On the management of a tropical reservoir fishery

J.S. Pet

Stellingen

1. Voor een duurzame exploitatie van *Oreochromis mossambicus* in Sri Lanka moet de wettelijke minimum maaswijdte van 76 mm gestrekte maas gehandhaafd worden.
   Dit proefschrift.

2. De visvangst uit Sri Lankaanse reservoirs kan worden verdubbeld door gerichte exploitatie van de inheemse cyprinide *Amblypharyngodon melettinus*.
   Dit proefschrift.

3. Holistische studies volgens de "ecosysteem benadering" (Schiemer & Duncan, 1988) in een beperkt aantal representatieve wateren leiden tot betere voorspellingen over de mogelijkheden voor visserijbeheer dan toepassing van ELEFAN (e.g. Pauly & Morgan, 1987) op grote schaal.
   Pauly, D. & Morgan, G.R. (1987). Length-based methods in fisheries research. Manila: ICLARM.
   Schiemer, F. & Duncan, A. (1988). The significance of the ecosystem approach for reservoir management. In: S.S. De Silva (ed.) Reservoir fishery management and development in Asia. Ottawa: IDRC.

4. Een hoge produktie aan hoogwaardige roofvis kan middels "culture-based" visserij of kooi-cultuur gerealiseerd worden op basis van de produktie van thans ongeëxploiteerde inheemse vissoorten in Sri Lankaanse irrigatie-reservoirs.

5. Het effect van predatie door *Lates calcarifer* op visgemeenschappen in ondiepe zuid-oost Aziatische reservoirs verdient onmiddellijke aandacht in het kader van de inventarisatie van mogelijke beheersscenario's voor de visserij in deze reservoirs.

6. Het belang van vis als voedsel in landen van de derde wereld is in het verleden al te vaak overdreven voorgesteld om hiermee onderzoek op het gebied van visteelt en visserij te verantwoorden. De balans dreigt op dit moment echter door te slaan naar éénzijdige aandacht voor de sociaal-economische positie van viskwekers en vissers.

7. Zoetwatervis is van toenemend belang als eiwitrijk voedsel voor de groeiende en arme bevolking in de droge laaglanden van Sri Lanka.

8. De toepasbaarheid van de wet van Murphy (Bloch, 1977) is omgekeerd evenredig met de afstand tot de evenaar.
   Bloch, A. (1977). Murphy's Law, and other reasons why things go wrong. Los Angeles, California: Price/Stern/Sloan Publishers.

9. De prestatiecurve van onderzoekers in de tropen, als functie van het aantal vakantiedagen, vertoont een optimum tussen de 0 en 365 dagen per jaar. Het is echter nooit bewezen dat dit optimum bij 24 dagen ligt.

10. Het feit dat visserijbiologische processen sneller verlopen onder tropische dan onder gematigde klimaatsomstandigheden (e.g. Longhurst & Pauly, 1987) kon ten volle worden benut door dit visserijbiologische proefschrift te schrijven gedurende de heetste zomer van de laatste 300 jaar (c.f. Verreth, 1994).

Longhurst, A.R. & Pauly, D. (1987). Ecology of tropical oceans. San Diego, California: Academic Press.
Verreth, J.A.J. (1994). Nutrition and related ontogenetic aspects in larvae of the African catfish, *Clarias gariepinus*. Thesis. Dept. of Fish Culture and Fisheries, Wageningen Agricultural University.

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Voorwoord

Toen ik tijdens mijn studie aan de Landbouwuniversiteit wel eens nadacht over het doen van promotie-onderzoek als vervolg op mijn visserij-opleiding zag ik dat nauwelijks als een haalbare optie. "Hoe krijg ik dat ooit voor elkaar: een zinvol onderzoeksvoorstel maken, een programma opzetten, dit uitvoeren en last but not least een aantal wetenschappelijke artikelen schrijven?". Ik realiseerde mij toen nog onvoldoende dat de onderzoeker in opleiding slechts één van de leden is van een team dat gezamenlijk werkt aan het eindresultaat.

Elk facet van het hierbij gepresenteerde onderzoek is het resultaat van een goede samenwerking tussen verschillende capabele mensen die mij telkens geholpen hebben een stapje verder te komen. Toen ik in 1991 in dienst kwam bij NWO hoefde ik geen onderzoeksvoorstel te maken want dit was reeds geformuleerd door Koos Vijverberg en Wim van Densen, ingediend bij WOTRO en toegekend onder het nummer w84-313. Dit voorstel betrof de niche-segregatie tussen geïntroduceerde tilapia's en inheemse cypriniden in Sri Lankaanse reservoirs. Het waren vooral Koos Vijverberg en het toenmalige Limnologisch Instituut die mij met dat onderzoek op gang hielpen, zowel in Nederland als ter plekke in Sri Lanka.

Op de Ruhuna Universiteit kon ik rekenen op de ondersteuning van de lokale coördinator van wat inmiddels bekend stond als het "WOTRO Project on Inland Fisheries". De heer Senaratne, hoofd van het Department of Zoology en lokaal coördinator, en mijn lokale collega's Amarasinghe en Guruge, stonden borg voor de overleving van het project. Vooral Bandu Amarasinghe heeft veel van zijn kostbare tijd gegeven om mij te helpen bij het inrichten en uitproberen van steeds weer aangepaste versies van het bemonsterings-programma. Het heeft zelfs mij verbaasd dat hij daarbij steeds bleef meedenken zonder naar zijn voorhoofd te gaan wijzen.

Wim van Densen heeft mij in die periode vooral gestimuleerd bij de formulering van een voorstel voor aanvullend onderzoek onder de paraplu van de Landbouwuniversiteit. Het feit dat Bram Huisman en Rudy Rabbinge van het begin af aan bereid zijn geweest om bij dit onderzoek als promotoren op te treden, is gedurende de gehele verdere periode een steun in de rug geweest. Het voorstel voor aanvullend onderzoek lag op het gebied van de visserijbiologie en het beheer van kieuwnet-visserijen, wat nog meer bij mijn persoonlijke interesses en capaciteiten aansloot. Nadat dit voorstel werd gehonoreerd, hebben alle betrokkenen zich ingezet voor een naadloze overgang en zorgde mijn enthousiaste collega Gerjan Piet voor de broodnodige versterking van de wetenschappelijke ploeg in Sri Lanka en voor de voortgang van het niche-segregatie onderzoek.

Inmiddels begon het vertrouwen op een goede afloop zeer vaste vorm aan te nemen met een begeleidingscommissie die naast de beide promotoren bestond uit Wim van Densen, Marcel Machiels, Koos Vijverberg en Frans Witte. Vanaf het begin is het mogelijk geweest om een uitgebreid programma aan veldwerk uit te voeren door de inzet van de lokale assistenten Rohana, Samaraweera, Jayasuriya, Munideewa, Shantha en Sanath. De dagelijkse logistieke en overige problemen werden opgelost met de altijd beschikbare medewerking van chauffeur, kapitein, koerier, onderhandelaar, huisgenoot, manus van alles, rots in de

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branding en boven alles drinkebroeder Gunasekera.

Wim van Densen heeft vanaf het begin structuur in het onderzoek gebracht en gehouden door de begeleiding te sturen via vijf duidelijke titels van hoofdstukken die de bouwstenen van dit proefschrift vormen. Verschillende studenten konden worden ingezet onder de afzonderlijke titels, zowel in hoofdvakken als in stages. Deze studenten, Lida Soede, Jeroen Wijsman, en Ingrid Gevers, hebben met hun werk in Sri Lanka en in Nederland een belangrijke bijdrage geleverd aan het tot stand komen van de verschillende hoofdstukken.

Mijn goede vriend en collega Peter Mous bleek buiten zijn eigen onderzoek nog energie over te hebben om inhoudelijk mee te denken en statistische analyses uit te voeren waar mijn kennis van de benodigde software tekort schoot. Aissah van Eer wil ik nog apart bedanken voor haar enthousiaste en niet aflatende pogingen om grotere aantallen tilapia's op leeftijd te brengen aan de hand van groeistructuren in de gehoorsteentjes. Vervolgens zijn het vooral Wim van Densen, Marcel Machiels en Koos Vijverberg geweest die ervoor zorgden dat mijn eerste schrijfselen langzaam maar zeker de vorm van wetenschappelijke publikaties begonnen aan te nemen. Collega's van de vakgroep zorgden voor de noodzakelijke relativerende praatjes boven kopjes koffie tussen het schrijven door. Bram Huisman en Rudy Rabbinge hebben met hun structurele commentaar zorg gedragen voor het uiteindelijke resultaat in de vorm van dit proefschrift.

Tenslotte is het natuurlijk het thuisfront wat er vooral voor zorgt dat motivatie en inzet op peil blijven. Lida Soede heeft gedurende het hele onderzoek de grootste invloed gehad op mijn motivatie en werklust. Ook mijn ouders en schoonouders hebben ervoor gezorgd dat ik steeds gemotiveerd naar het einddoel ben blijven streven. Daarnaast werden de moeilijke momenten in Sri Lanka opgevuld door goede vrienden als Paul en Rosemary Crowe, Errol en Yasmin Arnolda, Ramesh Meegama en Ranjith Samarage. In Nederland is mijn geklaag boven glazen bier telkens weer gewillig aangehoord door Joost Backx, Vera Minten, Tom Buijse, Peter Mous, Dirk Drijver, Jolanda Logtenberg, Hans van der Weide, René Remmerswaal en vele andere vrienden die me er telkens van wisten te overtuigen dat ik gewoon door moest gaan. Het resultaat van hun aanmoedigingen ligt thans voor U.

Het is waarschijnlijk onmogelijk om een dankwoord te schrijven waarin alle mensen genoemd worden die op de een of andere manier een positieve invloed hebben gehad op het ontstaan van dit proefschrift. Ik hoop dat niemand beledigd zal zijn wanneer hij of zij niet met name wordt genoemd. Het mag duidelijk zijn dat ik een ieder hartelijk wil danken die betrokken is geweest bij het tot een goed einde brengen van mijn promotieonderzoek.

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Samenvatting

De binnenvisserij in Sri Lanka vormt de voornaamste bron van inkomsten voor meer dan 5 000 vissers-gezinnen. De jaarlijkse oogst in deze visserij bedraagt ongeveer 27 000 tot 30 000 ton, ofwel 20% van de totale visvangst in Sri Lanka. De beschikbaarheid van goedkope zoetwatervis is vooral van belang in de onderontwikkelde gebieden rond de irrigatie-reservoirs in het droge noorden, oosten en zuid-oosten van het land. Het grootste deel van de aangevoerde zoetwatervis is afkomstig uit de grotere (> 100 ha) irrigatie-reservoirs, die een gezamenlijk oppervlak hebben van ongeveer 100 000 ha. De maximale diepte in deze reservoirs is vaak minder dan 5 m, terwijl het waterniveau aanzienlijke schommelingen vertoont. De biologische visproduktie werd in deze studie geschat op 5 400 kg/ha/jr voor Tissawewa, een irrigatie-reservoir van *ca.* 200 ha, dat representatief is voor het droge laagland van zuid-oost Sri Lanka.

De hoge biologische visproduktie is mogelijk door de specifieke structuur van de visgemeenschap. Een groot deel van de vis-biomassa (*ca.* 54%) bestaat namelijk uit de kleine inheemse cyprinide *Amblypharyngodon melettinus* (max. lengte 10 cm), die zich voedt met phytoplankton en detritus. De instroom van allochtoon materiaal (detritus) is als basis voor de visproduktie misschien wel belangrijker dan de primaire produktie, die niet bijzonder hoog is (netto 4 000 kgC/ha/jr). Detritus is het voornaamste voedsel voor de geïntroduceerde cichlide *Oreochromis mossambicus* (max. lengte 30 cm, *ca.* 7% van de vis-biomassa). De barbelen (*ca.* 25% van de vis-biomassa), die zich vooral voeden met kleine benthische organismen, vormen een tweede groep van veel voorkomende cypriniden. Deze groep bestaat uit *Barbus chola* (max. lengte 15 cm), *B. dorsalis* (max. lengte 20 cm) en *B. sarana* (max. lengte 30 cm). Zoöplanktivore vis vertegenwoordigt minder dan 10% van de biomassa en piscivore vis minder dan 5% (alen niet meegerekend). De totale visgemeenschap wordt dus gekarakteriseerd door kleine soorten die zich op een laag trofisch niveau bevinden.

De hoge biologische visproduktie in de reservoirs wordt niet volledig benut door de commerciële visserij. Een oogst van *ca.* 10% van de totale visproduktie moet als haalbaar worden gezien, maar de reservoir-visserij oogst op dit moment nog geen 5% (200 tot 250 kg/ha/jr). De voornaamste reden hiervoor is dat de visserij zich bijna volledig concentreert op de geïntroduceerde tilapia *O. mossambicus* (*ca.* 70% van de aanvoer tot medio 1993), die slechts een klein deel van de vis-biomassa vormt. Het overige deel van de vangst bestond tot 1993 vooral uit grote Indiase karpers, die als pootvis werden uitgezet en die zich in Sri Lankaanse reservoirs niet konden voortplanten. Deze karpers worden sinds 1990 niet meer uitgezet en zijn sinds 1993 uit Tissawewa verdwenen. De vangst bestaat sindsdien voor een nog groter deel (95%) uit tilapias, en daarbij is recent ook het aandeel van *Oreochromis niloticus* groter geworden. De selectieve visserij op tilapias in Tissawewa is kenmerkend voor de visserijen in laagland reservoirs in Sri Lanka. *O. mossambicus* wordt in alle reservoirs bevist met kieuwnetten, meestal met mazen van 64 tot 88 mm. De wettelijke minimum maaswijdte in de Sri Lankaanse reservoirs is 76 mm gestrekte maas, maar deze wet wordt sinds enige jaren niet meer gehandhaafd.

De meest voorkomende soorten in de reservoirs, in termen van biomassa, worden tot op

heden dus niet geëxploiteerd door de commerciële visserij. Deze grote bestanden aan cypriniden waren echter reeds eerder opgemerkt en een aanvullende visserij met kleine mazen, voor de exploitatie van deze soorten, werd al in 1987 voorgesteld. Daarbij werd verondersteld dat de cypriniden geëxploiteerd kunnen worden zonder grote schade aan de bestaande visserij op *O. mossambicus* toe te brengen. De juvenielen van *O. mossambicus* en van de cypriniden zouden namelijk vooral in de oeverzone voorkomen terwijl de volwassen stadia van beide categorieën vooral in het open water geconcentreerd zouden zijn. Tevens werd aangenomen dat de gehele kieuwnet-visserij zich op het open water zou concentreren. Bij het bevissen van de volwassen cypriniden, met kieuwnetten met 15 en 30 mm gestrekte maas, zouden in dat geval nauwelijks juvenielen van *O. mossambicus* worden gevangen en zou de bestaande visserij dan ook geen schade leiden.

Tegelijkertijd werd echter gewaarschuwd dat het gebruik van kieuwnetten met te kleine mazen, in de visserij op *O. mossambicus*, moet worden voorkomen omdat dit zou kunnen leiden tot overbevissing van deze soort. Deze ogenschijnlijk tegenstrijdige geluiden moeten als afzonderlijke beheers-problemen worden beoordeeld. Ten eerste moet worden ingeschat of een aanvullende visserij op de inheemse cypriniden mogelijk is, zonder door technische interakties schade toe te brengen aan de bestaande visserij op *O. mossambicus*. Daarnaast moet worden aangegeven welke beheersmaatregelen, in termen van maaswijdtes en visserij-inspanning, nodig zijn om de bestaande visserij te optimaliseren. De algemene doelstelling van deze studie was daarom de formulering van wetenschappelijk onderbouwde beheersadviezen voor de reservoir-visserij in Sri Lanka, zowel voor de bestaande tilapia-visserij als voor eventuele aanvullende visserijen op nu nog ongeëxploiteerde soorten.

Een van de belangrijkste uitgangspunten van dit onderzoek was de hypothese rond de ruimtelijke segregatie tussen volwassen cypriniden en juveniele tilapias. Om deze hypothese te toetsen werden habitat bezetting en habitat overlap bestudeerd voor *O. mossambicus* en de inheemse vissoorten. Maandelijks werden in Tissawewa de vier verschillende macro-habitats bevist, zowel overdag als 's nachts, met kieuwnetten met maaswijdtes van 12.5 tot 90 mm gestrekte maas. De vier habitats waren de begroeide oeverzone, met een diepte van ongeveer 1 m, het onbegroeide overgangsgebied, met een diepte van ongeveer 2 m, de onderste 1.5 m van het ongeveer 3 m diepe open water en de bovenste 1.5 m van dit open water (dieptes bij vol reservoir).

Er werd geconcludeerd dat de volwassen stadia van de verschillende *Barbus* soorten en de juvenielen van *O. mossambicus* (7-10 cm) in hetzelfde gebied geconcentreerd zijn, vlak buiten de vegetatie van de oeverzone. Verder werd vastgesteld dat de volwassen stadia van *A. melettinus* grotendeels ruimtelijk gescheiden zijn van de jongste stadia van *O. mossambicus* (0-4.5 cm), welke laatste geconcentreerd zijn in het meest ondiepe deel van de oeverzone. *A. melettinus* komt voor vanaf het diepere deel van de oeverzone tot overal in het open water. Op grond van deze resultaten werd de stelling over de mogelijkheden van een aanvullende visserij genuanceerd. Er werd vastgesteld dat exploitatie van *Barbus* soorten met kieuwnetten van 30 mm gestrekte maas aanzienlijke schade zou kunnen opleveren voor de bestaande visserij op *O. mossambicus*, omdat de in deze maaswijdte vangbare lengte-klassen van de verschillende soorten een grote mate van habitat-overlap vertonen. Hierbij werd verondersteld dat de visserij zich concentreert op de plaats waar de

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vis-dichtheid het grootst is, waarbij de oeverzone niet wordt gemeden. Exploitatie van *A. melettinus* met 15 mm gestrekte maas, werd als minder schadelijk aangemerkt, vanwege de ruimtelijke scheiding tussen de in deze maaswijdte vangbare lengteklassen van *O. mossambicus* en *A. melettinus*.

Evaluatie van beheersmaatregelen is alleen mogelijk wanneer een betrouwbare schatting van de jaarlijkse oogst gemaakt kan worden. Hierbij is een systeem benodigd voor het verzamelen van vangst- en inspannings-gegevens, waarbij nauwkeurigheid en kosten goed tegen elkaar zijn afgewogen. De huidige totale oogst uit Tissawewa (200 tot 250 kg/ha/jr) werd tijdens deze studie geschat op basis van de gemiddelde oogst per visdag. Deze schatting bleek aanzienlijk lager dan de officiële schattingen van 600 tot 900 kg/ha/jr voor dit reservoir. Een overschatting van de totale vangst in de officiële statistieken bleek evident voor meerdere reservoirs in het zuid-oosten van Sri Lanka.

Om aan te geven hoe het systeem voor het verzamelen van vangst- en inspannings-gegevens kan worden geoptimaliseerd, werd de bestaande visserij gekarakteriseerd aan de hand van een maandelijkse, 4-daagse bemonstering. Naast de schatting van de totale vangst omvatte deze beschrijving de temporele en spatiële dynamiek in de vangst, in de visserij-inspanning en in de vangst per eenheid van inspanning. Tevens werden de gebruikte maaswijdten en de grootte-structuur van de vangst per soort bepaald. Hierbij bleek dat relatief kleine mazen (veelal 64 en 70 mm) werden gebruikt, waardoor *O. mossambicus* al werd gevangen vanaf een minimum lengte van 10 cm. Grotere aantallen werden gevangen vanaf 13 cm en de modale lengte in vangst lag op 15.5 cm. Verder bleek dat de visserij zich niet beperkte tot het open water van het reservoir. De vissers volgden vermeende concentraties van *O. mossambicus* namelijk tot in de vegetatie van de oeverzone.

De dynamiek in vangst, visserij-inspanning en vangst per vistrip werd statistisch geanalyseerd. Hierbij werd onderzocht in hoeverre de gemiddelde vangst per vistrip significante verschillen vertoonde tussen de verschillende vistuigen, habitats, bemonsterings-maanden en/of water-niveaus. Het bleek dat 30% van de variantie in de vangsten per vistrip verklaard kon worden door significante verschillen tussen de bemonsterings-maanden. Met deze identificatie van strata in het gegevens-bestand is het mogelijk om de bemonstering ten behoeve van de visserij-statistiek te optimaliseren. Indien ieder reservoir een dag per maand bemonsterd wordt, waarbij uit een minimum van acht vistrips de gemiddelde vangst per vistrip wordt berekend, kan de totale jaarlijkse vangst worden geschat met een nauwkeurigheid van 28%. Daarbij moet dan tevens het totaal aantal vistrips per dag voor die maand worden vastgesteld. Bij genoemde nauwkeurigheid kan een halvering van de geschatte jaarlijkse vangst als een significante daling worden aangemerkt. De voorgestelde strategie betekent een afname van 50% in bemonsterings-inspanning in vergelijking tot het bestaande systeem van twee bemonsterings-dagen per maand, dat door de overheid wordt gehanteerd en dat in principe een nauwkeurigheid van 19% kan opleveren. Met de voorgestelde strategie wordt niet de systematische fout gemaakt die op dit moment ontstaat doordat men rekent met aantallen geregistreerde kano's, i.p.v. vissende kano's, als maat voor de visserij-inspanning.

Om een beheersadvies voor de kieuwnetvisserij te kunnen onderbouwen was naast de karakterisering van deze visserij ook een goede schatting voor de selectiviteit van het

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gebruikte netwerk nodig. De populatie-dynamica van de belangrijkste soorten zou namelijk bestudeerd moeten worden door middel van analyse van lengte-frequentie verdelingen van kieuwnet-vangsten, welke eerst voor netselectiviteit gecorrigeerd moesten worden. De netselectiviteit moest ook nauwkeurig geschat zijn om juiste voorspellingen over de effecten van maaswijdte-reguleringen te kunnen geven. Daarom werden verschillende methoden voor het schatten van de kieuwnetselectiviteit vergeleken voor de tien meest voorkomende vissoorten in Tissawewa. Het model van Holt, waarin verondersteld wordt dat de vorm van de selectiecurve kan worden beschreven door een normale verdeling, werd vergeleken met het model van Sechin waarin de selectiviteit wordt geschat aan de hand van de morfologie van de vis. Het model van Holt werd daarbij uitgebreid tot een model waarbij de standaard afwijking in de selectie-curve lineair toeneemt met de optimale selectie-lengte. Het model van Sechin werd eveneens uitgebreid, tot een model waarbij de standaardafwijking in de lichaams-omtrek per lengte-klasse lineair toeneemt met de lichaams-omtrek.

De selectie-curves volgens de uitgebreide Holt- en Sechin-modellen werden vergeleken met lengte-frequentie verdelingen van de vangst voor de grootst beschikbare monsters per soort en per maaswijdte. Hierbij werd aangenomen dat deze lengte-frequentie verdelingen de eigenlijke selectie-curves het dichtst benaderen, omdat ze zijn verkregen uit een gestratificeerd bemonsterings-programma over alle habitats en over een lange tijds-periode. Het uitgebreide Holt model werd geprefereerd boven het uitgebreide Sechin model, omdat het Sechin model resulteert in selectie-curves die systematisch smaller zijn dan lengte-frequentie verdelingen van de vangst en selectie-curves volgens het Holt model.

Met behulp van de geschatte netselectiviteit werden de populatie-structuren van *O. mossambicus* en de inheemse cypriniden gereconstrueerd uit de lengte-frequentie verdelingen van experimentele kieuwnet-vangsten. De dynamiek in deze grootte-structuren, met aanvullende informatie over de recruterings-patronen, werd gebruikt bij het bepalen van groei en totale mortaliteit van de verschillende soorten. De recruterings-patronen werden onderzocht aan de hand van de gonaden-ontwikkeling en het voorkomen van vislarven, waarbij alle soorten in deze studie verhoogde voortplantings-aktiviteit vertoonden gedurende de regenseizoenen rond mei en november. Voor de ongeëxploiteerde cypriniden was de natuurlijke mortaliteit gelijk aan de totale mortaliteit. De natuurlijke mortaliteit van *O. mossambicus* werd verondersteld gelijk te zijn aan de mortaliteit van vergelijkbare lengte-groepen van cypriniden. Na het schatten van de groei en mortaliteit werd de bestands-omvang van *O. mossambicus* bepaald met behulp van een lengte-gestructureerde cohort-analyse. Hierbij werd gebruik gemaakt van de geschatte totale commerciële vangst en de grootte-structuur van die vangst. De bestands-omvang van de overige soorten werd afgeleid uit de gewichts-aandelen van die soorten in voor selectiviteit en visserij-inspanning gecorrigeerde experimentele kieuwnet-vangsten.

O. mossambicus bleek te groeien tot een geschatte lengte van 14 cm in diens eerste levensjaar en tot 21 cm in het tweede. De natuurlijke mortaliteit van *O. mossambicus* (mortaliteits-coëfficiënten 1.9 en 1.7 jr^{-1} voor vrouwtjes en mannetjes) en cypriniden (1.3 tot 4.7 jr^{-1}) is hoog, mogelijk als gevolg van predatie door vogels. De visserij-mortaliteit van *O. mossambicus* is ook hoog, met een gemiddelde van 1.6 jr-1 voor de totale geëxploiteerde lengte-range van 10.0 tot 19.0 cm. De omvang van het totale visbestand werd geschat op

1 829 kg/ha, met 128 kg/ha *O. mossambicus*, 1 098 kg/ha kleine pelagische cypriniden (90% *A. melettinus*), 457 kg/ha *Barbus* spp. en 146 kg/ha overige vissoorten. De totale biologische visproduktie werd geschat op 5 400 kg/ha/jr waarvan 400 kg/ha/jr wordt geproduceerd door *O. mossambicus* en 3 200 kg/ha/jr door *A. melettinus*. Verhoging van de vis-oogst van 5% naar 10% van de biologische visproduktie bleek dus haalbaar door additionele exploitatie van de tot nu toe onbevistte *A. melettinus*, echter alleen wanneer technische interaktie met de bestaande visserij op *O. mossambicus* voorkomen kan worden. Als alternatieve beheersmaatregel werd voorgesteld *A. melettinus* indirekt te exploiteren door controleerbare (niet-reproducerende) bestanden aan roofvis (bijvoorbeeld *Lates calcarifer*) uit te zetten.

