with population levels at carrying capacity determined by resource limitations and coexisting species avoiding competitive exclusion through biotic interactions such as resource partitioning (Schoener 1974). In contrast, a community is stochastically regulated when the environment is not stable enough to allow an equilibrium to persist. The relative abundances of species in a community are determined largely through differential responses to unpredictable environmental changes, rather than through biotic interactions.

A community in equilibrium can be distinguished from a non-equilibrium community by examining the persistence of the community structure. Since the structure of a community in equilibrium should display persistence, the relative abundances of species from different consecutive collections during equilibrium should display a high degree of similarity whereas a non-equilibrium community should display a low degree of similarity (Grossman *et al.* 1982). Transition states where the community is shifting toward or away from equilibrium will display a gradually increasing or decreasing similarity between consecutive collections. Ascertaining the mechanism regulating community structure on this deterministic-stochastic continuum depends on the type of disturbance and community characteristics such as resistance or resilience. The characterisation of the mechanism regulating community structure, depends on the number and types of taxa included as part of the community (Rahel *et al.* 1984).

In contrast to the temperate zone, where water bodies are mainly affected by a warm and a cold season, most tropical water bodies are affected by a wet and a dry season. In most tropical water bodies these seasons are the main cause of environmental variation having a direct impact on the water level, which in turn affects availability of resources such as food, space and spawning area (Kalk *et al.* 1979). In order to study the effect of water level fluctuations on a fish community at different levels of organisation (*viz.* organism, population and community), I investigated a reservoir in which the changing water level affects resource availability, thus causing a transient disturbance. In the reservoir this disturbance recurs yearly and its magnitude increases with decreasing water level. During this study the reservoir dried up completely and filled up again a few months later, after which a different environment had developed. This presented a rare chance to study the effect of a persistent environmental disturbance on a community and its organisms. Environmental conditions over the periods before and after drought demonstrate two extremes experienced by the ecosystem and make it possible to put the smaller seasonal fluctuations and recurrent minor perturbations into perspective. The following questions are addressed: 1) is the fish community affected by a transient disturbance in the form of a changing water level; 2) is the response of the fish community affected by the magnitude of this transient disturbance; 3) is the fish community affected by a persistent disturbance in the form of a drought and subsequent environmental change; 4) what mechanism is regulating community structure; and 5) what factors determine this characterisation?

## Material and methods

### *Study area*

As in many other areas in SE Asia, Sri Lanka has no natural lakes but many artificial reservoirs, covering a total area of around 100,000 ha. The main function of these reservoirs is irrigation of paddyfields. Fisheries are a second function and water management of the reservoir is dictated by the demands of the paddy farmers. Tissawewa is a typical shallow lowland reservoir (mean depth = 1.2 m, average maximum depth = 2.6 m) in the dry SE corner of Sri Lanka. This reservoir is part of the Kirindi Oya Irrigation Scheme with the main river Kirindi Oya feeding the major reservoir Lunugamwehera

(3000 ha) from which five smaller downstream reservoirs, including Tissawewa, are fed. The water level is high after the rains in November and December, slowly decreasing to a minimum around August and September, and rapidly increasing with the onset of the NE monsoon in October. The SW monsoon during May and June has only little influence on the decreasing water level. Data on daily water levels and rainfall were obtained from the Sri Lankan Irrigation Department. These data have been recorded since January 1987. The surface area and volume of the reservoir at any water level were calculated using a model described by Pet *et al.* (1995c).

### *Sampling strategy*

To study disturbances caused by a changing water level on the fish community at different levels of organisation, the fish community in the reservoir was sampled between September 1991 and January 1994 on a monthly basis, unless circumstances (extreme low water level or drought) prevented this. To detect the effect of the magnitude of the transient disturbance three water level ranges were distinguished: high (more than 2.5 m. at deepest point), intermediate (between 1.5 and 2.5 m) and low (less than 1.5 m). The littoral zone with its macrophytes and associated invertebrates (Kalk *et al.* 1979, Dvorak & Best 1982, Rabe & Gibson 1984) is only available at high water level (Fig. 6.1). The effect of a persistent disturbance on the fish community was studied by distinguishing two periods: Period 1 (September 1991 - September 1992) consisting of 13 sampling occasions before the drought and period 2 (December 1992 - January 1994) consisting of 12 sampling occasions after the drought.

Environmental changes caused by water level changes were monitored by measuring the following physico-chemical parameters at three depths, covering the entire water column, on a monthly basis: temperature, pH, turbidity using a Secchi disk, suspended inorganic matter (Strickland *et al.* 1968), suspended particulate organic matter or seston (Golterman *et al.* 1978), chlorophyll-a (Moed & Hallegraeff 1978) and dissolved oxygen using the Winkler method (Mackereth *et al.* 1978). The concentration of detritus was calculated by subtracting the phytoplankton concentration from the seston concentration.

In the sampling program three types of fishing gear were employed at different habitats and different times of day in order to catch the entire size range (> 3 cm) of all fish species present in the reservoir. Not all gears could be applied every month at each habitat or every time of day because physical properties of the environment sometimes prevented employing every fishing gear. Only gillnets were employed every sampling month. The gillnets used were multi-mesh monofilament nets consisting of seven panels of different lengths with randomly distributed mesh sizes ranging from 12.5 up to 50 mm stretched mesh. Because ontogenetic stages often are differently affected by environmental factors all species were divided into six size-classes (Table 6.1). For gut content and gut fullness analysis each sampling month a maximum of ten specimens per species, size-class, gear type, habitat and time of day were pooled. For determination of length-weight relationships, a maximum of six specimens per species, per 0.5 cm-class, per habitat and per time of day were measured, thus assuring the length-weight relationship to be derived from the broadest possible size-range of each species.

Table 6.1 Total length ranges of each size-class

Size-class	1	2	3	4	5	6
Total length (cm)	3.0-4.4	4.5-6.9	7.0-9.9	10.0-13.9	14.0-18.9	≥ 19.0

The most important fish species in experimental gillnet catches and bottom trawl surveys in Tissawewa were: two small pelagic cyprinids *Amblypharyngodon melettinus* (Valenciennes) and *Rasbora daniconius* (Hamilton), three barbs *Barbus chola* (Hamilton), *Barbus dorsalis* (Jerdon) and *Barbus sarana* (Hamilton), one goby *Glossogobius giuris* (Hamilton), the estuarine halfbeak *Hyporhamphus gaimardi* (Valenciennes), two catfishes *Mystus gulio* (Hamilton) and *Mystus vittatus* (Bloch) which for practical reasons were combined into *Mystus spp.*, and two introduced exotic tilapias *Oreochromis mossambicus* (Peters) and *Oreochromis niloticus* (Linnaeus).

The feeding behaviour of each species was described by the quantity and the quality of the food items ingested, which were determined from analysis of gut fullness and gut contents. Fullness of the stomach or anterior one-third part of the gut was estimated according to five fullness categories (Table 6.2). The relative biovolumes of food items in gut/ stomach were estimated according to the point's method (Hynes 1950) using a microscope. The following categories of contents were distinguished: Fish, insects (both aquatic and terrestrial, but not benthic), zooplankton (cladocerans, cyclopoid and calanoid copepods), gastropods, shrimps, fish eggs, chironomids, microbenthos (mainly ostracods and some benthic cladocerans), porifera, macrophytes, epiphytic filamentous algae, phytoplankton and unrecognisable matter (digested matter and/or fine particulate detritus). The method does not distinguish between macrophytes which were directly consumed or those consumed as detrital matter.

Table 6.2 Gut fullness categories and estimated percentage of fullness (slightly modified according to Haram &amp; Jones 1971).

Gut fullness category	Fullness (%)
Completely filled and swollen	90-100
Just filled over full length, not swollen	70-89
Contents divided in different patches	30-69
Very few food particles	10-29
Completely empty	0-9

Each month the biomass per species, subdivided into size-classes, was determined from gillnet catches corrected for effort, at the same times of day (dawn and dusk) in the same habitat (entire water column, deep, open water). The total biomass caught per month in this standardised manner was used as an indicator of the fish density.

### Data analysis

The effect of environmental perturbation was analysed distinguishing two types of disturbances: transient and persistent. The transient disturbance was studied by comparing the three water level ranges before the drought, and the persistent disturbance was studied by comparing the two periods before and after drought. To prevent bias when analysing the effect of environmental perturbation, different selections of the dataset were made depending on the type of disturbance. First, comparison between the water levels is based

on the data of the first period only because during this period the lowest water level was reached. Second, comparison between periods is based on fish caught with a gillnet at high and intermediate water levels only because no low water level was recorded after the drought.

The effect of the disturbances on the fish community was monitored at three levels of organisation: organism, population and community. For each level different response variables were used as indicators of this effect. The two response variables describing the feeding behaviour (gut fullness and diet) were chosen as indicators of environmental effects at the level of the organism. In contrast, condition and abundance were chosen as indicators at the level of the population. The condition was only determined for the six most abundant species (both in numbers as well as in biomass). From these species the length and weight throughout the sampling period were measured at each sampling month up to July 1993. From these measurements a length-weight relationship per species per month was calculated. For those species for which sufficient fish belonging to different size-classes were caught each month, the average weight of each species was calculated per month and used as an indicator of the species' condition. This average weight was calculated for each month by multiplying the weight of each size-class during this month, with the relative abundance in terms of numbers of this size-class, over the entire sampling period. The weight of a size-class per month was calculated for the mid-range length of this size-class using the length-weight relationship for each particular month. The relative abundance per species is expressed as the percent composition each species contributes to the total biomass. The response variables at the level of the organism were expected to be instantaneous indicators while the response variables at higher levels of organisation were expected to reflect the effect of the environment with a certain time lag. Therefore only average values per water level and per period were calculated for the gut fullness and gut contents of a species while for the condition and abundance both the average value as well as the change over time were calculated. The calculated average value was based on all fish caught at that water level or period. The change over time was determined from the slope of the linear regression through the calculated values of the consecutive months belonging to that water level or period. For comparison between species, relative values ( $RV_{WP}$ ) per water level or period were calculated per species for both the average value as well as the rate of change of each of the response variables.

$$RV_{WP} = \frac{V_{WP}}{A_{TOT}}$$

In this formula  $V_{WP}$  is the average value or the rate of change of a response variable during a specific water level or period,  $A_{TOT}$  is the average value for this response variable over the entire sampling period. For the environmental variables and the biotic response variables differences between water levels and/or periods were tested with respectively the t-test and ANalysis Of VAriance (ANOVA) unless variables were not normally distributed (Shapiro-Wilks W-test,  $p < 0.05$ ) and the non-parametric Mann-Whitney U-test was used.

Per month the diet overlap for every species pair was calculated using Schoener's (1970) formula:

$$S = 1 - 0.5 * \sum_i (P_{xi} - P_{yi})$$

Where  $S$  is an index of similarity with 0 indicating no overlap and 1 indicating maximum overlap and  $P_x$  and  $P_y$  are the proportions of food item  $i$  in the guts of species  $x$  and  $y$ . The average diet overlap for the fish community is the average of all possible species pairs. The relation between the water level at the moment of sampling and the diet overlap was determined using linear regression. Differences in average diet overlap between the water levels and between the two periods were tested using the Mann-Whitney U-test.

The abundance rankings of species through time is a measure of community persistence and can be tested using Kendall's concordance. Because Rahel *et al.* (1984) found that the correlation among the abundance ranks of species increased as the number of species included in the assemblage increased, the coefficient of concordance is presented depending on the number of species included in the analysis. Selection of species was according to their relative abundance, discarding the species with the lowest relative abundance. Cluster analysis was used to detect any chronological pattern among the monthly collections per period. The similarity in community structure between consecutive months distinguishes between equilibrium and non-equilibrium communities, while a consistent decrease or increase of similarity along the time axis was considered an indication of the community structure changing respectively toward or away from equilibrium. The Spearman rank correlation was used to test the significance of changes in species abundances over time. This test is more appropriate than the frequently used Kendall's tau when the reliability of close ranks is uncertain (Ross *et al.* 1985). Differences in relative abundances of species- and trophic groups were tested with the Mann-Whitney U-test.

## Results

### *Environmental conditions*

At full supply level the total surface area of Tissawewa is around 300 ha and the maximum depth is around 4 m. Since water level recording started in 1987 considerable water level fluctuations have been observed but extreme situations did not occur as often as during this sampling period. Prior to this sampling period, water level had been above 1.5 m maximum depth, for more than 92% of the time. In contrast, during this sampling period it was only 76% of the time. "High" and "intermediate" water levels can thus be considered the upper and lower ranges within regular water level boundaries while a "low" water level only occurs occasionally. Only once before the beginning of the sampling period did the reservoir run dry for a period of only a few days, during this sampling period the reservoir was dry for almost two months. After filling a different ecosystem evolved. Before the drought Tissawewa had vegetation only in the shallow, inshore zone and a high turbidity due to resuspension of the thick layer of detritus on the bottom (Table 6.3). After the drought vegetation was found all over the reservoir, covering the entire water column, and the water was significantly clearer due to significantly lower concentration of suspended detritus and algae (Table 6.3). The concentration of suspended detritus during period 2 decreased considerably from the first measurement in December

Table 6.3 Physical and chemical parameters per water level and per period. Three water level ranges are distinguished during period 1: H (High: 2.5-4.0 m), I (Intermediate: 1.5-2.5 m) and L (Low: 0-1.5 m). Periods 1 and 2 comprise all sampling occasions respectively before and after the drought excluding those during low water level. Analysis of variance showed the effect of water level and period to be highly significant ( $p < 0.01$ ) for all parameters except for the effect of period on the phytoplankton biomass which was less significant ( $p < 0.05$ ).

Period	1			1	2
Water level	H	I	L	H,I	
Secchi-depth (cm)	34	27	6	30	127
Inorganic matter (mg dry weight.l <sup>-1</sup> )	22	43	568	33	19
Detritus mass (mg C.l <sup>-1</sup> )	5	10	118	7	2
Phytoplankton biomass (mg C.l <sup>-1</sup> )	0.4	0.6	9.0	0.5	0.3
Conductivity (μS.cm <sup>-1</sup> )	586	743	504	664	518

(4.6 mg C.l<sup>-1</sup>) to the last measurement in April (0.8 mg C.l<sup>-1</sup>). Conductivity was significantly lower during period 2. With decreasing water level, the concentrations of suspended inorganic matter, detritus and algae increased significantly, resulting in a significantly lower water transparency. Other environmental variables such as pH ( $8.3 \pm 0.4$ ), temperature ( $28.1 \pm 1.8$  °C) or dissolved oxygen ( $7.3 \pm 0.7$  mg.l<sup>-1</sup>) did not differ significantly between water levels or periods. The water level changed considerably throughout the sampling period (Fig. 6.2), affecting both the surface area as well as the volume of the waterbody. Comparison of the three water level ranges (High, Intermediate, Low) showed that both the largest surface area decrease (39% of the maximum area) as well as the largest volume decrease (64% of the maximum volume) occurred between the high water level boundaries (Fig. 6.3).

#### Feeding behaviour

The feeding behaviour of the fish was determined by two variables: diet and gut fullness. These variables were chosen as indicators of the effect of environmental change at the level of the organism. Both the quality as well as the quantity of the ingested food items differed for most species markedly between the different water levels as well as between the two periods (Table 6.4). Comparison between water levels and between periods showed for both tilapias a similar inverse relation between the proportions of macrophytes and epiphytic algae on the one hand and the proportions of phytoplankton and detritus/ digested matter on the other. When macrophytes and epiphytic algae were available in the environment they at least partially replaced phytoplankton and fine particulate detritus as a food source. This applied even more for *O. niloticus* than for *O. mossambicus*. The herbivorous/ detritivorous small pelagic, *A. melettinus*, showed only slight variation in its diet: within regular water level boundaries the proportion of detritus was significantly higher at intermediate water level, replacing phytoplankton. The proportions of zooplankton and detritus in the gut of *A. melettinus* during period 1 were significantly higher and lower respectively, than during the second period. The guts of the



Fig. 6.1 Map of Tissawewa indicating reservoir surface area at high (H), intermediate (I) and low (L) water level. Hatched area indicates the presence of vegetation during period 1. During period 2 vegetation was present all over the reservoir.

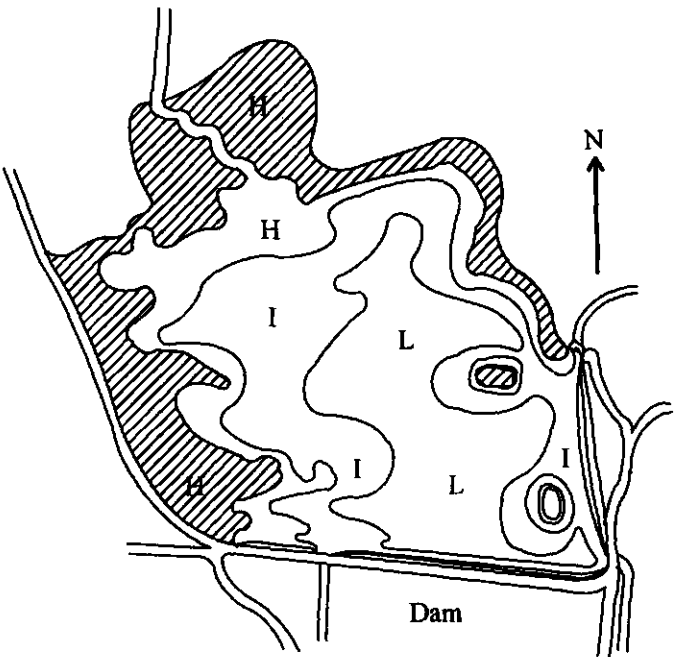


Fig. 6.2 Water level at deepest point throughout the sampling period. Dots indicate the water level at sampling dates. Ranges of high (H), intermediate (I) and low (L) water level as well as periods before (1) and after the drought (2) are indicated.

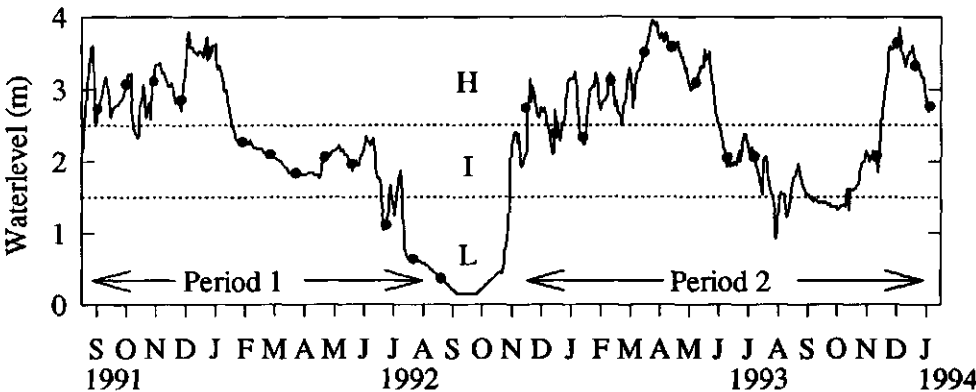
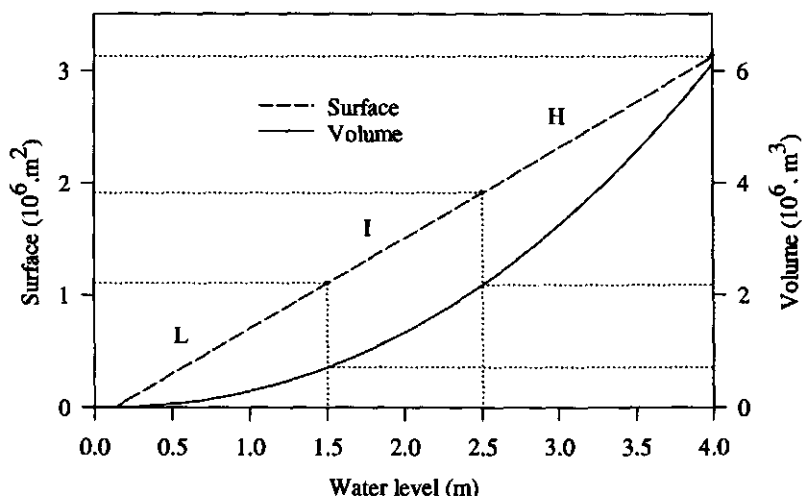


Fig. 6.3

Relationship between surface area ( $\text{m}^2$ ), volume ( $\text{m}^3$ ) and water level of Tissawewa reservoir at different water levels. Ranges of high (H), intermediate (I) and low (L) water level are indicated.



benthivorous barbs contained a higher proportion of zooplankton and gastropods with decreasing water level, while the proportions of insects, chironomids and microbenthos decreased. At low water level all three barbs had a significantly higher proportion of unrecognisable matter, suggesting that detritus was consumed. The piscivorous species, *G. giuris* and *Mystus spp.*, showed similar differences between the two periods: The proportions of fish and zooplankton were lower during the second period while the proportions of insects, chironomids and (only for *G. giuris*) shrimps were higher. The proportion of fish in the gut of *G. giuris* was higher at lower water levels. *Mystus spp.* showed a decrease in the proportion of insects with decreasing water level and a significantly higher proportion of zooplankton at intermediate water level. In the diet of the two zooplanktivorous/ insectivorous pelagics *H. gaimardi* and *R. daniconius*, the main food source during period 1, zooplankton, was replaced by insects and macrophytes during period 2. The main effect of water level changes on the diet of these two species was the significant increase in the proportion of unrecognisable matter with decreasing water level.

Regression analysis showed the gut fullness of most species was negatively correlated ( $p \leq 0.05$ ) with the water level. The only exceptions were the piscivores *Mystus spp.* and *G. giuris*. These piscivores, together with *B. sarana* and the zooplanktivorous/insectivorous *H. gaimardi* and *R. daniconius* were the only species for which gut fullness during period 2 was not significantly lower than during period 1. For *H. gaimardi* and *G. giuris*, gut fullness during period 2 was significantly higher.

The average diet overlap of the community increased during period 1 with decreasing water level and was higher during period 2 than during period 1.

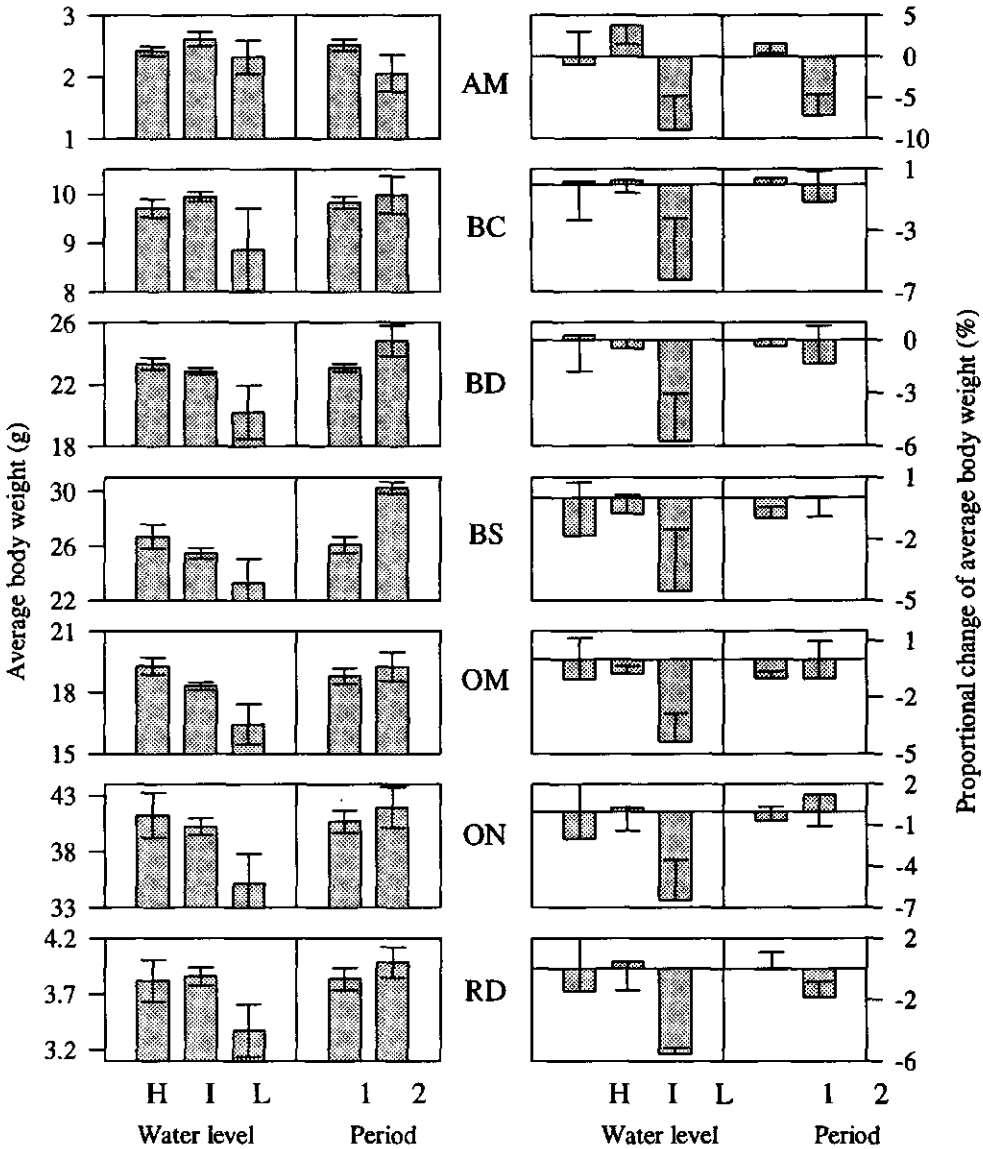
Table 6.4. Results of analysis of the gut contents and -fullness per water level and per period. Gut contents expressed as the proportion (%) of the recognizable matter (= total gut contents - digested matter and detritus) per food category. Because only the most important food items are included, the recognizable matter will not always equal 100%. Gut fullness indicated by the percentage of the gut filled. N is the number of fish used for these analysis. <sup>W</sup> and <sup>P</sup> indicate significant ( $p \leq 0.05$ ) differences between respectively water levels and periods. Average diet overlap was calculated for all species pairs using Schoener's (1970) formula.