Er werd tevens geconcludeerd dat het gebruik van steeds kleinere mazen het voornaamste probleem is in de huidige visserij op *O. mossambicus*. In Tissawewa is 64 mm bijvoorbeeld al een algemeen gebruikte maaswijdte. Hierdoor wordt de vis al bij een lengte van 15 cm weggevangen. De grens van geslachtsrijpheid lag hier enige jaren geleden nog rond de 16 cm maar is inmiddels gezakt naar 13 cm. *O. mossambicus* groter dan 20 cm is op dit moment zeldzaam in Tissawewa en deze 2 jaar oude vissen groeien nog slechts langzaam in vergelijking met situaties waarin deze soort pas gevangen wordt bij lengtes boven de 20 cm. Deze vorm van stunten is een bekend verschijnsel in met kieuwnetten geëxploiteerde cichliden-bestanden en kan alleen voorkomen worden door de vangst te beperken tot lengte-klassen boven de maximale grens van geslachtsrijpheid. Daarom wordt gesteld dat handhaving van de wettelijke minimum maaswijdte van 76 mm gestrekte maas, prioriteit zou moeten krijgen als beheersmaatregel ter voorkoming van overbevissing van *O. mossambicus*.

De effecten van verschillende optionele beheersmaatregelen op de bestaande visserij konden vervolgens worden gekwantificeerd met behulp van een lengte-gestructureerd simulatie-model, en de geschatte parameter-waarden voor netselectiviteit, recrutering, groei en mortaliteit. Het in deze studie ontwikkelde analytische model simuleert de dynamiek in de vis-populatie en de invloed van de visserij, rekening houdend met de ruimtelijke verspreidings-patronen en de migratie van de vis tussen de onderscheiden habitats. De dagelijkse recrutering van vis, bij een theoretische startlengte van 0 cm, wordt gesimuleerd met een variabel temporeel patroon. Hierdoor is het model algemeen toepasbaar, ook in tropische situaties waar de recrutering niet beperkt is tot één korte periode per jaar. Het model is gedifferentieerd naar sexe en de groei van de vissen wordt bepaald door hun lengte. De dispersie van vissen over de lengte-klassen in het model wordt gesimuleerd met de 'fractional boxcar train' methode. De natuurlijke mortaliteit wordt constant verondersteld voor alle geëxploiteerde lengte-klassen. De visserij-mortaliteit is een functie van de vis-lengte, gebaseerd op een combinatie van kieuwnet selectiviteits-curves voor verschillende maaswijdten. De ruimtelijke verspreiding van de vissen, over de verschillende habitats binnen het model, is gebaseerd op waargenomen patronen in de lengte-afhankelijke habitat bezetting. Het model geeft voorspellingen over de voortschrijdende effecten van optionele beheersmaatregelen op de omvang en grootte-samenstelling van de populatie en de vangst in de verschillende habitats. De commerciële kieuwnet-visserij op *O. mossambicus* in Tissawewa werd gebruikt als voorbeeld en de simulatie-resultaten voor dit reservoir

kwamen goed overeen met onafhankelijke schattingen voor output-parameters.

Op basis van model-berekeningen bleek dat de totale oogst in de visserij op *O. mossambicus* op dit moment dicht bij het maximaal haalbare niveau ligt. Er werd aangetoond dat het uitbannen van maaswijdtes kleiner dan 76 mm gestrekte maas inderdaad de kans op groei-overbevissing zal doen afnemen. De modale lengte van de gevangen vis in Tissawewa zal na een dergelijke maatregel namelijk verschuiven van 15 cm naar 17-18 cm waardoor een groter deel van de vissen zich zal kunnen voortplanten bij een lengte van 16 cm. Een aanzienlijke verhoging (60%) van de vangst per eenheid van inspanning kan bereikt worden door een halvering van de inspanning. Hierbij zou de totale oogst echter afnemen met 20%. Dit is niet wenselijk omdat het inkomen van de vissers, in deze visserij met goedkope kieuwnetten, vooral wordt bepaald door hun totale vangst. Bovendien is de totale vangst een belangrijke bron van goedkoop eiwitrijk voedsel voor de plattelands-bevolking. Er werd geadviseerd de visserij-inspanning te beperken tot het huidige niveau, omdat een stijging met 50% slechts een zeer geringe verhoging (5%) van de vangst zou opleveren. De vangst per eenheid van visserij-inspanning zou hierbij afnemen met 30%.

De conclusies voor het beheer van de visserij op *O. mossambicus* werden geëxtrapoleerd tot het kader van de totale Sri Lankaanse reservoir-visserij, door gebruik te maken van gegevens over geschatte groei en mortaliteit uit de literatuur over populaties in verschillende Sri Lankaanse reservoirs. Modelberekeningen met deze literatuur-waarden voor input parameters toonden aan dat conclusies voor het beheer van Tissawewa toepasbaar zijn op de gehele reservoir-visserij in Sri Lanka. Omdat *O. mossambicus* in verschillende reservoirs waarschijnlijk een grotere maximale lengte bereikt dan in Tissawewa, zal de optimale minimum maaswijdte misschien zelfs nog iets hoger liggen dan 76 mm. Het gebruik van maaswijdtes kleiner dan 76 mm, in de visserij op *O. mossambicus*, moet dus voorkomen worden in alle reservoirs van Sri Lanka.

Na simulatie van kieuwnet-visserijen met 15 en 30 mm gestrekte maas in verschillende habitats, werd geconcludeerd dat invoering van 30 mm kieuwnetten, voor de exploitatie van *Barbus* soorten, inderdaad grote schade zal toebrengen aan de bestaande visserij. Hierbij werd aangenomen dat deze aanvullende visserij zich vlak buiten de vegetatie van de oeverzone zou gaan concentreren, omdat de dichtheid aan volwassen *Barbus* hier relatief hoog is. Bij het bemonsteren van de visserij in Tissawewa werd al aangetoond dat de vissers vermeende concentraties van vis volgen tot in de oeverzone van het reservoir. Er werd verder geconcludeerd dat de invoering van 15 mm kieuwnetten, voor exploitatie van de pelagische *A. melettinus*, slechts weinig schade zal opleveren aan de bestaande visserij. Hierbij werd aangenomen dat deze visserij zich buiten de ondiepste delen van de oeverzone zal concentreren. Dit laatste is waarschijnlijk omdat *A. melettinus* vooral voorkomt vanaf de diepere delen van de oeverzone tot overal in het open water, waar deze soort gemakkelijk te bevissen is.

Abstract

The major factor in the development of Sri Lankan inland fisheries was the introduction, in 1952, of the exotic cichlid *Oreochromis mossambicus* (Peters) which dominated the catch ever since. The most important water bodies for the inland fisheries are the larger (> 100 ha) man-made reservoirs in the dry lowlands of north, east and south east Sri Lanka. The reservoirs cover a total surface area of around 100 000 ha. They are shallow with maximum depths often less than 5 m and exhibit considerable fluctuations in water level. Supply of irrigation water is the main purpose of these reservoirs and fish production is a secondary function of recent origin. The mean annual yield is estimated at 270 to 300 kg/ha/yr which is high for tropical lacustrine fisheries. The total catch from inland fisheries was low before the introduction of *O. mossambicus*, because a fishery for indigenous fresh water species hardly existed. The commercial fisheries still use only a small proportion of the available fish biomass. Although large stocks of indigenous minor cyprinids are present in the lowland reservoirs of Sri Lanka, these species form only a minor part of the catch.

An additional fishery for the unexploited cyprinid resources, with small-meshed gillnets, was recently proposed for the improvement of inland fisheries yield. While considering such additional small-meshed fisheries, however, the conservation of the presently successful fishery for *O. mossambicus* should remain a first priority for the reservoir fishery management. Formulation of a management strategy is therefore necessary, both for the existing fishery on *O. mossambicus* and for optional subsidiary fisheries on presently unexploited species.

The fish community structure, fish population dynamics and characteristics of the reservoir fishery were studied in Tissawewa, a typical irrigation reservoir of 200 ha. in the south eastern lowland of Sri Lanka. The major part of the fish community in Tissawewa consists of a group of eleven common species, including two introduced tilapias: *O. mossambicus* and *O. niloticus (L.)*. The other species are indigenous to Sri Lanka, including five riverine cyprinids: *Amblypharyngodon melettinus* (Valenciennes), *Barbus chola* (Hamilton), *B. dorsalis* (Jerdon), *B. sarana* (Hamilton) and *Rasbora daniconius* (Hamilton); two riverine catfishes: *Mystus gulio* (Hamilton) and *M. vittatus* (Bloch); one riverine goby: *Glossogobius giuris* (Hamilton) and one estuarine halfbeak: *Hyporamphus gaimardi* (Valenciennes). Several other species are present in the reservoir, but only in small quantities.

A major part of the fish biomass (54%) is formed by the small (max. length 10 cm) pelagic cyprinid *A. melettinus*, which feeds directly on phytoplankton and detritus. Detritus is the most important food item for *O. mossambicus* (max. length 30 cm), which represents 7% of the fish biomass. The group of minor *Barbus* spp. (max. length 30 cm), representing 25% of the fish biomass, feeds mainly on small zoobenthos, which is also the main item in the diet of *Mystus* spp. (max. length 30 cm). These catfish are partly piscivorous at larger sizes. Zooplanktivorous fish, like *R. daniconius* (max. length 15 cm) and *H. gaimardi* (max. length 20 cm), represent less than 10% of the fish biomass and piscivorous species like, *G. giuris* (max. length 30 cm), even less than 5%. The total fish biomass is estimated at 1 829 kg/ha, with a total biological fish production of 5 400 kg/ha/yr. The biological fish

production per species (-group) is 3 600 kg/ha/yr small pelagic cyprinids (90% *A. melettinus* and 10% *R. daniconius*), 1 100 kg/ha/yr *Barbus* spp., 400 kg/ha/yr *O. mossambicus* and 300 kg/ha/yr other species.

The commercial fishery in Tissawewa is typical for Sri Lankan lowland reservoirs, with gillnets fished from outrigger canoes as the most important gear. Daily effort remains around 9 fishing trips as long as water levels do not drop too low. A fishing trip normally includes one or two fishermen who set two gillnets of about 225 m long, usually during the night. The most common mesh sizes are 64, 70 and 76 mm stretched mesh, used in a ratio of 4:4:1 in terms of numbers of nets in operation. The mean catch per trip in the period 1991-1992 was around 14 kg and the annual yield in this period was 242 kg/ha, with *O. mossambicus* accounting for about 70% of the catch. *O. niloticus* accounted for 5% and stocked Indian carps for 20% of the catch in this period. The relative importance of *O. niloticus* seems to be increasing during recent years. Indigenous species represented only 5% of the total catch.

O. mossambicus in Tissawewa are growing to about 14 cm in one year and are caught in gillnets during their second year of life. The modal length in commercial catch length frequency distributions is invariably found at 15.5 cm. The mean instantaneous fishing mortality (F) for the length-range of 15.0 to 18.5 cm is high, with $F = 4.7$ yr^{-1} and $F = 5.5$ yr^{-1} for males and females respectively. The mean fishing mortality for the total exploited length-range of 10.0 to 19.0 cm is 1.6 yr^{-1}. The instantaneous natural mortality (M) for length classes from 10 cm upwards is also high, with $M = 1.7$ yr^{-1} and $M = 1.9$ yr^{-1} for males and females respectively. Due to the high fishing pressure, specimen of *O. mossambicus* larger then 19 cm are rare in Tissawewa, although estimates of potential growth indicate that lengths above 25 cm could be reached after 3 to 5 years (for males and females respectively). The size at maturity of female *O. mossambicus* has decreased from 16 to 13 cm during recent years, and a danger of growth overfishing is clearly present.

The management options for Sri Lankan reservoir fisheries can be divided in three major categories. The first category is formed by management measures related to the exploitation of introduced tilapias. The conservation of the fishery for *O. mossambicus*, in view of its present importance, should have the greatest priority, not only within in this category but in the overall context of reservoir fishery management. A large (> 25%) increase in the catch is not expected from any management measure in this fishery, which is near the level of maximum sustainable yield (*MSY*). Conservation of the existing fishery, by re-enforcement of the legal minimum mesh size of 76 mm stretched, is therefore recommended in the present study. This mesh size would reduce the chance of stunting in *O. mossambicus* populations since the peak in the catch length-frequency distributions would shift from 15 to 17-18 cm, leaving more fish of 16 cm a chance to reproduce. The results of this '76 mm option' should be monitored through catch and effort data recording. If catch levels would increase with more than 10%, following this measure, and if *O. mossambicus* of 18 cm would become dominant in the catch, a legal minimum mesh size of 82 mm could be implemented. Larger mesh sizes would certainly be beneficial when *O. niloticus* would replace *O. mossambicus* as the most abundant tilapia species, but legal minimum mesh sizes above 88 mm stretched mesh are not recommended for the fishery on *O. mossambicus*. Any

increase in fishing effort in this fishery should be prevented but forced reduction of the effort is not recommended either, since this would lead to a decrease in total yield. Since the costs of fishing are very low in this fishery, the income of the fishermen is determined by their total returns rather than by the catch per unit of effort. The total catch from inland fisheries is also important as a source of high-protein food for the rural population.

The second category of management options contains all measures related to the direct exploitation of indigenous species. Two groups of minor cyprinids, the *Barbus* spp. and *A. melettinus*, have been identified as candidates for proposed additional fisheries parallel to the existing fishery for tilapias. These two groups both represent a major part of the fish biomass and production in the reservoirs. These additional fisheries, however, would lead to the use of even smaller mesh sizes as presently operated, since the cyprinids are smaller than the exploited tilapias (Fig. A). Mesh sizes as small as 30 and 15 mm stretched mesh would be needed to exploit the *Barbus* spp. and *A. melettinus* respectively. Therefore these additional fisheries should only be considered if technical interactions with the existing fishery can be prevented. In case of the *Barbus* spp. this is not possible since these species show considerable habitat overlap with the juveniles of *O. mossambicus*. Since the smallest stages of *O. mossambicus*, vulnerable to mesh sizes of 15 mm, are spatially segregated from *A. melettinus*, this additional fishery may be feasible without causing serious damage to the existing fishery. Based on the large biomass and production of *A. melettinus*, a subsidiary fishery with 15 mm stretched mesh gillnets and/or lift nets may at least equal the present yield of *O. mossambicus*.

The third category of management options contains all measures related to culture-based fisheries with exotic species. A government enhanced stocking program with major Indian carps was ended in 1990, apparently for religious reasons. Poor returns left this program open to criticism and privatization has sofar not taken place. A culture-based fishery with controllable (non-reproducing) piscivorous fish is proposed in the present study, as a means of indirect exploitation of the large production of small indigenous species. The effect of piscivorous fish on the existing fishery must be carefully examined in isolated situations since such predators are presently rare in reservoir fish communities in Sri Lanka. The best candidate for such a culture-based fishery seems 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. *L. calcarifer* is a prized consumption fish all over south east Asia. Due to food conversion, the resulting increase in catch from this option will be an order of size lower than in the case of direct exploitation of small cyprinids, but the product will be of a much higher quality.

The inland fishermen in Sri Lanka are relatively well organized in fishermen societies which exist around all the major reservoirs. These small units show a considerable amount of internal control and are able to practice a limited access to the fishery of each reservoir. The fishermen societies form a useful interface for fisheries management and can easily be contacted by extension workers. Fishermen societies are willing to accept management regulations, if these are unanimously agreed upon and if they are strictly enforced by the government. This situation should be taken advantage of when management measures are to be implemented.
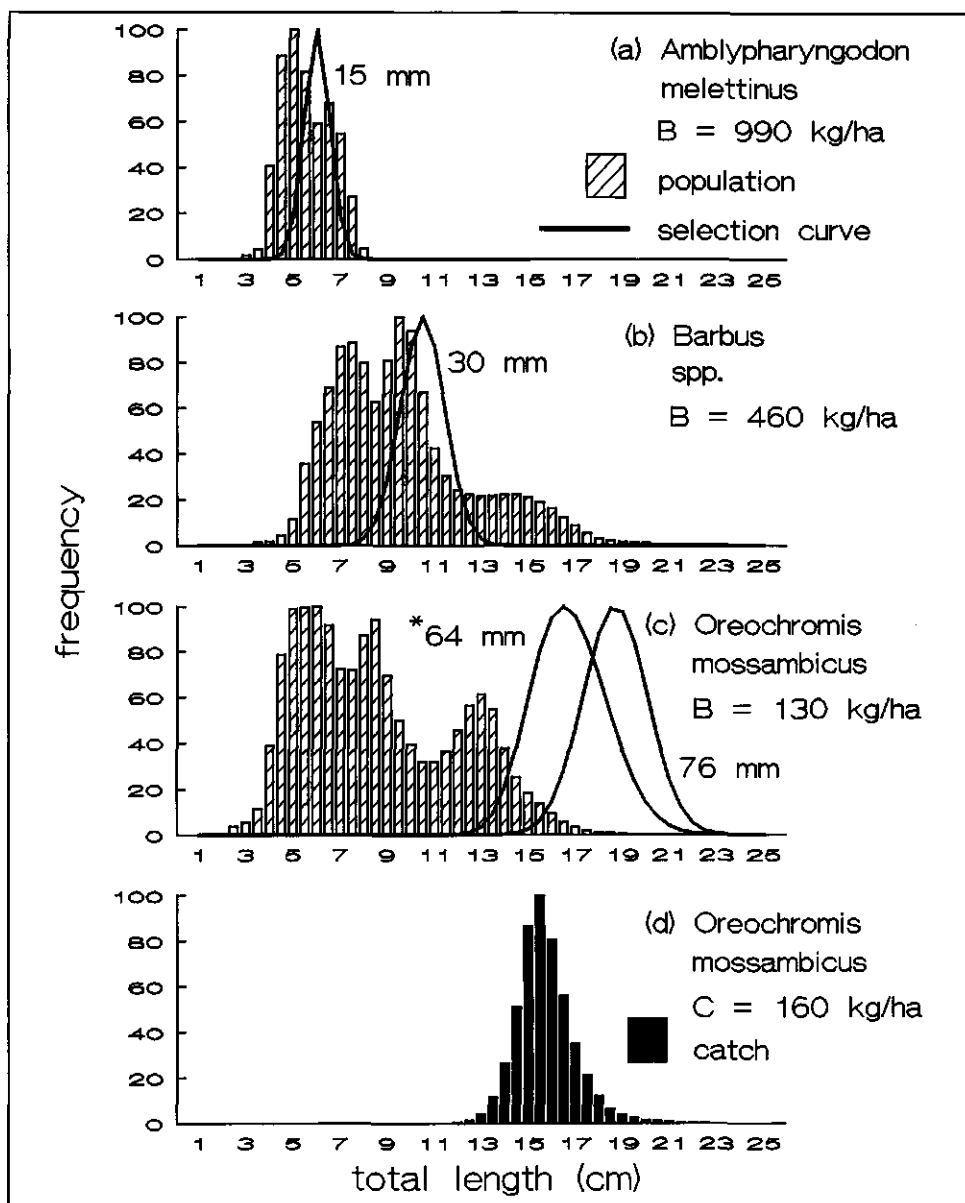
Fig. A. Population size structure and gillnet selectivity curve of proposed 15 mm mesh size (recommended in the present study) for *A. melettinus* (a). Population size structure and gillnet selectivity curve of proposed 30 mm mesh size (not recommended) for *Barbus* spp. (b). Population size structure and gillnet selectivity curves of presently operated *64 mm mesh size (*in combination with 70 an 76 mm) and recommended minimum mesh size of 76 mm for *O. mossambicus* (c). Size structure of the catch from presently operated mesh sizes (d). B = biomass of the population, C = annual catch.

Chapter 1

General introduction

Sri Lankan inland fisheries, problems and study objectives

The contribution of inland fisheries to the total fish production in Sri Lanka has increased from almost 0 to about 20% during the last decades (Jayasekera, 1990). The major factor in this development was the introduction, in 1952, of *Oreochromis mossambicus* (Peters) which dominated the catch ever since (Fernando & Indrasena, 1969; De Silva, 1988a). Stocking of exotic major carps further improved the inland fisheries, but stocking programs ended in 1990. The mean annual yield is estimated at 270 to 300 kg/ha/yr (De Silva, 1988a), which is high compared to the average annual yield of 80 kg/ha from this type of fisheries in other tropical countries (Oglesby, 1985). Based on official data, the maximum sustainable yield (*MSY*) for Sri Lankan reservoirs was estimated at 256 kg/ha/yr (De Silva *et al.*, 1991), but official data are considerably biased (Amarasinghe & Pitcher, 1986; Chandrasiri, 1986; Amarasinghe, 1992) and the estimate for *MSY* takes into account only the fishery for introduced tilapias. In 1990 the Sri Lankan government abandoned its active involvement in inland fisheries management, apparently for religious reasons (Amarasinghe, 1992). Renewed involvement is expected since the change of government in 1994.

The most important water bodies for Sri Lankan inland fisheries are the larger (> 100 ha) man-made reservoirs in the dry lowlands of north, east and south east Sri Lanka (De Silva, 1988a). There are hardly any natural lakes in Sri Lanka. The reservoirs, many of them being 500 to 2 000 years old (Fernando & Indrasena, 1969), cover a total surface area of around 100 000 ha. They are shallow with maximum depths often less than 5 m and exhibit considerable fluctuations in water level. Large parts of most lowland reservoirs are similar to the natural marshes which are formed during the wet seasons and are characterised by extensive littoral zones (Schiemer & Duncan, 1988). Supply of irrigation water is the main purpose of these reservoirs and the Irrigation Department of the Sri Lankan government is responsible for water management. Fish production is a secondary function of recent origin (De Silva, 1988a). This pattern of multi-purpose use is a feature of the inland fisheries of most Asian countries (Petr, 1985; De Silva, 1988b).

The inland fisheries of Sri Lanka is characterized by its small-scale gear, mainly outrigger canoes and multifilament gillnets. The fishery exploits mainly introduced tilapias, *O. mossambicus* and *O. niloticus* (Linneaus), with gillnets of 64 to 100 mm stretched mesh. The total catch from inland fisheries was low before the introduction of *O. mossambicus* in 1952, because a fishery for indigenous fresh water species hardly existed (De Silva, 1988a). The Sri Lankan fish fauna lacks indigenous lacustrine species (Fernando & Indrasena, 1969) and the man-made reservoirs were occupied by riverine and estuarine fish (Schiemer & Duncan, 1988). The fish communities are presently characterized by small adult sizes of the most important species, which largely feed directly on phytoplankton and detritus (Schiemer & Duncan, 1988).

The commercial fisheries use only a small proportion of the available fish biomass (Schiemer & Duncan, 1988). Although large stocks of indigenous minor cyprinids are present in the lowland reservoirs of Sri Lanka, these species form only a minor part of the catch (De Silva, 1985; De Silva, 1988a). The introduced tilapia *O. mossambicus* presently accounts for 80% of the total annual catch from inland waters (De Silva, 1988a). An additional fishery for the unexploited cyprinid resources, with small meshed gillnets, was recently proposed for the improvement of inland fisheries yield (De Silva & Sirisena, 1987, 1989; Sirisena & De Silva, 1988, 1989). The minor cyprinid resources would be exploitable with a subsidiary gillnet fishery, using 15 and 30 mm gillnets, without any detrimental effect on the existing commercial fishery for tilapia. Adult stages of minor cyprinids and *O. mossambicus* were assumed to occupy the open water zone whereas juveniles of all species would stay in the littoral areas. If this were true, and if the commercial gillnet fishery would be confined to the open water zone, an additional small-meshed gillnet fishery for minor cyprinids would be possible without technical interactions with the existing fishery for *O. mossambicus*. Adult minor cyprinids would then be caught in the open water with small mesh sizes, leaving juvenile *O. mossambicus* unharmed in the littoral zone. The potential catch of minor cyprinids was expected to exceed the present catch of *O. mossambicus* (De Silva & Sirisena, 1989).

While considering additional small-meshed fisheries, the conservation of the presently successful fishery for *O. mossambicus* should remain a first priority for the reservoir fishery management. Stocks of *O. mossambicus* in Sri lankan reservoirs have been reported to be subject to growth overfishing (Amarasinghe, 1988; Amarasinghe, 1992). An alarming trend of decreasing mesh sizes and sizes of landed fish has been recorded, with mesh sizes operated below the legal minimum of 76 mm stretched mesh. Neither the present legal minimum mesh size nor the recently proposed increase to 100 mm (Amarasinghe, 1992) were based on thorough scientific research and/or predictive analytical modelling.

Formulation of a management strategy is necessary, both for the existing fishery on *O. mossambicus* and for optional subsidiary fisheries on presently unexploited species. The main objective of the present study was therefore to formulate a scientifically supported management advice for the Sri Lankan reservoir fishery. The problem to be solved was which mesh size or combination of mesh sizes should be used, in combination with which level of fishing effort, to optimize the yield in this gillnet fishery. Detailed studies on ecology and population dynamics of the fish stocks and on characteristics of the existing fisheries were carried out to provide a thorough scientific basis for the answer to this question.

The study area and sampling program

Tissawewa reservoir
Tissawewa was chosen as the study area, since this is a typical irrigation reservoir, 2 000 years old (De Silva, 1988a) and situated in the dry south eastern lowland of Sri Lanka. This reservoir is part of the Kirindi Oya Irrigation Scheme in the Hambantota district. The main

river is the Kirindi Oya which feeds the main reservoir Lunuganwehera (*ca.* 3000 ha) from which three minor downstream reservoirs, Yodawewa (*ca.* 500 ha), Weerawila wewa (*ca.* 400 ha) and Tissawewa (*ca.* 200 ha), are fed. The reservoir has a mean surface area of 195 ha and a mean maximum depth of 3 m since January 1987 (data from Sri Lankan Irrigation Dept.). The mean surface area during the main study period, 1991-1992, was 175 ha. Maximum depth and surface area fluctuations follow the patterns in rainfall. Two monsoon periods occur annually in the southern and eastern lowland of Sri Lanka. The major rainy season is during the north east monsoon around November and a minor peak in rainfall occurs during the south west monsoon around May.

Fishery dependent data

Data on the commercial fisheries in Tissawewa were collected from September 1991 to July 1993. No commercial fishing took place from September 1992 to February 1993 due to extreme low water levels and a resulting massive fish kill. Such periodical draughts occur every five to ten years in this area. After the draught it took several months for the fish densities to increase and the fishermen collectively started fishing again in March 1993. From September 1991 to August 1992, the commercial fisheries were sampled for four full days during each month. From September 1992 to July 1993 this was done for two full days each month. Data recorded per fishing trip included: date of trip and name of canoe owner, number of fishermen, type of gear, method of fishing, number of gear units, size and mesh size per unit, duration of fishing trip, total weight of catch per species, length frequency distribution per species and location of the fishing operation.

Fishery independent data

Experimental fishing with gillnets was carried out on a monthly basis from September 1991 to August 1992 and from December 1992 to July 1993 in Tissawewa. A total of 480 meters of multi-mesh monofilament gillnets contained ten different mesh sizes from 12.5 to 90 mm stretched mesh respectively. Panel lengths increased from 5 to 15 meters with increasing mesh size. Two nets of 60 m * 1.5 m were set simultaneously at each station, one with the smaller (12.5 to 37 mm) and one with the larger (50 to 90 mm) meshes. Mesh sizes were randomly distributed within the nets. Each month four sets of netting were set, at four different stations. One sampling station was chosen within each macro-habitat in the reservoir. This was done four times each month, twice at daytime and twice at night. Day time settings were from 06.00 hours to 08.00 and from 06.00 to 18.00 hours for small and large meshes respectively. Night time settings were from 18.00 hours to 20.00 and from 18.00 to 06.00 hours. Additional fishing for fish fry and juveniles was carried out with a bottom fishing beam trawl (3 * 1.5 m mouth opening, 10 mm stretched mesh), a fine meshed scoop net and a fine meshed hoop net. The major fishery independent data base, was formed by length-frequency distributions per species, station, setting time and mesh size from experimental gillnets. Additional catch information included the biomass per species, station, setting time and mesh size and the way fish were caught in the net. Biological data were collected in the form of measurements on total length, maximum and gill girth and body weight, gonad weight and gonad development stage.

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Introduction to the various chapters

Spatial distribution of the fish in relation to fisheries management

Studies of resource partitioning among species and size classes within species in fish communities provide insight into the nature of intra- and interspecific interactions, and essential information for the development of production models for fisheries management (Werner et al., 1977; Schiemer & Duncan, 1988). The result of any management strategy will depend on the size-related spatial and temporal distribution patterns of the fish and fishermen. **Chapter 2** of this dissertation relates the commercial fisheries to spatial distribution patterns of the fishes on the basis of habitat electivity, habitat overlap, seasonality and reservoir periodicity. In this chapter the hypothesis is tested that introduction of a small meshed gillnet fishery, targeting minor cyprinids with 15 and 30 mm stretched mesh gillnets, is feasible without damaging the existing fishery for *O. mossambicus* (De Silva & Sirisena, 1987, 1989; Sirisena & De Silva, 1988, 1989). The main problem to be solved is whether the adult stages of the minor cyprinids are sufficiently separated in space from the juveniles of *O. mossambicus*. Introduction of an additional fishery can only be recommended when the predicted effects on the existing fishery are limited. A revised hypothesis on the effects of small meshed gillnets is put forward, providing more detail in the recommendations on exploitation patterns in terms of species and mesh sizes.

Monitoring fisheries input and output

Catch and effort data are often the only data available to managers of tropical fisheries (Larkin, 1982), especially when it comes to country-wide historical data sets. An efficient system for the collection of catch and effort data should be a first priority when it comes to investments in information gathering in any type of fishery. Collection of basic statistical data remains a problem and Sri Lanka is no exception in this (Marr, 1982; Amarasinghe & Pitcher, 1986; De Silva, 1988a; Amarasinghe, 1992). Inaccuracy is often caused by systematic errors in catch and effort data recording systems (Dudley & Harris, 1987). An accuracy of 30% is needed if a serious decline (reduction of 50%) in total catch is to be detected timely. The accuracy is a combination of bias and precision and it is improved by a well designed sampling program, increased sampling effort and removal of bias.

Chapter 3 describes a typical Sri Lankan reservoir fishery in terms of spatial and temporal patterns in catch, effort, catch per unit of effort (*CpUE*), mesh sizes and size distributions of the catch. A general analyses of variance (Sokal & Rohlf, 1969) is applied to identify strata in the *CpUE* data set. The main objective of this study is to indicate how the system for collection of catch and effort data could be optimised and how the accuracy of the data could be improved. An accurate description of the existing fishery, in terms of effort, *CpUE*, mesh sizes and size distributions of the catch, is needed to achieve this objective and to enable predictions on the effects of different management strategies on the existing fishery.

Estimation of gillnet selectivity

A precise description of gillnet selectivity per species is necessary to obtain accurate predictions on the results of mesh size regulations (Reddin, 1986; Van Densen, 1987; Reis & Pawson, 1992; Buijse *et al.*, 1992). Accurate estimates of selectivity are also needed for the interpretation and analyses of gillnet catch statistics in population studies (Winters & Wheeler, 1990; Spangler & Collins, 1992). Gillnets are size-selective and fish sizes differing more than 20% from the optimum length will hardly be retained (Hamley, 1975). Gillnet selectivity is usually described by a bell-shaped curve, which is broader and more positively skewed when more fish are caught tangled, and may approach the normal curve when most fish are caught wedged. The most reliable way of estimating gillnet selectivity is directly, by fishing a known population (Hamley, 1975). This is expensive since large numbers of fish have to be tagged (Borgström, 1989) or the population has to be sampled simultaneously with gear of known selectivity (Winters & Wheeler, 1990).

The indirect methods developed by Holt (1957) and Sechin (1969a, b) are still preferred by many workers, mainly because of ease of application. The Holt model is based on the assumption that the selection curve can be described by a normal distribution with constant efficiency for all mesh sizes. The input for this model is the catch ratio per length category of fish in two different mesh sizes. The Sechin model assumes a unimodal selection curve, which is positioned along the length axis by the ratio between mesh perimeter and body girth. Extended versions of the Holt and Sechin models are applied in **Chapter 4**. The first objective of this study is to compare these models for estimation of gillnet selectivity. The second objective is to obtain estimates of gillnet selectivity for the most important fish species in Sri Lankan reservoirs. The third objective is to derive a new method for rapid estimation of gillnet selectivity.

Analyses of stock dynamics

Growth, recruitment and mortality are important input parameters in analytical yield models, but are often difficult to estimate for fish stocks from tropical regions (Pauly & Murphy, 1982; Sparre *et al.*, 1989) although length-based methods are available (Pauly & Morgan, 1987; Gulland & Rosenberg, 1992). Length-based methods, however, should be supported with information on recruitment patterns and, whenever feasible, with some information on length at age (Macdonald & Pitcher, 1979).

Size distributions of commercial catches have been used in earlier studies to assess growth and mortality parameters of *O. mossambicus* in Sri Lankan reservoirs (Amarasinghe, 1987; De Silva *et al.*, 1988; Amarasinghe *et al.*, 1989) and recruitment peaks were reported to occur during the rainy seasons (De Silva & Chandrasoma, 1980; De Silva, 1983). Several cyprinid species were reported to migrate upstream from the reservoirs into the rivers for spawning (Silva & Davis, 1986) and reproduction periods have been reported to coincide with the rainy seasons (Chandrasoma & De Silva, 1981; De Silva, 1983; De Silva *et al.*, 1985). This kind of ecological information, however, has not been used as extra input in the assessment of stock dynamics. Recruitment patterns, in studies on growth and mortality, are usually presented as output of length-frequency analyses, instead of input parameters which can be used to define the starting points of growth curves. Fisheries mortality is

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commonly estimated after calculating the natural mortality with an empirical formula, without any consideration of the ecological characteristics of the system. The lack of integrated ecological information seems to be a general character of recent stock assessment studies from tropical regions (Yap, 1984; Amarasinghe, 1987; De Silva *et al.*, 1988; Amarasinghe *et al.*, 1989; De Silva, 1991; Getabu, 1992).

In **Chapter 5**, the scope for an increase in fisheries yield is estimated for a typical Sri Lankan reservoir, on the basis of a length-based stock assessment, supported by ecological information and direct ageing. The estimates for gillnet selectivity from **Chapter 4** are used to reconstruct population structures from the length-frequency distributions of experimental gillnet catches. The dynamics in corrected length frequency distributions are used to quantify stock dynamics. The supporting ecological information consists of recruitment patterns on the basis of developments in gonado somatic index (*GSI*) and larval abundance, temporal patterns in juvenile abundance and estimates of natural mortality for unexploited species. Integration of this ecological information leads to an upgraded use of the length-based methods. The feasability of the proposed exploitation of minor cyprinids is discussed on the basis of estimated biomass and production of different species (-groups).

Modelling and management of the fisheries

Predicting the results of different management alternatives is essential for fisheries management (Gulland, 1983; Hilborn and Walters, 1992) and simulation models are important tools to obtain such predictions (Jørgensen, 1994). For fish stocks in temperate regions these predictions were traditionally obtained from classical yield models (Beverton and Holt, 1957; Ricker, 1958), which were based on the concept of age-structured populations. These early analytical models assumed constant fishing mortality after knife-edge recruitment to the fishery. This is not realistic in case of gillnet fisheries with their gradual size-selective impact on the fish stocks. The realism of predictive models was improved by more modern age-structured models which include a gradual recruitment to the fishery (Pitcher and Hart, 1982; Jacobsen and Taylor, 1985) and can predict the progressive effects of management regulations (Hightower and Grossman, 1987). However, the selection of fish by gillnets is through size and not through age. Moreover, age-structured models are difficult to apply in tropical situations where reproduction shows variable temporal patterns and where estimates of age are hard to obtain (Pauly and Murphy, 1982).

Various methods are available to estimate population parameters from size-structured information on fish stocks from tropical regions (Pauly and Morgan, 1987; Sparre *et al.*, 1989; Gulland and Rosenberg, 1992). To generate predictions on the effects of management regulations in gillnet fisheries, however, these parameters should be used as input in a size-structured model and not in traditional models which are only age-structured. A size-structured dynamic simulation model is particularly needed for gillnet fisheries which heavily exploit short-lived tropical species. A size-structured model will give predictions on the effects of optional management measures in terms of length-frequency distributions of population and catch, in addition to predictions in terms of catch levels. Such a model will show the consequences of management regulations more precisely, and with more

detail than models which are only age-structured (Sissenwine, 1977; Buijse *et al.*, 1992). Moreover, a size-structured model has the advantage that it can be validated by comparison of the size-structured output with independently obtained length-frequency distributions of the catch.

The age- and size-structured simulation model which was developed earlier for the Lake IJssel fishery (Buijse *et al.*, 1992), lacked generality since it could not be used with variable recruitment patterns as encountered in tropical situations. Furthermore it lacked realism since it did not account for spatial effects, which are known to be important in reservoir fisheries (Siler *et al.*, 1986; Amarasinghe *et al.*, 1989). Finally it lacked precision in the simulated dispersion of cohorts over the length-classes in the model, which was correct over time intervals of one year, but not over shorter time or length intervals.

In **Chapter 6**, a simulation model is developed which is generally applicable in situations with variable recruitment patterns in both temperate and tropical situations. In this model the individual fish are not regarded as members of a certain age-group, but only as members of a length-class. The importance of a spatial dimension is recognized by accounting for size-dependent spatial distribution patterns of the fish, and their consequences for fisheries management. The gillnet fishery for *O. mossambicus* in Tissawewa is used as an example to show the possibilities of this model. Conclusions in respect to the fisheries management of this specific reservoir are put in a country-wide perspective, using data sets from the literature.

In this concluding chapter, information from the previous chapters is combined to predict the most likely effects of optional management measures on the gillnet fisheries for *O. mossambicus* in Sri Lankan reservoirs. The size-structured simulation model simulates the temporal patterns in recruitment, the developments in population length-frequency distributions and the gradual size-selective impact of the gillnet fishery. Migration and size-dependent habitat occupation are simulated according to the observed patterns described in **Chapter 2**. Characteristics of the fishery, in terms of operated mesh sizes and length-frequency distributions of the catch, are available from **Chapter 3**. These characteristics are used partly as input (mesh sizes) and partly as validation of the output (length-frequency distributions of the catch). **Chapter 4** provides the estimates for gillnet selectivity parameters, which describe the shape and position of the selection curves of various mesh sizes. The parameter values for growth, recruitment and mortality, which describe the stock dynamics of *O. mossambicus* in Tissawewa, are obtained from **Chapter 5** and compared with literature data for other Sri Lankan reservoirs. Several management measures are proposed in **Chapter 5**, to conserve the existing fishery for *O. mossambicus* and to improve the total catch from the reservoirs. The effects of these optional management strategies on the fishery for *O. mossambicus* are evaluated by means of the simulation model. Recommendations for management of the stocks of *O. mossambicus* are presented in terms of mesh sizes and levels of fishing effort. Finally, the simulation model is used to test the revised hypothesis from **Chapter 2**, on the feasability of introducing small-meshed gillnet fisheries for minor cyprinids, in addition to the existing fishery for *O. mossambicus*.

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Chapter 2

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

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Abstract

Habitat occupation and habitat overlap of the introduced tilapia *Oreochromis mossambicus* and co-occurring indigenous fish species were studied in a shallow lowland reservoir in Sri Lanka. Results were used to discuss the possible existence of empty habitats in reservoirs and the position of the introduced *O. mossambicus* in the fish community. Predictions were made on the effects of a subsidiary small meshed gillnet fishery for indigenous minor cyprinids on the yield of tilapia. The zooplanktivorous halfbeak *Hyporamphus gaimardi*, an indigenous invader from brackish water estuaries and lagoons, has successfully colonized the pelagic habitat in this reservoir. The habitat of the introduced *O. mossambicus* overlapped significantly with those of the indigenous minor cyprinids. Only the smallest size classes of *O. mossambicus* (below 45 mm) are spatially segregated from these cyprinids. Spatial distribution patterns are influenced by the rainy seasons which trigger an inshore movement of *O. mossambicus* and several other species around November and May. *Barbus* spp. (Cyprinidae) need riverine habitats for spawning, but for all other species the available habitats within the reservoir are suitable to complete their full life cycle. Exploitation of *Barbus* spp. with gillnets with a mesh size of 30 mm stretched mesh is predicted to have considerable detrimental effects on the existing fishery for *O. mossambicus*. However, a gillnet fishery with 15 mm stretched mesh to exploit *Amblypharyngodon melettinus, Rasbora daniconius* and *H. gaimardi* in the open water zone is expected to be successful without harming the existing fishery for *O. mossambicus* or the populations of *Barbus* spp.

Introduction

Studies of resource partitioning among species and size classes within species in fish communities provide insight into the nature of intra- and interspecific interactions, and essential information for the development of production models for fisheries management (Werner et al., 1977; Schiemer & Duncan, 1988). Fishing activities will have different effects in the varying habitats within a reservoir. The result of any management strategy will depend on the size-related spatial and temporal distribution patterns of the fish and fishermen.

There are no natural lakes in Sri Lanka, but more than 100 reservoirs larger than 100 ha were built in the dry zone of the country for irrigation of paddy fields (De Silva, 1988). The total surface area of these reservoirs is around 100 000 ha. Many of these reservoirs are 500 to 2 000 years old and they are the most important water bodies for Sri Lankan inland fisheries. No indigenous lacustrine species exist (Fernando & Indrasena, 1969). The reservoirs were occupied by indigenous riverine and estuarine fish. The reservoir fishery has developed after the introduction of exotic lacustrine cichlids (Fernando & Indrasena, 1969; De Silva, 1988). *Oreochromis mossambicus* (Peters) accounts for 80% of the total catch. Stocking of exotic riverine major carps further improved the inland fisheries, but stocking programs ended in 1990. The mean annual yield is estimated at 283 kg/ha (De Silva, 1988). The commercial fisheries use only a small proportion of the available fish biomass (Schiemer & Duncan, 1988). Although large stocks of indigenous minor cyprinids are present in the lowland reservoirs in Sri Lanka, indigenous species are rarely represented in the catch (De Silva, 1985; De Silva, 1988). The production of inland fisheries in Sri Lanka, before the introduction of exotics in 1952, was low because a fishery for indigenous fresh water species hardly existed in the reservoirs (De Silva, 1988).

Large parts of most lowland reservoirs are similar to the natural marshes which are formed during the wet season. The shallow, lowland, irrigation reservoirs are characterised by extensive littoral zones, where competition for food is probably severe (Schiemer & Duncan, 1988). Indigenous riverine fish may not be successful in fully utilizing all available niches in the reservoirs (Schiemer & Duncan, 1988).

Hypotheses on habitat occupation are at the basis of recent proposals to improve inland fisheries production through exploitation of non-conventional fish resources (De Silva & Sirisena, 1987; Sirisena & De Silva, 1988; Sirisena & De Silva, 1989; De Silva & Sirisena, 1989). The minor cyprinid resources would be exploitable with a subsidiary gillnet fishery, using 15 and 30 mm gillnets, without any detrimental effect on the existing commercial fishery for tilapia. This assumes spatial segregation between adult minor cyprinids and juvenile *O. mossambicus*. Adult stages of both minor cyprinids and *O. mossambicus* were assumed to occupy the open water zone whereas juveniles stay in the littoral areas. A small-meshed gillnet fishery for minor cyprinids would be possible if this were true and if the commercial gillnet fishery would be confined to the open water zone. The potential catch of minor cyprinids was expected to exceed the present catch of *O. mossambicus*.

The use of small meshed gillnets in the sub-littoral or littoral areas may have undesirable effects on the existing fishery (Sirisena & De Silva, 1988). The present study relates the

commercial fisheries to spatial distribution patterns of the fishes on the basis of habitat electivity, habitat overlap, seasonality and reservoir periodicity.

Materials and methods

The size-related spatial and temporal distribution patterns for the ten most abundant fish species were recorded in Tissawewa, a shallow lowland reservoir of c. 200 ha in the dry south east corner of Sri Lanka. Four different types of macro-habitat are available within the reservoir, and one sampling station was chosen within each of these four habitats (Fig. 2.1). The four types of habitat are characterised by a set of micro-habitat parameters (Table 2.1). Data on fish distribution are included for monthly samples from September 1991 to July 1992. Data for August 1992 are not included since extremely low water levels after July drastically changed pre-defined macro-habitats.

Data on fish distribution were collected using multi-mesh monofilament gillnets with ten different mesh sizes; 12.5, 16, 20, 25, 33, 37, 50, 60, 76 and 90 mm stretched mesh respectively, randomly distributed over the net. Panel lengths were 5, 5, 10, 10, 15, 15, 15, 15, 15 and 15 meters respectively. Two nets of 60 m * 1.5 m were set simultaneously at each station, one with the smaller (12.5 to 37 mm) and one with the larger (50 to 90 mm) meshes. The net at station B was set at the surface, the nets at all other stations were set at the bottom. The nets with smaller meshes were set for two hours to prevent saturation. The nets with larger meshes were set for twelve hours. Day time settings were from 06.00 hours to 08.00 and from 06.00 to 18.00 hours for small and large meshes respectively. Night time settings were from 18.00 hours to 20.00 and from 18.00 to 06.00 hours. Sampling was at monthly intervals. The total of eight nets were set four times during each monthly sampling session; twice during day and twice at night.

Fish fry and juveniles were sampled with a fine meshed scoop net in the littoral zone and with a bottom trawl (10 mm stretched mesh) and a fine-meshed hoop net in the open water zone.

Since habitat preference will differ for different size classes of each species (Keast, 1978; Werner & Gilliam, 1984), we analysed the catches separately for each size class. Length frequency distributions were corrected for fishing effort and gillnet selectivity, before they were used in further analyses. Gillnet selectivity factors were estimated using the method of Holt (Hamley, 1975) with standard deviations of the selection curves assumed to be proportional to the optimum selection length.

The length range of all species combined was divided into six classes to group individuals of comparable size and to facilitate comparison within and between species. Size classes and sample sizes per species are presented in Table 2.2. Relative activity at a specific time of day was calculated as the corrected catch during that time, divided by the total corrected catch (day + night). The biomass per species and size class was calculated using length-weight relationships obtained during the present study. For the statistical evaluation of spatial distribution patterns per species and size class, the gillnet catches were used, without correction for fishing effort or gear selectivity.
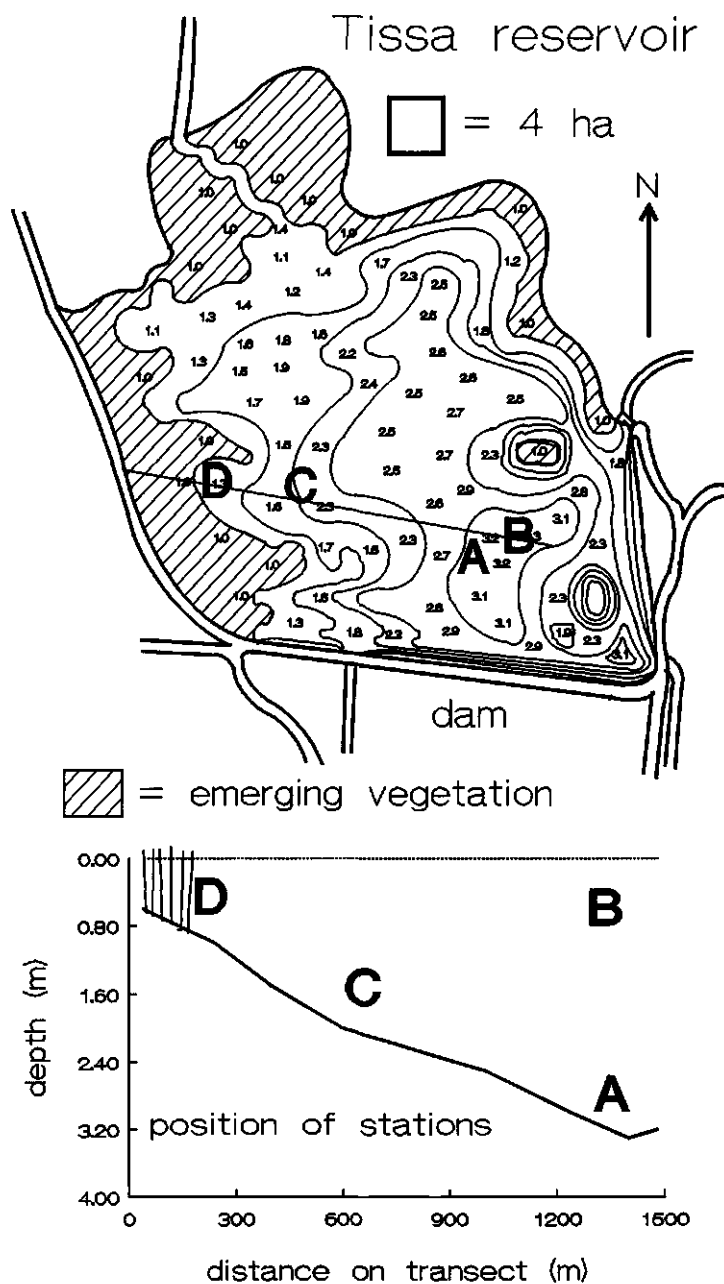
Fig. 2.1. Morphometric map of Tissawewa, with water depths measured at a water level of 4.2 m and a maximum depth of 3.3 m. Positions of the sampling stations are indicated on a transect from West (left) to East (right).

Table 2.1. Habitat parameters for each pre-defined macro-habitat
available in Tissawewa at three different water levels.

Macro-habitat[*]:	A	B	C	D
Maximum water level 3.5 m				
water column depth (cm)	250-350	250-350	150-250	0-150
relative depth[#] (cm)	200-350	0-150	100-250	0-150
distance to shore (m)	100-800	100-800	50-800	0-400
distance to vegetation (m)	600-800	600-800	100-400	0
availability (ha)	59	59	73	123
Intermediate level 2.5 m				
water column depth (cm)	150-250	150-250	50-150	0- 50
relative depth[#] (cm)	100-250	0-150	0-150	0- 50
distance to shore (m)	50-600	50-600	50-600	0-200
distance to vegetation (m)	600-800	600-800	100-400	0
availability (ha)	59	59	73	46
Low water level 1.5 m				
water column depth (cm)	50-150	50-150	0- 50	0
relative depth[#] (cm)	0-150	0-150	0- 50	-
distance to shore (m)	50-400	50-400	0-100	-
distance to vegetation (m)	-	-	-	-
availability (ha)	59	59	32	0
Independent of water level				
substrate particle size (mm)	0-0.25	-	0-0.42	0-2.54
dissolved oxygen (mg/l)	5-9	5-9	5-9	5-9
water temperature (°C)	25-29	26-30	25-30	25-31
pH	7.7-8.8	7.7-8.8	7.8-8.9	7.8-8.9
secchi disk visibility (cm)	19-53	19-53	17-48	18-53

[*]Macro-habitats: A, Bottom layer of open water zone; B, Pelagic zone (surface layer of open water); C, Shallow intermediate zone; D, Littoral zone with vegetation.
[#]Relative depth indicates the distance from net to surface.

All size classes of each species were tested for showing spatial distribution patterns significantly different from the expected ratio of 1:1:1:1 over four macro-habitats. We used the G-test for goodness of fit ($\alpha = 0.05$), for single classification frequency distributions (Sokal & Rohlf, 1969).

Jacobs' (1974) formula was used to calculate electivity for all combinations (species, size class and time) which showed spatial distribution patterns significantly different from 1:1:1:1. Jacobs' formula:

$$D_i = \frac{r_i - p_i}{r_i + p_i - 2 * r_i * p_i}$$

where r_i is the proportional occupation of habitat i, and p_i is the availability of habitat i in the environment. The availability p_i of each type of four macro-habitats was always equal to 25% given the equal fishing effort in all four habitats. Electivity D_{xi} for species x and

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Table 2.2. Species, size classes and sample sizes. Samples collected from September 1991 to July 1992.