Species		Water level			Period	
		H	I	L	1	2
<i>Amblypharyngodon melettinus</i>	N	887	974	398	1438	531
	Zooplankton <sup>P</sup>	9	3	4	5	20
	Phytoplankton <sup>W</sup>	89	97	89	93	67
	Digested/detritus <sup>W P</sup>	76	83	77	80	75
	Gut fullness <sup>W P</sup>	71	72	44	70	48
<i>Barbus chola</i>	N	753	1211	432	1516	979
	Insects <sup>P</sup>	5	2	5	4	8
	Zooplankton <sup>W P</sup>	12	24	17	17	8
	Gastropods	3	7	16	3	5
	Chironomids <sup>W P</sup>	38	28	25	32	36
	Microbenthos <sup>W</sup>	35	21	13	31	25
	Digested/detritus <sup>W P</sup>	26	61	57	48	33
<i>Barbus dorsalis</i>	N	655	663	397	1077	819
	Insects <sup>P</sup>	5	5	1	5	12
	Zooplankton <sup>W P</sup>	6	14	11	9	2
	Gastropods <sup>W P</sup>	11	37	47	22	5
	Chironomids <sup>W P</sup>	47	28	19	40	54
	Microbenthos <sup>W</sup>	24	11	9	19	16
	Digested/detritus <sup>W</sup>	16	25	55	20	27
<i>Barbus sarana</i>	N	192	323	273	243	524
	Insects <sup>W P</sup>	26	3	0	21	26
	Zooplankton <sup>P</sup>	3	5	6	4	2
	Gastropods <sup>W P</sup>	45	65	56	47	19
	Chironomids <sup>W P</sup>	8	3	9	8	23
	Macrophytes	6	13	5	8	9
	Benthic/epiphytic <sup>P</sup>	3	1	0	4	9
<i>Glossogobius giuris</i>	N	259	317	60	89	645
	Fish	30	46	95	82	49
	Insects <sup>P</sup>	8	13	2	3	24
	Zooplankton <sup>P</sup>	14	22	2	5	1
	Shrimp <sup>P</sup>	0	0	0	0	13
	Chironomids	42	13	1	9	11
	Digested/detritus <sup>P</sup>	23	36	23	33	20
<i>Glossogobius giuris</i>	Gut fullness <sup>P</sup>	42	30	35	39	47

Species		Water level			Period	
		H	I	L	1	2
<i>Hyporhamphus gaimardi</i>	N	293	528	29	304	379
	Insects <sup>P</sup>	11	5	0	21	37
	Zooplankton <sup>P</sup>	82	92	100	74	9
	Macrophytes <sup>P</sup>	2	2	0	2	40
	Digested/detritus <sup>W P</sup>	28	46	58	38	16
	Gut fullness <sup>W P</sup>	53	28	40	37	70
<i>Mystus spp.</i>	N	385	435	218	355	561
	Fish <sup>W P</sup>	54	32	55	49	7
	Insects <sup>W P</sup>	17	9	3	8	28
	Zooplankton <sup>W P</sup>	19	55	26	30	21
	Chironomids <sup>P</sup>	7	3	8	10	38
	Digested/detritus <sup>W</sup>	14	48	34	35	40
	Gut fullness	51	40	44	43	42
<i>Oreochromis mossambicus</i>	N	684	1158	404	714	510
	Insects	6	1	0	4	8
	Zooplankton	11	11	11	10.	7
	Macrophytes <sup>W P</sup>	20	7	3	10	22
	Benthic/epiphytic <sup>P</sup>	9	3	4	8	20
	Phytoplankton	47	67	75	59	27
	Digested/detritus	55	69	67	61	35
	Gut fullness <sup>W P</sup>	73	63	43	55	47
<i>Oreochromis niloticus</i>	N	15	223	82	10	315
	Zooplankton <sup>W</sup>	42	2	11	10	4
	Macrophytes <sup>W</sup>	53	41	8	22	49
	Benthic/epiphytic	0	2	0	0	10.
	Phytoplankton <sup>W</sup>	5	40	80	33	19
	Digested/detritus <sup>W P</sup>	39	66	59	66	28
	Gut fullness <sup>W P</sup>	75	75	61	53	52
<i>Rasbora daniconius</i>	N	718	952	256	1122	638
	Insects <sup>W P</sup>	29	8	20	26	55
	Zooplankton <sup>W P</sup>	65	85	61	67	17
	Chironomids <sup>W P</sup>	3	3	19	3	8
	Macrophytes <sup>P</sup>	1	3	1	2	10
	Benthic/epiphytic <sup>P</sup>	0	0	0	0	8
	Digested/detritus <sup>W</sup>	21	41	62	31	26
	Gut fullness <sup>W</sup>	66	48	36	55	50
Fish Community	Average diet overlap	0.45	0.53	0.57	0.49	0.53

Fig. 6.4

Condition of the seven most abundant species for three water levels, High (H), Intermediate (I) and Low (L) as well as the periods before (1) and after (2) the drought. The condition is expressed as the average body weight per species. Presented are the absolute value (left) and the rate of change relative to the average body weight over the entire sampling period (right). Error bars indicate 95% confidence limits. For species abbreviations see table 1.2

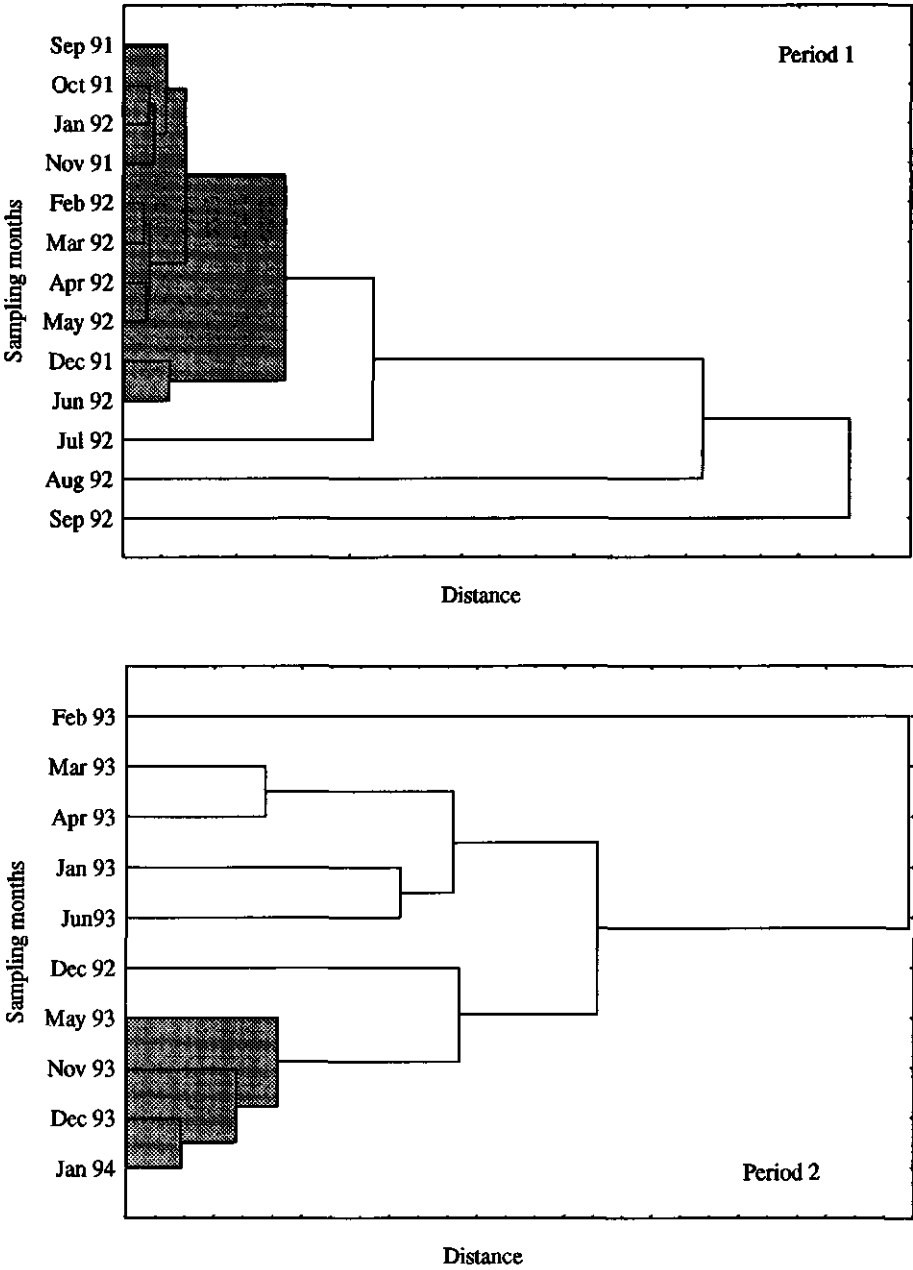


difference between the herbivorous/ detritivorous *A. melettinus* and the tilapias *O. mossambicus* and *O. niloticus*. The first period, where the relative abundance of the most abundant species, *A. melettinus* was increasing while that of the tilapias was decreasing, contrasts with the second period where it was the other way around. Similar, but less conspicuous are the inverse relationships between the relative abundances of the benthivorous barbs *B. chola* and *B. dorsalis* as well as the piscivores *Mystus spp.* and *G. giuris*.

#### Community structure

For each period separately, cluster analysis was used to group months together based on the similarity in community structure (Fig. 6.6). As distance between clusters increases, similarity decreases. The similarity of a cluster of consecutive months, indicating community stability, is represented by the distance of the smallest possible cluster grouping these months together. For each period one cluster of consecutive months is selected based on two criteria: 1) maximisation of the number of consecutive months, 2) minimisation of the distance between these months and 3) community structure must be stable as determined by Kendall's concordance ( $p \leq 0.01$ ). For period 1 the community structure was considered stable, and therefore at equilibrium from the beginning of the sampling period, September 1991, until the start of the low water phase in June 1992. For period 2 the same applied for the last sampling months: November 1993 until January 1994. The fact that Kendall's concordance remained significant ( $p \leq 0.05$ ) for each equilibrium as long as at least three species were included in these equilibria confirms that the conclusion that the community is at equilibrium is not biased by the number of species included as part of the assemblage (Fig. 6.7). Spearman correlation was used to compare the community structure of each month of period 1 to the equilibrium before the drought, and each month of period 2 to the equilibrium after drought. This showed how, from July onwards, the decreasing water level forces the community structure away from equilibrium, while after the drought the community structure gradually changed toward a new equilibrium which was reached in November (Fig. 6.8). Comparison of the community structure of each month of period 2 to the equilibrium community structure before drought showed a significant correlation for the months of December ( $p = 0.07$ ) and January ( $p = 0.05$ ) indicating the structure of the upstream community, entering the reservoir, resembled the equilibrium community structure of period 1. Spearman rank correlation showed the community structures at equilibrium of periods 1 and 2 were not similar ( $p = 0.56$ ). Comparison between periods of the relative abundance of each species at equilibrium showed a significantly lower ( $p \leq 0.05$ ) relative abundance during period 2 for *A. melettinus*, *H. gaimardi* and *R. daniconius* while the relative abundances of *O. mossambicus*, *O. niloticus*, *B. chola* and *G. giuris* were higher. The trophic structure however, hardly differed between the equilibria of period 1 and 2: only the planktivorous/ insectivorous trophic group consisting of *H. gaimardi* and *R. daniconius* was significantly ( $p \leq 0.05$ ) less abundant during period 2.

Fig. 6.6 Dendrograms, showing similarity of assemblage composition among sampling months of respectively periods 1 (top) and 2 (bottom). Similarity is inversely related to the calculated distance. This distance is based on the relative abundances in biomass of the 10 most abundant species of the assemblage.



## Discussion

### *Transient disturbance*

The response variables at both the organism level and population level are markedly affected by changes in resource availability, which in turn are affected by the water level. The decreasing water level causes a decrease in the availability of space and food, the former indicated by the increasing fish density, the latter by the decrease of area (bottom and surface) and volume of water per fish, which involves availability of all major food items except for prey fish. The food availability is affected in both a quantitative and qualitative way, which is reflected in the correlation of gut fullness with water level for all fish species except for the piscivores, and the increase in diet overlap with decreasing water level.

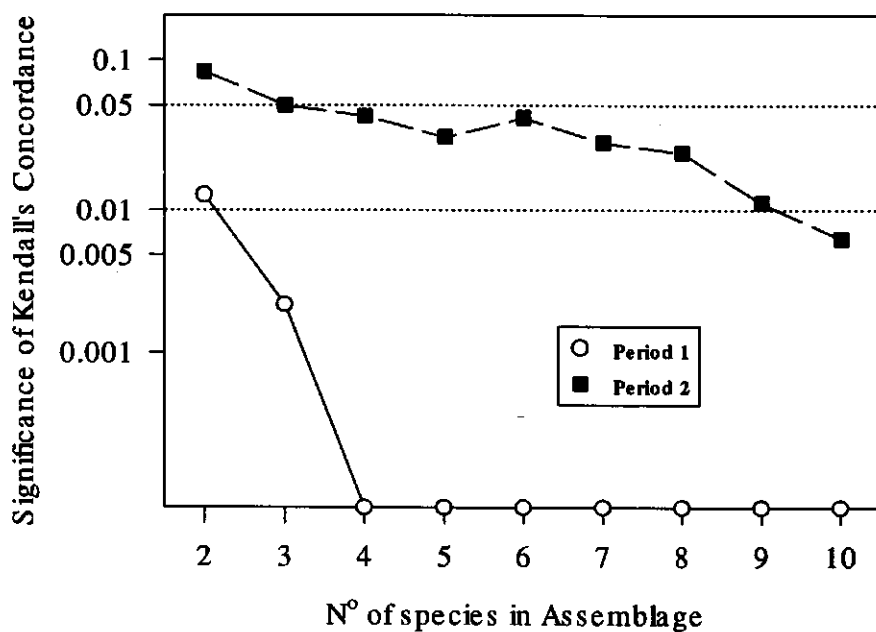
The impact of the magnitude of the transient disturbance caused by a changing water level can be determined by comparing the difference from high to intermediate water level with the difference between high and low water level. The loss of the littoral zone between high and intermediate water level is reflected in the gut contents where, at intermediate water level, most species contain a significantly lower proportion of invertebrates and the herbivorous/ detritivorous tilapias contain a significantly lower proportion of macrophytes. As the layer of water becomes thinner the resuspension of the bottom layer of detritus and sediment increases, resulting in a higher concentration of suspended detritus and inorganic matter in the water column indicated by an increase in turbidity. From this, only the detritivorous, filter feeding *A. melettinus* benefits which is reflected in the higher proportion of detritus and the higher gut fullness causing a marked increase of condition because of a higher rate of energy intake. All other species have a lower gut fullness during intermediate water level. At the population level these changes have only minor implications: At intermediate water level two small pelagics, *A. melettinus* and *R. daniconius*, show an increase in condition related to an apparently higher availability of their main food sources, detritus and zooplankton respectively, whereas two other species, *B. sarana* and *O. mossambicus*, show a decrease in condition. In general there are no differences in abundance between the two water level ranges. Thus, the main difference between high and intermediate water level is at the level of the organism which is forced to adjust to changes in the type of food available. This is reflected in the community structure which remains at equilibrium within regular water level boundaries.

Gut contents at low water level do not differ much from the contents at intermediate water level. As their regular food becomes scarce, the barbs increasingly feed on gastropods and, as for all non-detritivorous species, the proportion of unrecognisable matter increases, partly because retention time of the gut contents increases with decreasing gut fullness and partly because of the high detritus content in the water. Often inorganic matter was observed in the gut (pers. observations) caused by an extremely high concentration of suspended inorganic matter. In a study on the Lake Chilwa ecosystem (Kalk *et al.* 1979), an extremely high concentration of suspended solids was observed at very low water level, causing a sudden depletion of oxygen, leading to massive fish kills. In Tissawewa, however, dissolved oxygen concentrations below 5 mg/l were never observed. Food availability appears to be more important: at low water level gut fullness is markedly lower, which also explains the considerable decrease of condition for all species.



Fig. 6.7

Relationship between significance of Kendall's concordance and the number of species included in the assemblage for the community at equilibrium during period 1 and 2.

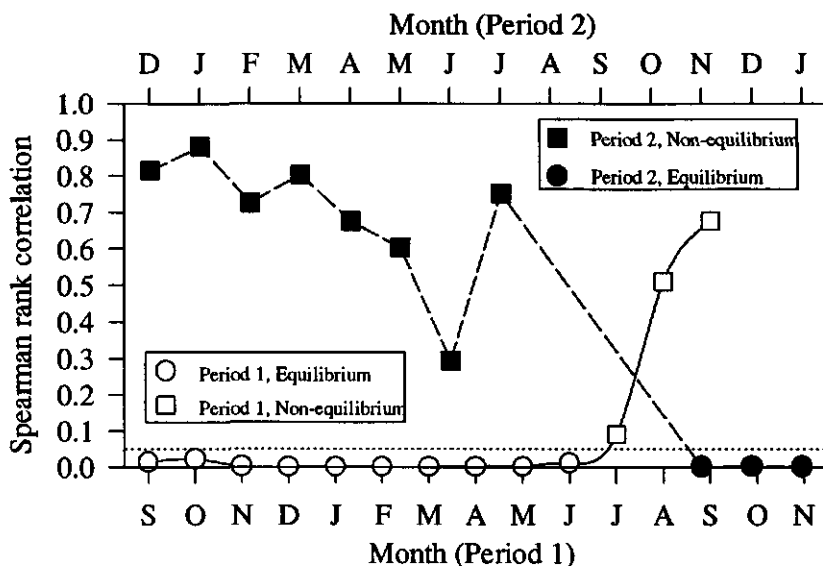


The relative abundance during low water level reflects the tolerance of species to these harsh conditions. The small pelagics *A. melettinus* and *R. daniconius* show the biggest decrease while the other small pelagic *H. gaimardi* completely disappeared after one month of low water level. The faster decline during harsh conditions of smaller-bodied species relative to larger-bodied ones is as predicted by Pimm (1991), and can be explained by the observation of Calder (1984) on mammals, that with increasing body mass the stored amount of fat increases more than do the energetic needs. The benthivorous barbs and to a lesser extent the herbivorous/ detritivorous tilapias are apparently better adapted and manage to persist. This difference between barbus and cichlid species is confirmed by the landings of the fishery during the recession of Lake Chilwa (Kalk *et al.* 1979). Thus, below regular water level boundaries, the decrease of resource availability not only affects the assemblage at the organismal level but at the population level as well, causing the community structure to shift from equilibrium towards a new steady state. This steady state was never reached because the water level did not stabilise and the reservoir ran dry.

When looking at the impact of a transient disturbance on a fish community at different levels of organisation, the magnitude of this disturbance is of major importance. With increasing magnitude the community will be affected at a higher level of organisation while at lower levels this disturbance will have an increasingly larger effect.

Fig. 6.8

Spearman rank correlation, comparing the community structure of each month belonging to one period to the community structure at equilibrium of that particular period. Months with  $p$ -values  $\leq 0.05$  are considered significantly similar to the community structure at equilibrium. Months of the different periods are indicated on the upper and lower x-axis.



### Persistent disturbance

Comparison of the response variables between the periods illustrates how the environment influences the community structure by affecting the assemblage at a lower level (organism, population). When comparing the relative abundance of a species between periods, the relative abundance at equilibrium is considered to be a better indicator than the average relative abundance over each period. Although, by definition, equilibria are considered stable, Kendall's concordance shows the equilibrium before the drought to be more stable than that after the drought, suggesting that equilibria are not necessarily equally stable. However this lies mainly in the fact that the equilibrium before drought covers a longer time period and thus more sampling months than that after the drought. Another effect of the short time at equilibrium during period 2 might be a bias of the relative abundances at equilibrium caused by migration of species. *Barbus* species, for example, are known to migrate out of the reservoirs, to spawn in riverine habitats (De Silva *et al.* 1986). To eliminate possible seasonal migration effects, the months in which the community was at equilibrium during period 2 were compared with the same months during period 1. However, the observed differences remained, confirming that they are caused by the changed environment alone.

There are two factors that explain the decreased turbidity during period 2. First, the lower concentration of suspended detritus caused by the decomposition of the organic material on the bottom during the drought is expected under well-aerated conditions and prevailing high surface temperature (Kalk *et al.* 1979). Second, the abundance of

macrophytes decreases the effect of the wind on the resuspension of the bottom layer thereby decreasing the concentration of inorganic matter and detritus in the water column. The different effect these changes have on the various herbivorous/ detritivorous species follows from differences in feeding behaviour between these species. The small pelagic cyprinid, *A. melettinus*, feeds mainly on suspended phytoplankton and fine particulate detritus (Bitterlich 1985, Pethiyagoda 1991). In contrast, the tilapias *O. mossambicus* and *O. niloticus*, feed mainly on the bottom deposits (Bowen 1979, 1980, 1981, Schiemer & Duncan 1987). Therefore the decrease of suspended matter during period 2 mainly affected *A. melettinus*, resulting in a lower gut fullness, condition and abundance at equilibrium. The shift from fine particulate detritus and phytoplankton during period 1 to macrophytes (or detritus from macrophyte origin) during period 2, exhibited by the tilapias, is probably caused by a change in composition of their food source, the benthic detrital aggregate, rather than a change in feeding behaviour of the fish. Although this switch resulted in a lower gut fullness, the condition increased and the abundance at equilibrium was higher for both species.

The second abundant trophic group, consisting of the mainly benthivorous barbs *B. chola*, *B. dorsalis* and *B. sarana*, switches from food items like zooplankton and gastropods during period 1 to insects and chironomids during period 2, resulting in a lower gut fullness. The higher condition during period 2, however, indicates that foraging or food conversion during this period is more efficient, but this is only reflected in a significantly higher abundance at equilibrium for *B. chola*. Foraging efficiency might well be higher during a period of higher water transparency (Diehl 1988).

The small pelagics *H. gaimardi* and *R. daniconius* first feeding almost entirely on zooplankton were forced to switch to other food sources. Gut content analysis showed respectively macrophytes and insects to be the main alternatives of which the first, mainly found in the gut of *H. gaimardi*, is a remarkable choice for a species which, based on a gut length to total length ratio below 0.4 (Piet Chapter 2), is ill equipped to utilise plant matter (Moyle & Senanayake 1984). A probable explanation is that macrophyte uptake was accidental and digestion slower, which accounts for the high gut fullness of *H. gaimardi* during period 2. Because of low density, it was not feasible to measure the condition of *H. gaimardi*. The higher condition of *R. daniconius* during period 2 suggests that the species is sufficiently adapted to the new environment. However, this is contradicted by the significantly lower abundance at equilibrium.

The gut contents of the piscivores *G. giuris* and *Mystus spp.* are markedly affected by the low abundance of their main prey fish *A. melettinus*, which is partially replaced with insects and chironomids larvae (*Mystus spp.*) or insects and shrimps (*G. giuris*). The significantly higher abundance at equilibrium of *G. giuris* compared with *Mystus spp.* suggests that the higher visibility improves the foraging efficiency of *G. giuris* but not of *Mystus spp.*. This corroborates with the possession of barbels by *Mystus spp.* (Pethiyagoda 1991, Piet Chapter 2).

The easy adaptation of most species of the community to this "new" environment is not surprising since this environment resembles, to a certain extent, the littoral zone which is available in the lowland reservoirs during the wet season and which in turn resembles the natural marshes which are formed during the wet season. Therefore differences in feeding behaviour observed between periods 1 and 2 are somewhat similar

to those observed between respectively intermediate and high water level. Food sources which were preferred during period 1 at high water level when the littoral zone was available and competition was less severe, are abundant during period 2.

Thus, a persistent disturbance results in changes at every level of organisation. The organism adapts its feeding behaviour to the food availability. Changes in terms of foraging- and food conversion efficiency affect the fitness of the organisms which in turn affect the populations. The community structure depends on the relative abundances of the populations and changes to an equilibrium in which the relative abundances of each species reflects the ability of the organism to adjust to this environment. The relation between environmental characteristics and community structure was also observed by Tonn & Magnuson (1982). The fact that the trophic structure was considerably less affected than the taxonomic structure corresponds with Grossman *et al.* (1982).

#### *Regulation of community structure*

Sufficient knowledge of the disturbances acting on the community and the subsequent responses of that community, are essential when studying the mechanisms regulating community structure. The outcome of this study can be biased by the length of the sampling period and the frequency at which sampling was conducted. Results from the present study, combined with water level recordings over a longer period, can illustrate this. A sampling period starting when the water level was first recorded up to the drought would characterise the community as deterministically regulated with an occasional "crunch" at extreme low water levels, with the frequency of these "crunches" depending on sampling frequency. In contrast, a sampling period more or less equally distributed before and after the drought would result in characterisation of the community as being stochastically regulated or if the sampling period would continue long enough for the "new" environment to return to its "old" state the community would be considered to be deterministically regulated with a "crunch". Thus far characteristics of both the community response or the disturbance have not been taken into account when determining the mechanisms regulating community structure (Grossman *et al.* 1982, Ross *et al.* 1985).

Any environmental disturbance will force the organism to adjust, almost instantaneously, to the new circumstances. Changes at higher levels of community organisation are only observed after a certain time lag. Because, in case of the decreasing water level, the magnitude of the disturbance increased with the passing of time, it is uncertain whether changes at higher levels of organisation occurred with a certain time lag after the lower level was affected, or whether a bigger magnitude of disturbance was required for an instantaneous response at a higher level of organisation, or whether it was a combination of both. But no matter what the mechanism, the observed discrepancy between change at the level of the organism versus change at the level of the community, indicates that the resistance increases with increasing level of organisation. The present study shows, that as soon as the water level started decreasing, the first changes in feeding behaviour were observed, while only after six months in which the magnitude of the disturbance increased considerably, the community structure was affected. In case the disturbance persisted long enough the community would eventually reach an equilibrium in which the relative abundance of each species reflected its ability to adjust to these circumstances. The time between the occurrence of a "new" environment and the

establishment of an equilibrium is a measure of the resilience of the community (Pimm 1991). About one year after the drought, the community has reached a new equilibrium. The relatively low persistence of this equilibrium compared with the equilibrium before the drought, is probably because of its recent establishment and is expected to increase with time.