Size class	Total length (cm)	Sample sizes[*] per species[a] and size class								
		AM	BC	BD	BS	GG	HG	MY	OM	RD
1	3.0- 4.4	87	19	0	0	0	0	0	40	0
2	4.5- 6.9	62879	1322	94	43	21	0	4	1155	3358
3	7.0- 9.9	18108	3912	914	153	8	263	164	1114	4856
4	10.0-13.9	0	2393	2671	259	11	1023	976	3037	32
5	14.0-18.9	0	0	2011	903	77	0	205	1855	0
6	≥19.0	0	0	10	615	345	0	85	23	0

[*]Samples smaller than 40 fish per size class per species were not used in calculations on habitat occupation. Total sample size is 115 061 fish.
[a]Species: AM, *Amblypharyngodon melettinus*; BC, *Barbus chola*; BD, *Barbus dorsalis*; BS, *Barbus sarana*; GG, *Glossogobius giuris*; HG, *Hyporamphus gaimardi*; MY, *Mystus gulio* & *Mystus vittatus*; OM, *Oreochromis mossambicus*; RD, *Rasbora daniconius*.

habitat i could be calculated directly from the proportion r_i of habitat i in the distribution of species x. Five categories of electivity values were used in this study: high preference (D≥0.5), low preference (0.1≤D<0.5), neither preference nor avoidance (-0.1≤D<0.1), low avoidance (-0.5≤D<-0.1) and high avoidance (D<-0.5).

The G-test for heterogeneity (Sokal & Rohlf, 1969) was used to test for significantly (α = 0.05) different spatial distribution patterns between all pairs of combinations of species, size class and time. Schoener's (1970) formula was used to calculate habitat overlap for all pairs of combinations which showed significantly different spatial distribution patterns,

$$S = 1 - 0.5 * \sum | p_{x_i} - p_{y_i} |$$

where p_{xi} is the proportion of habitat i in the spatial distribution of species x. Three categories of overlap values were used in this study: low overlap (S≤0.33), intermediate overlap (0.33<S<0.67) and high overlap (S≥0.67).

Results

Species composition and spatial distribution
The ten most important fish species in gillnet catches in Tissawewa are listed in Table 2.3. These species formed 95% of the fish biomass, and an even larger numerical proportion. *O. mossambicus* is an introduced lacustrine cichlid from African lakes (De Silva, 1988). *Hyporamphus gaimardi* (Valenciennes) is an estuarine species which invades the reservoirs from river mouths and lagoons (Munro, 1955; Schiemer & Hofer, 1983). The other eight important indigenous species are riverine fish. Table 2.3 also lists the species which were caught in smaller numbers (not included in further study), and species which were never caught but which are known to be present in the reservoir.

Table 2.3. Fish species common in Tissawewa.

Species	Food[*]
Most important	
Amblypharyngodon melettinus	suspended phytoplankton and detritus
Barbus chola	small zoobenthos
Barbus dorsalis	small zoobenthos
Barbus sarana	macrophytes, periphyton, fish and littoral fauna
Glossogobius giuris	fish
Hyporamphus gaimardi	zooplankton
Mystus gulio & *M. vittatus*	zoobenthos
Oreochromis mossambicus	benthic diatoms and detritus
Rasbora daniconius	zooplankton, fish fry, periphyton and air borne material
Caught in small numbers	
Anabas testudineus (Bloch)	
Channa striata (Bloch)	
Cyprinus carpio (Linnaeus)	
Esomus danrica (Hamilton)	
Heteropneustes fossilis (Bloch)	
Lepidocephalichthys thermalis (Valenciennes)	
Mugil cephalus (Linnaeus)	
Ompok bimaculatus (Bloch)	
Oreochromis niloticus (Linnaeus)	
Tilapia rendalli (Boulenger)	
Not caught but known to be present	
Anguilla bicolor (McClelland)	
Anguilla nebulosa (McClelland)	
Catla catla (Hamilton)	
Labeo rohita (Hamilton)	

[*]Information on feeding ecology based on studies in Parakrama Samudra reservoir (Schiemer & Hofer, 1983; Schiemer & Duncan, 1988).

Numerous fry of *O. mossambicus* were caught with the fine meshed scoop net in the shallowest parts of the littoral zone. The bottom trawl and hoop net yielded fry and juveniles of all other species except *Barbus* spp.

The species composition of gillnet catches (Fig. 2.2) shows the numerical dominance of *Amblypharyngodon melettinus* (Valenciennes). Although small (< 100 mm), this species also dominated the total biomass. Trawl surveys confirmed the dominance of *A. melettinus*. The second smallest cyprinid, *Rasbora daniconius* (Hamilton), was next in numerical importance. These two small pelagic minor cyprinids account for over 60% of the corrected biomass in gillnets. The benthic *Barbus* spp., *B. chola* (Hamilton), *B. dorsalis* (Jerdon) and *B. sarana* (Hamilton) account for 25% of the biomass. *O. mossambicus* accounts for 7% of the biomass in gillnets and 23% in bottom trawl catches.
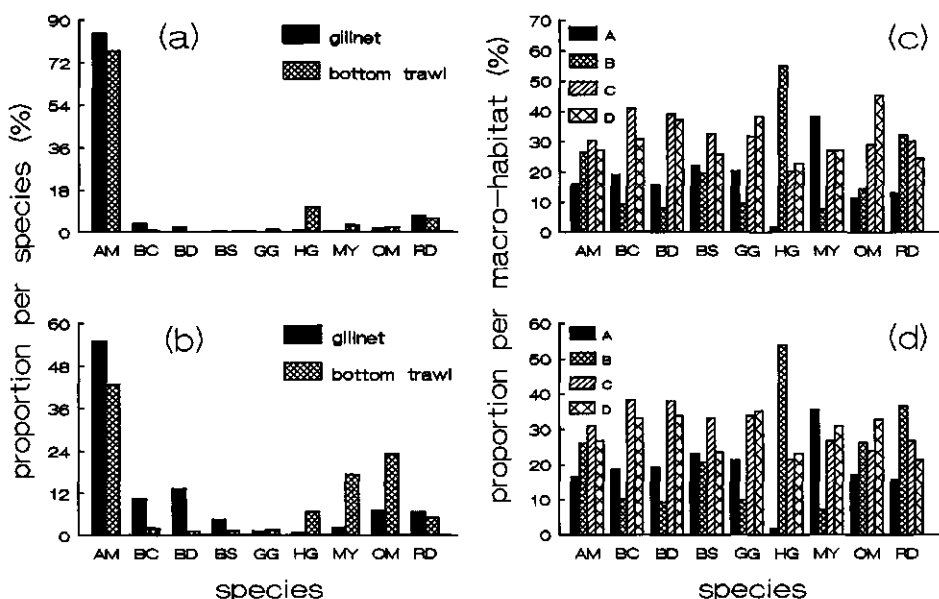
Fig. 2.2. Species composition of gillnet and bottom trawl catches in numbers (a) and biomass (b), after correction for selectivity and fishing effort. Habitat occupation per species in numbers (c) and biomass (d). Habitats: A, bottom layer of open water zone; B, surface layer of open water; C, shallow intermediate zone; D, littoral zone with vegetation. Abbreviations for species names as in Table 2.2.

Mystus gulio (Hamilton) and *Mystus vittatus* (Bloch) are relatively important in bottom trawl catches but were under-represented in gillnet catches. Fig. 2.2 also shows the gross habitat occupation per species, expressed in numbers and biomass. *B. chola, B. dorsalis* and *Glossogobius giuris* (Hamilton) prefer the littoral and intermediate zone (C and D) and avoid the surface layer of the open water (B). The open water surface layer is also avoided by *Mystus* spp., but it is preferred by *H. gaimardi*. *O. mossambicus* prefers the littoral zone in terms of numbers, but not in terms of biomass.

Size-related habitat occupation and electivity

The habitat occupation of all species changes with size class and time (Fig. 2.3 & 2.4). The distributions of most combinations of species, size class and time were significantly different from the expected distribution of 1:1:1:1. Electivity values for all combinations are presented in Table 2.4. *A. melettinus* is most active during the day, when all size classes show preference for the intermediate zone. This preference is stronger for the smallest size class, which avoids the open water during the day. At night, this species spreads out along the surface of the open water. The bottom layer of the open water is always avoided.

B. chola and *B. dorsalis* are most active during the night. They avoid the open water, and especially the surface layer. Avoidance of the open water is strongest for the smaller size classes. The larger specimens rise in the water column during the night. There is a preference

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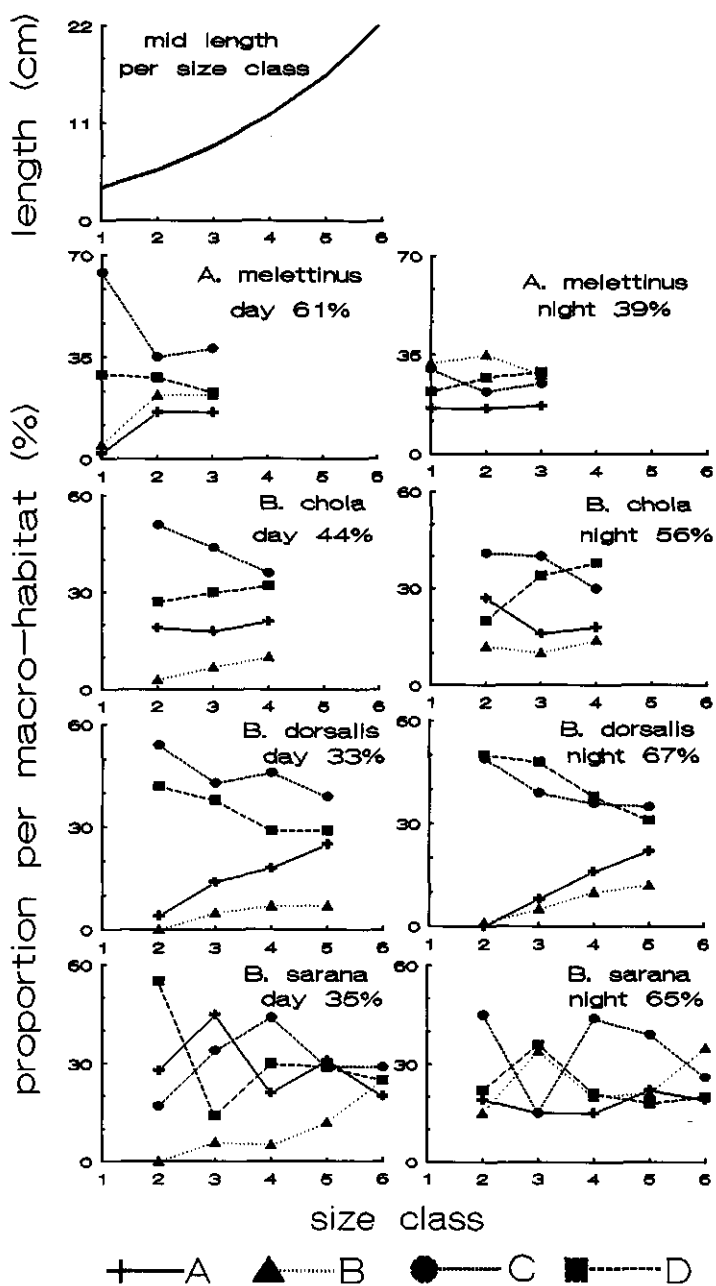
Fig. 2.3. Habitat occupation and relative catch per size class during day time and at night, for *A. melettinus*, *B. chola*, *B. dorsalis* and *B. sarana*. A, bottom layer of open water zone; B, pelagic zone (surface layer of open water); C, shallow intermediate zone; D, littoral zone with vegetation.
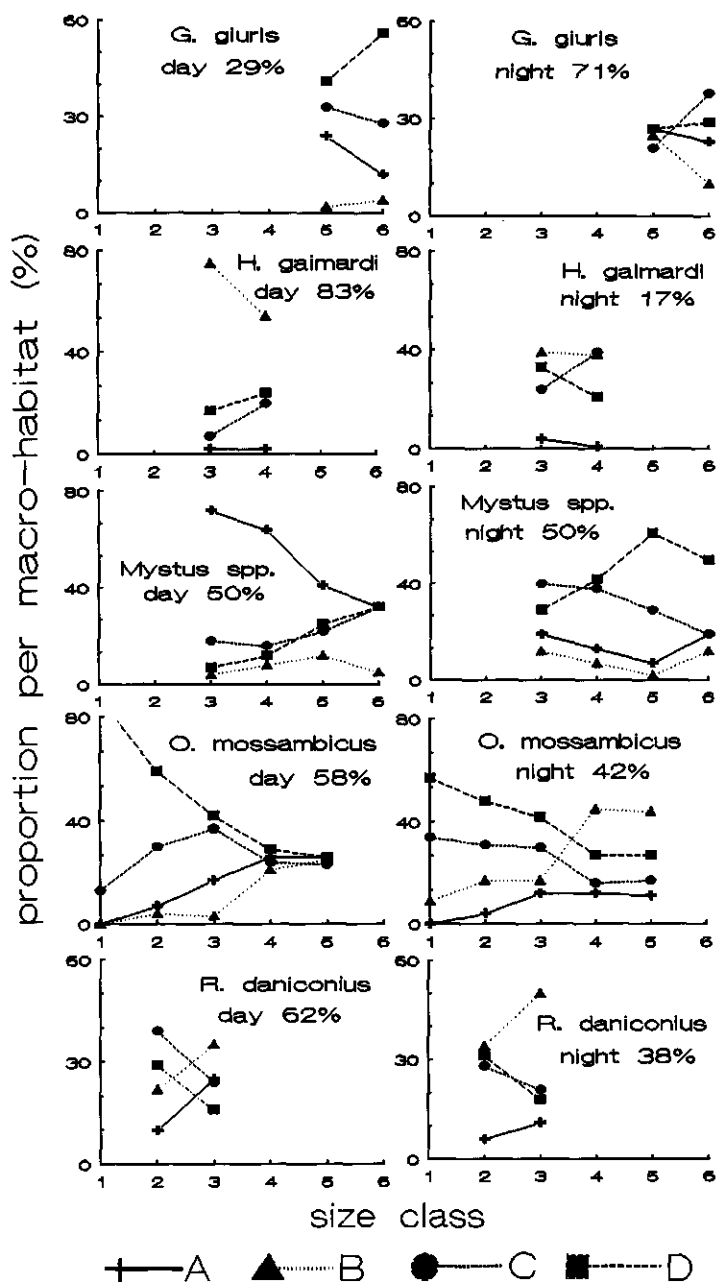
Fig. 2.4. Habitat occupation and relative catch per size class during day time and at night, for *G. giuris*, *H. gaimardi*, *Mystus* spp., *O. mossambicus* and *R. daniconius*. A, bottom layer of open water zone; B, pelagic zone (surface layer of open water); C, shallow intermediate zone; D, littoral zone.

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Table 2.4. Habitat electivity for Tissawewa fishes.

Species	Size class	Electivity* per macro-habitat#							
		Day time				Night time			
		A	B	C	D	A	B	C	D
A. melettinus	1	--	--	++		x	x	x	x
	2	-		+		-	+		
	3	-		+		-			+
B. chola	2	-	--	++			-	+	-
	3	-	--	+	+	-	--	+	+
	4	-	-	+	+	-	-	+	+
B. dorsalis	2	--	--	++	+	--	--	+	+
	3	-	--	+	+	--	--	+	+
	4	-	--	+		-	-	+	+
	5		--	+	+		-	+	+
B. sarana	2		--	-	++	x	x	x	x
	3	+	--	+	-	-	+	-	+
	4	-	--	+	+	-	-	+	-
	5	+	-	+			-	+	-
	6	x	x	x	x	-	+		-
G. giuris	5	x	x	x	x	x	x	x	x
	6	-	--		++	-	+	+	
H. gaimardi	3	--	++	--	-	--	+		+
	4	--	++	-		--	+	+	
Mystus spp.	3	++	--	-	--	-	-	+	+
(*M. gulio* &	4	++	--	-	-	-	--	+	+
M. vittatus)	5	+	-			--	--	+	++
	6	+	--	+	+	x	x	x	x
O. mossambicus	1	--	--	-	++	--	--	+	++
	2	--	--	+	++	--	-	+	+
	3	-	--	+	+	-	-	+	+
	4		-		+	-	+	-	
	5	x	x	x	x	-	+	-	
R. daniconius	2	-		+	+	--	+		+
	3		+		-	-	++	-	-

*Positive electivity is indicated by ++ for values of D≥0.5 and by + for values of 0.1≤D<0.5. Negative electivity is indicated by - for values of -0.5≤D<-0.1 and by -- for values of D<-0.5. Absence of positive or negative electivity is indicated by a blank for values of -0.1≤D<0.1 and by x for distributions which are not significantly different (α=0.05) from 1:1:1:1 over four stations.
#Macro-habitats: A, bottom layer of open water zone; B, pelagic zone (surface layer of open water); C, shallow intermediate zone; D, littoral zone with vegetation.

for the intermediate zone and, to a lesser extent, for the littoral zone. *B. chola* move from the intermediate zone into the littoral zone with increasing size. Size class 2 of *B. chola* moves towards the open water at night. Larger *B. chola* and all *B. dorsalis* move into the littoral zone at night.

B. sarana is most active at night and does not show a clear pattern of habitat preference. Size class 1 does prefer the littoral zone during the day. The surface of the open water is

avoided during the day by all but the largest size class.

G. giuris is most active at night. Size class 6 shows a strong day time preference for the littoral zone and the surface is avoided. At night, size class 6 shows a preference for the intermediate and littoral zone.

H. gaimardi is most active during the day when they strongly prefer the surface layer of the open water. With increasing size they spread out into the intermediate and littoral zone. The bottom layer of the open water is always strongly avoided. At night, *H. gaimardi* spreads out from the open water into the intermediate and littoral zone.

Mystus spp. are equally active during day and night. The smaller size classes of *Mystus* spp. show a strong preference for the bottom layer of the open water but with increasing size they spread out into the intermediate and littoral zones. The surface is always avoided. During the night, all size classes move towards the shore. Size class 3 stays in the intermediate zone.

O. mossambicus is most active during the day, when the smallest size classes show a strong preference for the littoral zone. With increasing size, they gradually spread out from littoral zone through intermediate zone into the open water. The largest size classes become indifferent to macro-habitat during the day. At night, *O. mossambicus* moves into the surface layer of the open water zone, but small size classes still show a preference for the littoral and intermediate zone. Schiemer and Hofer (1983) also reported a strong vertical migration of *O. mossambicus* in Parakrama Samudra during the night.

R. daniconius is most active during the day, when size class 2 shows preference for the intermediate and littoral zone, whereas size class 3 prefers the surface layer of the open water. At night, size class 2 spreads out into the surface layer of the open water whereas the bottom layer is avoided. At night, size class 3 is even more concentrated in the surface layer of the open water.

Seasonal migration

Seasonality in south east Sri Lanka is characterized by two monsoonal periods. The north east monsoon blows from October to March, and the south west monsoon from April to September. The north east monsoon is the wettest of the two seasons, with rain from October to January and a peak in rainfall during the month of November (Fig. 2.5). A second period with some rain extends from March to May. February and August are usually very dry. Mean water levels follow the patterns of rainfall, with lowest levels in August, a peak level around December and a second minor peak around April.

Most species may have two spawning periods. Peaks in Gonado Somatic Index (*GSI*) were observed during the monsoon rains around November and May. During the wet seasons a concentration in the littoral zone of Tissawewa was recorded for *A. melettinus*, *B. chola*, *O. mossambicus* and *Mystus* spp. (Fig. 2.5).

Size-related habitat overlap

Overlap of macro-habitat in Tissawewa fish community is high, with 70% high overlap values (Table 2.5). Habitat overlap is slightly higher during the night (0% low and 78% high values), than during the day (6% low and 62% high values).
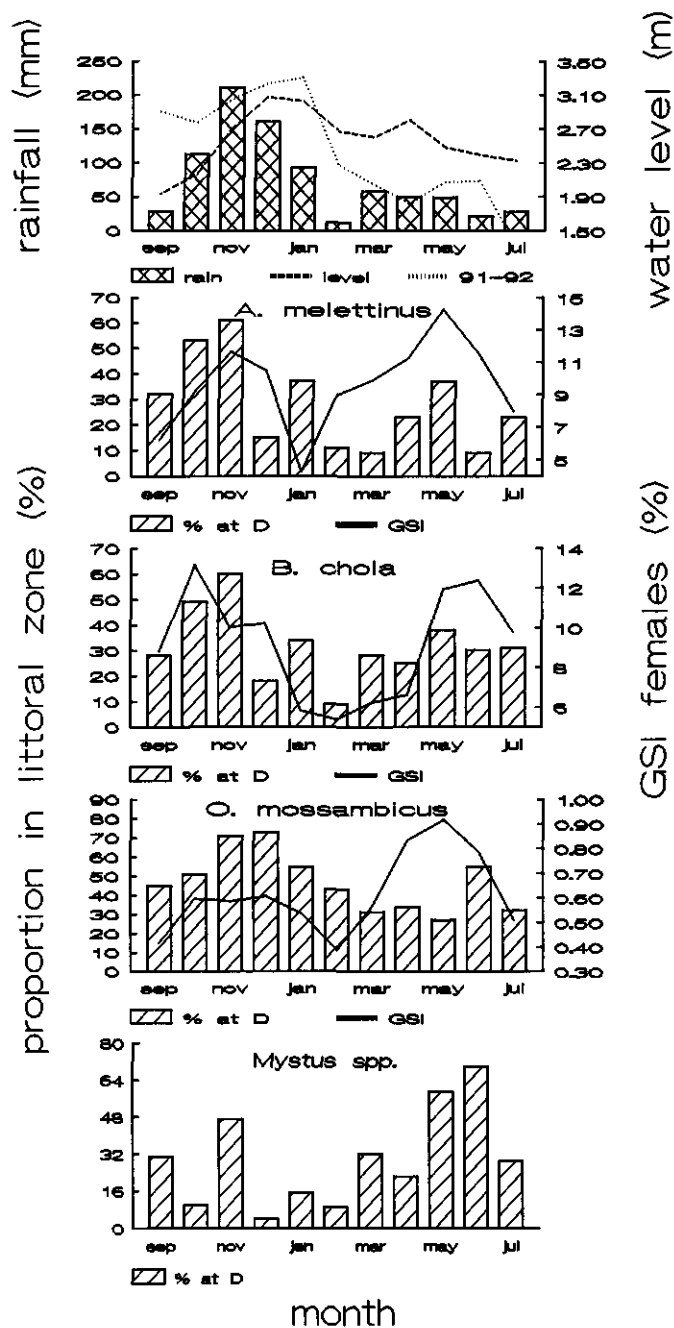
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Fig. 2.5. Temporal patterns in utilization of the littoral zone (D) by *A. melettinus*, *B. chola*, *O. mossambicus* and *Mystus* spp. Relations with patterns in rainfall, water level and mean *GSI*.

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Table 2.5. Habitat overlap* for Tissawewa fishes#.

```
\D   AM      BC      BD        BS            GG   HG   MY         OM          RD
N\   1 2 3   2 3 4   2 3 4 5   2 3 4 5 6     5 6  3 4  3 4 5 6    1 2 3 4 5   2 3

AM1  \ + + + + + X + + +         +                 -       -         +         +         +
2    x \ + + + +   + + +   + X + X X +       +           + +     + + + + + +
3    x + \ + + +   + + +   + + + + X +       +           + +       + + + + +
BC2  + + + \ + + X + + +     X X + + X + -             + X     + + + + +
3    + + + + \ + X X X X X X X X + + X + -             + X     + + + + +
4    + + + + + \ + + + X X X X X + X +               + X     + + + + + +
BD2          + + \ X X + X     X     X X -       - - -   +     X X       +
3        + + + + + \ X + X + X + + X X -               X       + X + + +
4    + + + + X + + + \ X     X X + + X + -             + X     + + + + +
5    + + + + + +   + + \ X X X X + X + -             + X       + + + + + +
BS2  x + x x x x + + x x \ x x x     x x -             x x x x x + +
3    x x x     + +     + +   \ x x + x     -       x x x x -     + x +       +
4    x + + x + +   + + + x + \ x + x x -               x x     + x + + +
5    x + + + + +   + + + x + x \ + x +                 x x     + + x + + +
6    x x + + + +   + + x + + + \ x +       +           + +       + x x + +
GG5  x x x + + +   + + x x + x x \ x -               x x     x x x x x x
6    + + + + + + + + x x + + + + \ -               + + x x +     +
HG3  x x +   + +     + +   x +     + +   \ +       - -   - - - -
4    + + + + +       + + + + + + + + + x \ -             + + + +
MY3  x + + x x x + + x x x + x x + x x + + \ x +         -
4    + + + + x + + + x + x + + +     + + + + x \ +         -
5          + + + x + +           +       + + \ x         x x + +
6    x x x + x x + x x x x x x x + + x x x   x x x \     + x + + + +
OM1          + + x x + +           +       + x x x \ x         -
2    + + +   + + + + + + + + + +     + + + + + + + x x \ +       +
3    x + + + + x + + + + x + + + + + + + + x + + x x + \ + + +
4    x + +     +       +   x + + + +   x + +       +     + \ x + +
5    x + +     +       +   x + + + +   x + +       +     + x \ + +
RD2  x + +   + +   + + + + + + + + + + x + + + + + + + + + \ +
3    x + +           + + + + +   x +           + + + \
```

*Low overlap (S≤0.33) is indicated by -, intermediate overlap (0.33<S<0.67) by a blank and high overlap (S≥0.67) by +. Combinations which did not show significantly (α=0.05) different spatial distribution patterns are indicated by x. Separate values are given for day (upper right) and for night (lower left).
#Species abbreviations and size class codes explained in Table 2.2.

The only species which is spatially segregated from the others is the pelagic *H. gaimardi*. This species shows 33% low, 53% intermediate and only 14% high overlap values during the day, when it is active in its preferred habitat (the surface layer of the open water zone).