For the fish community in Tissawewa, characterisation of the mechanisms regulating community structure is not dependent on the number of species included as part of the assemblage but does depend on the persistence, frequency and magnitude of the disturbance. The persistence indicates the time a disturbance lasts which theoretically is between zero and infinite. However, since no disturbance will last infinitely, categorisation of a disturbance to be transient or persistent depends on the time scale at which this disturbance acts. This, in turn, depends on the response at the level of organisation being studied. In the case of the Tissawewa fish community, a disturbance whose effect on the community extends longer than one year, can be classified as persistent. Assuming water level fluctuations are the main source of disturbance, then the frequency and magnitude of the disturbance follow directly from respectively the frequency and amplitude of the water level fluctuations.

The past seven years of water level monitoring give an idea of the disturbances acting on the Tissawewa community while observations presented in this study give a notion of the response of the community to disturbances of varying duration and magnitude. Based on these results the Tissawewa community can be characterised as deterministically regulated with occasional "crunches" when the water level drops for sufficiently long time below 1.5 m. The drought caused what can be categorised as a persistent disturbance during which, as long as it lasts, the community can experience other "crunches" depending on the water level. This implies that in spite of the considerable environmental variation, biotic interactions such as competition and resource partitioning are important. Competition, and therefore resource partitioning as a means to avoid competition (Schoener 1974), not only plays a major role during the "crunches" but, since resource partitioning increases as more resources become available during high water level, appear to be important at higher water levels as well.

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## Chapter 7

### ENVIRONMENTAL PERTURBATION AND THE STRUCTURE AND FUNCTIONING OF A TROPICAL AQUATIC ECOSYSTEM

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#### Abstract

In Tissawewa, a shallow, eutrophic reservoir in SE Sri Lanka, the ecosystem was studied from the perspective of the total fish community and the respective contributions of forage base groups to the fish production. For this, the primary production as well as the production and diets of the total size-structured fish assemblage were determined. The fish assemblage consists of 10 species, including two exotic tilapias, making up more than 98% of the fish biomass. A drought provided the opportunity to study two extreme states of this ecosystem: 1) a period where most primary production is sustained by phytoplankton, suspended fine particulate detritus is an important food source, total fish density is high and the impact of fish predation is insignificant versus 2) a period characterised by high macrophyte density, low concentration of suspended detritus, low total fish density of which a high proportion are piscivores. Gross primary production was estimated at 13034 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> and 6273 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> for respectively periods 1 and 2. For the fish production, transfer efficiencies of 1.9 % and 2.0 % were calculated. These relatively high efficiencies are probably caused by the short food chain. Total fish production, with emphasis on the relative importance of exotics versus indigenous species, is related to the yield of the commercial fishery and the consumption by birds. This shows that the importance of the exotic tilapia in Sri Lankan reservoirs is overrated because production estimates were based on commercial catches only. About 80% of the fish production in Tissawewa is sustained by indigenous species of which more than 95% is smaller than the selection range of the commercial fishery. The ecosystem is overall bottom-up controlled but after the perturbation an example of top-down control was observed. However, the structure of the foodweb prevents top-down effects from cascading down the foodchain.

## Introduction

One of the main goals of ecology can be defined as "prediction of the abundance and distribution of organisms in time and space" (Begon *et al.* 1986). With respect to the ecosystem research this means that the intention is to predict the changes in structure of an ecosystem over ecological time and how this is affected by functional aspects of this ecosystem such as the interactions between and among different populations as well as between these populations and their environment.

There is consensus that trophic interactions can be of major importance in determining ecosystem structure and functioning but there is an ongoing debate on whether primary control is by resources (bottom-up forces) or by predators (top-down forces). The theories propagating top-down control, where changes in abundance of the top predators will cascade down the foodweb are among others: the biomanipulation concept (Shapiro *et al.* 1975, 1982, Shapiro 1980), the cascading trophic interaction theory (Carpenter *et al.* 1985) and the food chain dynamics theory (Fretwell 1987, Oksanen 1988) which is an extension of the theories presented by Hairston *et al.* (1960) and Wiegert & Owen (1971). In contrast there are the theories propagating bottom up control such as the mutualism-cybernetics theory by Odum & Biever (1984) or the donor control-indirect effects theory (Vadas 1989). Recently, these two opposing viewpoints are incorporated in models in which the effects of ecological factors can cascade both up as well as down the trophic system. McQueen *et al.* (1986, 1989) predicts that the maximum attainable biomass is determined by resource availability, but that realised biomass is determined by the combined effects of top-down and bottom-up forces. In general, predator-mediated interactions are strong near the top of the foodweb whereas bottom-up regulation is strongest near the bottom of the foodweb. Hunter and Price (1992) introduced a "bottom-up template" on which two-way interactions of species and their environment on all trophic levels, can be superimposed. They argue that a true synthesis of "top-down" and "bottom-up" forces in terrestrial systems requires a model that encompasses heterogeneity, a term which may be expressed as the differences among species within a trophic level or in species interactions in a changing environment. This heterogeneity of interactions at roughly the same trophic level is probably the key factor explaining why consumption is so differentiated in speciose ecosystems that the overall effects of top-down forces are buffered and that consequently true trophic cascades can be considered a relatively unusual sort of food web mechanics (Strong 1992).

For aquatic ecosystems much of the evidence of trophic cascades is based on experiments involving four trophic levels, typical for the temperate zone: phytoplankton, zooplankton, planktivorous fish and piscivorous fish (Carpenter & Kitchell 1985, McQueen *et al.* 1986, 1989, Strong 1992). An important difference between the tropics and the temperate zone is that herbivorous fish, which compete with zooplankton for food and are directly consumed by piscivores, are frequent in the tropics (Moriarty *et al.* 1973, Leveque 1978) and that consequently heterogeneity at least at the level of the primary consumers can be expected to be higher in the tropics. Another difference between the tropics and the temperate zone is that at least one resource determining plant production, incident light, is higher in the tropics. Since plant production can determine the number of trophic levels in communities (Hunter and Price 1992, Power 1992) or the food web structure (Fretwell 1987), this might have

considerable consequences for the structure and functioning of tropical ecosystems compared to their temperate counterparts.

This paper presents results on the Tissawewa ecosystem in SE Sri Lanka from the perspective of the total fish community and the respective contributions of forage base groups to the fish production. This ecosystem is subject to considerable environmental variation and one particular perturbation provided the opportunity to study two extreme states of this ecosystem: a state characterised by high food availability and low predator abundance versus a state characterised by low food availability and a high predator abundance. In the present paper both structural and functional properties of the ecosystem are studied and compared with those in temperate ecosystems in order to explain the relatively high estimates of fish production and fish yield in the tropics. Furthermore the question is addressed to what extent the system is controlled by bottom-up or top-down forces and how the relative importance of these forces is related to environmental variation or trophic level heterogeneity.

## Material and methods

### *Study area*

Sri Lanka has a large number of artificial reservoirs and no natural lakes as is true for many other areas in SE Asia. In most of the tropical reservoirs in SE Asia the fish production is lower than would be expected on the basis of the high primary production (Henderson 1979, FAO 1980). This relatively low fish production is probably due to the origin of the fishes, mainly indigenous riverine carps, which may not be optimally adapted to the lacustrine conditions (Fernando 1984, Fernando & Holcik 1982, 1991). In the 1950s the African cichlids *Oreochromis mossambicus* and *Oreochromis niloticus* were introduced all over Sri Lanka. This introduction markedly increased the fish yield in the reservoirs (De Silva 1988).

Tissawewa is a shallow (mean depth = 1.2 m, average maximum depth = 2.6 m), lowland reservoir of about 200 ha in SE Sri Lanka, subject to considerable water level fluctuations. From daily water levels, obtained from the Sri Lankan Irrigation Department, and the water level-dependent volume of the reservoir, calculated using a model described by Pet *et al.* (1995c), a maximum retention time of 42 days was calculated for the water in this reservoir (Piet unpublished). The most abundant species are the cyprinids *Amblypharyngodon melettinus* (Valenciennes), *Barbus chola* (Hamilton), *Barbus dorsalis* (Jerdon), *Barbus sarana* (Hamilton) and *Rasbora daniconius* (Hamilton), one goby *Glossogobius giuris* (Hamilton), one halfbeak *Hyporhamphus gaimardi* (Valenciennes), two catfishes *Mystus gulio* (Hamilton) and *Mystus vittatus* (Bloch) which for practical reason were treated as *Mystus spp.* and two introduced exotic tilapias *Oreochromis mossambicus* (Peters) and *Oreochromis niloticus* (Linnaeus). These species together made up more than 98% of the biomass as determined from experimental gillnet catches and bottom trawl surveys.

### *Sampling program*

Sampling was conducted between April 1991 and January 1994. During this sampling program the reservoir dried up completely for two months (September/ October 1992) due to a long spell of extreme drought. After filling up of the reservoir, a different



ecosystem had evolved (Table 7.1): Before the drought Tissawewa had macrophytes only in the shallow, inshore zone and turbidity was high (Secchi-depth transparency = 30 cm) due to resuspension of a thick layer of detritus on the bottom. After the drought macrophytes were found all over the reservoir covering the entire watercolumn and there was relatively clear water (Secchi-depth transparency = 127 cm) because the detritus had vanished. To study the effect of this environmental change, two periods were distinguished: Period 1 covers the sampling occasions before the drought while period 2 covers the sampling occasions after the drought.

Table 7.1 Values of ecosystem parameters (mean  $\pm$  95% c.l.) for the periods before (1) and after drought (2).

	Period	
	1	2
Conductivity ( $\mu\text{S}\cdot\text{cm}^{-1}$ )	664 $\pm$ 47	518 $\pm$ 44
Secchi-depth transparency (cm)	30 $\pm$ 2	127 $\pm$ 18
Suspended detritus ( $\text{mgC}\cdot\text{m}^{-3}$ )	7328 $\pm$ 1599	2111 $\pm$ 1813
Phytoplankton biomass ( $\text{mgC}\cdot\text{m}^{-3}$ )	484 $\pm$ 93	143 $\pm$ 10
Vegetated area (%)	10	100
Gross primary production ( $\text{kgC}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ )	13034 $\pm$ 1792	6273 $\pm$ 1801
Fish biomass ( $\text{kgC}\cdot\text{ha}^{-1}$ )	170 $\pm$ 32	77 $\pm$ 19
Fish production ( $\text{kgC}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ )	243 $\pm$ 16	128 $\pm$ 10

Phytoplankton production was measured fortnightly from April 1991 to respectively July 1992 while phytoplankton biomass and concentration of suspended detritus were measured until April 1993. Phytoplankton production was estimated according to Vollenweider (1974). Phytoplankton biomass was determined from Chlorophyll-a measurements according to Moed & Hallegraeff (1978). The concentration of suspended detritus was calculated by subtracting the phytoplankton concentration from the seston concentration determined according to Golterman *et al.* (1978). For measurements which were not in  $\text{mg C}\cdot\text{m}^{-3}$  such as Chlorophyll-a ( $\text{mg}\cdot\text{m}^{-3}$ ) and seston ( $\text{mg dry weight}\cdot\text{m}^{-3}$ ) we used conversions of 1 g chlorophyll-a = 25 g carbon (Bailey-Watts 1974) and 1 g dry weight = 0.5 g carbon (Winberg *et al.* 1971). Fish were sampled on a monthly basis from September 1991 to January 1994. Each monthly sampling occasion consisted of setting 120 m of multimesh (12.5 - 90 mm stretched mesh) gillnets in four habitats (Pet & Piet 1993), twice during day-time and twice at night. Additional to the gillnets two active gears: bottom trawl and cast net were used. These gears ensured the entire size range (above 3 cm total length) of the available species was sampled. In order to distinguish any size-specific differences in feeding behaviour the total size range was divided into six size-classes (Table 7.2). For analysis of gut contents of the ten most abundant species, each month a maximum of 10 specimens per species, size-class, gear type, station and time of day were pooled. A maximum of twenty-four specimen per 0.5 cm class per month of the six most abundant species were measured, weighed and

dissected for data on respectively: body length and body weight, gonad weight and sex. In total 359920 fish were caught of which 20492 fish were used for gut content analysis and 14382 fish were dissected and used for determination of the length-weight relationship and gonado-somatic index.

Table 7.2 Total length ranges of each size-class of fish

Size-class	1	2	3	4	5	6
Total length (cm)	3.0-4.4	4.5-6.9	7.0-9.9	10.0-13.9	14.0-18.9	≥ 19.0

### *Stock assessment and production*

To determine the assemblage composition, the length-frequency distributions of the experimental gillnet catches were corrected for fishing effort and gillnet selectivity. Gillnet selectivity was estimated using the extended Holt model (Pet *et al.* 1995b). The standing stock biomass of *O. mossambicus*, over the full size-range, was calculated to be 128 kg/ha (Pet *et al.* 1995a). The standing stock biomass per month of all other species/ size-classes was calculated on the basis of species/ size-class composition in experimental gillnet catches and the estimated standing stock biomass of *O. mossambicus*. Production of each population for a given length of time is the sum of the growth increment of all specimens of the population. This growth increment involves not only somatic tissue but also that of gonads. The monthly growth of somatic tissue is calculated from the sex-dependent growth curves and length-weight relationships per period of each species. Growth was calculated using the von Bertalanffy growth curve (von Bertalanffy 1934) and the parameters  $K$  and  $L_{\infty}$  were partly derived from Pet *et al.* (1995a) and partly estimated on the basis of Length-Frequency Distribution Analysis (LFDA). For the sex-dependent growth curves, biomass increase per sex was calculated from a size-dependent sex-ratio per species (Pet *et al.* 1995a). Production of gonads was assumed to be only relevant for the female fish. For these fish the length-weight relationship was corrected for a size-dependent gonad weight while gonad production was estimated from the decreases in gonad weight when spawning which was assumed to occur twice a year (Pet *et al.* 1995a). Biomass is expressed in  $\text{kg C} \cdot \text{ha}^{-1}$  and production (gross for primary producers, net for primary and secondary consumers) in  $\text{kg C} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  where 1 kg C is assumed to be equal to 10 kg fresh weight (Winberg *et al.* 1971).

### *Diet composition and consumption*

To study the size-dependent diet composition of a species, the contents of the stomach or anterior 1/3 part of the gut were analysed. The relative biovolumes of food items in gut/stomach were estimated according to the point's method (Hynes, 1950) using a microscope. The following food items were distinguished: Fish, insects (both terrestrial and aquatic but not benthic), microcrustacean zooplankton (cladocerans, cyclopoid and calanoid copepods), gastropods, fish eggs, chironomids, microbenthos (mainly ostracods and some benthic cladocerans), macrophytes, epiphytic filamentous algae, phytoplankton and unrecognisable matter (digested matter and/or fine particulate detritus). In case fish was found in the gut, the species and size-class were determined when possible.

A three-way ANOVA was used to test for a species, size and environmental effect on the proportion of detritus in the gut. To distinguish between species ingesting detritus and those which did not, the species with the highest proportion of unrecognisable matter was excluded until no significant ( $p > 0.05$ ) species effect was observed. The excluded

species at that point were in the following order: *A. melettinus*, *O. mossambicus*, *O. niloticus* and *B. chola*. For the remaining species it was assumed all the unrecognisable matter was in fact digested matter. Thus, the proportion of digested matter per size-class and period could be determined from the linear regression between the proportion of digested matter and the mid-range size per size-class for each environment separately. With the following formulas the proportion (%) of digested matter per period (DM<sub>1</sub> and DM<sub>2</sub>) can be calculated for each size-class from the mid-range length (L) of that size-class:

$$DM_1 = 37.07 - 0.72 * L$$

$$DM_2 = 26.59 - 0.04 * L$$

The proportion of detritus was calculated by subtracting the proportion of digested matter from the observed proportion of unrecognisable matter.

Food consumption of each fish species was calculated from the production and the diet composition per size-class assuming a conversion efficiency (i.e. ratio of production of a consumer to consumption of its food) depending on food characteristics rather than consumer characteristics. Brett & Groves (1979) found conversion efficiencies of 20% for herbivorous fish and 29% for carnivorous fish. These conversion efficiencies were used for food items of plant and animal origin, respectively. Respiration losses of 37% for herbivores and 44% for carnivores, were assumed (Brett & Groves 1979).

#### *Bird predation*

The most important fish-eating birds around Tissawewa were: the Little Cormorant (*Phalacrocorax niger*), Large Cormorant (*Phalacrocorax carbo sinensis*), Indian Shag (*Phalacrocorax fuscicollis*), Grey Pelican (*Pelecanus philippensis*), Little Egret (*Egretta garzetta*), Large egret (*Casmerodius albus*), Grey Heron (*Ardea cinerea*), Painted Stork (*Mycteria leucocephala*), Spoon Bill (*Platalea leucorodia*), Open Bill (*Anastomus oscitans*) and White Ibis (*Threskiornis melanocephalus*). From August 1993 until June 1994 the number of each of these species foraging in Tissawewa were recorded during weekly one-day sessions lasting from sunrise until sunset. To cover the entire reservoir the reservoir was divided into four sections and during each session the birds of every section were counted once for one hour at alternating times of day. For ease of counting no distinction was made between the three cormorant species or between the two egret species.

Food consumption of the bird population was not measured directly but calculated. For the birds of the genus *Phalacrocorax* the average fish consumption per individual calculated by Winkler (1983) was used while for the other species the average fish consumption per individual was calculated by multiplying the total consumption with the estimated proportion of fish in their diet. Total consumption per individual was calculated per species from a regression by Drent *et al.* (1981):

$$\log(y) = 0.861188 * \log(x) - 0.3233879$$

where  $y$  is total consumption (g fresh weight) and  $x$  is average bird weight (g). Average bird weights and the proportion of fish in their diet were obtained per species from literature data (Cramp *et al.* 1977).

## Results

### Primary production

In Tissawewa primary production is realised predominantly by phytoplankton and macrophytes. Biomasses of these primary producers differed markedly before and after the drought. Average phytoplankton biomass was  $484 \text{ kg C.ha}^{-1}$  during period 1 and only  $143 \text{ kg C.ha}^{-1}$  during period 2. From the relation between phytoplankton biomass and production established during period 1, an average gross production of  $13034 \text{ kg C.ha}^{-1}\text{.yr}^{-1}$  during period 1 and  $6273 \text{ kg C.ha}^{-1}\text{.yr}^{-1}$  during period 2 was calculated from the mean biomasses during the respective periods (Fig. 7.1). Respiration was on average 54% of the gross production. In contrast to phytoplankton production, the production of macrophytes, judging from the area of the reservoir covered with vegetation, was markedly higher after the drought. During period 1 the area covered with vegetation took up 30% of the reservoir area at full supply level, decreasing with decreasing water level until it was negligible below a water level of 2.5 m. On average about 10% of the reservoir area during period 1 could be characterised as littoral zone whereas during period 2 this was close to 100%.

Fig. 7.1 Relationship for Tissawewa between phytoplankton biomass (B) and production (P). Indicated are the mean phytoplankton biomasses and the production estimates for the periods before (1) and after the drought (2).

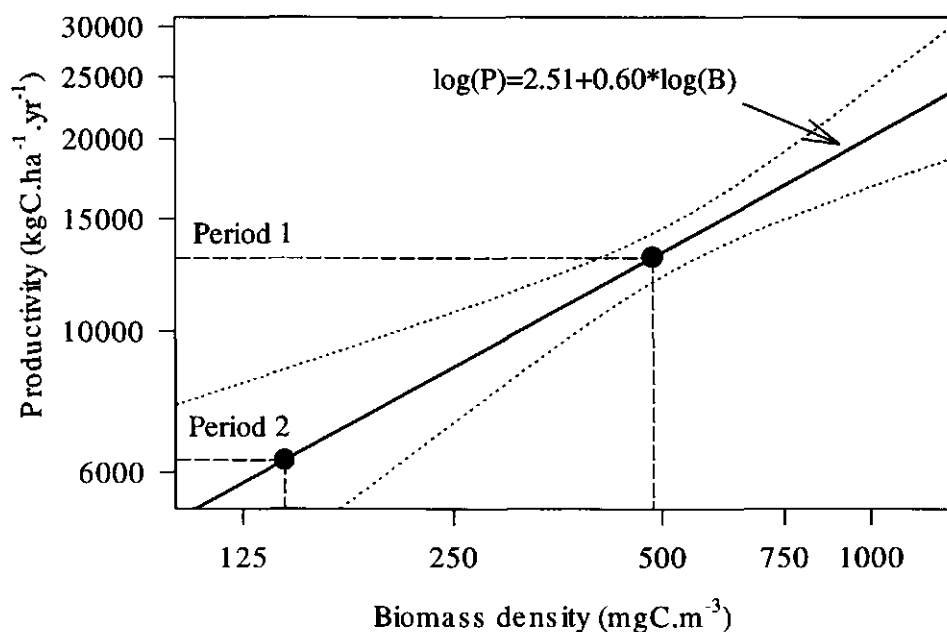
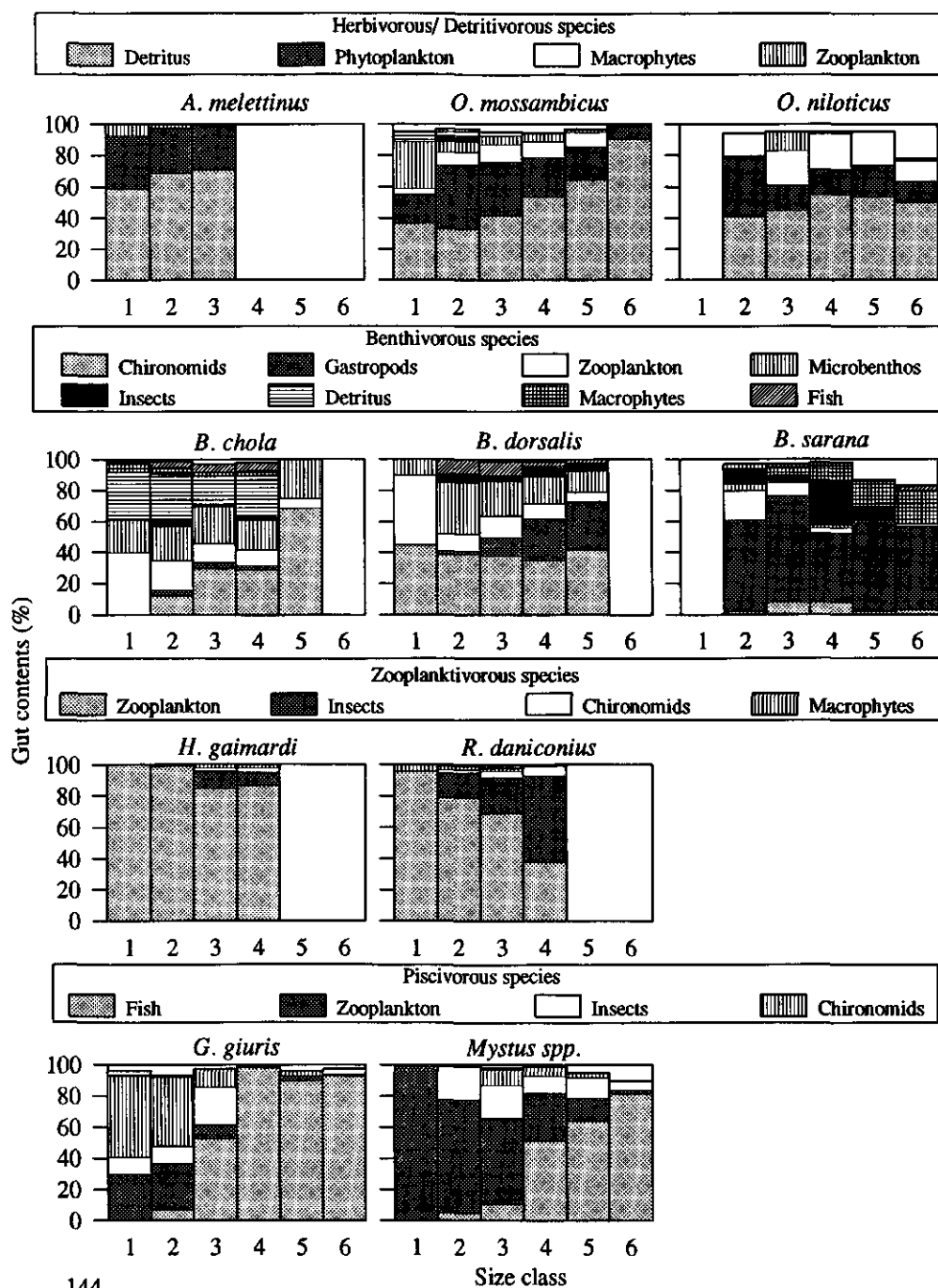
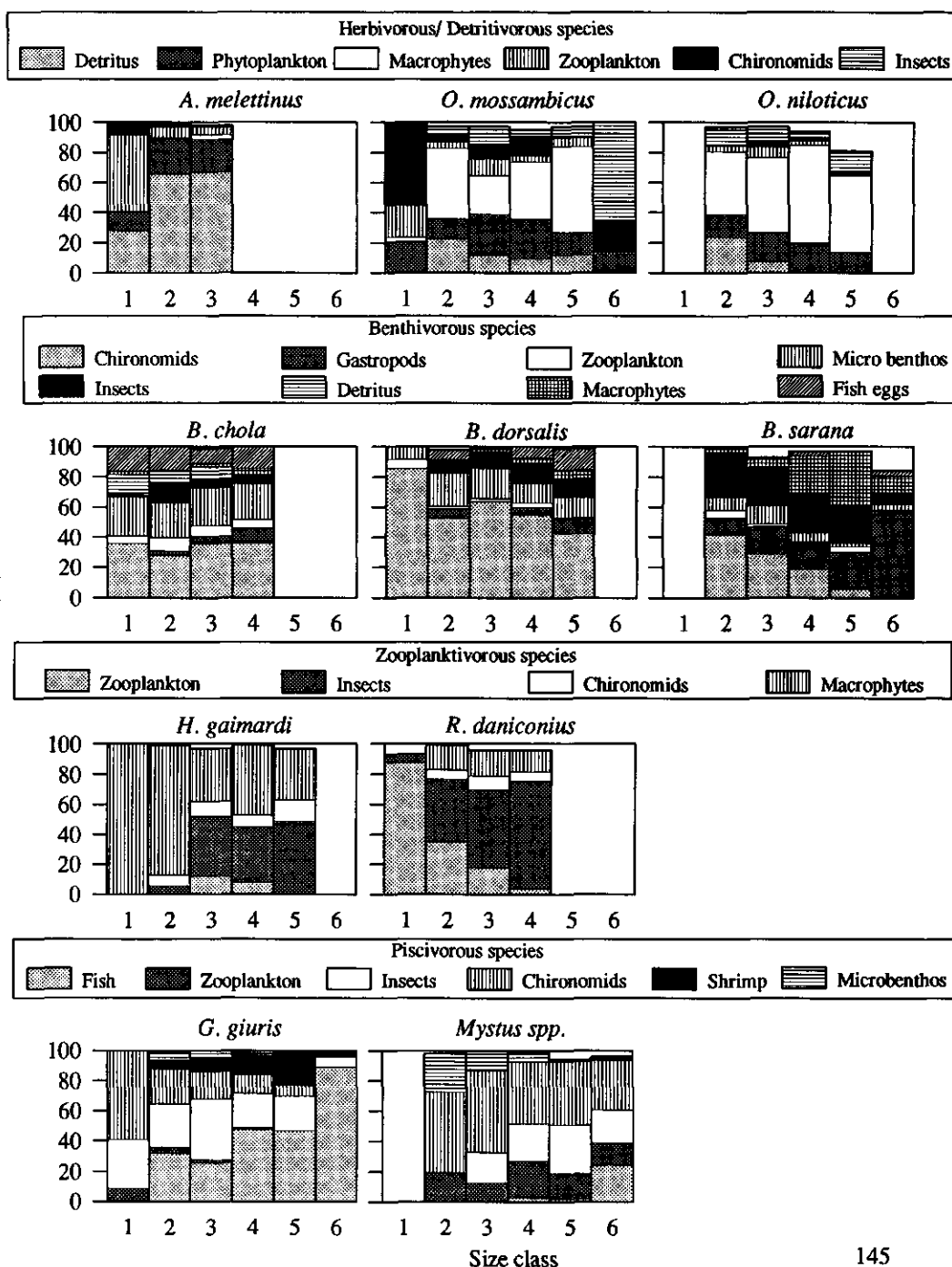


Fig. 7.2

Gut contents (%) on basis of biovolume per species, per size-class and per period. Species are grouped together according to their guild. Period 1 on left page, Period 2 on right page. For explanation of size-class numbers see table 7.1.





### Diet Composition

Based on the feeding behaviour throughout the entire sampling period the species of the Tissawewa fish assemblage were divided into four guilds: The herbivorous/ detritivorous guild consisting of *A. melettinus*, *O. mossambicus* and *O. niloticus*, the benthic carnivorous guild consisting of the barbs *B. chola*, *B. dorsalis* and *B. sarana*, the pelagic carnivorous guild consisting of *H. gaimardi* and *R. daniconius* and the piscivores consisting of *G. giuris* and *Mystus spp.* (Fig. 7.2). Within these guilds considerable differences in diet composition of a species were observed during ontogeny and between periods.

The diet of the herbivorous/ detritivorous species during period 1 consisted mainly of detritus and to a lesser extent phytoplankton and macrophytes. After the drought the proportion of detritus in the diet of the tilapias was lower whereas the proportions of macrophytes and epiphytic algae were higher. For the largest size-classes of *A. melettinus* no differences between periods were observed but the smallest size-class displayed a larger proportion of zooplankton in its diet.

During period 1 the main food items in the diet of the barbs *B. chola*, *B. dorsalis* and *B. sarana* were benthic food items such as chironomids, gastropods and microbenthos. Although the diets of the barbs were qualitatively similar throughout the entire sampling period the quantities of the different food items differed considerably, both between species and between periods. Comparison of the most important size-classes, in terms of biomass, of the barbs shows *B. chola* fed mainly on chironomids and microbenthos while the third important food item differed between periods: detritus during period 1 and fish eggs during period 2. *B. dorsalis* fed on chironomids while the second important food item during period 1, gastropods, was replaced by insects and microbenthos. The biggest difference between the periods was observed for *B. sarana*: the principal food item during period 1, gastropods, was largely replaced by insects.

Before the drought the pelagic carnivorous species, *H. gaimardi* and *R. daniconius*, fed almost entirely on zooplankton with, especially for the latter, an increasing proportion of insects with increasing size. During period 2 zooplankton was replaced by insects while a high proportion of macrophytes was observed in the gut.

The piscivores exhibited some distinct size-related changes in their diet. With increasing size both species switched from zooplankton to invertebrates to fish of increasing size. Overall, the most important prey fish was *A. melettinus* but this was dependent on predator size and abundance of *A. melettinus* (Fig. 7.3). The main alternative prey species were the carnivorous pelagics *H. gaimardi* and to a lesser extent *R. daniconius*. During period 2 the proportion of fish in the diet of both species was lower compared to period 1 and was replaced by insects, chironomids and (only for *G. giuris*) shrimps.

### Composition and production of fish assemblage

During period 1 the standing stock biomass was dominated by *A. melettinus*, which biomass almost equalled that of all other species combined. Other abundant species in terms of biomass were the cyprinids *B. dorsalis*, *B. chola*, *R. daniconius* and the tilapia *O. mossambicus*. Because of the relatively high P/B-ratios of the smaller species, *A. melettinus* was even more important in terms of production, representing 45% of the total

Table 7.3 Biomass (kg C.ha<sup>-1</sup>) and production (kg C.ha<sup>-1</sup>.yr<sup>-1</sup>) per species, per size-class and per period. For definition of size-classes see table 7.2. For species abbreviations see table 1.2.

Size-class	Period 1						Period 2					
	1	2	3	4	5	6	1	2	3	4	5	6
Species	Standing stock biomass (kgC.ha <sup>-1</sup> )											
AM	0.5	56.5	20.1	0.0	0.0	0.0	0.0	2.7	2.4	0.0	0.0	0.0
OM	0.0	1.5	2.7	5.3	3.2	0.1	0.0	0.1	0.7	3.4	1.9	0.3
ON	0.0	0.1	0.2	0.4	0.4	1.4	0.0	0.0	0.2	0.8	1.1	1.4
BC	0.0	1.6	11.1	5.9	0.0	0.0	0.0	1.1	3.0	1.3	0.0	0.0
BD	0.0	0.2	2.5	9.8	10.6	0.1	0.0	0.2	1.6	10.0	2.9	0.0
BS	0.0	0.1	0.3	0.9	3.4	1.3	0.0	0.2	0.6	2.3	1.7	0.1
HG	0.0	0.0	1.4	3.2	0.0	0.0	0.0	0.0	0.1	2.5	4.0	0.0
RD	0.0	5.2	11.5	0.1	0.0	0.0	0.0	1.7	9.1	0.4	0.0	0.0
GG	0.0	0.1	0.0	0.0	0.4	2.7	0.0	0.1	0.5	3.2	2.6	1.4
MY	0.0	0.0	0.4	4.1	1.2	0.2	0.0	0.0	1.7	7.7	2.0	0.0
	Production (kgC.ha <sup>-1</sup> .yr <sup>-1</sup> )											
AM	1.9	94.8	11.6	0.0	0.0	0.0	0.1	4.8	1.4	0.0	0.0	0.0
OM	0.5	10.2	12.0	16.1	4.9	0.0	0.0	0.5	3.6	11.2	3.3	0.1
ON	0.0	0.6	0.7	1.2	0.7	0.5	0.0	0.1	0.8	2.8	2.3	0.7
BC	0.1	3.9	12.2	2.4	0.0	0.0	0.2	3.2	3.5	0.7	0.0	0.0
BD	0.0	1.0	7.4	14.9	6.6	0.0	0.3	1.0	6.5	18.0	1.9	0.0
BS	0.0	0.2	0.7	1.3	2.4	0.3	0.0	0.8	1.4	3.5	1.3	0.0
HG	0.0	0.0	1.3	1.5	0.0	0.0	0.0	0.0	0.1	1.7	0.7	0.0
RD	0.0	13.1	10.6	0.0	0.0	0.0	0.1	5.8	11.5	0.1	0.0	0.0
GG	0.0	0.4	0.1	0.1	0.6	1.4	0.0	0.8	3.0	12.4	5.2	0.8
MY	0.0	0.0	0.6	3.2	0.4	0.0	0.0	0.0	2.7	7.8	0.9	0.0

fish production, followed by *O. mossambicus*, *B. dorsalis* and *R. daniconius*. The standing stock biomass of the entire fish assemblage as well as the abundances of the species differed considerably between periods. During period 1 the total standing stock biomass was 170.4 kg C.ha<sup>-1</sup> while during period 2 it was only 77.4 kg C.ha<sup>-1</sup> (Table 7.1). The species most affected by the environmental changes after the drought was *A. melettinus*, which density decreased from 77.1 kg C.ha<sup>-1</sup> during period 1 to 5.2 kg C.ha<sup>-1</sup> during period 2 (Table 7.3). The abundances through time of *A. melettinus* and its main predators, *G. giuris* and *Mystus spp.* before the drought and *G. giuris* after the drought, show how this predator-prey relationship affects the densities of the species involved (Fig. 7.3). The only other species showing, compared to the entire fish assemblage, a more than average decrease in density was *B. chola*. Remarkable is the observation that for some species their density increased in spite of the considerable overall decrease; for the piscivores *G. giuris* and *Mystus spp.* as well as the tilapia *O. niloticus* and the estuarine invader *H. gaimardi* a higher density during period 2 was observed. These changes in density markedly affected production of the fish assemblage (Table 7.3). The growth of somatic tissue was calculated using the K and L<sub>∞</sub> values per species in the von Bertalanffy growth equation and a length-weight relationship per period (Table 7.4). The production of eggs was determined from the calculated proportion of the body weight per size-class which is spent per year on development of gonads (Table 7.5). Fish production



in the reservoir, both in an absolute sense as well as relative to the surface area, was significantly ( $p < 0.01$ ) dependent on the water level (Fig. 7.4). Compared to the change in standing stock biomass, the change in production from  $243 \text{ kg C} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  to  $128 \text{ kg C} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ , is relatively smaller. The species with a markedly higher P/B-ratio during period 2 were *G. giuris*, *B. sarana* and *B. dorsalis* while those with a lower P/B-ratio were *H. gaimardi*, *O. mossambicus*, *A. melettinus* and *R. daniconius* (Table 7.3). After the drought the main producers of fish biomass were *B. dorsalis*, *G. giuris*, *O. mossambicus* and *R. daniconius*.

Fig. 7.3 Densities of predator and prey for the same months before (Period 1) and after drought (Period 2) and the size-specific proportion of herbivorous fish (*A. melettinus*) in the gut of the piscivores. During period 1 the piscivores are *G. giuris* and *Mystus spp.* while during period 2 this was only *G. giuris*.

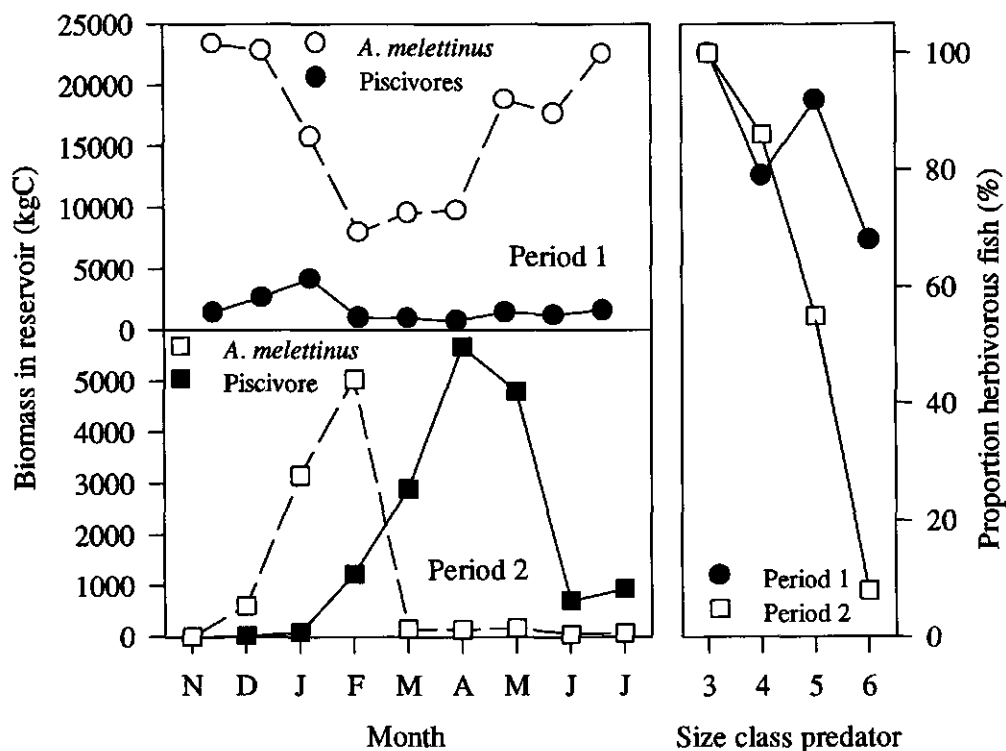


Fig. 7.4

Significant ( $p < 0.01$ ) relationship between water level and fish production. The fish production per surface area ( $P_A$ ) is fitted with a first order equation, the total fish production in the reservoir ( $P_R$ ) is fitted through the origin using a second order equation.

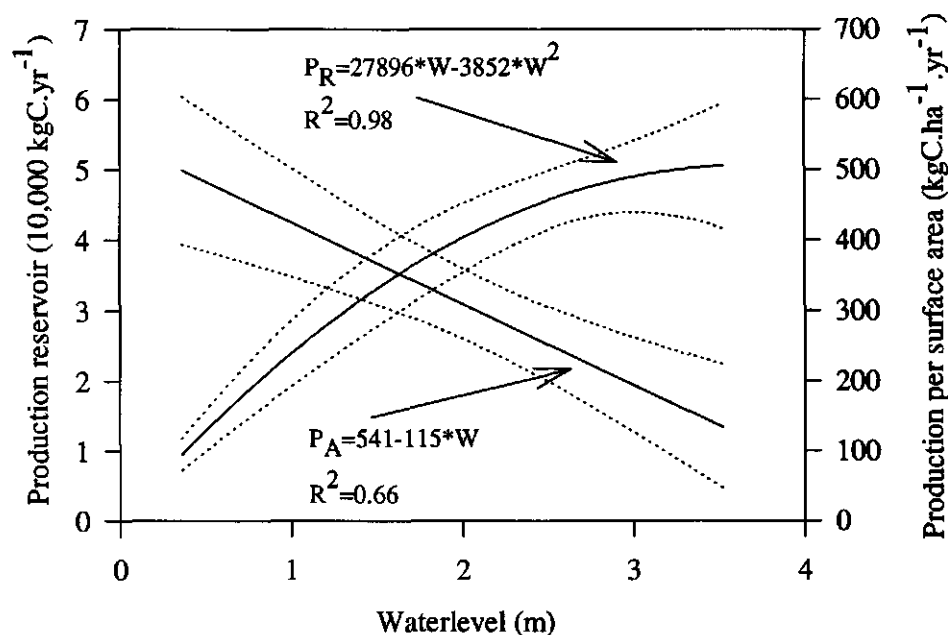


Table 7.4

Calculated parameters used for determination of somatic growth.  $K$  and  $L_{\infty}$  of species with abbreviations in bold were calculated by Pet *et al.* (1995a) for females (f) and males (m). The length-weight relationship is described by  $\ln(W) = a + b \cdot \ln(L)$  with total length (L) in millimeters and weight (W) in grams fresh weight. For species abbreviations see table 1.2.

Species	Von Bertalanffy growth curve				Length-Weight relationship			
	K		L <sub>∞</sub>		Period 1		Period 2	
	f	m	f	m	a	b	a	b
AM	1.50	1.60	8.0	7.0	-11.97	3.11	-11.97	3.10
OM	0.75	0.65	26.0	30.0	-10.79	2.97	-10.36	2.89
ON		0.61		30.0	-10.86	3.00	-11.11	3.06
BC	1.00	1.10	12.0	10.5	-11.74	3.14	-11.20	3.02
BD	0.85	0.95	19.0	17.0	-11.89	3.13	-11.28	3.01
BS	0.40	0.45	26.0	22.0	-11.21	2.99	-11.80	3.14
HG		0.21		19.7	-12.76	3.02	-12.76	3.02
RD	1.10	1.20	11.0	10.0	-11.68	3.02	-11.69	3.03
GG		0.59		30.2	-11.39	2.94	-11.39	2.94
MY		0.29		22.3	-11.09	2.95	-11.09	2.95

Table 7.5 Proportion (%) of the body weight per year spent as gonads per species and per size-class as determined during period 1. For definition of size-classes see Table 7.1. For species abbreviations see table 1.2.

Species	Sizeclass				
	2	3	4	5	6
AM	11.5	17.8			
OM		0.8	1.1	0.9	
ON			0.1	0.7	2.5
BC		4.4	13.4	15.3	
BD		6.8	9.8	17.0	
BS			2.4	7.4	7.3
HG		16.0	13.0	8.5	
RD	32.1	25.9	17.1		
GG			1.2	3.7	3.6
MY			1.2	3.7	3.6

### Foodweb

The major food items to sustain the fish production during period 1 were detritus (46%) and phytoplankton (20%) (Table 7.6). Other plant material such as macrophytes and epiphytic algae are not important food sources during this period, sustaining only about 3% of the total fish production. Zooplankton and chironomids are the main animal food sources sustaining respectively 11% and 6% of the fish production. The production of the barbs *B. chola*, *B. dorsalis* and *B. sarana* relied for more than 70% on benthic food items of which the chironomids, sustaining 30% of the barb production, are much more important than gastropods (19%) or ostracods (18%). The production of the piscivores *G. giuris* and *Mystus spp.* was sustained mainly by prey fish (55%) while production of *R. daniconius* and *H. gaimardi* relies almost entirely on zooplankton (76%) and to a lesser extent on insects (18%). For the entire fish assemblage 72% of the insects were from terrestrial origin. Of all the prey fish consumed, herbivorous fish (mainly *A. melettinus*) contributed 74% during period 1 and 77% during period 2.

In contrast to period 1, the importance of plant material to sustain fish production was markedly lower during period 2, with macrophytes and epiphytic algae as the main food sources sustaining 17% of the fish production while detritus and phytoplankton sustained only 7% respectively 6% (Table 7.6). Consequently, the relative importance of the animal food sources was higher after the drought. Chironomids and insects were the most important animal food sources sustaining respectively 23% and 19% of the fish production. These two food items are the main replacement for food items such as the gastropods for the barbs, fish and zooplankton for the piscivores and zooplankton for the pelagic carnivores. The relatively high importance of insects during period 2 is possible due to an increased consumption of insects of aquatic origin; only 46% of the insects consumed in this period by the entire fish assemblage were from terrestrial origin.

### Bird predation

Based on recordings of the numbers of the most important bird species in and around Tissawewa combined with literature data of these species indicating average weight per individual and proportion of fish in the diet, it appears that in terms of numbers and fish

Table 7.6 Calculated consumption ( $\text{kgC}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ) by fish species before (Period 1) and after the drought (Period 2).

Species Food items	Period 1										Period 2									
	AM	OM	ON	BC	BD	BS	HG	RD	GG	MY	AM	OM	ON	BC	BD	BS	HG	RD	GG	MY
Fish	0	1	0	0	0	0	1	0	0	7	7	0	0	0	0	0	0	0	0	34
Insects	0	3	0	2	6	3	1	18	0	2	0	5	2	3	13	7	4	34	22	13
Zooplankton	8	10	0	10	12	1	10	71	1	5	2	4	1	2	3	1	1	17	1	8
Gastropods	0	0	0	3	28	11	0	0	0	0	0	0	0	0	1	4	5	0	0	0
Shrimps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chironomids	0	1	0	19	45	1	0	3	1	1	0	8	1	10	62	6	1	6	10	19
Fish eggs	1	0	0	4	6	0	0	0	0	0	0	1	1	4	7	0	0	0	0	0
Micro benthos	0	0	0	17	22	0	0	0	0	0	0	1	0	7	17	2	0	1	1	1
Macrophytes	2	21	4	3	1	3	0	2	0	0	0	38	21	1	4	7	5	15	0	1
Phytoplankton	155	67	4	0	0	0	0	0	0	0	7	23	6	0	0	1	0	1	0	1
Detritus	374	103	9	20	0	0	0	0	0	0	21	10	0	3	0	0	0	0	0	0

Table 7.7

Average bird density and 95% confidence limits with data from the literature to calculate the average fish consumption per species/ genus. For the genus marked with <sup>1)</sup> data were from Winkler (1983), for the species marked with <sup>2)</sup> the data were from Cramp *et al.* (1977) while for the remaining species average weight per individual was derived from Cramp *et al.* (1977) and consumption was calculated using the regression of Drent *et al.* (1981).

Bird species		Bird density (#ha <sup>-1</sup> ) average $\pm$ 95% c.l.	Weight (g)	Consumption (kgC.bird <sup>-1</sup> .yr <sup>-1</sup> )	Proportion fish in diet (%)	Consumption (kgC.ha <sup>-1</sup> .yr <sup>-1</sup> )
Cormorant/Shag	<i>Phalacrocorax spp.</i> <sup>1)</sup>	14.3 $\pm$ 5.8		6	100	14.3
Egret	<i>E. garzetta</i> , <i>C. albus</i>	2.8 $\pm$ 0.9	750	5	70	2.8
Grey Heron	<i>A. cinerea</i>	1.7 $\pm$ 0.8	1500	15	80	1.7
White Ibis	<i>T. melanoccephalus</i>	0.2 $\pm$ 0.1	1500	9	40	0.2
Open bill Stork	<i>A. oscitans</i> <sup>2)</sup>	12.4 $\pm$ 10.2		66	70	12.4
Painted Stork	<i>M. leucocephala</i> <sup>2)</sup>	16.2 $\pm$ 9.1		66	80	16.2
Grey Pelican	<i>P. philippensis</i>	5.5 $\pm$ 2.5	10000	48	100	5.5
Spoon bill	<i>P. leucorodia</i>	0.3 $\pm$ 0.2	1500	9	70	0.3

consumption, cormorants and shags (genus *Phalacrocorax*) are the most important bird species in Tissawewa (Table 7.7). Although second in numbers the importance of the egrets as a fish predator is exceeded by the considerably less numerous pelicans and storks. Cormorants, storks and pelicans take up more than 90% of a total fish consumption by birds in the reservoir of 53 kg C.ha<sup>-1</sup>.yr<sup>-1</sup>. Apart from the pelicans and an occasional cormorant, birds are hardly ever observed in the open water zone.

## Discussion

### *Detritus*

For a long time it has been recognised that non-living organic matter plays a very important role in the structure and function of aquatic ecosystems (Mann 1988). In Tissawewa, detritus is the most important food source for the fish assemblage before the drought, whereas after the drought, the proportion of detritus in the diets of the fish species as well as the abundance of the main detritivore has decreased considerably. In this study the importance of detritus as a food source is based on the size-specific biomass production by the species of the fish assemblage and the proportion of detritus in the gut contents of these species. When determining the proportion of detritus in the diet from gut contents alone it should be realised that 1) it is difficult to distinguish detritus from formerly living matter, digested in the gut of the fish, and 2) the term detritus covers a broad range of dead organic matter from different origin. The first argument has been accounted for by the correction for the proportion of digested matter in the gut although the proportion of detritus might still be slightly overestimated because digestion rates of herbivorous species are higher than those of non-herbivorous species (Fänge & Grove 1979). The latter argument can be partially solved by considering the feeding behaviour of the main detritivorous species: *A. melettinus* is a filter feeder feeding on phytoplankton and suspended detritus in the watercolumn (Bitterlich 1985, Pethiyagoda 1991) whereas the tilapias prefer surface-grazing to filter-feeding (Dempster *et al.* 1993) and feed mainly on the benthic detrital aggregate (Bowen 1979, 1980, 1981, Schiemer & Duncan 1987).

During period 1 there was a thick layer of fine particulate detritus on the bottom which disappeared during the drought (pers. observations). Based on the relatively high gross production by phytoplankton and relatively small area covered with macrophytes, the autochthonous part of this detritus mainly originated from phytoplankton. During the drought the organic material on the bottom decomposed, which is to be expected under well-aerated conditions and prevailing high surface temperature (Kalk *et al.* 1979), and was blown away. Therefore, after the drought, accumulation of detritus had to recommence. As the reservoir was refilling, the shallowness of the reservoir and the relatively low turbidity allowed access light to reach the bottom, thus promoting macrophyte growth (Blazka *et al.* 1980). The presence of macrophytes covering the entire reservoir area had considerable consequences for food availability of the herbivores, limiting phytoplankton growth and resuspension of detritus (Wetzel & Manny 1972). Because after the drought phytoplankton biomass was markedly lower while macrophyte biomass was higher, a considerably higher proportion of the autochthonous detritus formed after the drought will have been from macrophyte origin. Through time this will only be amplified because the decomposition rate of fine particulate organic matter is

markedly higher than that of particulate leaf organic matter (Anderson 1987). The abundant vegetation affects the availability of suspended detritus in the pelagic zone in a two-fold manner: by decreasing turbulence in the water column and because resuspension of relatively large particulate leaf organic matter can be expected to be less than that of finer particulate organic matter from algal origin. These arguments explain the observed changes in feeding behaviour and density of the herbivorous/ detritivorous fish. The availability of suspended fine particulate organic matter, the main food source of *A. melettinus*, decreased while the composition of the bottom deposits, the main food source of the tilapias changed from mainly small particles of algal origin to larger particles of macrophyte origin. The apparent change in consumption by the tilapias from mainly detritus to macrophytes represents a change in composition of their food source rather than a change in feeding preference of the fish.