R. daniconius is concentrated in the open water pelagic zone only at night, when it is not very active. *R. daniconius* is not spatially segregated from other species in Tissawewa with 65% high overlap values. Size classes 3 and 4 of *Mystus* spp. show spatial segregation from other species during the day, when they concentrate in deep water, with 15% low and only 7% high overlap values.

Except for size class 1, *O. mossambicus* is not spatially segregated from the minor cyprinids. Size class 1 of *O. mossambicus* shows spatial segregation from minor cyprinids,

with 12% low and only 6% high overlap values during the day, when it is most active. Most overlap values for this size class are intermediate. All other size classes of *O. mossambicus* show 77% or more high overlap values with minor cyprinids. Overlap of *O. mossambicus* with *A. melettinus* is high, especially for their larger size classes. Overlap of size class 1 of *O. mossambicus* with *A. melettinus* is only intermediate.

Discussion and conclusions

Habitat occupation, overlap and temporal patterns
    The feeding ecology of the species under consideration was studied by Schiemer and Hofer (1983) and Schiemer and Duncan (1988) in Parakrama Samudra reservoir, in east Sri Lanka (Table 2.3).
    The pelagic zooplanktivorous *H. gaimardi* seems to be filling the niche which is often available in man-made lakes (Fernando & Holcik, 1982). *H. gaimardi* shares its habitat, the pelagic zone of the open water, with *Ehirava fluviatilis* (Deraniyagala) in other reservoirs (Schiemer & Hofer, 1983; Schiemer & Duncan, 1988). This small zooplanktivorous clupeid fish, which invades the reservoirs from estuarine habitats, was not present in Tissawewa during our survey. *H. gaimardi*, which is also an invader from the brackish water estuaries and lagoons, may experience little competition for food and space in Tissawewa.
    Size classes 3 and 4 of *Mystus* spp. are spatially segregated during the day from their possible food competitors, namely *Barbus* spp. Both the smaller *Mystus* spp. and the *Barbus* spp. are feeding on zoobenthos, but only *Mystus.* spp. show a preference for the bottom layer of the open water, during the day.
    Cormorants prey on fish in the open water zone of Tissawewa during day time, which may lead many species to avoid this habitat. *Barbus* spp. and juvenile tilapia are an appropriate size prey (130 mm) for the Large Cormorant, *Phalacrocorax carbo sinensis* (Shaw), which feeds in the open water zone (Schiemer & Duncan, 1983). During the night, the bottom layer of the open water is avoided by all species in the reservoir. Escape from eels might be a reason for *Barbus* spp. and juvenile tilapia to avoid the open water zone during the night. Little is known about stock densities of eels (Wickström & Enderlein, 1988) but they grow to considerable sizes and might be important predators in the reservoirs. Eels are active during the night, and large eels were caught at night by fishermen and by the authors on the bottom of the open water on hook and line, using tilapia or barb for bait.
    The size of the pelagic minor cyprinids *A. melettinus* and *R. daniconius* is below the preferred size range of prey for the Large Cormorant and they are spatially segregated from benthic predators like eels and catfish. These two smaller cyprinids are more vulnerable to the Little Cormorant, *Phalacrocorax niger* (Stephens) and the Indian Shag, *Phalacrocorax fiscicolis* (Vieillot), which normally hunt near and in the littoral zone (Schiemer & Duncan, 1983).
    Size class 1 of *O. mossambicus* and *Barbus* spp. were vulnerable to the smallest mesh size in the net, but very few were caught (Table 2.2). *O. mossambicus* of size class 0 (0 to

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29 mm), were caught with a fine meshed scoop net in the shallowest parts (5 to 20 cm depth) of the littoral zone, where numerous *O. mossambicus* of size class 1 were also observed. Other species were hardly ever observed here. This leads to the conclusion that overlap of size class 1 of *O. mossambicus* with other species is probably even less than could be shown from our results. Our scoop net catches and visual observations indicated that *O. mossambicus* fry are spatially segregated from other species in the shallowest part of the littoral zone. The cover of vegetation, which is available in the littoral zone in the rainy seasons, may lower the predation risk for juvenile fish (Werner et al., 1983; Savino & Stein, 1989) around November and May. The largest size classes are indifferent to macro-habitat during the day, whereas the cyprinids prefer the intermediate and littoral zone. At night there is a spatial segregation from *Barbus* spp. These factors may explain part of the successful introduction, although competition for food with *A. melettinus* is likely to occur.

Size classes 0 and 1 of *A. melettinus, G. giuris, H. gaimardi, Mystus* spp. and *R. daniconius* are too small to catch in the smallest mesh size in the gang. However, all these species were present and sometimes abundant in bottom trawl and hoop net (surface trawl) catches from the intermediate and open water zone. Few fry of *A. melettinus* and *R. daniconius* were encountered in scoop net catches from the littoral zone. Schiemer and Duncan (1983) reported periodic high densities of planktonic larvae of *Hemiramphidae* spp. in the open water zone of Parakrama Samudra. All these species are most probably spawning successfully in the reservoir.

The absence of juvenile indigenous *Barbus* spp. in Parakrama Samudra reservoir was reported by Schiemer and Duncan (1988), and also observed in Tissawewa. These *Barbus* spp. migrate out of the reservoirs, to spawn in riverine habitats (Silva & Davis, 1986). Schut et al. (1984) reported that current and structure (i.e. pebbles and rocks) are necessary conditions for successful spawning of *Barbus* spp. This type of habitat was not available within the reservoir.

The reproductive cycle of many tropical fish is closely related to the rainy seasons (Lowe-McConnell, 1975). Recruitment peaks for both *O. mossambicus* (De Silva & Chandrasoma, 1980; Schiemer & Hofer, 1983) and *Barbus* spp. (Chandrasoma & De Silva, 1981; De Silva, 1983; De Silva et al., 1985) occur during the rainy seasons around November and May. Earlier studies in Tissawewa have led to similar conclusions (N.D.N.S. Wijegoonawardana, unpublished data). Enderlein and Wickström (1991) concluded that *A. melettinus* and *R. daniconius* are very short-lived, and spawn only once and die thereafter. Concentration in the littoral zone occurred simultaneously with peaks in GSI in *O. mossambicus* and several other species in Tissawewa. This does not prove that the spawning of these species also takes place in the littoral zone of the reservoir. Breeding seasons probably coincide with seasons when food and shelter are abundant. The inshore movement of one or more of these species could be a feeding activity. Spawning sites of *O. mossambicus* were concentrated in the littoral zone of Parakrama Samudra reservoir (De Silva & Chandrasoma, 1980; De Silva & Sirisena, 1988). During the drought of September 1992, spawning sites in Tissawewa were spread out all over the reservoir bed.

Introduction of a small-meshed gillnet fishery

Table 2.6 gives the size classes of *O. mossambicus* and minor cyprinids which are expected in the catch of several mesh sizes of gillnets. These size classes are calculated using Holt's method for estimation of gillnet selectivity.

Table 2.6. Vulnerable size classes of *O. mossambicus* and minor cyprinids for different mesh sizes of gillnets.

	Mesh size* in mm stretched mesh							
	Day				Night			
	15	20	25	30	15	20	25	30
O. mossambicus	1,D	2,C+D	2,C+D	3,C+D	1,D	2,C+D	2,C+D	3,C+D
B. chola	2,C+D	2,C+D	3,C+D	3,C+D	2,A+C	2,C+D	3,C+D	3,C+D
B. dorsalis	2,C+D	3,C+D	3,C+D	4,C+D	2,C+D	3,C+D	3,C+D	4,C+D
B. sarana	2,A+D	3,A+C	3,A+C	4,C+D	2,X	3,B+D	3,B+D	4,C
A. melettinus	2,B+C +D	3,B+C +D			2,B+C +D	3,B+C +D		
R. daniconius	3,A+B +C	3,A+B +C			3,B	3,B		

*Mesh sizes below 15 mm stretched mesh are not included. Habitats which are not avoided are given for each species and size class: A, bottom layer open water; B, surface layer open water; C, intermediate zone; D, littoral zone; X, no significant preference.

Sirisena and De Silva (1989) argued that 15 mm stretched mesh would be an appropriate mesh size to exploit *A. melettinus* and *R. daniconius*, whereas 30 mm would be correct for *Barbus* spp. Our results confirm these findings and show that the vulnerable sizes of *O. mossambicus* for 15 and 30 mm meshes would be around 41 and 82 mm total length, or size classes 1 and 3 respectively.

Juvenile *O. mossambicus* over 45 mm total length (size class 2 and larger) show high overlap of macro-habitats with *Barbus* spp. Both small *O. mossambicus* and adult *Barbus* spp. show preference for the intermediate and littoral zone. Introduction of mesh sizes targeting *Barbus* spp. (30 mm stretched mesh) will seriously affect the presently successful fishery on *O. mossambicus* since commercial fishermen will follow concentrations of target species into the littoral zone. Vulnerable size classes of juvenile *O. mossambicus* are abundant in this habitat.

A mesh size of 15 mm stretched mesh is appropriate to catch *A. melettinus* and *R. daniconius* in water deeper than one meter. The vulnerable size class 1 of *O. mossambicus* remains safely within the shallowest parts of the littoral zone. The vulnerable size class 2 of *Barbus* spp. are not abundant in the reservoir. The proposal of De Silva and Sirisena (1987) could be accepted for the two smallest minor cyprinids, *A. melettinus* and *R. daniconius*. Since these two species also represent the major part of fish biomass in the

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reservoir, a successful fishery might be developed.

Exploitation of *Barbus* spp. with a mesh size of 30 mm stretched mesh will damage the existing fishery for *O. mossambicus* by removing pre-recruits. Whether the output of such a fishery will make up for the loss of *O. mossambicus* remains to be assessed. *A. melettinus* and *R. daniconius* can be exploited efficiently with a mesh size of 15 mm stretched mesh, in water over one meter deep. This fishery should not be harmful to the existing fishery for *O. mossambicus* nor to the populations of indigenous *Barbus* spp. and it will also yield adult *H. gaimardi* (size class 4), which is prized locally for human consumption. Exploitation of *A. melettinus* may be beneficial to the existing fishery since possible interspecific competition between *O. mossambicus* and *A. melettinus* will be reduced due to a declining stock size of the latter species.

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Chapter 3

Characteristics of a Sri Lankan reservoir fishery and consequences for the estimation of annual yield

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Abstract

A quantitative analysis of dynamics in catch, effort and catch per unit of effort (*CpUE*) was applied to indicate how a system for the collection of catch and effort data could be optimised and how the accuracy of fisheries statistics could be improved. Temporal and spatial patterns in the commercial fisheries were studied in Tissawewa, a representative irrigation reservoir in Sri Lanka. Considerable fluctuations of water level in shallow waters are important characteristics of the irrigation reservoirs in Sri lanka. Reservoir water level and surface area in Tissawewa fluctuated around means of 2.30 m and 175 ha respectively. The reservoir almost ran dry halfway through the study period. After two months the reservoir filled up again. The total annual catch from Tissawewa was estimated at 42 431 kg/yr over the first year, and 11 011 kg/yr over the second. The annual yield was estimated to range from 150 to 250 kg/ha/yr depending on the occurrence of dry periods. The main fishing methods were normal (stationary) gillnetting, cast netting, seining with gillnets and "water beating". Normal gillnets, usually with 64 or 70 mm stretched mesh, were by far the most important gear. The *CpUE* was defined as the catch of a single fishing trip by an outrigger canoe. Strata in the *CpUE* data set were identified to enable the development of an efficient catch and effort data recording system (*CEDRS*). The overall mean catch per trip was not significantly different between fishing methods or between fishing areas. Significant differences, explaining 30% of the total variance in *CpUE*, were observed between sampling months. A *CEDRS* with an accuracy of 28% for the estimated annual catch, 17% for the catch per unit of effort, and 11% for the effort was proposed for the reservoir fishery. Not more than one sampling day per month is needed to achieve this accuracy in a reservoir like Tissawewa. This is a 50% reduction in sampling investments compared to the former official *CEDRS* for Sri Lankan reservoirs. Application of the proposed *CEDRS* will remove the bias which presently occurs in the official data, which are based on the number of registered canoes and not on actual recordings of effort.

Introduction

The contribution of the inland fisheries to the total fish production in Sri Lanka has increased from almost 0 to about 20% during the last decades (Jayasekera, 1990). The major factor in this development was the introduction of *Oreochromis mossambicus* (Peters) in 1952, which has dominated the catch ever since (Fernando and Indrasena, 1969; De Silva, 1988a). Mainly outrigger canoes and multifilament nylon gillnets are used to catch tilapia. The most important water bodies for Sri Lankan inland fisheries are the larger (>100 ha) irrigation reservoirs in the dry lowlands of north, east and south-east Sri Lanka. They are shallow reservoirs with maximum depths often less than 5 m and considerable fluctuations in water level. These reservoirs, many of them being 500 to 2 000 years old (Fernando and Indrasena, 1969), cover a total surface area of around 100 000 ha. Supply of irrigation water is the main purpose and the Irrigation Department of the Sri Lankan government is responsible for water management. Fish production is a secondary function of recent origin (De Silva, 1988a). This pattern of multi-purpose use is a feature of the inland fisheries of most Asian countries (Petr, 1985; De Silva, 1988b).

The total annual catch from Sri Lankan reservoirs is estimated at 27 000 to 30 000 metric tonnes (De Silva, 1988a) which indicates an average yield of 270 to 300 kg/ha/yr. This is high compared to the average annual yield of 80 kg/ha from this type of fisheries in other tropical countries (Oglesby, 1985). Based on official data, the maximum sustainable yield for Sri Lankan reservoirs is estimated at 256 kg/ha/yr and the optimum effort at 3.2 boats per km^2 (De Silva *et al.*, 1991), but the official estimates are considerably biassed (Amarasinghe and Pitcher, 1986; Chandrasiri, 1986; Amarasinghe, 1992). In 1990 the Sri Lankan government abandoned its active involvement in inland fisheries management, apparently for religious reasons (Amarasinghe, 1992).

Catch and effort data are often the only data available to managers of tropical fisheries (Larkin, 1982), especially when it comes to country-wide historical data sets. Collection of basic statistical data remains a problem and Sri Lanka is no exception in this (Marr, 1982; Amarasinghe and Pitcher, 1986; De Silva, 1988a; Amarasinghe, 1992). Inaccuracy is often caused by systematic errors in data recording systems (Dudley and Harris, 1987). An accuracy of 30% is needed if a serious decline (reduction of 50%) in total catch is to be detected on time. The accuracy is a combination of bias and precision and it is improved by a well designed sampling program, increased sampling effort and removal of bias.

The present study describes a typical Sri Lankan reservoir fishery in terms of spatial and temporal patterns in catch, effort, catch per unit of effort (*CpUE*), mesh sizes and size distributions of the catch. A general analysis of variance (Sokal and Rohlf, 1969) was applied to identify strata in the *CpUE* data set. The primary aim of this study is to indicate how the system for collection of catch and effort data can be optimised and how the accuracy of the data can be improved. The second aim is to accurately describe the existing fishery in terms of effort, *CpUE*, mesh sizes and size distributions of the catch. This description is needed to enable predictions on the results of different management strategies.

Materials and methods

Study site and climate

Dynamics of the commercial inland fisheries were studied in Tissawewa, a typical lowland reservoir which is 2 000 years old (De Silva, 1988a) and situated in the dry south east corner of Sri Lanka. This reservoir is part of the Kirindi Oya Irrigation Scheme in the Hambantota district. The main river is the Kirindi Oya which feeds the major reservoir Lunuganwehera (*c.* 3 000 ha) from which three smaller downstream reservoirs, Yodawewa (*c.* 500 ha), Weerawila wewa (*c.* 400 ha) and Tissawewa (*c.* 200 ha), are fed.

A morphometric map of Tissawewa was constructed using an echo-sounder and surface areas within depth contour lines were calculated by planimeter. The reservoir volume at each depth contour was calculated from volumes per depth stratum (Orth, 1983).

$$V = \Sigma V_s = \Sigma \left(\frac{h_s}{3} * (A_{1s} + A_{2s} + \sqrt{A_{1s} * A_{2s}}) \right)$$

where V = reservoir volume (m³),
   V_s = volume of stratum s (m³),
   h_s = height of stratum s (m),
   A_{1s} = area of the upper surface of stratum s (m²) and
   A_{2s} = area of the lower surface of stratum s (m²).

Data on daily water levels and rainfall were obtained from the Sri Lankan Irrigation Department. Calculated surface areas and volumes from all depth contours were plotted on water levels and models were fitted to enable calculation of surface areas and volumes at any water level,

$$S = 10^3 * (808 * D - 106)$$

$$V = 29 * 10^4 * D^{2.2}$$

where D = maximum water depth in the reservoir (m),
   S = surface area (ha) and
   V = reservoir volume (m³).

Mean depths were calculated from volumes and surface areas. The morphometric map was constructed when the level at the main sluice was 4.20 m and the deepest point in the reservoir was 3.30 m. The map was divided in sections of 4 ha each, to record the location of fishing operations. Three fishing areas (Fig. 3.1) were chosen: a deep water area at depths above 2.50 m, a more shallow area at depths from 1.50 to 2.50 m and a littoral area with vegetation from 0.00 to 1.50 m (all at a maximum depth of 3.30 m). Boundaries of fishing areas were not shifted with changing water levels.

Sampling the fisheries and estimation of catch and effort

Data on the commercial fisheries in Tissawewa were collected from September 1991 to
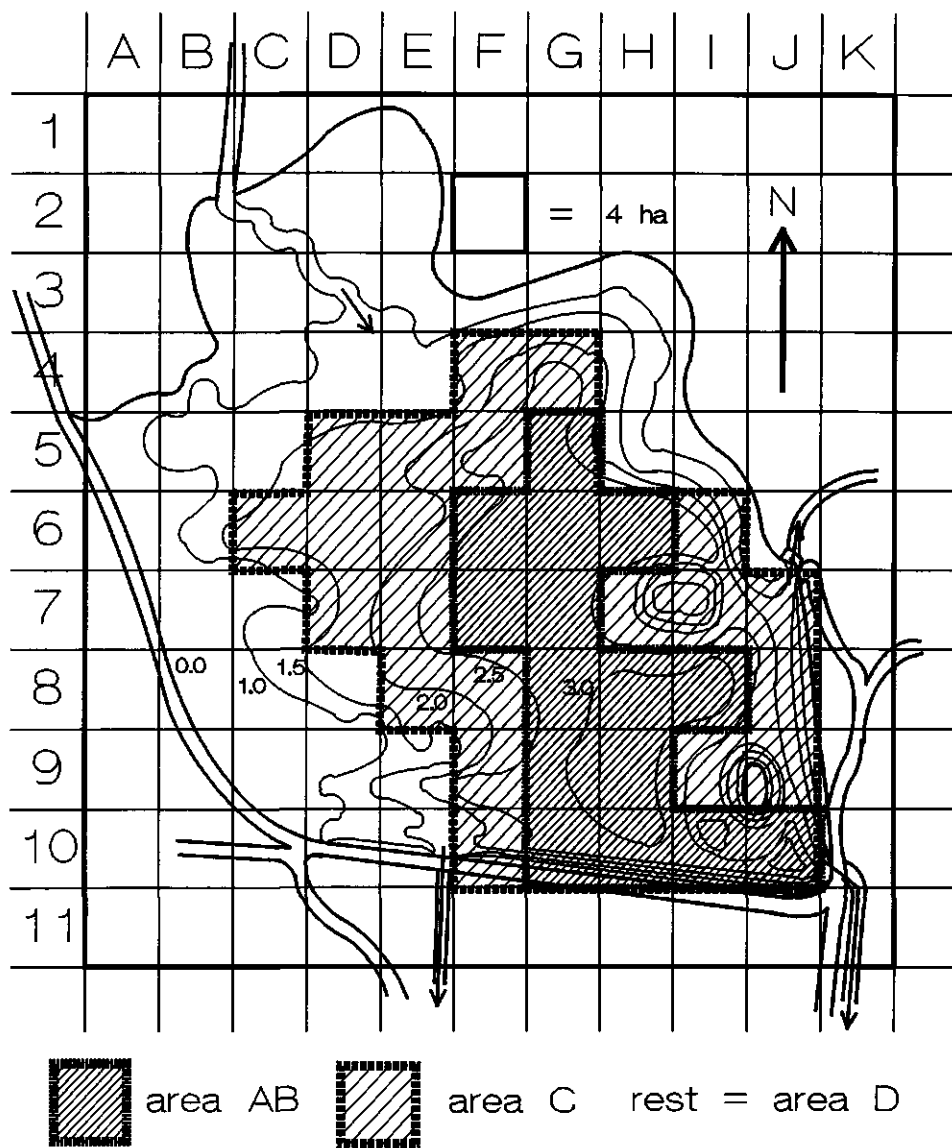
Fig. 3.1. Morphometric map of Tissawewa. The inflow is in the North, dam and outflow are in the South. One
block is equivalent to 4 ha. Fishing areas: *AB*, open water zone with deeper water; *C*, inshore shallow
open water; *D*, littoral zone with vegetation.

July 1993. No fishing took place from September 1992 to February 1993 due to extremely
low water levels and a resulting fish kill. After the drought it took several months for the
fish densities to increase and the fishermen collectively started fishing again in March 1993.

From September 1991 to August 1992, the commercial fisheries were sampled for four full days during each month. From September 1992 to July 1993 this was done for two full days each month. Sampling days were always chosen a few days before or after full moon. Three teams covered the main landing sites of the gillnet fishermen at sunrise. Data recorded from one fishing trip included: date of trip and name of canoe owner, number of fishermen in the canoe, type of fishing gear (gillnet or cast net), method of fishing (normal gillnetting, seining, beating), number of units (number of nets), size (m) and mesh size (mm) per unit, duration of fishing trip in hours, total weight of catch per species in 0.1 kg, length frequency distribution (half cm below, total length) per species and location of the fishing operation.

The fishermen from all landing canoes were interviewed as they landed and length frequency distributions per species were recorded for the entire catch on almost all sampling days. Sub-sampling of length frequencies was only necessary when catches per trip were relatively high in January 1992. The location of the fishing operation was identified from direct observations, made when the fishermen were lifting their nets, and this was verified during the interview at the landing site. After the morning landings by gillnet fishermen, beach seiners, water beaters and cast net fishermen took over and were active throughout the rest of the day. Their activities were monitored through field glasses and each landing craft was intercepted and sampled in the same way as the gillnet fishermen in the morning. Since the size of the reservoir and the number of fishermen were small, all fishing operations were sampled on a given sampling day.

Estimates for total annual catch and yield were calculated for different time intervals. Daily estimates were calculated directly as total landings. The relative importance of different gear types and fish species was calculated for individual months and over the total study period. The statistical population was defined as the number of fishing days in each time interval. Mean and standard deviation were calculated over the sample of fishing days. Total annual catch with 95% confidence limits was calculated with

$$C_{est} = \frac{\Sigma c_i}{n} * N \ +/- \ \frac{t * N * s}{\sqrt{n}} * \sqrt{1 - (n \ / \ N)}$$

where C_{est} = estimated total annual catch,
      c_i = total landings on fishing day i,
      n = number of fishing days in the sample,
      N = number of fishing days in the time interval,
      t = 1.96 at 95% confidence limits and
      s = standard deviation of mean daily catch.

The maximum relative error was calculated as a percentage of the total annual catch. The annual yield was calculated for each time interval by two different methods. The first estimate was based on the actual mean surface area during the time interval. The second estimate was made using the mean surface area since January 1987.

A one-way analysis of variance (Sokal and Rohlf, 1969) was applied on the effort data set to test for significant ($P<0.05$) differences in effort between sampling months. Means

of individual months were compared by means of a Student-Newman-Keuls multiple range test (SAS Institute Inc., 1989).

Analysis of variance for individual catches

Strata were identified within the *CpUE* data set, to enable the development of an efficient catch and effort data recording system (*CEDRS*). A general analysis of variance (Sokal and Rohlf, 1969) was applied on ln-transformed data, since *CpUE* distributions within cells were slightly skewed. Potential sources of variance were water level, sampling month, fishing area, fishing method and interaction terms. Water level and sampling month were correlated. Two models were tested, based on two different hypotheses. The first hypothesis was that part of the variance in *CpUE* can be explained by water level fluctuations. The second hypothesis was that this variance can be explained by temporal patterns,

1) $CpUE = wa + ar + me + wa * ar + wa * me + ar * me + wa * ar * me$

2) $CpUE = mo + ar + me + mo * ar + mo * me + ar * me + mo * ar * me$

where *ar* = area: *AB*, *C* and *D*,

   me = method: normal gillnet, cast net, beating and seining,

   mo = month: September 1991 to July 1993,

   wa = water level category: 0-2 m, 2-3 m and >3 m.

Both models were tested separately for tilapia and for the group of "other species". All zero catches were omitted when the data set for tilapia was analysed. Zero catches only existed for mesh sizes of 202 and 254 mm stretched mesh, which were targeting Indian carps and were too large to catch tilapia. Zero catches did exist within the group of other species and they were changed to catches of 0.1 kg (one small fish) before ln-transformation.

It was assumed that overall mean *CpUE* values were not significantly different among sampling days within sampling months. This assumption was tested with a model where the sampling date was nested within the sampling month.

A catch and effort data recording system was designed using the results of analysis of variance. *CpUE* data, including all species and gear types between September 1991 and August 1992, were used to calculate required annual sample sizes. Only the fishery for Indian carps, with mesh sizes of 202 and 254 mm, was excluded from the analysis since stocking of these species had stopped in 1990 (Pet and Piet, 1993) and these fish do not reproduce naturally in Sri Lankan waters.

A first approximation for the required sample size, at 5% significance level and a variable maximum relative error, was calculated using the formula for stratified random sampling with proportional allocation (Cochran, 1977),

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$$n_0 = \frac{t^2 * \Sigma \ (W_h * s_h^2)}{r^2 * Y_m^2}$$

where n_0 = first approximation of sample size,
        t^2 = 3.84, at 5% significance level,
        W_h = weight factor = $N_h \ / \ N$,
        N_h = total number in stratum h,
        N = total number in population,
        s_h = standard deviation in stratum h,
        r = maximum relative error and
        Y_m = estimated mean in the population.