Apart from the autochthonous primary production, an influx of allochthonous organic matter can be expected for a small reservoir with a short retention time (Wetzel 1990). However, the influx of allochthonous organic material is unknown and is therefore not incorporated in the estimation of the total production of detritus thereby underestimating this production. The net autochthonous production of detritus and probable influx of allochthonous organic matter is in correspondence with the observed thick layer of detritus on the bottom of the reservoir during period 1. The importance of suspended detritus from this pool as a food source corroborates with the fact that the concentration of suspended detritus in the pelagic zone where the species with the highest production, *A. melettinus*, feeds, is about 15 times as high as the phytoplankton concentration.

#### *Primary production and fish production*

Gross primary production and respiration of the phytoplankton were estimated during period 1 at 13034 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> and 7091 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> respectively, resulting in a net primary production of 5943 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> or 46% of the gross primary production. This gross primary production is roughly in the same range as that reported for other shallow eutrophic tropical waterbodies such as Lake George, with 19726 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> (Ganf 1972), or Lake Chad with 5500 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> (Carmouze 1983). Observed respiration loss for Tissawewa is high compared to the range of 21 - 37% found in other studies, predominantly based on waterbodies in the temperate region (Vollenweider & Nauwerck 1961, Lewis 1974, Capblancq 1982, Sondergaard *et al.* 1985, Garnier & Mourelatos 1991). However, this is not surprising considering that bacterial respiration per unit of biomass is often higher than algal respiration (Westlake 1980), the relatively high concentration in Tissawewa of suspended detritus with associated bacteria, and the elevated water temperatures in this tropical reservoir.

During period 1 the total fish biomass is estimated at 171 kg C.ha<sup>-1</sup> and the total fish production at 243 kg C.ha<sup>-1</sup>.yr<sup>-1</sup>. Fish production is 1.9 % of the gross primary production. This is a high transfer efficiency (i.e. ratio of production of the particular step of the trophic chain to the gross primary production) compared to transfer efficiencies reported for other lakes and reservoirs ranging from 0.2% to 1.6% (Blazka *et al.* 1980). An explanation for this high transfer efficiency of fish production lies in the fact that it is caused by a short food chain: primary producers take up 71% of the total energy consumed by the fish assemblage, various invertebrate primary consumers 26% while fish, of which only 18% consists of primary consumers, takes up a meagre 2%. The estimated fish production of 540 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> by Pet *et*

*al.* (1995a) is not only extremely high compared to the production estimated in the present study but its calculated transfer efficiency is also extremely high compared to the transfer efficiencies reported for other lakes and reservoirs (Blazka *et al.* 1980). The overestimation of the fish production is probably because the steady state assumption that fish production equals the estimated mortality (Pauly 1983, 1984a, b) is not realistic over a relatively short period (ten months) in a system subject to considerable water level fluctuations.

Fish production in Tissawewa is exploited mainly by the commercial fisheries and birds. In Parakrama Samudra, another Sri Lankan reservoir, the predation by cormorants alone was estimated by Winkler (1983) at 15 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> which corresponded to the yield of the commercial fisheries (Schiemer & Duncan 1987). The impact commercial fisheries and bird predation have on the fish assemblage as well as the possible competition between these two can be assessed by estimating the amount of fish consumed by birds and by comparing the composition of the birds' diet with that of the commercial catches. The commercial catches were estimated at 24.2 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> for period 1 and 16.7 for period 2 (Pet *et al.* 1995c). During period 1, the utilisation of the biological fish production in terms of fish yield was 10.0 %, a value equal to the utilisation efficiency (i.e. ratio of fish yield to fish production) which, according to Blazka *et al.* (1980), can be obtained from lakes and reservoirs. During period 2 an even higher utilisation efficiency of 13.0% was achieved. Tilapia is by far the most important species in the commercial catches; before the drought 72% of the total catches consisted of tilapia while after the drought this was 95% (Pet *et al.* 1995c).

#### *Bird predation*

In Tissawewa predation by cormorants alone was estimated at 14 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> while the total bird predation was estimated at 53 kg C.ha<sup>-1</sup>.yr<sup>-1</sup>. Similar to Parakrama Samudra, predation by cormorants in Tissawewa after the drought, was comparable to the fisheries yield. Because Parakrama Samudra is a much larger reservoir than Tissawewa, covering an area of 2262 ha at full supply level (Winkler 1983), the ratio of inshore zone (where most birds forage) versus total area is lower, suggesting a higher predation by birds can be expected in Tissawewa. Considering the apparent correspondence between cormorant predation and commercial yield together with the commercial yield in Tissawewa before the drought it is probable that cormorant predation and thereby bird predation was affected by the relatively low fish density after the drought. The quantity of fish consumed by *Phalacrocorax spp.*, depends on the composition of the population. According to Winkler (1983) *Ph. carbo* consumes more fish per individual than *Ph. fuscicollis* which in turn consumes more fish than *Ph. niger*. Because these three species were not distinguished during the aquatic avifauna survey of Tissawewa an average fish consumption per individual, equal to that in Parakrama Samudra was assumed for *Phalacrocorax spp.* For *Phalacrocorax spp.* the main prey species can be determined from the preferred size ranges of consumed fish reported for the three species by Winkler (1983) and the assumption that selection of a fish species for consumption depends entirely on the relative abundance of a particular species within this size range. For Tissawewa during period 1, which is representative of a typical shallow, dry zone reservoir, 80% of the fish consumed by cormorants would consist of *A. melettinus* while tilapia would take up only 6%. Based on the calculated fish consumption and the preferred size ranges of prey (Cramp *et al.* 1977), storks and pelicans are probably the main consumers of tilapia and thereby the main competitor of the commercial fisheries.

### *Indigenous fish species versus exotics*

The argument of Fernando (1984) and Fernando & Holcik (1982, 1991) that fish yield in reservoirs depends on the nature of the fish community, i.e. origin with regard to lacustrine or riverine habitat, is in contradiction with the findings in this study. Although fish yield of the indigenous riverine species in Tissawewa is low, comparison of the production of indigenous and exotic species, respectively 80% and 20% during both periods, shows the indigenous species, once exploited, are capable of sustaining a much higher yield than the current yield of exotic species. The overrated importance of the exotic tilapia in Sri Lankan reservoirs is because thus far production estimates were based on commercial catches only (Fernando 1971, De Silva 1985). In a fish assemblage consisting of indigenous and exotic species, the question arises to what extent the introduction of the exotics has harmed the native fishes. Because of their lacustrine origin, the exotic tilapias, *O. mossambicus* and *O. niloticus* should be able to occupy a niche previously unfilled by the riverine indigenous species (Fernando & Holcik 1982, 1991). Although there is one indigenous species, *A. melettinus*, which also exploits the food sources phytoplankton and detritus, it cannot be considered a true competitor of the tilapias because *A. melettinus* takes its food in suspended form (Pethiyagoda 1991) whereas the tilapias feed mainly on the bottom deposits (Bowen 1979, 1980, 1981, Schiemer & Duncan 1987).

### *Estimation production of primary invertebrate consumers*

Although production of primary invertebrate consumers in Tissawewa was not measured in the present study, it can be assessed from the adjoining trophic levels, either below (primary production) or above (fish consumption) and compared to estimates for Tissawewa or similar water bodies, in other studies. Based on a gross primary production of 13034 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> the total secondary production by zooplankton and benthic invertebrates was estimated at 1659 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> using a linear relationship between total secondary invertebrate production and gross primary production calculated for waterbodies in the temperate zone (Blazka *et al.* 1980). Assuming both zooplankton and benthos are strictly herbivorous then the total secondary invertebrate production can be divided, based on the relative transfer efficiencies (Brylinski 1980), into 1253 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> zooplankton and 406 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> benthic invertebrates. Because these correlations only apply for temperate waterbodies where gross primary productions above 3500 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> were not observed and benthos was also included, the high transfer efficiency into net secondary production of 12.5% should be considered with caution. Also, since benthos production seems to be related to mixing depth (Brylinski 1980) the ratio zooplankton production to benthic invertebrate production will be smaller in a well-mixed reservoir such as Tissawewa. From estimates of zooplankton net production for the period October 1990 until June 1992 the zooplankton production during period 1 was estimated at 118 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> while for the period October 1990 until September 1991, zooplankton production was estimated at 83 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> (Amarasinghe unpublished) which is markedly lower than the estimates based on correlations with the gross primary production. For other shallow, eutrophic waterbodies in the tropics, such as Lake George (Burgis 1974, Burgis & Dunn 1978) and Lake Chad (Carmouze *et al.* 1983) zooplankton production was estimated at 216 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> and 237 kg C.ha<sup>-1</sup>.yr<sup>-1</sup> resulting in an approximate transfer efficiency of respectively 1.1% and 4.3%. Although these



values are low compared to that of the temperate zone, they are markedly higher than the transfer efficiency of 0.9% calculated for Tissawewa by Amarasinghe *et al.* (unpublished). Furthermore the estimated zooplankton production of  $118 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  is in contradiction with the calculated zooplankton consumption of  $127 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  by the entire fish assemblage. Because the zooplankton production in Tissawewa estimated by Amarasinghe *et al.* (unpublished) is not consistent with observations in comparable waterbodies or with the estimated zooplankton consumption by fish in the present study and because there are no estimates of the benthic invertebrate production in Tissawewa, the total production of invertebrate primary consumers is estimated from the consumption of the entire fish assemblage. For fish feeding on invertebrates an ecological efficiency (i.e. ratio of the food requirements of one trophic level to the production of the previous level) of 40% is used (Vijverberg *et al.* 1990). This results in estimates of zooplankton production of  $318 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  for period 1 and  $100 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  for period 2. The transfer efficiencies for zooplankton of respectively 2.4% and 1.6% are within the range observed for Lakes George and Chad. For the primary invertebrate consumers an ecological efficiency of 70 % (Winberg 1980) and a ratio of respiration to production of 1.5 (Morgan 1980) are used. Furthermore it is assumed all invertebrates are herbivorous and their diet consists of phytoplankton and detritus in the same ratio as that of the herbivorous fish, respectively 30% and 70%.

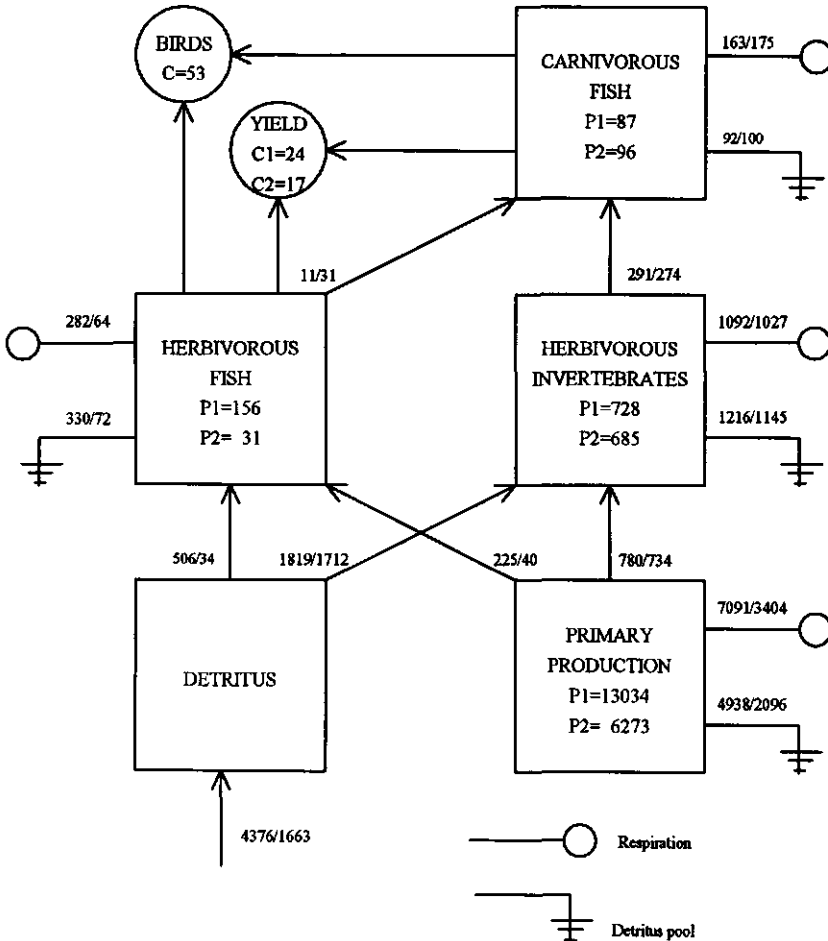
#### Foodweb

From the estimates of primary production, consumption and production of the fish assemblage together with data on commercial fisheries and bird predation as well as the above formulated assumptions pertaining to the production of primary invertebrate consumers, a foodweb for the Tissawewa ecosystem was constructed for the periods before and after drought (Fig. 7.5). Comparison of the carbon fluxes in these foodwebs clearly shows the impact of environmental change on the Tissawewa food web. During period 1 gross primary production by phytoplankton was estimated at  $13034 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  and respiration at  $7091 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$ . For the phytoplankton production during period 2, the same gross production per biomass and fraction of respiration were assumed as were measured during period 1 resulting in a gross primary production of  $6273 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  and respiration of  $3404 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$ . For the respective periods, fish production was  $243 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  and  $128 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$ . Based on the fish consumption and assumed ecological efficiency, the production by primary invertebrate consumers is calculated at  $728 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  during period 1 and  $685 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  during period 2. The consumption of the primary invertebrate consumers during period 1 is calculated to be  $780 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  of phytoplankton and  $1819 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  of detritus. The gross primary production minus respiration and a total consumption of primary consumers (both fish and invertebrates) of  $1005 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  leaves  $4938 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  to flow into the detritus pool. Adding to this comes production which is not utilised by higher trophic levels and excretion which contributes to respectively  $124 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  and  $423 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  for fish and  $437 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  and  $780 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$  for the invertebrates. From phytoplankton, invertebrates and fish there is a net autochthonous detritus production during period 1 of  $4376 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$ . Similarly the net production of autochthonous detritus for period 2 is calculated at  $1663 \text{ kg C.ha}^{-1}.\text{yr}^{-1}$ . The fact that most of the production is sustained by detritus and associated bacteria agrees with Mann (1988) who states that most of the primary production is transmitted to other trophic levels from dead decomposing plant matter rather than from living tissue. The

importance of detritus in sustaining fish production is emphasised when considering that stomachless fish such as *A. melettinus* cannot utilise phytoplankton (Bitterlich 1985) implying phytoplankton as a food source for fish in the pelagic zone is overestimated while detritus is underestimated.

According to Slobodkin (1960) efficiencies of 10% can be expected between trophic levels. The transfer efficiency to the primary consumers of 6.8% during period 1, is low relative to less productive systems, confirming the suggestion of Hillbricht-Ilkowska *et al.* (1972) that transfer efficiency decreases with increasing trophic because of the increasing importance of larger and presumably inedible algae in more eutrophic waters. The relatively high transfer efficiency during period 2 follows from the fact that primary production by macrophytes and epiphytic algae was not taken into account. The

Fig. 7.5 Foodweb distinguishing the main trophic groups in the Tissawewa ecosystem. Indicated are the energy fluxes between the compartments and the calculated respiration and flow into the detritus pool. Production (P) and consumption (C) are indicated for the periods before and after drought using numerals (resp. 1,2) while for the energy fluxes they are separated with a slash (Period 1/ Period 2).



**Table 7.8** Overview of the four major pathways of energy flow in the Tissawewa foodweb. Production ( $\text{kg C.ha}^{-1}.\text{yr}^{-1}$ ) is given for primary and secondary consumers. In case of fish consumers the name of the species is given. For species abbreviations see table 7.3. The differences between periods in fish species partaking in a specific pathway are indicated as follows: Period 1/ Period 2

Primary producer (%)	Primary consumer	Secondary consumer
	Pelagic fish: AM	GG+MY/GG
Period 1: 38	108	7
Period 2: 4	6	22
	Pelagic invertebrates	HG+RD
Period 1: 16	343	27
Period 2: 17	242	20
	Benthic fish: OM+ON	Commercial fisheries
Period 1: 15	47	17
Period 2: 14	25	16
	Benthic invertebrates	BC+BD+BS/BC+BD+BS+MY
Period 1: 30	384	53
Period 2: 65	443	53

efficiencies between primary consumers (herbivores) and secondary consumers (carnivores) are close to 10% for both periods. The observation that efficiencies in this tropical reservoir are similar compared to temperate waterbodies, strongly suggests that the high levels of fish production and fish yield in the tropics compared to the temperate zone are caused by only two factors: 1) the high level of primary production and 2) the short food chain. To what extent Tissawewa is representative for tropical waterbodies is difficult to determine because contrary to the present study of Tissawewa, the estimated fish production of most other tropical communities is based on commercial catches only, which generally exclude the smaller sized species and therefore underestimate total fish production. In Tissawewa about 90% of the total fish production is realised by size-classes 1-4 which consist of fish smaller than the gillnet selection range of the commercial fishery. Thus, the observation that in most of the tropical reservoirs in SE Asia the fish production (i.e. fish yield) is lower than would be expected on the basis of the high primary production (Henderson 1979, FAO 1980) reflects the low efficiency with which commercial fisheries exploit the entire fish assemblage rather than represents a true estimate of biological fish production.

The two environmental states of the ecosystem exemplify the inverse relationship between the two sources of primary production because of their competition for resources and confirm the hypotheses that food web structure is largely determined by plant production. During period 1 primary production by phytoplankton was high compared to period 2 when macrophytes and associated epiphytic algae were abundant. Production of macrophytes and epiphytic algae during period 2 will be higher than can be expected from the increase in area alone because the area covered with macrophytes expanded into the deeper parts of the reservoir covering the entire watercolumn and because turbidity of the water decreased. Although the total primary production was not assessed, the relative changes of the two primary producers together with the disappearance of the layer of detritus have considerable impact on the distribution of energy through the different food chains and consequently affect the food web structure and functioning.

In the Tissawewa foodweb four major pathways can be distinguished (Table 7.8): For both the pelagic and the benthic zone two pathways can be distinguished based on the nature of the primary consumers, respectively fish and invertebrates. The pelagic herbivorous fish species was the filter-feeder *A. melettinus*, the benthic herbivorous fish species were the tilapias *O. mossambicus* and *O. niloticus*. The impact of the environmental changes follows not only from the difference in the absolute amount of energy flowing through the various pathways but also from the changes in the relative contributions of these pathways to the total energy flow through the food web. These quantitative changes also affect some of the pathways qualitatively. Before the drought the benthic and pelagic pathways were about equally important as were the fish and invertebrate pathways. In the pelagic zone most of the energy was consumed by the fish while in the benthic zone this applied for the invertebrates. When the commercial fisheries are considered the main predator of the tilapias, all pathways basically consisted of three trophic levels. After the drought most of the energy flows through the benthic invertebrate pathway to the detriment of the pelagic fish pathway. The pelagic fish pathway is mainly affected by the decrease of the concentration of suspended detritus and phytoplankton together with the high predation pressure on *A. melettinus*. Contrary to the other pathways through which the flow of energy decreased, the benthic invertebrate pathway is the only pathway through which the same amount of energy flows as before the drought resulting in its relative importance. There is a two-fold explanation for this: 1) The higher turnover rate of invertebrates compared to fish allows them to recover faster (i.e. reach carrying capacity) after a catastrophe and 2) apparently the amount of dead organic matter produced by phytoplankton, macrophytes and epiphytic algae during period 2 is sufficient for a similar carrying capacity. These quantitative changes cause a major qualitative shift to occur: the piscivores *G. giuris* and *Mystus spp.* which were mainly exploiting *A. melettinus* during period 1 and were thus secondary consumers in the pelagic fish pathway switched toward exploitation of the invertebrate pathways during period 2. However, while *Mystus spp.* consume mainly the benthic invertebrates during period 2 and remain secondary consumers, *G. giuris* switches to consumption of the pelagic fish, thereby becoming a tertiary consumer and adding one more trophic level to this pathway.

#### *Bottom-up versus top-down control*

Several patterns of ecosystem organisation emerge when considering the energy fluxes in the foodweb and observed changes along the various pathways. The competition for resources between the primary producers was already established. For the second trophic level consisting of herbivorous fish and invertebrates, detritus is the main food source. Changes in quantity and quality of this food source had a considerable impact mainly on the pelagic herbivores. Biomass and production of both vertebrates (*A. melettinus*) and invertebrates (zooplankton) decreased with decreasing availability of suspended detritus suggesting that the plant-herbivore interaction was donor-controlled. This, together with the observed importance of competition for resources and accommodative processes such as resource partitioning at the second and third trophic levels (Piet *et al.* Chapter 5) strongly suggest that the Tissawewa ecosystem is overall bottom-up controlled. However, one example of top-down control was observed. During period 2 the biomass and production of *A. melettinus* was clearly controlled by *G. giuris*. The fact that this example of top-down control was not observed during period 1

confirms the hypotheses that changing environments can affect species interactions (Dunson & Travis 1991, Hunter & Price 1992) and that top-down forces between secondary and primary consumers can be modulated by the primary producers (Power 1992). The apparent increase in efficiency with which *G. giuris* exploits *A. melettinus* in an environment, with relatively clear water and sufficient cover for predators, such as that present after the drought, follows from the increased top-down force (Power 1992) and corresponds with the observed preference of *G. giuris* for the littoral zone during period 1 (Pet & Piet 1993, Piet *et al.* Chapter 4). A notion of the trophic relationships in Tissawewa also clarifies why trophic cascades are not likely to occur in this system. All major pathways consist of three trophic levels implying that predator control will affect the level of the primary consumers. Since both the pelagic and the benthic trophic chains consist of an invertebrate and fish pathway, predator control on species of one of these pathways will inevitably result in the species belonging to the other pathway, taking advantage and thereby preventing the top-down effect from cascading down the food chain. This is corroborated by a comparison of the energy fluxes in the foodwebs and efficiencies between trophic levels for the two ecosystem states showing that in spite of the drastic changes in the pathways of the energy fluxes and the composition of the various trophic levels, the overall transfer efficiency remains fairly constant. The decrease of *A. melettinus* due to predation and the subsequent shift of its predator to the pelagic secondary consumers revealed another stabilising effect in the Tissawewa food web: the lower abundance of *A. melettinus* will result in an increase in the zooplankton density which, in turn will increase the density of the zooplanktivorous fish, *H. gaimardi* and *R. daniconius*, which are suffering from an increased predation pressure by the shifting piscivore. This corresponds to the premise of Strong (1992) that the occurrence of trophic cascades in the community sense is restricted to fairly low diversity communities where great influence can be issued from one or a few species. Although there are several studies based on a variety of aquatic systems, indicating that even complex, highly interconnected webs can respond to perturbations of higher trophic levels with chain like dynamics (for review see Power 1982), the results of the present study emphasise the importance of multi-trophic studies on speciose ecosystems in order to comprehend and predict how trophic interactions can determine the structure and functioning of an ecosystem.

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## CHAPTER 8

### CONSEQUENCES OF THE ECOSYSTEM PERSPECTIVE FOR THE MANAGEMENT OF A TROPICAL RESERVOIR FISHERY

G.J. Piet

#### Introduction

When considering the application of ecosystem-based approaches to fisheries management, several concepts of hierarchical organisation can be distinguished: a primary organisational feature of aquatic ecosystems is their hierarchical structure which, in part, is captured by the familiar concept of levels of organisation. This hierarchical structure can be either nested or non-nested. An example of the former are ecosystems which are composed of individual organisms, populations and communities, representing a stepwise progression in complexity. Each level of the hierarchy is composed of the elements of the next lower level. The dynamics at each level, however, are influenced by biotic and abiotic factors interacting within and between levels. In contrast, an example of a non-nested hierarchical organisation is that based on the particle-size distribution. According to O'Neill *et al.* (1986) this concept of hierarchical organisation presents a more flexible and precise approach which emphasises a "function-preserving fractionation" that identifies structural discreteness and associated differences in process rates. The central premise of hierarchy theory is that organisation in complex systems results from differences in process rates (Allen & Starr 1982) and thereby recognises the functional redundancy inherent in the taxonomic diversity of ecological systems. However, since fisheries management is primarily concerned with determining the sustainable yield from a standing stock of a particular species (Larkin 1977, Maclean & Evans 1981), the effective ecosystem models must be interpretable at the species level.

There is a growing awareness that variation in abundance of fishes in a population depends on parental stock size and structure, intra- and interspecific interactions and abiotic environmental factors. Until relatively recently, process-oriented studies have been aimed primarily at the effects of stock size and environmental variability on fish populations, with little attention to interspecific effects. At present, fisheries managers require models which also include the effects of competitive and predatory interactions between species on the structure and production dynamics of the fish communities they wish to manage (Evans *et al.* 1987). Both these interactions are body size dependent. The extent to which the fish assemblage demonstrates characteristics of stability can also have important implications for fisheries management because this implies that a certain degree of stress can be tolerated without causing transformation of the whole system (Kerr 1977, Evans *et al.* 1987).

In this chapter the relevance of an ecosystem perspective for the management of a tropical reservoir fishery is discussed on the basis of a case study. In Tissawewa, a shallow Sri Lankan reservoir subject to considerable environmental perturbation, the entire fish

community was sampled together with important environmental parameters. The impact on the fish community of competition, predation, water level management and species introductions are discussed as well as their consequences for management of the fisheries. Within the fish community, the study distinguished taxonomic components, body sizes and different levels of complexity.

## Competition

The niche occupation of the ten most important fish species was determined along three dimensions: the trophic, the spatial and the temporal dimension (Chapter 5). The position along the trophic dimension depends on the diet of the species, the position along the spatial dimension on the distribution over the various habitats in the reservoir, and the position along the temporal dimension depends on the time of day the species are actively foraging. Because the body size of fish can increase several orders of magnitude during ontogeny which, in turn, can have considerable consequences for the niche occupation of an individual, each species was subdivided into size-classes for which niche occupation was determined separately. At best, this approach will lead to the formulation of hypotheses pertaining to the effect of intra- and interspecific interactions in determining the structure of the fish community, which can be determined much clearer if experimental manipulations of competitors or resources are performed. This, although unintentionally, was achieved by the drought which reduced fish density and affected availability of important resources such as the primary producers, detritus and primary invertebrate consumers such as zooplankton thereby distinguishing two different environmental states. Comparison of resource use and the degree of resource partitioning between these environmental states showed that resource partitioning increased with increasing fish density. This strongly suggests competition and resource partitioning are important factors structuring the fish community (Schoener 1983). In general the fish species belonging to the same guilds experience the same habitat profitability for their main food items (Chapter 4) and forage at the same time of day (Chapter 3) which implies that resource partitioning along each of the resource dimensions or predator avoidance will result in suboptimal foraging which in turn can affect fish production through a decrease of growth and reproductive rates.