The required sample size was corrected for finite populations, taking the ratio of sample size to population size into account. The correction factor for stratified random sampling programs (Cochran, 1977) was used,

$$n = n_0 \ / \ (1 + (n_0 \ / \ N))$$

where n = sample size, n_0 = first approximation of sample size and
       N = total number in the population.

Required sample sizes, were calculated for different sampling strategies with a precision of 20% in the estimated mean *CpUE*. The most efficient sampling strategy was chosen and the actual precision of *CpUE*, effort and catch estimates was calculated for this strategy and compared with the required precision. The official *CEDRS* for Sri Lankan reservoirs (Chandrasiri, 1986), which existed before 1990, will be discussed in terms of precision, accuracy, bias and efficiency.

Results

Study site and environmental factors

Fluctuations in water level, surface area and volume follow the patterns in rainfall (Fig. 3.2a). Annual rainfall at Tissawewa varies from 600 to 1 000 mm. The main rainy season is during the north east monsoon from October to January, with peak rainfall in November. A second minor rainy season extends from March to May, during the south west monsoon.

The maximum depth in Tissawewa ranged from 0.14 to 3.95 m with a mean of 2.55 m since January 1987. The mean maximum depth during the study period was 2.30 m. The maximum depth of 5.0 m as reported by De Silva and Sirisena (1987) refers to the maximum recorded water level at the main sluice, which was approximately 1 m more than the actual maximum depth in the reservoir. The reservoir surface area and volume at any moment followed from reservoir water levels (Fig. 3.2b). The total surface area fluctuated between 1 and 312 ha, with a mean of 195 ha, since January 1987. The mean surface area during the study period was 175 ha and the mean depth was 1.06 m.
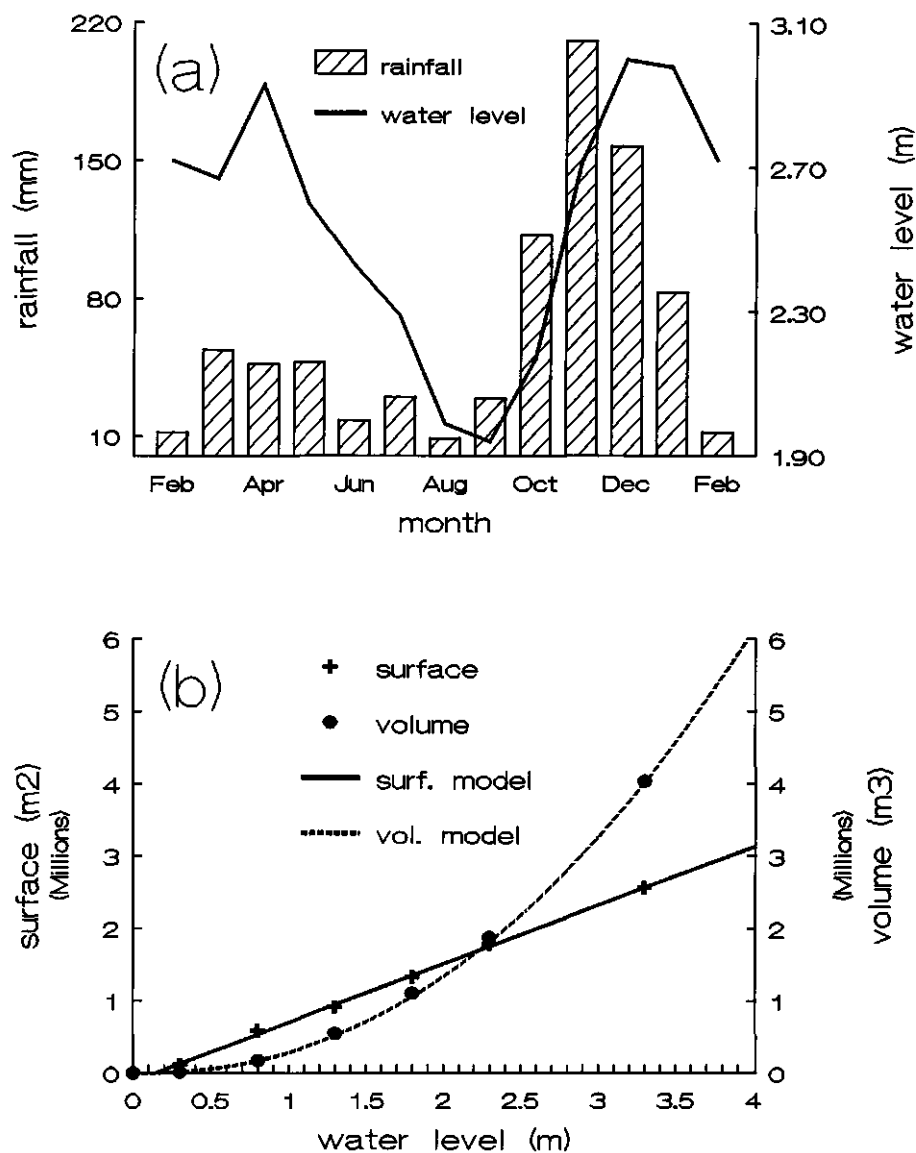
Fig. 3.2. Mean monthly rainfall and water level from January 1987 to July 1993 (a). Calculated surface and volume at different water levels with fitted models for interpolation and extrapolation (b).

Tissawewa fisheries

There are about 13 active fishermen living around Tissawewa. Fishing is mainly by non-motorized outrigger canoes, equipped with gillnets and cast nets. Gillnets are used mainly as passive gear, with setting times of 12 hrs from dusk to dawn (Table 3.1).

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Table 3.1. Specification of mean fishing effort parameters per fishing
trip for all gear types and fishing methods.

Gear	Method	N units	Size*	Duration*	N people	N#
Gillnet	normal	2.1 (0.8)	225 (50)	12 (2)	1.4 (0.6)	399
Gillnet	seining	1.0 (0.0)	200 (70)	5 (2)	3.6 (1.3)	28
Gillnet	beating	1.1 (0.3)	200 (35)	4 (2)	2.3 (0.7)	24
Cast net		1.0 (0.0)	6.4 (1.1)	4 (2)	1.8 (0.6)	63

*Size: gillnets, length (m); cast nets, diameter (m). *Duration: setting time or fishing
time (hr). #N: number of observations. Standard deviations are given between brackets.

A fishing trip with gillnets usually includes 2 nets, each with a mean length of 225 m.
Only 1 or 2 people are involved in a normal gillnet fishing trip. Gillnets are also used in
an active way, as a beach seine and sometimes in a method named "water beating"
(Amarasinghe and Pitcher, 1986). Seining and beating trips usually include 2 to 5 people.
These trips take place during daytime and they have a mean duration of 4 hrs. The second
type of gear is the cast net, a circular throw net with a mean diameter of 6.4 m. Cast net
trips usually take place during daytime, with a mean duration of 4 hrs and involving 1 or
2 fishermen. Fishermen using normal gillnets land every morning on a fixed landing place.
Canoes which operate other methods and gear land throughout the day, usually near the
house of the canoe owner. Based on religious reasons, the commercial fishery is inactive
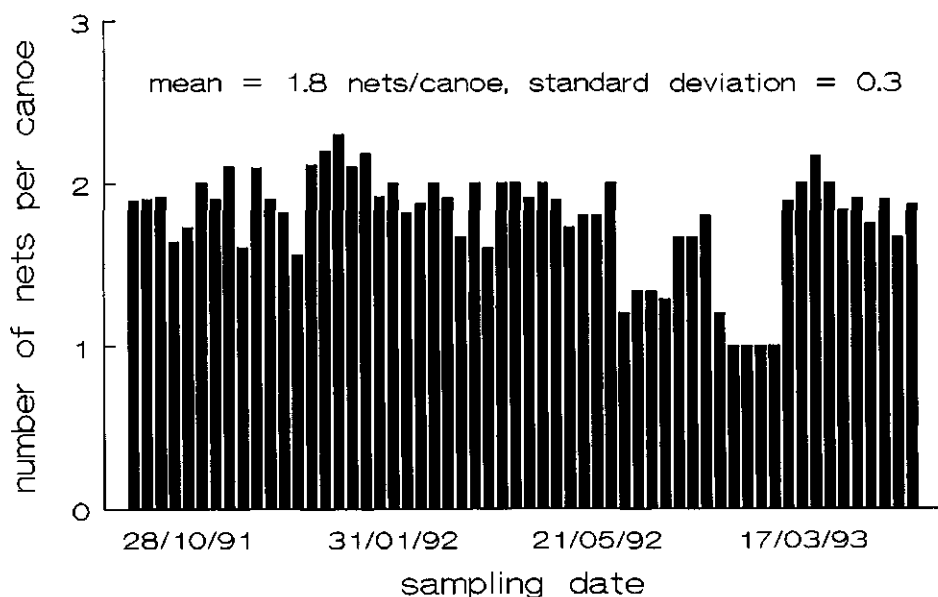during 2 days around full moon.

Fig. 3.3. Mean number of nets per canoe, irrespective of fishing gear, for all sampling days in the study period.

The daily mean number of nets per canoe, irrespective of gear type, varied from 1.0 to 2.3 (Fig. 3.3). The mean number was 1.8 nets per canoe with a standard deviation of 0.3. There was no trend in the number of nets per canoe during the study period. Since the number of nets was proportionally related to the number of fishing trips, and for reasons of manageable sampling, a unit of effort was defined as a single fishing trip of an outrigger canoe.

After a long period of high water levels, a severe drought and high water demands from paddy farmers caused the reservoir to run almost dry in September 1992 (Fig. 3.4a). This situation occurs once every 5 to 10 years in Tissawewa (Irrigation Dept., pers. comm.), the previous case being in 1987. During most years, including 1988 to 1991, the water levels stay sufficiently high for the fishermen to remain active throughout the year. After the drought period of 1992, the reservoir filled up again in November 1992.

Peak values in $CpUE$ of tilapia occurred in January 1992 and August 1992 (Fig. 3.4b). The mean number of trips per day was not significantly ($P>0.05$) different between months until June 1992. The mean daily effort in the tilapia fishery, excluding mesh sizes of 202 and 254 mm, was 9.2 trips per day with a standard deviation of 1.8. Most fishermen fish every day, except on full moon days. Access is limited by the Fishermen's Societies of each reservoir, which do not accept outsiders to fish in "their" water. The fishing effort decreased after May 1992, with decreasing water level and surface area, to an absolute zero in September 1992 (Fig. 3.4c). All fishermen started fishing again in March 1993 when adult tilapia had migrated into Tissawewa from the larger upstream reservoir which had not fallen dry in 1992.

Both before and after the drought period normal gillnetting has always been by far the most important fishing method, accounting for 81% of all fishing trips and for 76% of the total catch (Fig. 3.4c and 3.4d). Cast net, beach seine and water beating account for 11, 4 and 4% of the effort respectively in terms of number of trips and 13, 6 and 5% of the catch in terms of weight.

Table 3.2. Species composition in the commercial catch from Tissawewa between September 1991 and July 1993.

Group	Species	Composition (%)	
		period 1*	period 2*
Tilapia	*Oreochromis mossambicus* (Peters)	64.8	49.4
	Oreochromis niloticus (Linnaeus)	5.0	45.6
	Tilapia rendalli (Boulenger)	2.2	0.0
Indian	*Catla catla* (Hamilton)	20.7	0.0
carps	& *Labeo rohita* (Hamilton)		
Indigenous	*Barbus dorsalis* (Jerdon)	0.5	0.2
species	*Barbus sarana* (Hamilton)	2.6	0.6
	Channa striata (Bloch)	2.8	2.9
	Glossogobius giuris (Hamilton)	0.9	1.1
	Mystus gulio (Hamilton)	0.5	0.2

*Period 1, September 1991 - August 1992; period 2, September 1992 - July 1993.
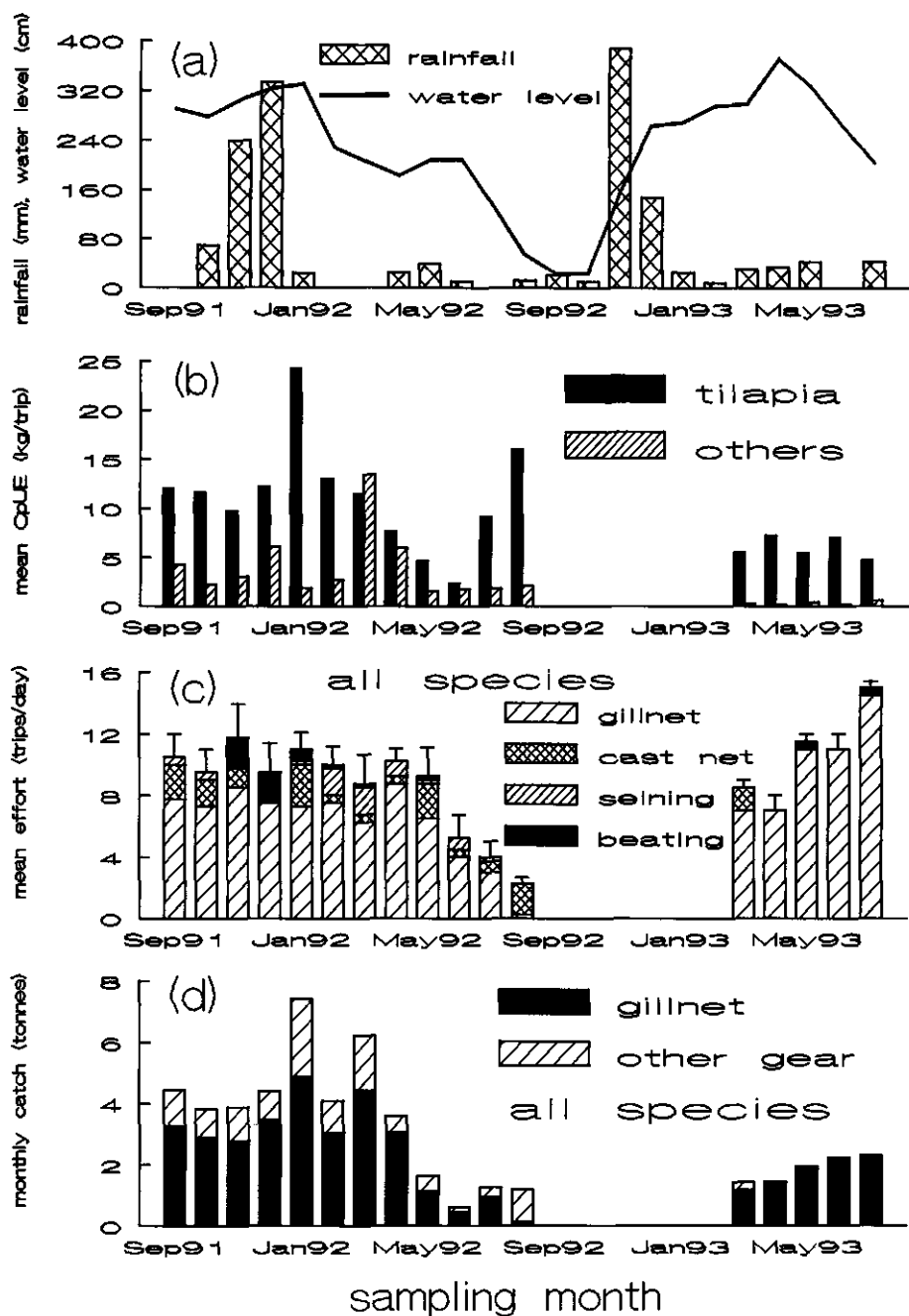
Fig. 3.4. Patterns in rainfall and water level during the study period (a) compared to patterns in *CpUE* per species (b), mean daily effort per gear type with standard deviations (c) and total monthly catch per gear type (d).

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The overall most important species, in terms of catch by weight, was *O. mossambicus* accounting for 64.8% of the catch before and 49.4% after the drought period (Table 3.2). The total group of tilapia, including *Oreochromis niloticus* (L.) and *Tilapia rendalli* (Boulenger), accounted for 72% of the catch before the drought period and 95% after that. Stocked Indian carps represented 20.7% of the catch before the drought.

Species composition of the catch had changed drastically after the period of drought and Indian carps and *T. rendalli* were no longer present. This partly explains the lower overall mean *CpUE* after the drought period. The dominance of *O. mossambicus* was no longer evident and the relative importance of *O. niloticus*, already the dominant species in the main upstream reservoir, had increased from 5.0% before the drought to 45.6% after that.

Mesh sizes and size distribution of the catch

The four different fishing methods showed similar size distributions of the catch (Fig. 3.5) since similar mesh sizes were used for all gear types. Size distributions of tilapia were almost identical for normal gillnet and water beating since these nets were standing passively in the water for both methods. When the gillnets were used as a beach seine, they were dragged through the water so large fish were encircled and could not escape.
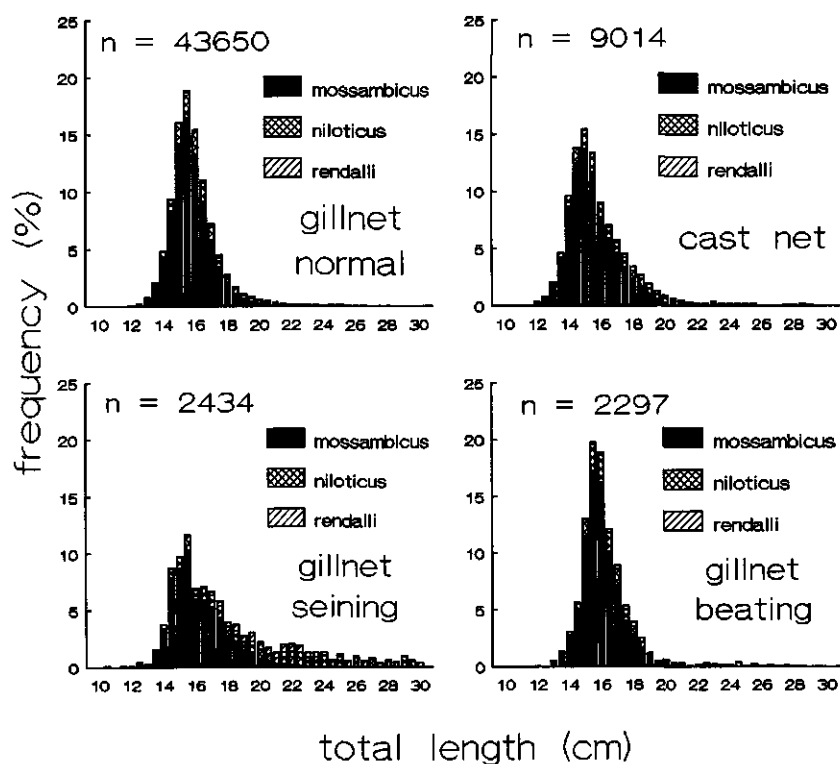

Fig. 3.5. Cumulated length frequency distributions of the catch, per gear type and fishing method for three species of tilapia: *Oreochromis mossambicus*, *O. niloticus* and *Tilapia rendalli*.

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Beach seines yielded relatively large numbers of larger *O. niloticus* and showed a positively skewed length frequency distribution. Cast nets operated in Tissawewa sometimes had relatively small mesh sizes, down to 58 mm. The active way of fishing also resulted in a slight positive skewness of the length frequency distribution.

The legal minimum mesh size in Sri Lankan inland fisheries is 76 mm stretched mesh (Amarasinghe, 1987). The range of mesh sizes encountered during this study included 58, 64, 70, 76, 82, 88, 100, 112, 202 and 254 mm stretched mesh. Meshes from 58 to 112 mm were aimed at tilapia, 202 and 254 mm were meant to catch Indian carps. The latter two mesh sizes were only used before the drought period, since Indian carps were no longer present after that. In the tilapia fisheries, 64 and 70 mm were by far the most common mesh sizes from September 1991 to August 1992, occurring in similar frequencies. During this period the length frequency distributions didn't change much from month to month, they showed a common modus of 15.5 cm and hardly any skewness (Fig. 3.6a). The mean mesh size, based on frequency of occurrence data, was 67 mm for most months in this period (Fig. 3.6c) and dropped to 64 mm in August 1992, after the mean length of *O. mossambicus* started to decrease in March 1992.

Between September 1992 and July 1993, after the drought, the length frequency distribution of the catch was positioned more to the right with modes from 16.5 to 17.0 cm. The cumulated curve for this period is positively skewed (Fig. 3.6b) due to the presence of larger *O. niloticus* and the occurrence of larger mesh sizes, especially at the end of this period. The most common mesh size used was 76 mm. In the first months of this period, 76 mm was used in combination with 70 mm. During later months, when fishermen noticed the presence of relatively large numbers of *O. niloticus*, 76 mm was used in combination with mainly 82 and 88 mm. During both periods the mean length of the overall most important species in the catch, *O. mossambicus*, closely followed the patterns in mean mesh size (Fig. 3.6c).

Table 3.3. Annual catch and yield of tilapia.

Period	Surface (ha)	N	n	Catch (kg/yr)	Y_{mn} (kg/ha/yr)	Y_{195} (kg/ha/yr)	E_{max} (%)	P (%)
09/91 - 08/92	175	340	48	30560	175	157	18.3	72
09/92 - 08/93	173	170	10	10472	61	54	13.0	95
01/92 - 12/92	125	227	32	18634	149	96	28.2	72
09/91 - 02/92	227	170	24	44639*	197*	229*	16.5	79
09/91 - 08/93	175	510	58	21677*	124*	111*	16.6	74

*Doubled values from 6 months period. *Mean values from 2 years period. Abbreviations: N, no. of fishing days in time interval; n, number of fishing days in sample; Y_{mn}, yield from mean surface per period; Y_{195}, Y from mean surface (195 ha) since 01/01/87; E_{max}, maximum relative error; P, percentage tilapia in total catch and yield.

The estimation of annual yield for Tissawewa

Using the mean surface area over each time interval, tilapia yields of 175 kg/ha/yr and 61 kg/ha/yr were calculated for the periods September 1991 to August 1992 and September
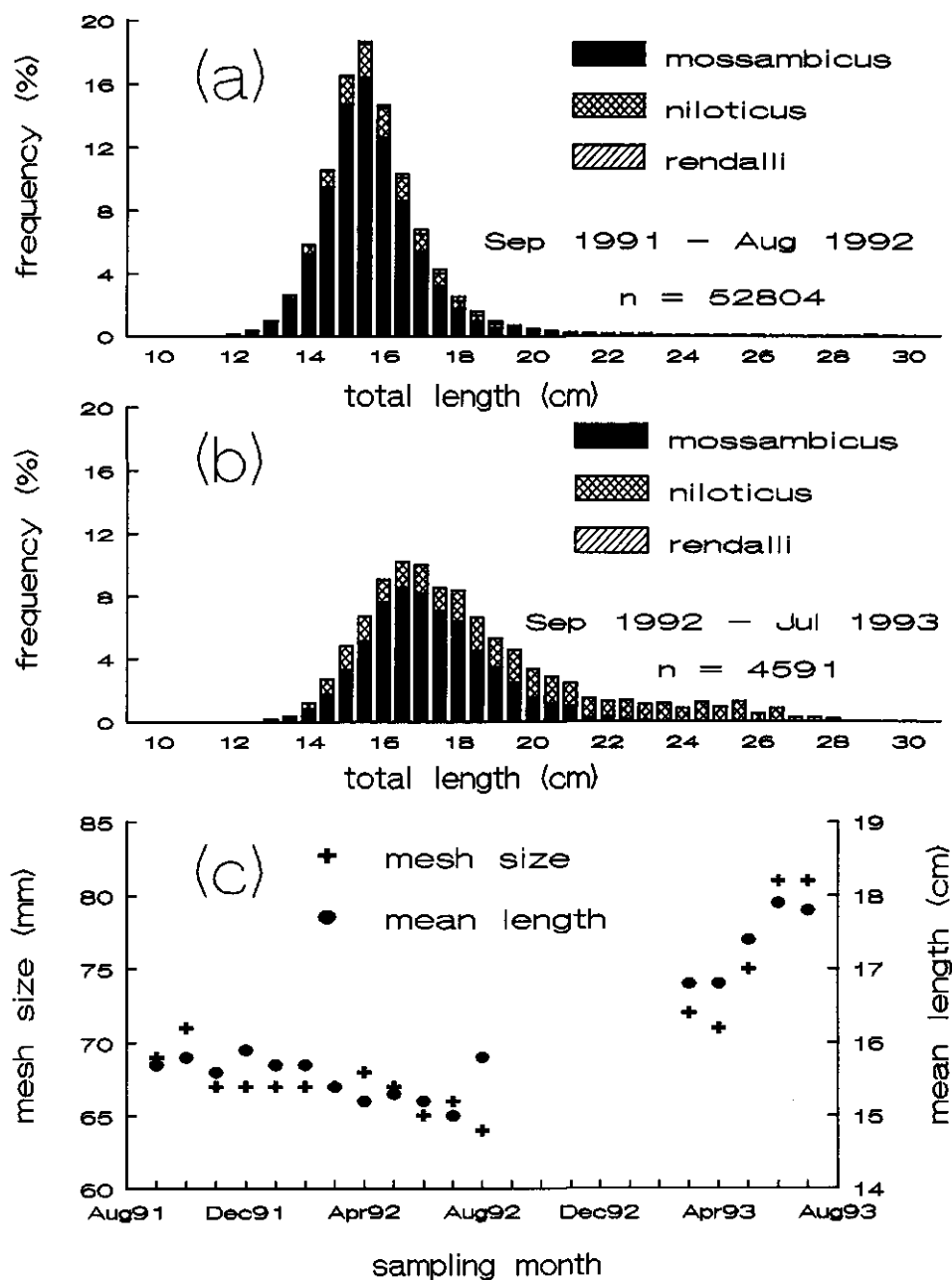
Fig. 3.6. Catch length frequency distributions, for sampling period September 1991 to August 1992 (a) and September 1992 to July 1993 (b) for three species of tilapia: *Oreochromis mossambicus, O. niloticus* and *Tilapia rendalli*. Mean lengths of *O. mossambicus* in the catch are compared with mean mesh sizes (c).