The most important species for the commercial fisheries in Tissawewa are the exotic tilapias *O. mossambicus* and *O. niloticus* (Pet *et al.* 1995c). Based on the niche occupation of the fish species in Tissawewa there is only one potential competitor for the tilapias: *A. melettinus*. Both the tilapias and their potential competitor utilise phytoplankton and detritus as their major food sources. Because these food sources do not appear to be limiting (Chapter 7), exploitative competition is probably not important for these species. In contrast, interference competition most probably is very important, because under the conditions prevailing in most Sri Lankan reservoirs, the density and biomass of *A. melettinus* in Tissawewa are about forty, respectively five times, that of the tilapias. Studying the size-specific niche occupation shows that the juveniles of all species, including the tilapias, feed mainly on zooplankton, which means that the juveniles of the tilapias have to compete for this food source with the juveniles of the other fish species, and the adult zooplanktivores *H. gaimardi* and *R. daniconius* besides. Therefore a

subsidiary gillnet fishery aimed specifically at exploiting the small pelagic species *A. melettinus*, *H. gaimardi* and *R. daniconius* will most probably increase production of the tilapias. Because these small pelagics are spatially segregated from the juveniles of the tilapias this subsidiary gillnet fishery will not harm the existing fishery on tilapia (Pet & Piet 1993).

Competition at a higher trophic level, directly affecting fish yield, is that between the commercial fisheries and birds. The estimated fish consumption by birds is more than twice the yield of the commercial fisheries (Piet *et al.* Chapter 7). However, based on the preferred size ranges of each of the bird species only a minor part of the fish consumed by birds will consist of tilapias. In Tissawewa storks and pelicans are probably the main consumers of tilapia and thereby the main competitors of the commercial fisheries (Piet *et al.* Chapter 7).

### Predation

The most important piscivorous fish are *Mystus spp.* and *G. giuris*. These species feed mainly on adults of the species *A. melettinus*, *H. gaimardi* and *R. daniconius* (Chapter 4). Under the conditions normally prevailing in the Sri Lankan reservoirs the fish community structure in Tissawewa is regulated by bottom-up processes and the piscivores do not seem to be able to control the large stock of *A. melettinus*, resulting in the fish community being dominated by this species (Chapter 7). Possibly, the estuarine origin of the main indigenous piscivore, *G. giuris*, is the reason that this species is not sufficiently adapted to the lacustrine conditions preventing it from efficiently exploiting its potential prey species. This is confirmed by the fact that *G. giuris* appeared to be considerably more efficient when the transparency of the water was higher (Chapter 7). Similar communities in the temperate zone without large efficient piscivores were observed to be often dominated by stunted populations of a single species (Svärdson 1976).

A large body size and relatively long lifetime are key characteristics of predators as integrators of community structure. Storage of periodic recruitment success in the adults of long-lived predators contributes to the stability of the community. Piscivores were reported to promote diversity in temperate fish communities by maintaining prey species at more equitable densities than would otherwise be realised (Svärdson 1976). The density-dependent switch by the predators to alternative prey also observed by the indigenous piscivores *Mystus spp.* and *G. giuris* (Chapter 7) will maintain the abundance and diversity of prey species. Thus, introduction of a piscivore, more efficient at exploiting the small pelagic fish, notably *A. melettinus*, may increase diversity and stability of the fish community while at the same time converting the production of small pelagics into a product of much higher market quality. The possible benefits to the existing fishery on tilapias, of exploiting the small pelagics were already mentioned above. The best candidate for a stocking program in Sri Lankan lowland reservoirs was suggested by Pet *et al.* (1995a) to be *Lates calcarifer* (Bloch), an estuarine predator, indigenous to Sri Lanka, which grows well in fresh water reservoirs, but does not reproduce in land-locked situations (Senanayake & Fernando 1985).



## Water level management

The objective of fisheries managers to maintain stable and harvestable abundances of species can only be achieved if the integrity of the communities and ecosystems of which these species are part, are maintained. This, of course, is difficult in reservoirs of which the main purpose is the supply of irrigation water for the rice cultivation. However, the recent increase of the importance of freshwater fish production, both in terms of income as well as a source of protein, for the population in the dry zone, necessitates a quantitative study of the effect of water level fluctuations on fish production. This allows the irrigation departments to incorporate not only the production of rice but also the production of fish in their decisions on the management of the water level in the reservoirs.

Table 8.1 Water level dependent instantaneous total mortality ( $\text{yr}^{-1}$ ) for the six most abundant fish species. For all species except for *O. mossambicus* this is also their natural mortality. Note the relatively high total mortality during "low" water level compared to "high" or "intermediate" water level.

Species	Water level		
	High	Intermediate	Low
<i>A. melettinus</i>	3.2	3.3	3.8
<i>B. chola</i>	2.3	2.1	2.8
<i>B. dorsalis</i>	1.8	1.9	2.4
<i>B. sarana</i>	1.4	1.9	2.5
<i>R. daniconius</i>	2.3	3.3	3.8
<i>O. mossambicus</i>	6.3	5.4	7.2

The water level can affect fish production in Tissawewa both directly and indirectly. Directly because with the outflowing water there is also a loss of fish biomass which cannot be harvested and because with a decreasing water level the size of the reservoir decreases and consequently the total fish production in the reservoir per measure of time decreases (Chapter 6). The indirect effect of the water level on fish production can be caused by a loss of spawning sites and refuges for the juveniles which can limit the recruitment, and by increased competition for resources which causes a decrease in condition (Chapter 6) and an increase in natural mortality (Table 8.1). Furthermore it was shown that extreme low water levels (in case of Tissawewa below 1.5 m at the deepest point) disturb the equilibrium structure of the fish community. To study this, three water level ranges were distinguished in Tissawewa (Chapter 6): 1) high water level when competition for resources is minimal and the littoral zone is covered with water thereby providing optimal conditions for a successful recruitment, 2) intermediate water level when competition is higher and the littoral zone is dry and 3) low water level when due to increased natural mortality the equilibrium community structure is disturbed. A possible management strategy would be to maintain the water level within high water level boundaries at the onset of the monsoons, around November and May, when spawning activity is at its highest (Pet *et al.* 1995a) and to avoid at all times a "low" water level.

## Species introductions

The effect and success of an exotic species depends largely on 1) its ability to secure a portion of the energy available by either occupying an unfilled niche or 2) by successfully sharing a common niche while escaping predation, or 3) simply by displacing a potential competitor by its fitness (Evans *et al.* 1987). In the first case, the indigenous species will hardly be affected by the introduction while the latter two cases will result in various degrees of disruption of the indigenous fish community. It might be possible to predict the success of an introduction by comparing the niche characteristics throughout ontogeny and life-table parameters of the exotic with those of the indigenous species. Ecomorphology can be an important tool for predicting the niche occupation of the exotic after the introduction in a particular community, providing relationships are established between morphological characters and resource use. Although for only a few morphological characters a relationship with a species' diet was established, the predicted trophic structure of the Tissawewa fish community based on these morphological characters (Chapter 2) coincided with the actually observed trophic structure (Chapter 5), thereby confirming the potential of the ecomorphological approach. Also the niche occupation along the trophic dimension of the exotic tilapias was according to expectations based on their morphological characters. The negligible effect of predacious fish on the tilapias follows from the growth curves of the tilapias (Chapter 7) and the limited gape size of the indigenous predators (Chapter 2) which indicate the relatively small part of their life-span the tilapias are subject to predation by fish.

In contrast to the introduced exotic tilapias which occupied an unfilled niche, the possible management measure of the introduction of a larger, more efficient predator than the indigenous predators in Tissawewa will undoubtedly affect the indigenous piscivores. The exploitation of the tilapias by such an introduced predator can be prevented by choosing a predator which is constrained by morphological characters such as its gape width to utilise prey of the size of adult tilapias. Although the suggested piscivore, *Lates calcarifer* (Pet *et al.* 1995a), was reported to feed on smaller prey in other waterbodies, no morphological constraints are known which can prevent this species from exploiting the tilapia populations and thereby harming the existing fishery.

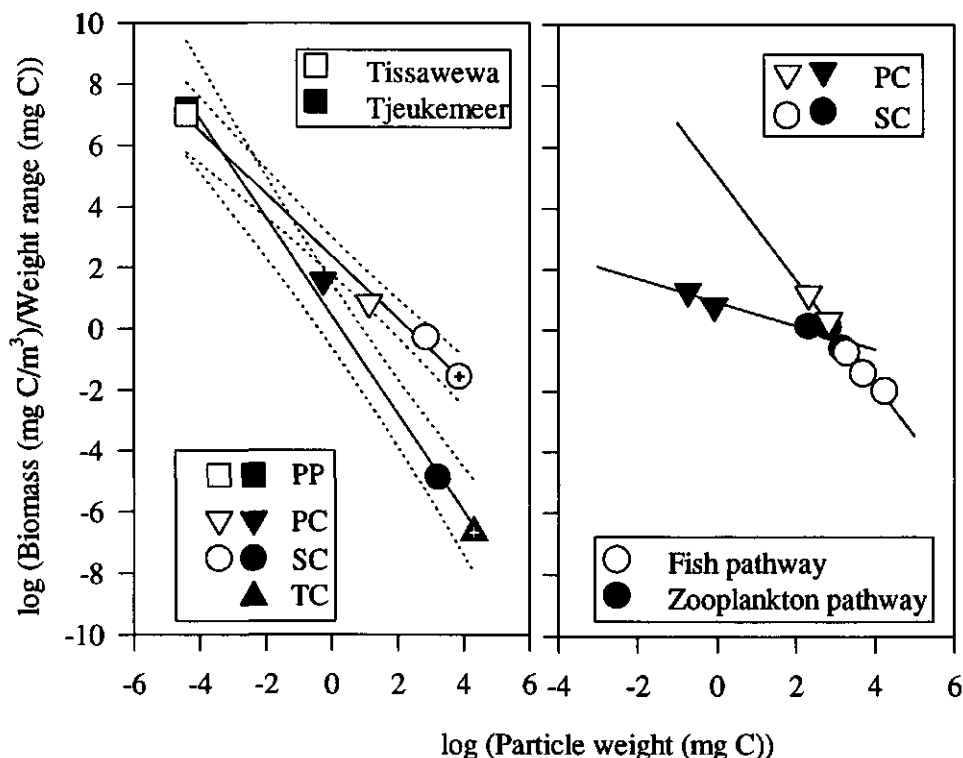
## Potential for management measures in a tropical reservoir

The potential for management measures in the Tissawewa ecosystem are discussed based on a concept in which two approaches are combined: the particle size approach and the food web approach (Evans *et al.* 1987). This concept is also used to compare a tropical aquatic ecosystem (Tissawewa) with a similar ecosystem located in the temperate zone (Tjeukemeer, Gons unpublished, Grift 1995, Mooij unpublished). Tjeukemeer is a shallow (mean depth = 1.5 m) eutrophic lake in the Netherlands. The lake is much exposed to wind and the water is very turbid (Secchi-depth transparency = 25 - 35 cm).

Particle size theory entails the size distribution within ecological systems, i.e. the relative frequency of size-classes rather than age or taxonomic classes. Observations on pelagic marine communities (Sheldon & Parsons 1967, Sheldon *et al.* 1972) and freshwater ecosystems (Sprules *et al.* 1983, Sprules & Munawar 1986) revealed that

particle concentrations conform to regular patterns when grouped into logarithmic size intervals. According to Sprules & Munawar (1986) a particular ecosystem can be quantitatively described by the "normalised" size distribution. These "normalised" size distributions can then be compared between ecosystems. Based on food web theory different trophic levels (e.g. primary producers, primary-, secondary and tertiary consumers) can be distinguished. In the temperate zone the main primary-, secondary and tertiary consumers are respectively herbivorous zooplankton, zooplanktivorous fish and piscivorous fish. In contrast, in Tissawewa and probably the tropics in general much of the piscivorous fish are in fact secondary consumers. Thus, for comparison of a tropical and a temperate ecosystem the following trophic groups were chosen: primary producers, primary consumers, zooplanktivorous fish and piscivorous fish.

Fig. 8.1 "Trophic group-standardised" size distributions of the pelagic zone. a) regressions for a tropical (Tissawewa) and a temperate (Tjeukemeer) ecosystem. Indicated are the primary producers (PP), the primary consumers (PC), the secondary consumers (SC) and tertiary consumers (TC). Symbols marked with "+" indicate piscivory. b) regressions for two energy pathways in the Tissawewa ecosystem. Indicated are different size ranges of the primary consumers (PC) and the secondary consumers (SC).



Particle size- and food web theory are combined into one concept by determining the size-range, average size and biomass of each of the trophic groups. This "trophic group-standardised" size distribution can be used to compare the Tissawewa and Tjeukemeer ecosystems (Fig. 8.1a). Similar to the "normalised" size distribution, the slope of the regression is proportional to the difference between the efficiency of converting small particles into larger ones and the exponent of the allometric relationship between body size and turnover rate (Borgmann 1982). The regressions for both ecosystems are highly significant ( $R^2=0.99$ ,  $p<0.01$ ). The significantly ( $p\leq 0.05$ ) steeper slope of the regression for Tjeukemeer indicates the efficiency of this ecosystem during the growing season is higher than that of Tissawewa. However, it should be realised that, contrary to the tropics where it is year-round, this growing season lasts only about half a year in the temperate zone. Consequently, on a yearly basis, efficiency will probably be lower in the temperate zone. Other notable differences between the two ecosystems are the larger size of the primary consumers, the smaller size of the piscivores and the lack of tertiary consumers in Tissawewa. The former is because the primary consumers in the pelagic zone of Tissawewa consist of both zooplankton and fish (*A. melettinus*) while those of Tjeukemeer consist of only zooplankton. Because of this, the biomass in Tissawewa allocated in fish-size particles is markedly higher than in Tjeukemeer. Therefore, there is potential for a much more efficient exploitation of the tropical ecosystem. The relatively high biomass and small size of the fish in Tissawewa compared to Tjeukemeer confirms the possibility of introducing a larger piscivore to exploit this large standing stock of small fish.

The implications of the fact that the primary consumers in the pelagic zone of Tissawewa consist of both fish and zooplankton are further studied by distinguishing two major pathways: the zooplankton and the fish pathway (Chapter 7). For each of these pathways, the "trophic group-standardised" size distributions are determined based on different size-ranges of the primary and secondary consumers (Fig. 8.1b). For both pathways the regressions are highly significant (fish pathway:  $R^2=0.98$ ,  $p\leq 0.01$  and zooplankton pathway:  $R^2=0.90$ ,  $p\leq 0.01$ ). The extrapolations of the "trophic group-standardised" size distributions for each pathway strongly suggest that in case of competition between zooplankton and *A. melettinus*, niche segregation will be realised by exploiting different size ranges of the resource: zooplankton utilising the smaller sized particles, and *A. melettinus* the larger. However, the exact ranges can only be determined if the size-spectra of their common resource are known. Considering the fact that the Tissawewa ecosystem is bottom-up regulated and the existence of two complementary pathways of energy, it is important to determine to what extent the relative importance of the two pathways is governed by the size-spectra of their common resource.

## Conclusions

Based on the findings of this case study on a tropical ecosystem and the comparison with an ecosystem in the temperate zone, it can be concluded that there is considerable potential for increasing the yield in Tissawewa and most probably tropical waterbodies in general. At present the fish yield in Tissawewa is 10% of the total biological fish production but there is a vast potential of unexploited fish populations in for

example the pelagic zone which can be harvested (either directly, or indirectly by the introduction of a predator) without harming the existing commercial fishery. Probably the existing gillnet fishery on tilapia, will even benefit from these measures because they will, at least partially, release the main target species of this fishery, from competition. Considering the current status of the fishery, and the potential for improvement, it can be concluded that the utilisation efficiency (yield/ production) of 10%, which is assumed that can normally be obtained from lakes and reservoirs (Blazka *et al.* 1980), is a considerable underestimation at least for Tissawewa, and most probably for all such waterbodies in the tropics. The reason this 10% value was considered to apply to fish communities in both the tropics and the temperate zone lies in the combination of anthropogenic and biological factors. In the temperate zone the estimates of the relatively low biological fish production were in general reliable because based on the entire fish community and exploitation of this fish production was relatively efficient. In contrast, in the tropics the relatively high fish production was underestimated because these estimates were based on the commercial catches only which, besides, were often less efficient in exploiting the fish production.

## REFERENCES

- Adamicka, P. 1983. Contributions to the functional anatomy of the feeding apparatus of five cyprinids of Parakrama Samudra (Sri Lanka). p.171-175. In: F. Schiemer (ed.) Limnology of Parakrama Samudra - Sri Lanka, W. Junk Publ., Den Haag.
- Adams, S.M. & McLean, R.B. 1985. Estimation of largemouth bass, *Micropterus salmoides* Lacepede, growth using the liver somatic index and physiological variables. J. Fish Biol. 26: 111-126.
- Alabaster, J.S. & Robertson, K.G. 1961. The effect of diurnal changes in temperature, dissolved oxygen and illumination on the behaviour of roach (*Rutilus rutilus* (L.)), bream (*Abramis brama* (L.)) and perch (*Perca fluviatilis* (L.)). Anim. Behav. 9: 187-192.
- Aleev, Y.G. 1969. Function and gross morphology in fish. Israel program for scientific translations, Jerusalem.
- Allen, T.F.H. & Starr, T.B. 1982. Hierarchy, perspectives for ecological complexity. University of Chicago Press, Chicago.
- Anderson, J.M. 1987. Production and decomposition in aquatic ecosystems and implications for aquaculture. p. 123-147. In: Moriarty D.J.W. & Pullin R.S.V. (eds.) Detritus and microbial ecology in aquaculture. ICLARM Conference proceedings.
- Anderson, O. 1984. Optimal foraging by largemouth bass in structured environments. Ecology 65: 851-861.
- Atchley, W.R., Gaskins, C.T., & Anderson, D. 1976. Statistical properties of ratios. I. Empirical results. Systematic Zoology 25: 137-148.
- Bailey-Watts, A.E. 1974. The algal plankton of Loch Leven, Kinross. Proc. R. Soc. Edinb. 74: 135-156.
- Baker, J.A. & Ross, S.T. 1981. Spatial and temporal resource utilization by southeastern cyprinids. Copeia 1: 178-189.
- Baldwin, M.F. 1991. Natural resources of Sri Lanka: conditions and trends. Natural Resources, Energy and Science Authority of Sri Lanka, Colombo. 280 p.
- Balon, E.K. 1985. Early life history of fishes. New developmental and evolutionary perspectives. In: E.K. Balon (ed.) Developments in Env. Biol. Fish. 5, Dr. W. Junk Publishers, Dordrecht.
- Baltz, D.M., Moyle, P.B. & Knight, N.J. 1982. Competitive interactions between benthic stream fishes, Riffle Sculpin *Cottus gulosus* and Speckled Dace, *Rhinichthys osculus*. Can. J. Fish. Aquat. Sci. 39: 1502-1511.
- Barel, C.D.N. 1983. Towards a constructional morphology of cichlid fishes (Teleostei, Perciformes). Neth. J. Zool. 33: 357-424.
- Barel, C.D.N., Anker, G.C., Witte, F., Hoogerhoud, R.J.C. & Goldschmidt, T. 1989. Constructional constraint and its ecomorphological implications. Acta Morphol. Neerl.-Scand. 27: 83-109.
- Begg, G.W. 1976. The relationship between the diurnal movements of some of the zooplankton and the sardine *Limnothrissa miodon* in Lake Kariba, Rhodesia. Limnol. Oceanogr. 21: 529-539.

- Begon, M., Harper, J.L., Townsend, C.R.** 1986. Ecology. Blackwell Scientific Publications, Oxford. 876 p.
- Bertalanffy, L. von** 1934. Untersuchungen über die Gesetzmäßigkeiten des Wachstums. Allgemeine Grundlagen der Theorie. Roux d'Arch. Entwicklungsmech. Org. 131: 613-653.
- Bhatt, V.S.** 1971. Studies on the biology of some freshwater fishes. Part V, *Mystus vittatus* (Bloch). J. Bombay Nat. Hist. Soc. 68: 556-572.
- Bitterlich, G.** 1985. The nutrition of stomachless phytoplankton fish in comparison with *Tilapia*. Hydrobiologia 121: 173-179.
- Blazka, P., Backiel, T. & Taub, F.B.** 1980. Trophic relationships and efficiencies. p. 393-410. In: E.D. Le Cren & R.H. Lowe-McConnell (eds.) The functioning of freshwater ecosystems. Cambridge University Press. London.
- Bock, W.J. & Wahlert, G. von** 1965. Adaptation and the form-function complex. Evolution 19: 269-299.
- Bock, W.J.** 1980. The definition and recognition of biological adaptation. Amer. Zool. 20: 217-227.
- Bolger, T. & Connolly, P.L.** 1989. The selection of suitable indices for the measurement and analysis of fish condition. J. Fish Biol. 34: 171-182.
- Booth, D.J. & Keast, J.A.** 1986. Growth energy partitioning by juvenile bluegill sunfish, *Lepomis macrochirus* Rafinesque. J. Fish Biol. 28: 37-45.
- Borgmann, U.** 1982. Particle size conversion efficiency and total animal production in pelagic ecosystems. Can. J. Fish. Aquat. Sci. 39: 668-674.
- Bowen, S.H.** 1978. Benthic diatom distribution and grazing by *Sarotherodon mossambicus* in Lake Sibaya, South Africa. Freshwat. Biol. 8: 449-453.
- Bowen, S.H.** 1979. Determinants of the chemical composition of periphytic detrital aggregate in a tropical lake (Lake Valencia, Venezuela). Arch. Hydrobiol. 87: 166-177.
- Bowen, S.H.** 1979. A nutritional constraint in detritivory by fishes: The stunted population of *Sarotherodon mossambicus* in Lake Sibaya, South Africa. Ecol. Monogr. 49: 17-31.
- Bowen, S.M.** 1980. Detrital nonprotein amino acids are the key to rapid growth of *Tilapia* in Lake Valencia, Venezuela. Science 207: 1216-1218.
- Bowen, S.H.** 1981. Digestion and assimilation of periphytic detrital aggregate by *Tilapia mossambica*. Trans. Amer. Fish. Soc. 110: 239-245.
- Bowen, S.H.** 1982. Feeding, digestion and growth - Qualitative considerations. In: R.S.V. Pullin & R.H. Lowe-McConnell (eds.) The biology and culture of tilapias. ICLARM Conference Proceedings 7, International centre of living aquatic resources management, Manila, Philippines.
- Bowen, S.H.** 1988. Detritivory and herbivory. p. 243-247. In: C. Lévêque, M.N. Bruton & G.W. Ssentongo (eds.) Biology and ecology of African freshwater fishes. Orstom. Paris.
- Bowers, M.A. & Brown, J.H.** 1982. Body size and coexistence in desert rodents: chance or community structure? Ecology 63: 391-400.
- Brett, J.R. & Groves, T.D.D.** 1979. Physiological energetics. In: W.S. Hoar, D.J.