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1992 to August 1993 respectively (Table 3.3). Total yields were 242 and 64 kg/ha/yr over the same periods (Table 3.4). Maximum relative errors of these catch estimates were below 20%. The estimated yield over the second period underestimates the minimum yield in any calendar year since it contains the entire non-fishing period. The total yield over the calendar year 1992 was 208 kg/ha/yr and the mean annual yield over the entire study period was 167 kg/ha/yr. The time interval with highest yields was the first six months of the study period, the end of a period without any major droughts. The estimated total annual yield over this period was 248 kg/ha/yr. The estimated yields for all time intervals were different when the long term mean surface area was used instead of the actual mean over the time interval.

Table 3.4. Annual catch and yield of "other species" and total.

Period	"Other Species"				Total			
	Catch (kg/yr)	Y_{mn} (kg/ha/yr)	Y_{195}	E_{max} (%)	Catch (kg/yr)	Y_{mn} (kg/ha/yr)	Y_{195}	E_{max} (%)
09/91 - 08/92	11870	68	61	29.1	42431	242	218	16.6
09/92 - 08/93	539	3	3	52.8	11011	64	56	13.5
01/92 - 12/92	7386	59	38	44.4	26020	208	133	25.5
09/91 - 02/92	11648*	51*	60*	22.0	56287*	248*	289*	12.7
09/91 - 08/93	7507*	43*	38*	30.7	29184*	167*	150*	16.0

*Doubled values from 6 months period. 'Mean values from 2 years period. Abbreviations: Y_{mn}, yield from mean surface per period; Y_{195}, Y from mean surface (195 ha) since 01/01/87; E_{max}, maximum relative error.

Analysis of variance for individual catches

The model with water level, fishing area and fishing method was significant (P<0.01) for tilapia but it explained only 9.4% of the total variance. Only fishing area and the three-way interaction term were significant at the 5% level. The first hypothesis, linking patterns in *CpUE* of tilapia to water level fluctuations, was therefore rejected (Fig. 3.7a).

The second model (Table 3.5) with sampling month, fishing area and fishing method was also significant (P<0.01) for tilapia and it explained 50% of the total variance. Therefore this model was adopted to describe patterns in *CpUE* of tilapia as temporal (Fig. 3.4b). Analysis of variance showed that different fishing areas or fishing methods by themselves (Fig. 3.7b and 3.7c) did not result in significantly (P>0.1) different mean catch per trip for tilapia. The only main effect which caused significant (P<0.01) fluctuations in *CpUE* of tilapia was the sampling month, which explained 30% of the total variance. The interaction between month and method was significant (P<0.01) and explained 9% of the total variance. During some months of the year some fishing methods show higher *CpUE* values than others (Fig. 3.8). Normal gillnetting showed the highest *CpUE* values in January 1992 and cast netting showed the highest values in July and August 1992. The interaction between month and area was significant (P<0.01) and explained 6% of the total variance.
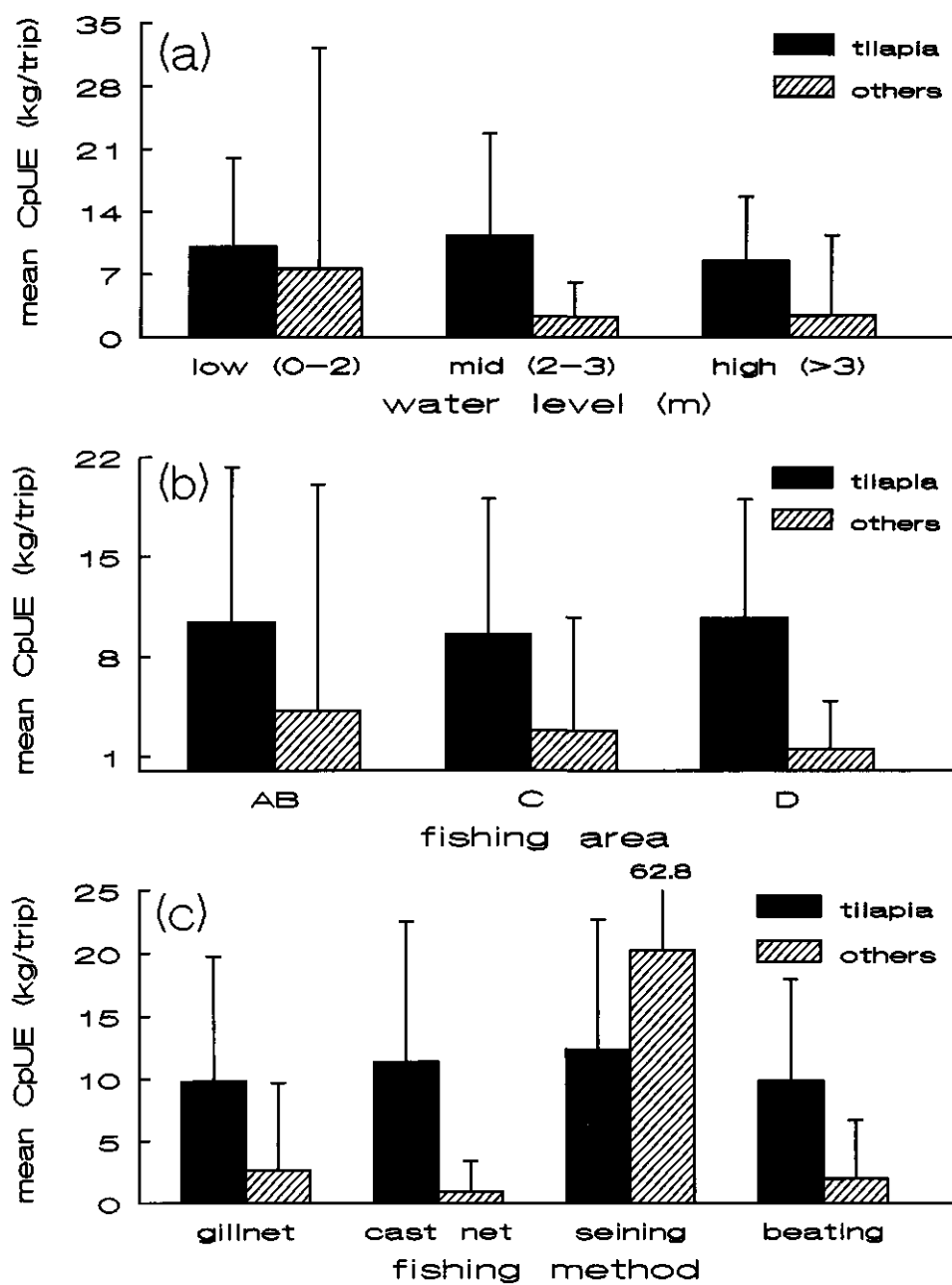
Fig. 3.7. Mean and standard deviation (bar) of catch per trip for tilapia spp. and "other species" over different categories of water level (a), fishing area (b) and fishing method (c).

Table 3.5. Analysis of variance for 485 catches of tilapia.

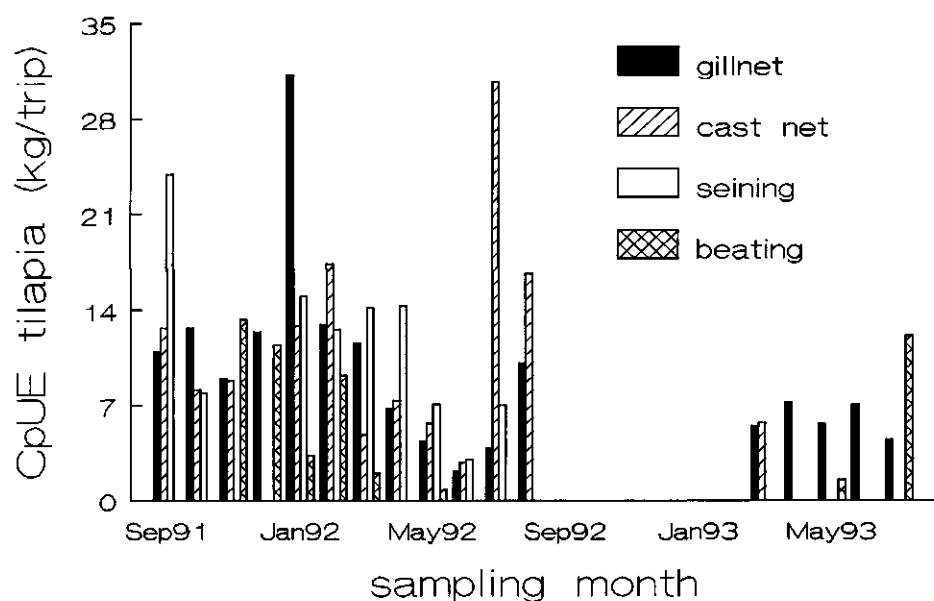| Source	df	SS	MS	F	P
MONTH	16	127.78	7.99	14.77	0.0001
AREA	2	2.00	1.00	1.85	0.1585
METHOD	3	2.42	0.81	1.49	0.2262
MONTH*AREA	25	27.15	1.09	2.01	0.0031
MONTH*METHOD	25	35.50	1.42	2.63	0.0001
AREA*METHOD	5	8.59	1.72	3.18	0.0079
MONTH*AREA*METHOD	9	10.33	1.15	2.12	0.0268
Model	85	213.78	2.52	4.65	0.0001
Error	399	215.80	0.54		
Corrected Total	484	429.58			

Fig. 3.8. Monthly changes in catch per trip for tilapia over four different fishing methods.

Different seasonal fluctuations were observed within the *CpUE* of tilapia for each fishing area. Whereas catch per trip in the deep water (area *AB*) showed the same pattern as the overall mean, the opposite was observed in the littoral zone (area *D*) which is most productive during the two rainy seasons, from April to June and from October to December (Fig. 3.9a). The shallow inshore zone (area *C*) always yields intermediate *CpUE* values. The fishermen react to spatial and temporal patterns in *CpUE*, by re-allocating their effort into the most productive area (Fig. 3.9b). The interaction between area and method (Fig. 3.9c) was significant at the 1% level and between month, area and method only at the 5% level. None of these terms explained more than 2% of the total variance.
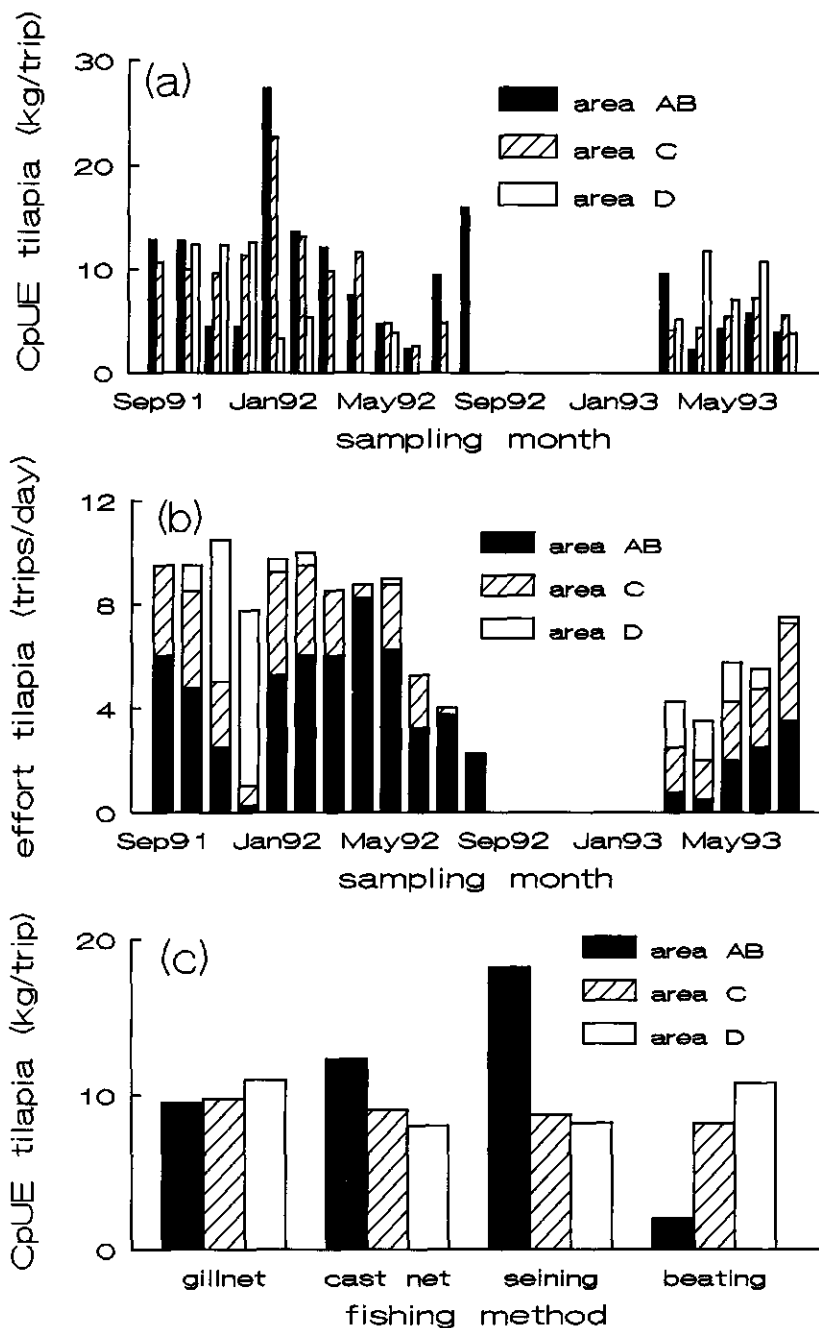
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Fig. 3.9. Interaction between fishing area and sampling month (a) compared with temporal patterns in the allocation of effort over different fishing areas (b). Interaction between fishing method and fishing area (c).

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Table 3.6. Analysis of variance for 514 catches of "other species".

Source	df	SS	MS	F	P
MONTH	16	234.27	14.64	6.84	0.0001
AREA	2	5.37	2.69	1.26	0.2861
METHOD	3	213.17	71.06	33.21	0.0001
MONTH*AREA	25	50.14	2.01	0.94	0.5528
MONTH*METHOD	25	66.29	2.65	1.24	0.1987
AREA*METHOD	5	24.19	4.84	2.26	0.0475
MONTH*AREA*METHOD	9	16.03	1.78	0.83	0.5865
Model	85	609.47	6.38	3.35	0.0001
Error	428	915.68	3.57		
Corrected Total	513	1525.15			

The model with sampling month, fishing area and fishing method explained 40% of the total variance in $CpUE$ for the group of "other species" (Table 3.6). The sampling month and fishing method resulted in significantly ($P<0.01$) different mean $CpUE$ values. These two main effects explained 15%, and 14% of the variance respectively. For seining the mean $CpUE$ of 'other species' was by far the highest (Fig. 3.7c) but the standard deviation was also high. The interaction between area and method was significant ($P<0.05$) in this model, although explaining only 2% of the total variance.

An ln-transformed model with sampling date nested within sampling month showed that overall mean daily $CpUE$'s were not significantly ($P>0.1$) different within sampling months.

An efficient catch and effort data recording system

The results of analysis of variance showed that temporal stratification is the most efficient way to reduce the variance in $CpUE$ values. Each monthly mean $CpUE$ value of tilapia was compared with values for all other months by means of an LSD-test for unequal cell sizes (Sokal and Rohlf, 1969), and nine groups of sampling months did not show significantly ($\alpha = 0.05$) different $CpUE$ values within groups (Table 3.7). Few months of the year occur in the same group as previous or subsequent months. It would be difficult to decide on any grouping of months in sampling intervals, especially since the short data set has no predictive value for patterns in future years.

Mean values for $CpUE$ and effort between September 1991 and August 1992 were used in the calculation of sample sizes and maximum relative errors. The estimated total catch in this period was 38 271 kg, excluding mesh sizes of 202 and 254 mm. The total effort was 2 677 trips during 340 fishing days, which resulted in a mean $CpUE$ of 14.3 kg/trip and a mean effort of 7.9 trips per day.

Sample sizes for stratified (1,2,3,4,6, or 12 strata per year) random sampling programs with maximum relative errors of 20% for total $CpUE$ varied for different combinations of sampling months within strata (Fig. 3.10a). A minimum number of 69 samples per year is needed to achieve a precision of 20% when sampling takes place on a monthly basis. Larger strata have the disadvantage that the sampling program has to be randomized, which

is more important than the small increase in sample size. Monthly samples can be taken in one day, since differences within months are not significant.

Table 3.7. Groups of months which do not show significant ($\alpha = 0.05$) differences in mean *CpUE* of tilapia after ln-transformation.

Month	Mean *CpUE* kg/trip	ln(kg/trip)	A	B	C	D	E	F	G	H	I
Sep 1991	12.1	2.298								*	*
Oct 1991	11.6	2.218						*	*	*	
Nov 1991	9.8	1.895				*	*	*	*		
Dec 1991	12.2	2.182						*	*	*	
Jan 1992	24.2	2.861									*
Feb 1992	13.0	2.340								*	
Mar 1992	11.4	2.152					*	*	*	*	
Apr 1992	7.7	1.852				*	*	*			
May 1992	4.7	1.341		*	*						
Jun 1992	2.4	0.704	*								
Jul 1992	9.1	1.619		*	*	*					
Aug 1992	16.0	2.450								*	*
Mar 1993	5.5	1.392		*	*						
Apr 1993	7.2	1.638			*	*					
May 1993	5.4	1.495		*	*	*					
Jun 1993	7.0	1.761			*	*	*				
Jul 1993	4.7	1.199		*							

Table 3.8. Populations, sample sizes, means and standard deviations per month for *CpUE* and effort from Sep. 1991 to Aug. 1992. All gear types and species except fishery for Indian carps.

Month	N_{trips}	n_{trips}	Catch/trip (kg) mean	sd	N_{days}	n_{days}	Trips/day mean	sd
Sep	266	38	16.5	7.7	28	4	9.5	1.5
Oct	276	38	13.8	8.9	29	4	9.5	1.5
Nov	294	42	12.5	9.2	28	4	10.5	2.2
Dec	225	31	15.9	13.8	29	4	7.8	1.9
Jan	283	39	25.8	18.9	29	4	9.8	1.1
Feb	260	40	15.7	11.7	26	4	10.0	1.2
Mar	239	33	17.5	19.2	29	4	8.3	1.9
Apr	245	35	10.4	9.2	28	4	8.8	0.8
May	261	36	6.0	3.9	29	4	9.0	1.9
Jun	147	21	4.1	2.1	28	4	5.3	1.5
Jul	116	16	10.9	13.5	29	4	4.0	1.0
Aug	65	9	18.1	19.6	29	4	2.3	0.4

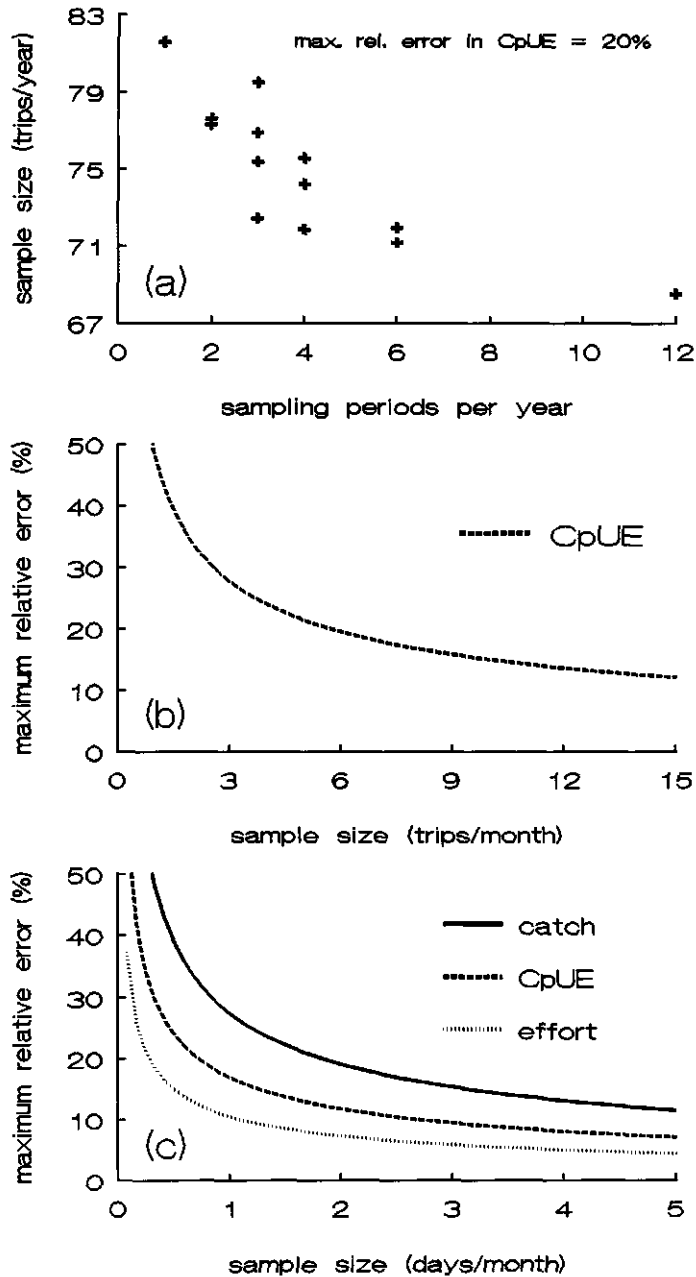Abbreviations: N, population size; n, sample size; *sd*, standard deviation.

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Fig. 3.10. Required annual sample sizes at different sampling strategies for various combinations of sampling months (a). Maximum relative error of the estimated mean annual *CpUE* at different sample sizes in terms of trips per month (b). Maximum relative error of the estimated mean annual *CpUE*, effort and catch at different sample sizes in terms of days per month (c).

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Monthly population and sample sizes, means and standard deviations (Table 3.8) were used to calculate the maximum relative error in *CpUE* and effort at different sample sizes in terms of sampling days per month. Sample sizes of 6 trips per month are sufficient to achieve a maximum relative error of 20% in the estimate of mean annual *CpUE* (Fig. 3.10b). These six samples can be taken in one day since an average of 7.9 trips is available each day and differences within months are not significant. When 7.9 trips are sampled in one day, the maximum relative error in the estimated mean *CpUE* and effort and in the estimated total catch are 17, 11 and 28% respectively (Fig. 3.10c). The maximum relative error in the estimated catch decreases to 19 and 13%, when the sample size is increased to 2 or 3 days per month respectively.

Discussion and conclusions

Temporal dynamics in effort, CpUE and yield

Daily effort in Tissawewa is constant as long as the water level remains above 2.0 m for the deepest point in the reservoir. Most fishermen fish daily, resulting in a mean effort of 9.2 trips per day in the tilapia fishery. Non-fishing periods occur when water levels drop below 0.5 m. After filling up of the reservoir, about 5 months are needed for fish densities to increase again to exploitable levels. This period is relatively short, due to immigration of fish from a large upstream reservoir through the main river.

A biannual pattern in *CpUE* of tilapia was observed in Tissawewa, with peak values in January and July/August. The actual second peak may be in July since *CpUE* values for July 1992 were possibly underestimated in the present study (Wijsman, 1992). De Silva (1988a) also noted peak landings in January in Tissawewa and in August in the downstream situated Yodawewa. Similar patterns were observed in five reservoirs in the Hambantota district (Chandrasiri, 1986). They are most probably caused by the recruitment of new cohorts of *O. mossambicus* to the fishery.

The modus in the size frequency distribution of the smaller mesh sizes is 15.5 cm. This is the mean length at which a cohort of *O. mossambicus* is fully recruited to the fishery. The fish will need about 14 months to reach this length in Tissawewa (Pet *et al.*, submitted).

The two recruitment peaks in January and July/August indicate two spawning periods around November and May/June, during the two rainy seasons. Similar spawning patterns were reported by other authors (De Silva and Chandrasoma, 1980; De Silva, 1983) and were confirmed by patterns in GSI (Pet and Piet, 1993) and in larvae and fingerling abundance in Tissawewa (Pet *et al.*, submitted). Patterns in *CpUE* per fishing area indicate that *O. mossambicus* migrates into the littoral zone during the spawning seasons, as reported earlier for Tissawewa (Pet and Piet, 1993).

Annual yields from reservoirs like Tissawewa should be calculated from actual mean surface areas since these are different from long term means. Using areas at full supply level will underestimate the actual fish production, and long term averages will give biased results for individual years. Since the overall mean annual yield during the present study includes periods just before, during and just after a major drought, it is assumed that 150

kg/ha/yr is a good estimate for the lower limit of the range of possible yields from Tissawewa. The upper limit of the range seems to be around 250 kg/ha/yr, as estimated from the first six months of the study period. Mean annual yields are expected to be between 200 and 250 kg/ha/yr since major droughts occur only once every 5 to 10 years.

Mesh sizes and growth overfishing

Overall mean mesh sizes and fish lengths in the present study were low compared to previous reports from Tissawewa and other reservoirs (Amarasinghe and Pitcher, 1986; Amarasinghe, 1987; De Silva *et al.*, 1988). Pet and Piet (1993) concluded that hardly any *O. mossambicus* of over 19 cm total length were present in Tissawewa between September 1991 and August 1992. Most fish were caught at a length of 15.5 cm. This is contrary to a maximum recorded length of 30 cm, a length at maturity of 16 cm and a length at capture of 16.5 cm, reported recently for Tissawewa (De Silva *et al.*, 1988).