- Randall and J.R. Brett (eds.) Fish physiology, Volume VIII, Bioenergetics and growth. Academic press, New York.
- Brylinski, M.** 1980. Estimating the productivity of lakes and reservoirs. p. 411-454. In: E.D. Le Cren & R.H. Lowe-McConnell (eds.) The functioning of freshwater ecosystems. Cambridge University Press. London.
- Burgis, M.J.** 1974. Revised estimates for the biomass and production of zooplankton in Lake George, Uganda. Freshwat. Biol. 4: 535-541.
- Burgis, M.J., Darlington, J.P.E.C., Dunn, I.G., Ganf, G.G., Gwahaba, J.J.G. & McGowan, L.M.M.** 1973. The biomass and distribution of organisms in Lake George, Uganda. Proc. R. Soc. Lond. 184: 271-298.
- Burgis M.J. & Dunn I.G.** 1978. Production in three contrasting ecosystems. p. 137-158. In: Gerking S.D. (ed.) Ecology of freshwater fish production Blackwell Sci. Publ., Oxford.
- Calder, W.A.** 1984. Size, function, and life history. Harvard University Press, Cambridge.
- Capblancq, J.** 1982. Phytoplankton et production primaire. p. 1-48. In: R. Pourriot, J. Capblancq, P. Champ & J. Meyer (eds.) Ecologie des eaux continentales. Masson, Paris.
- Capone, T.A., & Kushlan, J.A.** 1991. Fish community structure in dry-season stream pools. Ecology 72: 983-992.
- Carmouze, J.P., Durand, J.R. & Leveque, C.** 1983. Lake Chad: Ecology and productivity of a shallow tropical ecosystem. Monographiae Biologicae 53, Dr. W. Junk Publishers, The Hague, Boston.
- Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R.** 1985. Cascading trophic interactions and lake productivity. BioScience 35: 634-639.
- Chandrasoma, J. & De Silva, S.S.** 1981. Reproductive biology of *Puntius Sarena*, an indigenous species, and *Tilapia Rendalli* (melanopleura), an exotic, in an ancient man-made lake in Sri Lanka. Fisheries Management 12: 17-28.
- Charnov, E.L., Orians, G.H., & Hyatt, K.** 1976. Ecological implications of resource depression. Am. Nat. 110: 247-259.
- Chesson, P.L.** 1986. Environmental Variation and the Coexistence of Species. p. 240-256. In: J. Diamond, & T.J. Case (eds.) Community Ecology. Harper and Row, New York.
- Chesson, P. & Rosenzweig M.** 1991. Behavior, heterogeneity, and the dynamics of interacting species. Ecology 72: 1187-1195.
- Clark, C.W. & Levy, D.A.** 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. Am. Nat. 131: 271-290.
- Cody, M.L.** 1968. On the methods of resource division in grassland bird communities. Am. Nat. 102: 107-148.
- Colwell, R.K. & Fuentes, E.R.** 1975. Experimental Studies of the Niche. pp. 281-310.
- Colwell, R.K. & Futuyma, D.J.** 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.
- Cone, R.S.** 1989. The need to reconsider the use of condition indices in fishery science. Trans. Amer. Fish. Soc. 118: 510-514.
- Connell, J. H.** 1983. On the prevalence and relative importance of interspecific



- competition: Evidence from field experiments. *Am. Nat.* 122: 661-696.
- Craig, J.F.** 1977. Seasonal changes in the day and night activity of adult perch, *Perca fluviatilis* L. *J. Fish Biol.* 11: 161-166.
- Cramp, S., Simmons, K.E.L., Ferguson-Lees, I.J., Gillmor, R., Hollom, P.A.D., Brooks, D.J. Collar N.J. Dunn E. & Perrins C.M** 1993. Handbook of the birds of Europe, the Middle East and North Africa, The birds of the Western Palearctic. Oxford University Press, Oxford.
- Crowder, L.B. & Cooper, W.E.** 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63: 1802-1813.
- Crowder, L.B., Magnuson, J.J. & Brandt, S.B.** 1981. Complementarity in the Use of Food and Thermal Habitat by Lake Michigan Fishes. *Can. J. Fish. Aquat. Sci.* 38: 662-668.
- De Groot, S.J.** 1969. Digestive system and sensorial factors in relation to feeding behaviour of flatfish (Pleuronectiformes). *J. Const. int. Explor. Mer* 32: 385-395.
- Dempster, P.W., Beveridge, M.C.M. & Baird, D.J.** 1993. Herbivory in the tilapia *Oreochromis niloticus* - a comparison of feeding rates on phytoplankton and periphyton. *J. Fish Biol.* 43: 385-392.
- Dervo, B.K., Hegge, O., Hessen, D.O. & Skurdal, J.** 1991. Diel food selection of pelagic Arctic charr *Salvelinus alpinus* (L.), in brown trout, *Salmo trutta* L., in Lake Atnsjo, SE Norway. *J. Fish Biol.* 38: 199-210.
- De Silva, S.S.** 1983. Reproductive strategies of some major fish species in Parakrama Samudra reservoir and their possible impact on the ecosystem-a theoretical consideration. p. 185-192. In: F. Schiemer (ed.) *Limnology of Parakrama Samudra - Sri Lanka*, The Hague: Dr. W. Junk Publishers.
- De Silva, S.S.** 1985. Status of the cichlid *Sarotherodon mossambicus* (Peters) in the reservoir fishery of Sri Lanka: A management strategy and ecological implications. *Aquaculture and Fisheries Management* 1: 91-102.
- De Silva, S.S.** 1986. Reproductive biology of *Oreochromis mossambicus* populations of man-made lakes in Sri Lanka: a comparative study. *Aquaculture and Fisheries Management* 17: 31-47.
- De Silva, S.S.** 1988. Reservoirs in Sri Lanka and their fisheries. *FAO Fisheries technical paper* 298, 128 pp.
- De Silva, S.S. & Chandrasoma, J.** 1980. Reproductive biology of *Sarotherodon mossambicus*, an introduced species in an ancient man-made lake in Sri Lanka. *Env. Biol. Fish.* 5: 253-259.
- De Silva, S.S., Cumaratunga, P.R.T. & De Silva, C.D.** 1980. Food, feeding ecology and morphological features associated with feeding of four co-occurring cyprinids (Pisces: Cyprinidae). *Netherlands Journal of Zoology* 30: 54-73.
- De Silva, S.S. & Sirisena, H.K.G.** 1988. Observations on the nesting habits of *Oreochromis mossambicus* (Peters) (Pisces: Cichlidae) in Sri Lankan reservoirs. *J. Fish Biol.* 33: 689-696.
- Diehl, S.** 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. *Oikos* 53: 207-214.
- Doble, B.D. & Eggers, D.M.** 1978. Diel feeding chronology, rate of gastric evacuation,

- daily ration and prey selectivity in Lake Washington juvenile sockeye salmon (*Oncorhynchus nerka*). Trans. Am. Fish. Soc. 107: 36-45.
- Douglas, M.E.** 1987. An ecomorphological analysis of niche packing and niche dispersion in stream fish clades. p. 144-149. In: W.J. Matthew and D.C. Heins (eds.) Community and evolutionary ecology of North American stream fishes. University of Oklahoma press, Norman, Oklahoma, USA.
- Drenner, D.W., Vinyard, G.L. & Gophen M.** 1987. Experimental study of size-selective phytoplankton grazing by a filter-feeding cichlid and the cichlid's effects on plankton community structure. Limnol. Oceanogr. 32: 1138-1144.
- Drent, R., Ebbinge, B. & Weijland, B.** 1981. Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. Verh. Orn. Ges. Bayern 23: 239-264.
- Duncan, A., Gunatilaka A. & Schiemer F.** 1990. Limnological aspects of landscape management in Sri Lanka. Proceedings of the International Symposium "Ecology and Land Landscape Management in Sri Lanka". p. 381-395. In: W. Erdelen, C. Preu & C.M. Madduma Bandara (eds) Margraf Scientific Books.
- Dunn, I.G.** 1975. Ecological notes on the Haplochromis (Pisces: Cichlidae) species-flock of Lake George, Uganda (East Africa). J. Fish. Biol. 7: 651-666.
- Dunson, W.A. & Travis, J.** 1991. The role of abiotic factors in community organization. Am. Nat. 138: 1067-1091.
- Dvorák, J. & Best, E.P.H.** 1982. Macro-invertebrate communities associated with the macrophytes of Lake Vechten: structural and functional relationships. Hydrobiologia 95: 115-126.
- Eggold, B.T. & Motta, P.J.** 1992. Ontogenetic dietary shifts and morphological correlates in striped mullet, *Mugil cephalus*. Env. Biol. Fish. 34: 139-158.
- Emery, A.R.** 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. J. Fish. Res. Bd. Can. 30: 761-774.
- Evans, D.O., Henderson, B.A., Bax, N.J., Marshall, T.R., Oglesby, R.T., & Christie, W.J.** 1987. Concepts and methods of community ecology applied to freshwater fisheries management. Can. J. Fish. Aquat. Sci. 44: 448-470.
- Evans, F.C.** 1956. Ecosystem as the basic unit in ecology. Science 123: 1127-1128.
- Fänge, R. & Grove, D.** 1979. Digestion. p. 161-260. In: W.S. Hoar, D.J. Randall & J.R. Brett (eds.) Fish physiology Vol. VIII. Academic Press. New York.
- FAO** 1972. Fish populations of Kainji Lake, trends in their development and utilization. In: Kainji Lake research project. FAO Fish. Tech. Pap. 198: 1-46.
- Fenton, M.B.** 1972. The structure of aerial feeding bat faunas as indicated by ears and wing elements. Can. J. of Zool. 50: 287-296.
- Fernando, C.H.** 1971. The role of introduced fish in fish production in Ceylon's freshwaters. p. 285-310. In: Duffey, E. & Watt, A.S. (eds.) The Scientific Management of Animal and Plant Communities for Conservation. Blackwell, Oxford.
- Fernando, C.H.** 1977. Fisheries of natural lakes and man-made reservoirs. p. 9-12. In: I.G. Dunn (ed.) Symposium on the development and utilization of inland fishery resources.
- Fernando, C.H.** 1984. Reservoirs and lakes of southeast Asia (Oriental region). p. 411-

446. In: F. Taub (ed.). Lakes and reservoirs. Elsevier. The Netherlands.
- Fernando, C.H. & Furtado, J.I.** 1975. Reservoir fishery resources of South East Asia. Bull. Fish. Res. Stn. Sri Lanka 26: 83-95.
- Fernando C.H. & Holcik, J.** 1982. The nature of fish: A factor influencing the fishery potential and yields of tropical lakes and reservoirs. Hydrobiologia 97: 127-140.
- Fernando, C.H. & Holcik, J.** 1991. Fish in Reservoirs. Int. Revue ges. Hydrobiol. 76: 149-167.
- Fernando, C.H. & Indrasena, H.H.A.** 1969. The freshwater fisheries of Ceylon. Bulletin of the Fisheries Research Station Ceylon 20: 101-134.
- Findley, J.S.** 1976. The structure of bat communities. Am. Nat. 110: 129-139.
- Findley, J.S. & Black, H.** 1983. Morphological and dietary structuring of a Zambian insectivorous bat community. Ecology 64: 625-630.
- Fretwell, S.D.** 1987. Food chain dynamics: The central theory of ecology? Oikos 50: 291-301.
- Galis, F.** 1993. Interactions between the pharyngeal jaw apparatus, feeding behaviours, and ontogeny in the cichlid fish, *Haplochromis piceatus*: a study of morphological constraints in evolutionary ecology. J. Exp. Zool. 267: 137-154.
- Galis, F. & Jong, P.W. de** 1988. Optimal foraging and ontogeny; food selection by *Haplochromis piceatus*. Oecologia 75: 175-184.
- Ganf, G.G.** 1972. The regulation of net primary production in Lake George, Uganda, East Africa. p. 693-708. In: Z. Kayak & A. Hillbricht-Ilkowska (eds.) Productivity problems of fresh waters. Warsaw & Krakow: Polish Scientific publishers.
- Gascon, D. & Legget, W.C.** 1977. Distribution, abundance and resource utilization of littoral zone fishes in response to a nutrient/production gradient in Lake Memphremagog. J. Fish. Res. Bd. Can. 34: 1105-1117.
- Gatz, A.J.** 1979. Ecological morphology of freshwater stream fishes. Tulane Stud. Zool. Bot. 21: 91-124.
- Gatz, A.J.** 1979. Community organization in fishes as indicated by morphological features. Ecology 60: 711-718.
- Garnier, J. & Mourelatos, S.** 1991. Contribution of grazing in phytoplankton overall losses in a shallow French lake. Freshwater Biology 25: 515-523.
- Gascon, D. & Legget, W.C.** 1977. Distribution, abundance and resource utilization of littoral zone fishes in response to a nutrient/production gradient in Lake Memphremagog. J. Fish. Res. Board Can. 34: 1105-1117.
- Getachew, T.** 1989. Stomach pH, feeding and ingestion rate in *Oreochromis niloticus* L. (Pisces:Cichlidae) in Lake Awasa, Ethiopia. Hydrobiologia 174: 43-48.
- Gilbert, C.R. & Bailey R.M.** 1972. Systematics and zoogeography of the American cyprinid fish *Notropis (Opsopoeodus) emiliae*. Occ Pap. Mus. Zool., Univ. Michigan 664: 1-35.
- Gilliam, J.F.** 1982. Habitat use and competitive bottlenecks in size-structured fish populations. Thesis Michigan State Univ., East Lansing
- Gladfelter, W.B. & Johnson, W.S.** 1983. Feeding niche separation in a guild of tropical reef fishes (Holocentridae). Ecology 64: 552-563.
- Gliwicz, Z.M.** 1986. A lunar cycle in zooplankton. Ecology 67: 883-897.
- Goldschmidt, T., Witte, F. & Visser, J. de** 1990. Ecological segregation in

- zooplanktivorous haplochromine species (Pisces: Cichlidae) from Lake Victoria. *Oikos* 58: 343-355.
- Golterman, H.L., Clymo, R.S. & Ohnstad, M.A.M.** 1978. Methods for physical and chemical analysis of fresh waters. IBP Handbook 8, 2nd edition. Blackwell Scientific Publ., Oxford.
- Gordon, D.M.** 1991. Variation and change in behavioral ecology. *Ecology* 72: 1196-1203.
- Gosline, W.A.** 1973. Considerations regarding the phylogeny of cypriniform fishes with special reference to structures associated with feeding. *Copeia* 1955: 267-290.
- Greenfield, D.W., Rakocinski, C.F. & Greenfield T.A.** 1983. Spatial and trophic interactions in wet and dry seasons between *Gambusia luma* and *Gambusia sexradiata* (Pisces: Poeciliidae) in Belize Central America. *American Fieldiana Zool. N.S.* 14: 1-16.
- Gregg, W.W. & Rose, F.L.** 1985. Influences of aquatic macrophytes on invertebrate community structure, guild structure and microdistribution in streams. *Hydrobiologia* 128: 45-56.
- Grift, R.E.** 1995. A comparison of zooplankton community structures in tropical and temperate freshwater ecosystems, varying in trophic state. Thesis Wageningen Agricultural University.
- Grossman, G.D.** 1986. Food resource partitioning in a rocky intertidal fish assemblage. *J. Zool. Lond.* 1: 317-355.
- Grossman, G.D., Moyle P.B. & Whitaker, J.O.** 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: A test of community theory. *Am. Nat.* 120: 423-454.
- Hairston, N.G., Smith F.E. & Slobodkin, L.B.** 1960. Community structure, population control and competition. *Am. Nat.* 94: 421-425.
- Hall, D.J., Werner, E.E., Gilliam, J.F., Mittelbach, G.G., Howard, D. & Doner, C.G.** 1979. Diel foraging behavior and prey selection in the golden shiner (*Notemigonus crysoleucas*). *J. Fish. Res. Bd. Can.* 36: 1029-1039.
- Hall, D.J. & Werner, E.E.** 1977. Seasonal distribution and abundance of fishes in the inshore zone of a Michigan Lake. *Trans. Am. Fish. Soc.* 6: 545-555.
- Hamrin, S.F.** 1986. Vertical distribution and habitat partitioning between different size classes of vendace, *Coregonus albula*, in thermally stratified lakes. *Can. J. Fish. Aquat. Sci.* 43: 1617-1625.
- Haram, O.J., & Jones, J.W.** 1971. Some observations on the food of the gwyniad *Coregonus clupeoides pennantii* (Valenciennes) of Llyn Tegid (Lake Bala), North Wales. *J. Fish Biol.* 3: 287-295.
- Harrison, G.W.** 1979. Stability under environmental stress: Resistance, resilience, persistence, and variability. *Am. Nat.* 5: 659-669.
- Helfman, G.S.** 1978. Patterns of community structure in fishes: Summary and overview. *Env. Biol. Fish.* 3: 129-148.
- Henderson, H.F.** 1979. The significance of limnology in the development of fisheries in man-made lakes and river basins. *Proc. Int. Conf. on Kainji Lake and river basins development in Africa Vol 1*: 135-145.
- Herrera, C.M.** 1978. Individual dietary differences associated with morphological

- variation in Robins *Erithacus rubecula*. *Ibis* 120: 542-545.
- Hershey, A.E.** 1985. Effects of predatory sculpin on the chironomid communities in an arctic lake. *Ecology* 66: 1131-1138.
- Hillbricht-Ilkowska, A., Spodniewska, I., Weglenska, T. & Karabin, A.** 1972. The seasonal variation of some ecological transfer efficiencies and production rates in the plankton community of several Polish lakes of different trophic. p. 111-127. In: Z. Kayak & A. Hillbricht-Ilkowska (eds.) Productivity problems of fresh waters. Warsaw & Krakow: Polish scientific publishers.
- Hixon, M.A.** 1980. Competitive interactions between California reef fishes of the genus *Embiotoca*. *Ecology* 61: 918-931.
- Hofer, R.** 1991. Digestion. p. 55-79. In: I.J. Winfield & J.S. Nelson (eds.) Cyprinid fishes: systematics, biology and exploitation. Chapman & Hall. London.
- Hofer, R. & Schiemer, F.** 1983. Feeding ecology, assimilation efficiencies and energetics of two herbivorous fish; *Sarotherodon (Tilapia) mossambicus* (Peters) and *Puntius filamentosus* (Cuv. et Val.). In: Limnology of Parakrama Samudra - Sri Lanka, Schiemer F. (ed.), W. Junk Publ., The Hague.
- Horn, M.H.** 1989. The biology of marine herbivorous fishes. *Oceanogr. Mar. Biol. Annual Reviews* 27: 167-272.
- Hunter, M.D. & Price, P.W.** 1992. Playing Chutes and Ladders - Heterogeneity and the Relative Roles of Bottom-Up and Top-Down Forces in Natural Communities. *Ecology* 73: 724-732.
- Hutchinson, G. E.** 1978. An introduction to population ecology. Yale University Press, New Haven.
- Hynes, H.B.N.** 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.* 19: 36-58.
- Hyslop, E.J.** 1980. Stomach contents analysis - a review of methods and their application. *J. Fish. Biol.* 17: 411-429.
- Jacobsen, B.A. & Simonsen, P.** 1993. Disturbance events affecting phytoplankton biomass, composition and species diversity in a shallow, eutrophic, temperate lake. *Hydrobiologia* 249: 9-14.
- Jansen, W.A. & Mackay, W.C.** 1992. Foraging in yellow perch, *Perca flavescens*: biological and physical factors affecting diel periodicity in feeding, consumption, and movement. *Env. Biol. Fish.* 34: 287-304.
- Janssen, J. & Brandt, S.B.** 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in lake Michigan. *Can. J. Fish. Aquat. Sci.* 37: 177-184.
- Kalk, M., McLachlan A.J. & Howard-Williams C.** 1979. Lake Chilwa, Studies of change in a tropical ecosystem. Monographiae Biologicae Volume 35. Dr W. Junk Publishers, The Hague. 462 p.
- Karr, J.R. & James, F.C.** 1975. Ecomorphological configurations and convergent evolution in species and communities. p. 258-291. In: M.L. Cody and J.M. Diamond (eds.) Ecology and evolution of communities. Belknap, Cambridge, Massachusetts, USA.
- Keast, A.** 1977. Diet overlaps and feeding relationships between the year classes in the

- yellow perch (*Perca flavescens*). *Env. Biol. Fish.* 2: 53-70.
- Keast, A.** 1978. Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. *Env. Biol. Fish.* 3: 7-31.
- Keast, A.** 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. *Env. Biol. Fish.* 12: 119-129.
- Keast, A., Harker, J. & Turnbull, D.** 1978. Nearshore fish habitat utilization and species associations in Lake Opinicon (Ontario, Canada). *Env. Biol. Fish.* 3: 173-184.
- Keast, A. & Welsh, L.** 1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. *J. Fish. Res. Bd Can.* 25: 1133-1144.
- Kerr, S.R.** 1977. Structure and transformation of fish production systems. *J. Fish. Res. Board Can.* 34: 1989-1993.
- Khoo, H.W. & Tay, S.** 1992. Detritus production and its utilization by *Oreochromis mossambicus* in Selatar Reservoir. p. 62-72. In: S.S. De Silva (ed.) *Reservoir fisheries of Asia*. IDRC. Ottawa.
- Kimmel, B.L. & Groeger, A.W.** 1986. Limnological and ecological changes associated with reservoir aging. p. 103-109. In: *Reservoir Fisheries Management: Strategies for the 80's*. G.E. Hall & M.J. Van Den Avyle (eds.) Reservoir Committee, Southern Division.
- Kislalioglu, M. & Gibson, R.N.** 1976. Prey "handling time" and its importance in food selection by the 15 spined stickleback, *Spinachia spinachia* (L.). *J. Exp. Mar. Biol. Ecol.* 25: 115-158.
- Kortmulder, K.** 1987. Ecology and behaviour in tropical freshwater fish communities. *Arch. Hydrobiol.* 8: 503-513.
- Kortmulder, K., Padmanabhan K.G. & De Silva, S.S.** 1990. Patterns of distribution and endemism in some cyprinid fishes as determined by the geomorphology of south-west Sri Lanka and south Kerala (India). *Ichtyol. Explor. Freshwat.* 1: 97-112.
- Kotrschal, K. & Goldschmid, A.** 1983. Food preferences, morphology and arrangement of teeth of 14 species of Adriatic blennies (Pisces, Teleostei). *Thalassia* 19: 217-219.
- Krebs, C.J.** 1972. *Ecology*. Harper & Row, New York.
- Kumar, K.P.** 1985. Diurnal variations in the feeding of *Rasbora daniconius* (Hamilton). *Aquatic Biology* 5: 51-54.
- Kumar, K.P. & John, P.A.** 1985. Seasonal variations of the allochthonous fauna and flora and their influence on the diet of *Rasbora daniconius* (Hamilton). *Arch. Hydrobiol.* 102: 537-542.
- Kumar, K.P. & John, P.A.** 1987. Feeding ecology of the allochthonous feeder *Rasbora daniconius* (Hamilton) (Cyprinidae -Teleostei). *Int. Revue ges. Hydrobiol.* 72: 325-337.
- Kumar, K.P., Vijayakumar, B., Padmanabhan K.G. & Kortmulder, K.** 1986. Food and feeding habits of two cyprinids forage fishes, *Puntius* (=Barbus) *filamentosus* (Val.) and *P. amphibius* (Val.) from South Kerala, India. *Neth. J. Zool.* 36: 449-461.
- Kushlan, J.A.** 1976. Environmental stability and fish community diversity. *Ecology* 57:

- Lammens, E.H.R.R., de Nie, H.W., Vijverberg, J. & van Densen, W.L.T.** 1985. Resource partitioning and niche shifts of bream (*Abramis brama*) and eel (*Anguilla anguilla*) mediated by predation of smelt (*Osmerus eperlanus*) on *Daphnia hyalina*. Can. J. Fish. Aquat. Sci. 42: 1342-1351.
- Lampert, W. & Taylor, B.E.** 1985. Zooplankton grazing in a eutrophic lake: Implications of diel vertical migration. Ecology 66: 68-82.
- Larkin, P.A.** 1977. An epitaph for the concept of maximum sustained yield. Trans. Am. Fish. Soc. 106: 1-11.
- Larson, R.J.** 1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (sebastes) species. Ecol. Monographs 50: 221-239.
- Lauder, G.V.** 1983. Neuromuscular patterns and the origin of trophic specialization in fishes. Science 219: 1235-1237.
- Leveque, C.** 1978. Estimation du rapport P/B a partir de la longevite de especes. Verh. Internat. Verein. Limnol. 20: 2122-2126.
- Levins, R.** 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton.
- Levin, S.A. & Paine, R.T.** 1974. Disturbance, patch formation, and community structure. Proc. Nat. Acad. Sci. U.S.A. 71: 2744-2747.
- Levy, D.A.** 1990. Reciprocal diel vertical migration behavior in planktivores and zooplankton in British Columbia lakes. Can. J. Fish. Aquat. Sci. 47: 1755-1764.
- Lewis Jr., W.M.** 1974. Primary production in the plankton community of a tropical lake. Ecological Monographs 44: 377-409.
- Liem, K.F.** 1991. Toward a new morphology: pluralism in research and education. Amer. Zool. 31: 759-767.
- Liem, K.F.** 1993. Ecomorphology of the teleostean skull. p. 422-452. In: J. Hanken & B.K. Hall (eds.) The Skull, Functional and Evolutionary Mechanisms, Volume 3. The University of Chicago Press, Chicago.
- Loreau, M.** 1990. The Colwell - Futuyma method for measuring niche breadth and overlap: a critique. Oikos 58: 251-253.
- Love, R.M.** 1980. The chemical biology of fishes. Volume 2: Advances 1968-1977. Academic Press, London. 943 p.
- MacArthur, R.H.** 1955. Fluctuations of animal populations and a measure of community stability Ecology, 36: 533-536.
- MacArthur, R.H.** 1965. Patterns of species diversity. Biological reviews 40: 510-533.
- MacArthur, R.H.** 1972. Geographical ecology : patterns in the distribution of species. Harper and Row, New York.
- MacArthur, R.H. & Pianka, E.R.** 1966. On optimal use of a patchy environment. Am. Nat. 100: 603-609.
- Mackereth, F.J.H., Heron, J. & Talling, J.F.** 1978. Water analysis: some revised methods for limnologists. Freshwater Biological Association, Ambleside.
- Maclean, J.A. & Evans, D.O.** 1981. The stock concept, discreteness of fish stocks, and fisheries management. Can. J. Fish. Aquat. Sci. 38: 1889-1898.
- Maguire, B.** 1967. A partial analysis of the niche. Am. Nat. 101: 515-523.
- Maiorana, V.** 1978. An explanation of ecological and developmental constants. Nature

- Maitpe, P. & De Silva, S.S.** 1985. Switches between zoophagy, phytophagy and detritivory of *Sarotherodon mossambicus* (Peters) populations in twelve man-made Sri Lankan lakes. *J. Fish Biol.* 26: 49-61.
- Mann, K.H.** 1988. Production and use of detritus in various freshwater estuarine, and coastal marine ecosystems. *Limnol. Oceanogr.* 33: 910-930.
- May, R. M. & MacArthur, R.H.** 1972. Niche overlap as a function of environmental variability. *Proc. Nat. Acad. Sci. USA* 69: 1109-1113.
- McQueen, D.J., Johannes, M.R.S., Post, J.R., Stewart, T.J. & Lean, D.R.S.** 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecol. Monographs* 59: 289-309.
- McQueen, D.J., Post, J.R. & Mills, E.L.** 1986. Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. Aquat. Sci.* 43: 1571-1581.
- Meffe, G.K.** 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. *Ecology* 65: 1525-1534.
- Menge, B.A. & Sutherland, J.P.** 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* 130: 730-757.
- Menon, M.D. & Chacko, P.T.** 1958. Food and feeding of freshwater fishes of the Madras state. *J. Bombay Nat. Hist. Soc.* 55: 117-124.
- Miles, D.B. & Ricklefs, R.E.** 1984. The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology* 65: 1629-1640.
- Miller, G.L.** 1984. Seasonal changes in morphological structuring in a guild of benthic stream fishes. *Oecologia* 63: 106-109.
- Mittelbach, G.G.** 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62: 1370-1386.
- Moed, J.R. & Hallegraeff, G.M.** 1978. Some problems in the estimation of chlorophyll-a and phaeopigments from pre- and postacidification spectrophotometric measurements. *Int. Revue ges. Hydrobiol.* 63: 787-800.
- Montgomery, W.L.** 1977. Diet and gut morphology in fishes, with special reference to the monkeyface prickleback, *Cebidichthys violaceus* (Stichaeidae: Blenniodei). *Copeia* 1977: 178-182.
- Morgan, N.C.** 1980. Secondary production. p. 247-340. In: E.D. Le Cren & R.H. Lowe-McConnell (eds.) *The functioning of freshwater ecosystems*. Cambridge University Press, London.
- Moriarty, D.J.W.** 1973. The physiology of digestion of blue-green algae in the cichlid fish, *Tilapia nilotica*. *J. Zool. Lond.* 171: 25-39.
- Moriarty, D.J.W., Darlington, J.P.E.C., Dunn, I.G., Moriarty, C.M. & Tevlin, M.P.** 1973. Feeding and grazing in Lake George, Uganda. *Proc. R. Soc. Lond.* 184: 299-319.
- Moriarty, D.J.W. & Moriarty, C.M.** 1973. The assimilation of carbon from phytoplankton by two herbivorous fishes: *Tilapia nilotica* and *Haplochromis nigripinnis*. *J. Zool. Lond.* 171: 41-55.
- Moriarty, C.M. & Moriarty, D.J.W.** 1973. Quantitative estimation of the daily



- ingestion of phytoplankton by *Tilapia nilotica* and *Haplochromis nigripinnis* in Lake George, Uganda. *J. Zool. Lond.* 171: 15-23.
- Motta, P.J. 1988. Functional morphology of the feeding apparatus of ten species of pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. *Env. Biol. Fish.* 22: 39-67.
- Motta, P.J. 1989. Dentition patterns among Pacific and Western Atlantic butterflyfishes (Perciformes, Chaetodontidae): relationship to feeding ecology and evolutionary history. *Env. Biol. Fish.* 25: 159-170.
- Motta, P.J., Clifton, K.B., Hernandez, P. & Eggold, B.T. 1995. Ecomorphological correlates in ten species of subtropical seagrass species: diet and microhabitat utilization. *Env. Biol. Fish.* 44: 37-60.
- Motta, P.J. & Kotschal, K.M. 1992. Correlative, experimental, and comparative evolutionary approaches in ecomorphology. *Neth. J. Zool.* 42: 400-415.
- Moyle, P.B. 1973. Ecological Segregation Among Three Species Of Minnows (Cyprinidae) in a Minnesota Lake. *Trans. Am. Fish. Soc.* 4: 794-805.
- Moyle, P.B. & Senanayake, F.R. 1984. Resource partitioning among fishes of rainforest streams in Sri Lanka. *J. Zool. Lond.* 202: 195-223.
- Nagelkerke, L.A.J., Sibbing, F.A., Boggart, J.G.M., Lammens, E.H.R.R. & Osse, J.W.M. 1994. The barbs (*Barbus spp.*) of Lake Tana: a forgotten species flock?. *Env. Biol. Fish.* 39: 1-22.
- Nagelkerke, L.A.J., Sibbing, F.A. & Osse, J.W.M. 1995. Morphological divergence during growth in the large barbs (*Barbus spp.*) of Lake Tana, Ethiopia. *Neth. J. Zool.* 45: 431-454.
- Nikolsky, G.V. 1963. The ecology of fishes. Academic press, London, 352 p.
- Nilsson, N.A. 1978. The role of size-biased predation in competition and interactive segregation in fish. p. 303-325. In: S.D. Gerking (ed.) *Ecology of Freshwater Fish Production*. Blackwell Scientific Publications, Oxford.
- Norton, S.F. 1988. The role of the gastropod shell and operculum in inhibiting predation by fishes. *Science* 241: 92-94.
- Norton, S.F. 1991. Capture succes and diet of cottid fishes: the role of predator morphology and attack kinematics. *Ecology* 72: 1807-1819.
- Norton, S.F. 1995. A functional approach to ecomorphological patterns of feeding in cottid fishes. *Env. Biol. Fish.* 44: 61-78.
- Norton, S.F. & Brainerd, E.L. 1993. Convergence in the feeding mode of ecomorphologically similar species in the centrarchidae and cichlidae. *J. Exp. Biol.* 176: 11-29.
- Norton, S.F., Luczkovich, J.J. & Motta, P.J. 1995. The role of ecomorphological studies in the comparative biology of fishes. *Env. Biol. Fish.* 44: 287-304.
- O'Brien, W.J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. *Amer. Sci.* 67: 572
- Odum, E.P. & Biever, L.J. 1984. Resource quality, mutualism, and energy partitioning in food chains. *Am. Nat.* 124: 360-376.
- O'Neill, R.V., DeAngelis, D.L., Waide, J.B. & Allen, T.F.H. 1986. A hierarchical concept of ecosystem. *Monographs in population biology*. Princeton University Press. Princeton. 253 p.

- Oksanen, L. 1988. Ecosystem organization: Mutualism and cybernetics or plain darwinian struggle for existence?. *Am. Nat.* 131: 424-444.
- Osenberg, C.W. & Mittelbach, G.G. 1989. Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. *Ecol. Monogr.* 59: 405-432.
- Osman, R.W. 1978. The influence of seasonality and stability on the species equilibrium. *Ecology* 59: 383-399.
- Park, T. 1962. Beetles, competition, and populations. *Science* 138: 1369-1375.
- Pauly, D. 1983. Length converted catch curves. A powerful tool for fisheries research in the tropics. (Part 1). *ICLARM Fishbyte* 1: 9-13.
- Pauly, D. 1984a. Length converted catch curves. A powerful tool for fisheries research in the tropics. (Part 2). *ICLARM Fishbyte* 2: 9-17.
- Pauly, D. 1984b. Length converted catch curves. A powerful tool for fisheries research in the tropics. (Part 3). *ICLARM Fishbyte* 2: 9-10.
- Persson, L. 1986. Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). *Ecology* 67: 355-364.
- Persson, L. 1987. The effects of resource availability and distribution on size-class interactions in perch, *Perca fluviatilis*. *Oikos* 48: 148-160.
- Persson, L., Greenberg, L.A. 1990. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*) - roach (*Rutilus rutilus*) interaction. *Ecology* 71: 44-56.
- Pet, J.S., Gevers, G.J.M., Van Densen, W.L.T. & Vijverberg, J. 1995a. Management options for a more complete utilization of the biological fish production in Sri Lankan reservoirs. *Ecology of Freshwater Fish* 4: in press.
- Pet, J.S., Pet-Soede, C. & Van Densen, W.L.T. 1995b. Comparison of methods for the estimation of gillnet selectivity to tilapia, cyprinids and other species of Sri Lankan reservoir fish. *Fisheries Research* 24: 141-164.
- Pet, J.S. & Piet, G.J. 1993. The consequences of habitat occupation and habitat overlap of the introduced tilapia *Oreochromis mossambicus* (Peters) and indigenous fish species for fishery management in a Sri Lankan reservoir. *J. Fish Biol.* 43: 193-208.
- Pet, J.S., Wijsman, J.W.M., Mous, P.J. & Machiels, M.A.M. 1995c. Characteristics of a Sri Lankan reservoir fishery and consequences for the estimation of annual yield. *Fisheries Research* 24: 9-33.
- Pethiyagoda, R. 1991. Freshwater fishes of Sri Lanka. Wildlife Heritage Trust of Sri Lanka. 362 p.
- Petraitis, P.S. 1979. Likelihood measures of niche breadth and overlap. *Ecology* 60: 703-710.
- Pianka, E.R. 1976. Competition and niche theory. p. 114-141. In: R.M. May (ed.) *Theoretical ecology*. Blackwell Scientific Publications, Oxford.
- Pimm, S.L. 1991. The balance of nature: Ecological issues in the conservation of species and communities. The university of Chicago press, Chicago, 434 p.
- Ploskey, G.R. 1986. Management of the physical and chemical environment. p. 87-97. In: G.E. Hall & M.J. Van Den Avyle (eds.) *Reservoir Fisheries Management: Strategies for the 80's*. Reservoir Committee, Southern Division.
- Polis, G.A. 1984. Age structure component of niche width and intraspecific resource

- partitioning: Can age groups function as ecological species. *Am. Nat.* 123: 541-564.
- Power, M.E.** 1992. Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology* 73:1675-1688.
- Rabe, F.W. & Gibson, F.** 1984. The effect of macrophyte removal on the distribution of selected invertebrates in an inshore environment. *J. of Freshwater Ecology*: 359-371.
- Rahel, F.J.** 1984. Factors structuring fish assemblages along a bog lake successional gradient. *Ecology* 65: 1276-1289.
- Rahel, F.J., Lyons, J.D. & Cochran, P.A.** 1984. Stochasticity or deterministic regulation of assemblage structure? It may depend on how the assemblage is defined. *Am. Nat.* 124: 583-589.
- Randall, J.E.** 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* 5: 665-847.
- Rask, M.** 1986. The diet and diel feeding activity of perch, *Perca fluviatilis* L., in a small lake in southern Finland. *Ann. Zool. Fennici* 23: 49-56.
- Real, L. & Caraco, T.** 1986. Risk and foraging in stochastic environments. *Ann. Rev. Ecol. Syst.* 17: 371-90.
- Reilly, S.M. & Wainwright, P.C.** 1994. Conclusion: ecological morphology and the power of integration. In: P.C. Wainwright & S.M. Reilly (eds.) *Ecological Morphology, Integrative Organismal Biology*, University of Chicago Press, Chicago.
- Ricklefs, R.E.** 1966. The temporal component of diversity among species of birds. *Evolution* 20: 235-242.
- Ricklefs, R.E. & Travis, J.** 1980. A morphological approach to the study of avian community organization. *Auk* 97: 321-338.
- Ricklefs, R.E., Cochran, D. & Pianka, E.R.** 1981. A morphological analysis of the structure of communities of lizards in desert habitats. *Ecology* 62: 1474-1483.
- Robinson, C.L.K. & Tonn, W.M.** 1989. Influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. *Can. J. Fish. Aquat. Sci.* 46: 81-89.
- Ross, S.T.** 1986. Resource partitioning in fish assemblages: A review of field studies. *Copeia* 2: 352-388.
- Ross, S.T., Matthews, W.J. & Echelle, A.A.** 1985. Persistence of stream fish assemblages: effects of environmental change. *Am. Nat.* 126: 24-40.
- Roughgarden, J.** 1972. Evolution of niche width. *Am. Nat.* 106: 683-718.
- Roughgarden, J.** 1976. Resource Partitioning Competing Species - A Coevolutionary Approach. *Theoretical Population Biology* 9: 388-424.
- Roughgarden, J.** 1983. Competition and theory in community ecology. *Am. Nat.* 122: 583-601.
- Rudstam, L.G. & Magnuson, J.J.** 1985. Predicting the vertical distribution of fish populations: Analysis of Cisco, *Coregonus artedii*, and yellow perch, *Perca flavescens*. *Can. J. Fish. Aquat. Sci.* 42: 1178-1188.
- Sainsbury, K.J.** 1986. Estimation of food consumption from field observations of fish feeding cycles. *J. Fish Biol.* 29: 23-36.

- Sale, P.F. & Douglas, W.A.** 1984. Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology* 65: 409-422.
- Savino, J.F. & Stein, R.A.** 1989. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. *Env. Biol. Fish.* 24: 287-293.
- Schiemer, F. & Duncan, A.** 1987. The significance of the ecosystem approach for reservoir management. p. 183-194. In: S.S. de Silva (ed.). *Proc. regional workshop on reservoir fisheries management and development, Kathmandu, Nepal.*
- Schiemer, F. & Hofer, R.** 1983. A contribution to the ecology of the Parakrama Samudra Reservoir. p. 135-148. In: Schiemer F. (ed.) *Limnology of Parakrama Samudra - Sri Lanka.* W. Junk Publ., The Hague.
- Schmitt, R.J.** 1987. Indirect interactions between prey: apparent competition, predator aggregation, and habitat segregation. *Ecology* 68: 1887-1897.
- Schoener, T.W.** 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51: 408-418.
- Schoener, T.W.** 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2: 369-404.
- Schoener, T.W.** 1974. Resource partitioning in ecological communities. *Science* 185: 27-39.
- Schoener, T.W.** 1983. Field experiments on interspecific competition. *Am. Nat.* 122: 240-285.
- Schoener, T.W.** 1986. Overview: Kinds of ecological communities - Ecology becomes pluralistic. p. 467-479. In: J. Diamond & T.J. Case (eds.) *Community Ecology.* Harper and Row, New York.
- Schut, J., de Silva, S.S. & Kortmulder, K.** 1984. Habitat, associations and competition of eight *Barbus* (=Puntius) species (Pisces, Cyprinidae) indigenous to Sri Lanka. *Neth. J. Zool.* 34: 159-181.
- Senanayake, F.R. & Fernando, W.J.P.** 1985. Enhancement of fisheries potential in Sri Lanka's inland water bodies by addition of trophic diversity. p. 269-274. In: T. Panayotou (ed.) *Small scale fisheries in Asia: socioeconomic analysis and policy.*
- Shapiro, J.** 1980. The importance of trophic-level interactions to the abundance and species composition of algae in lakes. p. 105-116. In: Barica J. & Mur L.R. (eds.) *Developments in hydrobiology, vol. 2,* Junk Publ., Den Haag.
- Shapiro, J., Forsberg, B., Lamarra, V., Lindmark, G., Lynch, M., Smeltzer, E. & Zoto, G.** 1982. Experiments and experiences in biomanipulation. Interim Report No. 19 of the Limnological Research Center University of Minnesota, Minneapolis, Minnesota.
- Shapiro, J., Lamarra, V. & Lynch, M.** 1975. Biomanipulation: An Ecosystem Approach to Lake Restoration. *Proc. Symp. Waterquality Management through Biological Control.*
- Sheldon, R.W. & Parsons, T.R.** 1967. A continuous size spectrum for particulate matter in the sea. *J. Fish. Res. Board Can.* 24: 909-926.
- Sheldon, R.W., Prakash, A. & Sutcliffe Jr, W.H.** 1972. The size distribution of particles in the ocean. *Limnol. & Oceanograph.* 17: 327-339.
- Sibbing, F.A.** 1988. Specializations and limitations in the utilization of food resources by

- the carp, *Cyprinus carpio*: a study of oral food processing. *Env. Biol. Fish.* 22: 161-178.
- Sibbing, F.A. 1991. Food capture and oral processing. p. 377-412. In: I.J. Winfield & J.S. Nelson (eds.), *Cyprinid Fishes. Systematics, biology and exploitation*. Chapman & Hall, London.
- Sibbing, F.A., Nagelkerke, L.A.J. & Osse, J.W.M. 1994. Ecomorphology as a tool in fisheries: identification and ecotyping of Lake Tana barbs (*Barbus intermedius* complex), Ethiopia. *Netherlands Journal of Agricultural Science* 42-1: 77-85.
- Silva, E.I.L. & Davis, R.W. 1986. Movement of some indigenous riverine fish in Sri Lanka. *Hydrobiologia* 137: 263-270.
- Slobodkin, L.B. 1960. Ecological energy relationships at the population level. *Am. Nat.* 94: 213-236.
- Smirnov, S.A., Makeyeva, A.P. & Smirnov, A.I. 1995. Development of ecomorphology of fishes in Russia. *Env. Biol. Fish.* 44: 23-33.
- Smith, E.P. & Zaret, T.M. 1982. Bias in estimating niche overlap. *Ecology* 63: 1248-1253.
- Sondergaard, M., Riemann, B. & Jorgenson, N.O.G. 1985. Extracellular organic carbon during a diatom bloom in Lake Mosso: molecular weight fractionation. *Freshwater Biology* 12: 313-320.
- Sprules, W.G., Casselman, J.M. & Shuter, B.J. 1983. Size distribution of pelagic particles in lakes. *Can. J. Fish. Aquat. Sci.* 40: 1761-1769.
- Sprules, W.G. & Munawar, M. 1986. Plankton size spectra in relation to ecosystem productivity, size and perturbation. *Can. J. Fish. Aquat. Sci.* 43: 1789-1794.
- Starck, W.A. & Schroeder, R.E. 1971. Investigations on the grey snapper, *Lutjanus griseus*. *Stud. Trop. Oceanogr.* 10: 1-150.
- Stich, H.B. & Lampert, W. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature* 293: 396-398.
- Stoner, A.W. & Livingston, R.J. 1984. Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia* 1984: 174-187.
- Strickland, J.D.H. & Parsons, T.R. 1968. A practical handbook of seawater analysis. *Fish. Res. Bd. Canada Bulletin* 167.
- Strong, D.R. 1992. Are Trophic Cascades All Wet? Differentiation and Donor-Control in Speciose Ecosystems. *Ecology* 73: 747-754.
- Sturmbauer, C., Mark, W. & Dallinger, R. 1992. Ecophysiology of aufwuchs-eating cichlids in lake Tanganyika: niche separation by trophic specialization. *Env. Biol. Fish.* 35: 283-290.
- Svärdson, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. *Inst. Freshwater Res. Drottningholm Rep.* 55: 144-171.
- Taper, M.L. & Case, T.J. 1985. Quantitative genetic models for the coevolution of character displacement. *Ecology* 66: 355-371.
- Tilman, D. 1982. Space as a resource, disturbance, and community structure. p. 205-227. In: D. Tilman (ed) *Resource Competition and Community Structure*. University Press, Princeton.
- Thorman, S. 1982. Niche dynamics and resource partitioning in a fish guild inhabiting a

- shallow estuary on the Swedish West coast. *Oikos* 39: 32-39.
- Tonn, W.M. & Magnuson, J.J. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63: 1149-1166.
- Tonn, W.M., Paszkowski, C.A. & Moermond, T.C. 1986. Competition in *Umbra-Perca* fish assemblages: experimental and field evidence. *Oecologia* 69: 126-133.
- Townsend, R.E. & Winfield, I.J. 1985. The application of optimal foraging theory to feeding behaviour in fish. p. 67- 97. In P. Tytler and P. Calow (ed.) *Fish energetics - New perspectives*. Croom Helm, London.
- Trewavas, E. 1983. Tilapiine fishes of the genera *Sarotherodon*, *Oreochromis* and *Danakilia*. British Museum (Natural History), London.
- Tudorancea, C., Fernando, C.H. & Paggi, J.C. 1988. Food and feeding ecology of *Oreochromis niloticus* (Linnaeus, 1758) juveniles in Lake Awassa (Ethiopia). *Arch. Hydrobiol.* 2/3: 267-289.
- Turelli, M. 1978. Does environmental variability limit niche overlap?. *Proc. Nat. Acad. Sci. USA* 75: 5085-5089.
- Urban, T.P. & Brandt, S.B. 1993. Food and habitat partitioning between young-of-year alewives and rainbow smelt in southeastern lake Ontario. *Environ. Biol. Fish.* 36: 359-372.
- Vadas, R.L. 1989. Food web patterns in ecosystems: A reply to Fretwell and Oksanen. *Oikos* 56: 339-343.
- Vadas, R.L. 1990. Competitive exclusion, character convergence, or optimal foraging: which should we expect. *Oikos* 58: 123-129.
- Vergina, I.A. 1991. Basic adaptations of the digestive system in bony fishes as a function of diet. *J. Ichthyol.* 31: 8-20.
- Vollenweider, R.A. 1974. A manual on methods for measuring primary production in aquatic environments. IBP Handbook 12. Blackwell Scientific Publ., Oxford.
- Vollenweider, R.A. & Nauwerck, A. 1961. Some observations on the C14-method for measuring primary production. *Verhandlungen der internationalen vereinigung fur theoretische und angewandte limnologie* 14: 134-139.
- Vijverberg, J., Boersma, M., van Densen, W.L.T., Hoogenboezem, W., Lammens, E.H.R.R. & Mooij, W.M. 1990. Seasonal variation in the interactions between piscivorous fish, planktivorous fish and zooplankton in a shallow eutrophic lake. *Hydrobiologia* 207: 279-286.
- Wainwright, P.C. 1987. Biomechanical limits to ecological performance: mollusc-crushing by the Caribbean hogfish, *Lachnolaimus maximus* (Labridae). *J. Zool.* 213: 283-297.
- Wainwright, P.C. 1991. Ecomorphology: experimental functional anatomy for ecological problems. *Amer. Zool.* 31: 680-693.
- Wainwright, P.C. & Richard, B.A. 1995. Predicting patterns of prey use from morphology of fishes. *Env. Biol. Fish.* 44: 97-113.
- Wallace, R.K. 1981. An assessment of diet-overlap indexes. *Trans. Am. Fish. Soc.* 110: 72-76.
- Watson, D.J. & Balon, E.K. 1984. Ecomorphological analysis of fish taxocenes, in rainforest streams of northern Borneo. *J. Fish Biol.* 25: 371-384.
- Webster, J.R., Waide, J.B. & Patten, B.C. 1975. Nutrient recycling and the stability of

- ecosystems. p 1-27. In: F.G. Howell (ed) Mineral cycling in southeastern ecosystems. U.S.A.E.C. Symp. Ser. Conf. 74-0513.
- Werner, E.E.** 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. *J. Fish. Res. Bd. Can.* 31: 1531-1536.
- Werner, E.E.** 1986. The mechanisms of species interactions and community organization in fish. In: J. Diamond and T.J. Case (eds.). *Community Ecology*. Harper and Row, New York.
- Werner, E.E. & Gilliam, J.F.** 1984. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* 15: 393-425.
- Werner, E.E., Gilliam D.J., Hall D.J. & Mittelbach G.G.** 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540-1548.
- Werner, E.E. & Hall, D.J.** 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55: 1042-1052.
- Werner, E.E. & Hall, D.J.** 1977. Competition and habitat shift in two sunfishes (Centrarchidae). *Ecology* 58: 869-876.
- Werner, E.E., & Hall, D.J.** 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69: 1352-1366.
- Werner, E.E., Hall, D.J., Laughlin, D.R., Wagner, D.J., Wilsmann, L.A. & Funk, F.C.** 1977. Habitat partitioning in a freshwater fish community. *J. Fish. Res. Bd. Can.* 34: 360-370.
- Werner, E.E., Mittelbach, G.G. & Hall, D.J.** 1981. The role of foraging profitability and experience in habitat use by the bluegill sunfish. *Ecology* 62: 116-125.
- Werner, E.E., Mittelbach, G.G., Hall, D.J., & Gilliam, J.F.** 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology* 64: 1525-1539.
- Westlake, D.F.** 1980. Primary production. p. 141-246. In: E.D. Le Cren & R.H. Lowe-McConnell (eds.) *The functioning of freshwater ecosystems*. Cambridge University Press, London.
- Wetzel, R.G.** 1990. Reservoir ecosystems: conclusions and speculations. p. 227-238. In: K.W. Thornton, B.L. Kimmel & F.E. Payne (eds.) *Reservoir limnology: ecological perspectives*. John Wiley & Sons, New York.
- Wetzel, R.G. & Manny, B.A.** 1972. Decomposition of dissolved organic carbon and nitrogen compounds from leaves in an experimental hard-water stream. *Limnol. & Oceanogr.* 17: 927-931.
- Wiegert, R.G. & Owen, D.F.** 1971. Trophic structure, available resources and population density in terrestrial vs. aquatic ecosystems. *J. Theor. Biol.* 30: 69-81.
- Wiens, J.A.** 1977. On Competition and Variable Environments. *American Scientist* 65: 590-597.
- Wilbur, H.M.** 1988. Interactions between growing predators and growing prey. p. 157-172. In: B. Ebenman & L. Persson (eds.) *Size-structured populations*. Springer-Verlag, Berlin.
- Winberg, G.G. et al.** 1971. Methods for calculating productivity. p. 296-317. In: W.T. Edmondson and G.G. Winberg (eds.) *Secondary productivity in fresh waters*. Blackwell Scientific Publications Oxford.
- Winberg, G.G.** 1980. General characteristics of freshwater ecosystems based on Soviet

- IBP studies. p. 481-492. In: E.D. Le Cren & R.H. Lowe-McConnell (eds.) The functioning of freshwater ecosystems. Cambridge University Press, London.
- Winemiller, K.O.** 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Env. Biol. Fish.* 26: 177-199.
- Winemiller, K.O.** 1991. Ecomorphological Diversification in Lowland Freshwater Fish Assemblages from five Biotic Regions. *Ecological Monographs* 61: 343-365.
- Winkler, H.** 1983. The ecology of cormorants (genus *Phalacrocorax*). p. 193-199. In: F. Schiemer (ed.) *Limnology of Parakrama Samudra - Sri Lanka*. W. Junk Publ., The Hague
- Wijeyaratne, M.J.S. & Costa, H.H.** 1992. Resource Partitioning of two Commercially Important Cichlid Species in Three Minor Perennial Reservoirs in the Northwestern Province of Sri Lanka. *J. Aqua. Trop.* 7: 131-140.
- Wikramanayake, E.D.** 1990. Ecomorphology and biogeography of a tropical stream fish assemblage: evolution of assemblage structure. *Ecology* 71: 1756-1764.
- Wilson, D.S.** 1975. The adequacy of body size as a niche difference. *Am. Nat.* 109: 769-784.
- Wurtsbaugh, W. & Li, H.** 1985. Diel migrations of a zooplanktivorous fish (*Mendia beryllina*) in relation to the distribution of its prey in a large eutrophic lake. *Limnol. Oceanogr.* 30: 565-576.
- Zaret, T.M., & Rand, A.M.** 1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. *Ecology* 52: 336-342.
- Zihler, F.** 1982. Gross morphology and configuration of the digestive tracts of cichlidae (Teleostei, Perciformes): phylogenetic and functional significance. *Neth. J. Zool.* 32: 544-571.



### Curriculum vitae

Gerjan Piet werd op 19 november 1962 geboren in Eindhoven. In 1980 behaalde hij het HAVO diploma aan het Eindhovens Protestants Lyceum waarna begonnen werd aan de opleiding chemie aan de H.T.S. te Eindhoven. Hiervoor werd het diploma in 1985 behaald. Van 1985 tot 1991 studeerde hij Milieuhygiëne aan de Landbouw Universiteit in Wageningen waarvoor hij "*cum laude*" afstudeerde met als hoofdvakken Aquatische Ecologie, Ecotoxicologie en Theoretische Productie Ecologie. Op 1 januari 1992 trad hij in dienst als onderzoeker in opleiding bij NWO/WOTRO en werd gestationeerd bij de Afdeling Zoölogie van de Ruhuna Universiteit in Matara, Sri Lanka, van waaruit het veldwerk voor het in dit proefschrift beschreven onderzoek werd uitgevoerd. Van april 1994 tot en met december 1995 is het onderzoek afgerond door het schrijven van dit proefschrift op het Centrum voor Limnologie (CL) van het Nederlands Instituut voor Oecologisch Onderzoek (NIOO) te Nieuwersluis.