De Silva and Chandrasoma (1980) reported a decline in the length at maturity for *O. mossambicus* in Parakrama Samudra. A declining trend in the mean landing size of *O. mossambicus* in commercial catches has been reported for several reservoirs (De Silva and Fernando, 1980; Amarasinghe, 1988). This trend was attributed to growth overfishing by the use of small-meshed gillnets (Amarasinghe, 1988). Reservoirs with small landing sizes showed a low body condition of fish, which lead to the conclusion that *O. mossambicus* populations in Sri Lanka are in danger of becoming stunted. Stunting, in this case, was caused by selectively fishing out the larger and faster growing individuals, resulting in a positive selection for smaller and slower growing fish. (Rowell *et al.*, 1989; Smith *et al.*, 1991; McAllister and Peterman, 1992; McAllister *et al.*, 1992; Chambers, 1993). The theoretical weight at 20 cm total length was used as a measure for body condition of *O. mossambicus* (Amarasinghe, 1988). During "normal" water levels (>2 m) this was 139.5 g for Tissawewa, which is a value at the lower end of the range as reported for other reservoirs. These symptoms do indicate stunting in a cichlid population (Lowe-McConnell, 1982).

The catch and effort data recording system and annual yield

The *CEDRS* for Sri Lankan irrigation reservoirs should be stratified by sampling month. These reservoirs show considerable fluctuations of water level and the fishery is characterized by relatively small mesh sizes and high fishing effort (Pet *et al.*, submitted). These two characteristics of the reservoir fishery cause unstable temporal patterns in *CpUE* and the variance in estimated catch can only be efficiently reduced through temporal stratification. Results from the present study show that one sampling day per month results in a precision of 28% for total annual catch estimates in a reservoir like Tissawewa. Sampling days should be chosen at regular monthly intervals, to level out bias by systematic sampling. The conclusions do not change much when sampling months with very low (<2 m) water levels are omitted from the analysis. Proportional allocation of sampling effort is necessary since peaks in *CpUE* may shift a month or more from year to year.

Amarasinghe and Pitcher (1986) noted that catch and effort data needed to be stratified for different seasons in Parakrama Samudra reservoir. They attributed differences between

seasons to differences in water levels causing altered stock density and catchability. Neither in their study nor in the present one could a significant effect of water level on mean *CpUE* values be shown. Little is known about the migration of tilapia with incoming or outflowing water, although immigration in Tissawewa was very rapid after the drought period.

The effect of the fishing area on mean *CpUE* values was limited in this study. Larger reservoirs may have to be stratified in different sampling units when spatial differences become evident. Amarasinghe and Pitcher (1986) found significant differences between different reservoir areas in Parakrama Samudra. They did not sample different habitats within one reservoir but three separate basins, which should indeed be treated as separate systems (Schiemer and Duncan, 1983; Schiemer and Hofer, 1983).

A single fishing trip of an outrigger canoe should be used as the most convenient unit of effort. Amarasinghe and Pitcher (1986) noted that number of nets is the most appropriate unit, since it is directly related to the fishing mortality experienced by the fish stock. This is true but the same holds for number of trips, when this is proportionally related to the number of nets, as in Tissawewa fisheries (Fig. 3.3). Amarasinghe and Pitcher (1986) found that catch was overestimated using number of trips as a measure of effort. This was due to large differences in catch per trip between the three study areas, which should have been treated as separate systems. They also found significant differences between fishing methods when number of nets was used as the measure of fishing effort. This effect was not observed in Tissawewa where the number of trips was used, which makes it an even more convenient measure. Catch per trip can be measured directly at the landing site but this is not possible for the catch per net since catches from different nets are mixed in the boat. Amarasinghe and Pitcher (1986) also noted that net counts are bound to be subject to a certain amount of false reporting.

During each monthly catch assessment survey, a frame survey (Caddy and Bazigos, 1985) should be carried out to determine the mean daily effort. The mean catch per trip multiplied by the number of active canoes per day will result in the mean daily catch for that month. Mean daily catches, when multiplied by the number of fishing days in that month, give an estimate of the total monthly catch. Cumulating the values for each month will result in an estimate for the total annual catch,

$$C_y = \Sigma \ C_m = \Sigma \ (f_m * CpUE_m * n_m)$$

where C_y = total catch in year y (kg),
   C_m = total catch in month m (kg),
   f_m = mean effort in month m (canoe-trips per day),
   $CpUE_m$= mean catch per trip in month m (kg) and
   n_m = number of fishing days in month m.

The precision of the catch estimate was calculated for the total catch, which consisted of 95% tilapia and 5% other species since the Indian carps disappeared. *CpUE* values must be recorded for each species separately, in order to detect changes in species composition.

Amarasinghe and Pitcher (1986) reported a total annual yield of 120 kg/ha from Parakrama Samudra, only half the official figure, using the area at full supply level as the production unit. The present study shows that annual yields in Tissawewa are far below

previously reported values of 648 kg/ha and 918 kg/ha for this reservoir (De Silva and Sirisena, 1987; De Silva *et al.*, 1988). Although the annual yield may have decreased during recent years, the differences are enlarged by inaccuracies in the official data. The range of possible yields for Tissawewa as found in this study (150 to 250 kg/ha/yr) shows values which are less than one third of the official yield figures. This pattern of overestimated yield in official statistics is probably a general trend in the Sri Lankan reservoir fisheries (Chandrasiri, 1986; Amarasinghe, 1992).

Official statistics have been calculated from estimated values for the mean catch per boat, multiplied by the number of registered boats (Amarasinghe and Pitcher, 1986; Chandrasiri, 1986). The fish production in Sri Lankan reservoirs was officially estimated by fisheries inspectors, who were supposed to apply a sampling system as described in the present study, with two sampling days per month (Chandrasiri, 1986). Instead of sampling the fisheries at the reservoirs, the fisheries inspectors attended meetings of the fishermen societies where they obtained estimates for the catch per canoe per day. All members reported catches, including those who had illegally sold their subsidised fishing gear. Many people around the reservoirs obtained subsidised boats and nets in the past, but only part of them actively took part in the fisheries. Canoes were issued to 24 members of the Tissawewa fisheries society (Chandrasiri, 1986). Many of the subsidised boats were sold and only 13 members are active fishermen at present, together making an average of 9.2 trips each day. This source of bias results in an over-estimation of effort and catch by a factor 2.4 for Tissawewa. Similar situations were found in 4 other reservoir fisheries in south east Sri Lanka (Chandrasiri, 1986).

The official *CEDRS* for Sri Lankan reservoirs had a precision of 20% in the case of the Tissawewa fisheries and could be optimised by reducing the number of sampling days to one per month. This reduction of the sampling investment with 50% would result in a maximum relative error below 30% for the estimated total annual catch. The major source of inaccuracy in the official data was the biased estimate of effort which is based on numbers of registered boats rather than on frame surveys. Removal of this bias and introduction of the optimised *CEDRS* will result in data which are sufficiently accurate for management purposes.

Acknowledgements

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Chapter 4

Comparison of methods for the estimation of gillnet selectivity to tilapia, cyprinids and other fish species in a Sri Lankan reservoir

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Abstract

Methods based on the models of Holt (1957) and Sechin (1969a, b) were compared for the estimation of gillnet selectivity to two tilapiine, five cyprinid, two catfish, one goby and one halfbeak species, inhabiting a Sri Lankan reservoir. Holt's model was extended to the case where the standard deviation of the selection curve increases in proportion to the optimum selection length. Sechin's model was extended to the case where standard deviation of body girth increases in proportion to the body girth. Selection curves from extended Holt and Sechin models were compared with length frequency distributions of the catch (catch *LFD*) for the largest samples per species. A method for rapid estimation of the position and shape of selection curves was proposed. This method is based on the most common position of retention in gillnets, the length-girth relationship at that position and the ratio between mesh perimeter and body girth. A constant coefficient of variation of 9% was considered to be a good estimate for the standard deviation of the selection curves for non-tangled fish. Tangling percentages were low for all but one toothy species, *Glossogobius giuris* (Hamilton), which showed bimodality in the catch *LFD* due to high tangling percentages. The selectivity to different species was compared using the girth at the position of retention as the independent variable. Differences between species were small and a rough estimation for the most efficiently selected retention girth could be calculated as 2.10 times the stretched mesh size, or 1.05 times the mesh perimeter, independent of fish species. The Holt and Sechin models are only suitable to reconstruct population structures of species with low tangling percentages. The extended Holt model is preferred over the Sechin model, because the Sechin model results in selection curves which are systematically more narrow than the catch *LFD* and Holt selection curves.

Introduction

Gillnets are by far the most important gear in the Sri Lankan inland fishery. At present this fishery is mainly concentrated in the man-made reservoirs, exploiting tilapias, *Oreochromis mossambicus* (Peters) and *Oreochromis niloticus* (Linneaus), with gillnets of 64 to 100 mm stretched mesh (De Silva, 1988). A mixed gillnet fishery for tilapia and cyprinids, using additional small-meshed gillnets for catching cyprinids, has recently been proposed for Sri Lankan reservoirs (De Silva and Sirisena, 1987; Sirisena and De Silva, 1989).

A precise description of gillnet selectivity per species is needed to obtain accurate predictions on the results of mesh size regulations (Reddin, 1986; Van Densen, 1987; Reis and Pawson, 1992). Accurate estimates of selectivity are also necessary for the interpretation and analyses of gillnet catch statistics in population studies (Winters and Wheeler, 1990; Spangler and Collins, 1992). Estimates of gillnet selectivity are of importance for target and non-target species since both will influence the fishery, directly, as by-catch, or indirectly through the food web.

Gillnets are size-selective and fish sizes differing more than 20% from the optimum length will hardly be retained (Hamley, 1975). Gillnet selectivity is usually described by a bell-shaped curve, which is broader and more positively skewed when more fish are caught tangled.

The most reliable way of estimating gillnet selectivity is directly, by fishing a known population (Hamley, 1975). This is expensive since large numbers of fish have to be tagged (Borgström, 1989) or the population has to be sampled simultaneously with gear of known selectivity (Winters and Wheeler, 1990). The indirect methods developed by Holt (1957) and Sechin (1969a, b) are still preferred by many workers, mainly because of ease of application. The Holt model is based on the assumption that the selection curve can be described by a normal distribution with constant efficiency for all mesh sizes. The input for this model is the catch ratio per length category of fish in two different mesh sizes. The Sechin model assumes a unimodal selection curve, which is positioned along the length axis by the ratio between mesh perimeter and body girth.

The third "classical" model (Gulland and Harding, 1961) is based on the ratio between best mesh and mesh used, per length category of fish. This method was developed for a species (*Clarias mossambicus*, Peters) which systematically showed asymmetrical catch length frequency distributions (catch *LFD*). The selection curve, which is fitted through scattered data of relative efficiency per mesh size and length class, is not of a predetermined shape. The Gulland and Harding method was not applied in the present study since the important species did not show asymmetrical catch *LFD*.

Newly proposed methods (Boy and Crivelli, 1988; Helser, Condrey and Ceaghan, 1991; Henderson and Wong, 1991) for estimation of gillnet selectivity fit selection curves on the basis of catch *LFD*. The major disadvantage of these methods is that they require catch *LFD* to be reasonable estimates of the selection curve. This is only true in cases where all size classes vulnerable to a specific mesh size have been equally available to the sampling gear. Samples of this kind are rare. These models do not explain the retention and/or

tangling of fish in gillnets. Predictive models for the position and shape of the selection curve were not improved since Sechin (1969a, b) and Kawamura (1972) developed their deterministic models for the non-tangled part of the catch. These models explain retention of non-tangled fish with data on fish morphology.

Extended versions of the Holt and Sechin models were applied in the present study. The first objective was to compare these models for estimation of gillnet selectivity. The second objective was to obtain estimates of gillnet selectivity for the most important fish species in Sri Lankan reservoirs. The third objective was to derive a method for rapid estimation of gillnet selectivity.

Materials and methods

Data collection

Gillnet fishing was carried out on a monthly basis from September 1991 to July 1993 in Tissawewa (Pet and Piet, 1993). A set of gillnets was made of green monofilament webbing with ten different mesh sizes ranging from 12.5 to 90 mm stretched mesh (Table 4.1), a depth of 1.5 m and a hanging ratio of 0.4 (Sparre et al., 1989). Mesh sizes were randomly distributed within the nets.

Table 4.1. Sample sizes and sampling effort per mesh size and species.

mesh[*]	12.5	16	20	25	33	37	50	60	76	90
length[+]	(5)	(5)	(10)	(10)	(15)	(15)	(15)	(15)	(15)	(15)
time[#]	(2)	(2)	(2)	(2)	(2)	(2)	(12)	(12)	(12)	(12)
species[@]			sample	sizes						
Tilapias (Cychlidae)										
OM		220	529	866	1170	1326	5209	991	130	
ON							849	397	205	157
Cyprinids (Cyprinidae)										
AM	40335	36468	19457							
BC		483	2849	3688	3581	502				
BD		86	392	1862	3390	3241	1382			
BS			90	213	384	908	1593	314		
RD	3503	3867	1105							
Catfish (Bagridae)										
MY			97	436	649	568	215	95		
Gobies (Gobidae)										
GG	140	247	370	303	164	94				
Halfbeaks (Hemiramphidae)										
HG	1933	575	336							

[*]Mesh size in mm stretched mesh, [+]Panel length in m per set of gillnets, [#]fishing time in hrs per setting. [@]Species: AM, *A. melettinus*; BC, *B. chola*; BD, *B. dorsalis*; BS, *B. sarana*; GG, *G. giuris*; HG, *H. gaimardi*; MY, *M. gulio & M. vittatus*; OM, *O. mossambicus*; ON, *O. niloticus*; RD, *R. daniconius*.

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Twine sizes increased with mesh size from 0.1 to 0.2 mm. Each month four sets of netting were set, at four different stations, two times at daytime and two times at night. Data were analysed for all species caught in sufficient numbers (Table 4.1), including two tilapias: *O. mossambicus* and *O. niloticus*; five cyprinids: *Amblypharyngodon melettinus* (Valenciennes), *Barbus chola* (Hamilton), *B. dorsalis* (Jerdon), *B. sarana* (Hamilton) and *Rasbora daniconius* (Hamilton); and four other species: *Mystus gulio* (Hamilton), *M. vittatus* (Bloch), *Glossogobius giuris* (Hamilton) and *Hyporamphus gaimardi* (Valenciennes). Catch *LFD* were corrected for fishing effort (Pet and Piet, 1993).

The way fish were caught was recorded as tangled or non-tangled and retention of non-tangled fish was categorized as: 1. wedged at the maximum girth, 2. wedged between maximum and gill girth or 3. gilled (Sparre *et al.*, 1989). Tangling percentages were calculated per species and per mesh size. Additional measurements included total length (mm), maximum and gill girth (mm) and body weight (g).

The Holt model extended with constant coefficient of variation

The Holt (1957) model is based on the assumption that the selection curve can be described by a normal distribution.

$$S_{(ij)} = EXP \left(- \left(L_j - L_{opt_i} \right)^2 / \left(2 * \sigma_i^2 \right) \right) \tag{1}$$

Abbreviations used in this and all other formulas are presented in Table 4.2.

Table 4.2. Abbreviations.

a, b	= parameters in Holt model for gillnet selectivity
a_{pos}, b_{pos}	= coeff. and exponent in L-G_{pos} relationship
c_{pos}	= coeff. in approximated L-G_{pos} relationship
C, H, S	= Catch, Holt, Sechin
cv	= coefficient of variation in %
cvG_m, cvG_g	= cv in maximum and gill girth in %
D_c	= maximum deviation (%) in approximation of girth
G_{pos}	= girth in mm at maximum, gill or middle position
K_{pos}	= ratio of mesh perimeter and body girth at maximum, gill or middle girth.
$K_{max, gil, mid}$	= K value at maximum, middle and gill girth
K_{mn}	= mean girth/perimeter ratio over several species
k, k_{new}	= Holt's and new estimate of selection factor
L, L_{opt}	= total length in cm, optimum L in cm
LFD	= length frequency distribution
m, m_{opt}	= mesh size in mm stretched mesh, optimum m in mm
max, gil, mid	= maximum, gill and middle girth position
pos	= common position of retention, non-tangled fish
$S_{(ij)}$	= selectivity for length class j in mesh i
$tan\%$	= percentage of fish that were caught tangled
$\sigma, \sigma_{max}, \sigma_{gil}$	= standard deviation, σ of max. and gill girth
Φ	= cumulative normal distribution function

All selection curves were assumed to have a maximum efficiency of 1. L_{opt_i} and σ_i were estimated by comparing the catches of two different mesh sizes, m_1 and m_2 ($m_1 < m_2$), with overlapping selection ranges. Mesh sizes were expressed in mm stretched mesh and catches were corrected for fishing effort. The optimum selection length (L_{opt}), which is the most efficiently retained length in a certain mesh size, was assumed proportional to the mesh size m.

$$L_{opt_i} = k \, * m_i \tag{2}$$

Selection curves from two slightly different meshes were assumed to have equal standard deviations ($\sigma_1 = \sigma_2$).

$$\sigma_1 = \sigma_2 = \sqrt{\frac{2 * a * (m_2 - m_1)}{b^2 * (m_1 + m_2)}} \tag{3}$$

Input data for the analysis were the numbers caught per length class, C_1 and C_2, and the mesh sizes m_1 and m_2. A linear regression of $ln(C_1/C_2)$ on L yielded a and b, representing the intercept and the slope respectively (Holt, 1957; Hamley, 1975). Only the length range for which linearity was observed, was included in the analyses. The catch in each mesh size was compared with catches from the first smaller and larger mesh. For all species the plots of $-2a/b$ against $(m_1 + m_2)$ were expected to approximate straight lines through the origin with overall selection factors k as the slopes (Hamley, 1975).

$$k = \frac{-2 * a}{b * (m_1 + m_2)} \tag{4}$$

For a wide range of mesh sizes it is not realistic to assume a constant standard deviation of the selection curve. A constant coefficient of variation is more realistic (Regier and Robson, 1966; Hamley, 1975) and this extension was adopted in the present model. It was assumed that Holt's assumption of constant standard deviation is approximately correct for each pair of mesh sizes m_1 and m_2, and the coefficient of variation is constant for a wider range of meshes. In the present study, the coefficient of variation (cv) was expressed as a percentage of the mean.

$$cv = 100 * (\sigma_1 + \sigma_2) / (L_{opt_1} + L_{opt_2}) \tag{5}$$

The Sechin model with constant coefficient of variation in girth

Body girth rather than fish length is the decisive feature in gillnet selectivity (McCombie and Berst, 1969; Sechin. 1969a, b; Kawamura, 1972; Winters and Wheeler, 1990). Estimates based on catch frequency distributions only (McCombie and Berst, 1969) may be biased by the girth structure in the population. The modal length, width and skewness of catch LFD are expected to be poor estimates for the parameters defining the selection curve (Hamley, 1975), unless they are based on carefully selected samples. Models based

on assumptions about the mechanisms of selectivity (Sechin, 1969a, b; Kawamura, 1972) use girth measurements and ratios of mesh perimeter and body girth (perimeter/girth ratios) to estimate gillnet selectivity. Sechin's model was based on the assumption that all fish are fully selected whose maximum girth is greater but gill girth smaller than the mesh perimeter. Within the length class, the maximum and post-operculum girth were assumed to be normally distributed with a constant standard deviation.

$$S_{(ij)} = \phi \left(\frac{2m_i - K_{gil}G_{gil_i}}{\sqrt{\sigma_{gil_i}^2 + \sigma_{m_i}^2}} \right) * \left[1 - \phi \left(\frac{2m_i - K_{max}G_{max_i}}{\sqrt{\sigma_{max_i}^2 + \sigma_{m_i}^2}} \right) \right] \qquad (6)$$

A polynomial expression which approximates the integral of the normal probability distribution with a maximum error of $7.5 * 10^{-8}$ (Rohlf and Sokal, 1981) was used as an approximation for the cumulative normal distribution function. The standard deviation of each mesh size was assumed to be approximately zero in high quality machine-made nets. The standard deviations of both maximum and gill girth were expected to increase with the girth of the fish, as was reported for G_{max} by Kawamura (1972).

A constant coefficient of variation in body girth was assumed, contradicting Sechin's assumption of constant variance of girth. The mean and standard deviation of maximum and gill girth were calculated for each size class (0.5 cm), resulting in coefficients of variation for each length class and for both girths. The mean coefficient of variation was calculated for both girths over the length ranges where sufficient numbers of fish were available.

Length-girth relationships were modelled with a power function.

$$G_{pos} = a_{pos} * L^{b_{pos}} \qquad (7)$$

Coefficient and exponent were calculated for all species and the two girth positions by means of linear regression after natural log transformation. A t-test (Sokal and Rohlf, 1969) was used to test for which species and girths the exponent in the length-girth relationship was significantly ($\alpha < 0.05$) different from 1 (allometric growth). The average of maximum and gill girth, based on recordings from individual fish, was used as an estimate for the girth at the middle position. Length-girth relationships were used to estimate mean girths per length class (mm) and mean coefficients of variation were used to estimate the standard deviation in the girth. These estimated means and standard deviations of girth were used as input in the extended Sechin model.

The perimeter/girth ratio or K value, which quantifies the compressibility at retention girth, can be estimated from individual measurements on mesh perimeter and girth at mesh mark (Kawamura, 1972; Clarke and King, 1986; Ehrhardt and Die, 1988; Reis and Pawson, 1992).

$$K_{pos} = \frac{mesh\ perimeter\ of\ the\ retaining\ mesh\ (mm)}{girth\ at\ retention\ position\ (mm)} \qquad (8)$$

In the present study, data on the common position of retention (the most common

position in which a certain species is caught in the mesh), individual length-girth measurements and optimum mesh sizes (best mesh to catch fish of a certain size) per species were used in an indirect estimation of K values. The perimeter of the optimum mesh size ($2*m_{opt}$) can be calculated as the girth at the common position of retention (G_{pos}) multiplied by the K value for that position (K_{pos}).

$$2 * m_{opt} = G_{pos} * K_{pos} \tag{9}$$

Optimum mesh sizes (m_{opt}) were calculated for each species and length class (L) using the selection factor (k) from Holt's model.

$$m_{opt} = L / k \tag{10}$$

The K value at the most common position of retention was estimated by plotting $2L/k$ against the girth at this position for individual fish. These plots were expected to approximate straight lines through the origin with perimeter/girth ratios at the common position of retention (K_{pos}) as the slopes.

$$2 * L / k = K_{pos} * G_{pos} \tag{11}$$

In the present study it was assumed that perimeter/girth ratios were independent of mesh size.

For species commonly caught gilled, the calculated K_{gil} value was used in Sechin's model. The average K_{gil} value over all these species was used as the K_{gil} for all other species. K_{max} values were calculated for those species caught wedged at the maximum girth. Calculated K_{mid} values were assumed to be good estimates for K_{max} (Clarke and King, 1986) in species caught at the middle position. Therefore the average K_{mid} value was used as an estimate for K_{max} in species which were caught gilled. The two species normally caught wedged at maximum girth were highly compressible and therefore their average K_{max} value was not used for other species.

The maximum efficiency of estimated selection curves was assumed to be 1 for each mesh size. To compare estimated Sechin curves with Holt curves and catch LFD, the value of L_{opt}/m (similar to selection factor k) and the coefficient of variation of the Sechin selection curve were calculated for the largest sample of each species.

A method for rapid estimation of the selection curve

The most common position of retention, perimeter/girth ratio's (K values) at retention position and approximated length-girth relationships were used to derive a method for rapid estimation of the selection factor k. The position of retention in gillnets is important when K values are estimated, since compressibility in the bony area of the gill girth is less than around the maximum girth (Ehrhardt and Die, 1988; Winters and Wheeler, 1990). Values of perimeter/girth ratios can only be used for nets of similar elasticity. It was assumed, as in the extended Holt model, that the selection curve approximates a normal distribution with a constant coefficient of variation, which is equal for the non-tangled catch of all species

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in the present study. The maximum efficiency of the selection curve was assumed to be 1 for all mesh sizes.

Length-girth relationships can be combined with equation (11) to estimate the selection factor k.

$$2 * L / k = K_{pos} * a_{pos} * L^{b_{pos}}$$ (12)

$$k = 2 / (K_{pos} * a_{pos} * L^{b_{pos}-1})$$ (13)

In this model the selection factor k is dependent on fish length, since length/girth ratios are changing with fish length (allometric growth). The expression for k was simplified by making it independent of length. It was assumed that the length-girth relationship can be approximated by a linear function through the origin, with c_{pos} as proportionality factor, since b_{pos} is always very close to 1. Values for c_{pos} were calculated from linear regressions of G_{pos} on L.

$$G_{pos} = c_{pos} * L$$ (14)

The maximum relative deviation (D_c), caused by linear approximation of the length-girth relationship, was calculated for all species over the length range as caught during the present study. The selection factor k_{new} was estimated from two variables.

$$k_{new} = 2 / (c_{pos} * K_{pos})$$ (15)

The optimum selection length was calculated from the estimated selection factor (equation 2). A constant coefficient of variation was assumed for the selection curve which is described by a normal distribution. This coefficient of variation was assumed equal for all species and calculated as the mean over a range of species. The standard deviation was calculated from the optimum selection length and the constant coefficient of variation. The selection curve was estimated with equation (1). The variance in selection lengths is assumed to be explained partly by a variance in girth among fish of the same length-class and partly by variance in the position and girth of retention.

K values should be calculated from measurements on mesh sizes and retention girths (equation 8). In the present study K values were estimated indirectly, using k values from the Holt model as input (equation 11). Consequently the estimates of K were not independent of k (Holt) and the model could not be evaluated by comparison of k_{new} with k values from the Holt model. The model was therefore tested with data from the literature by comparing k_{new} values with values for L_{opt}/m. Values for c_{pos} were calculated by using modal lengths as input in length-girth relationships from the literature.

Comparison of selection curves with catch LFD

Estimating gillnet selectivity from catch *LFD* would be feasible when the fish population contained equal numbers of fish per size class. Such a population can be approximated by

considering a short section of the length range at a position where population numbers are most stable. At this position catch *LFD* should be accumulated over a long period of time to smoothen the effect of temporary peaks in abundance for certain length classes (Reis and Pawson, 1992). Catch *LFD* should preferably be used from mesh sizes in the middle of a range of sizes which all produced fish at the sampling site. The smallest mesh sizes may correspond with length ranges where abundance increases with length when juveniles recruit to the sampling site (Garrod, 1961; Sparre *et al.*, 1989; Pet and Piet, 1993). The largest mesh sizes correspond with length ranges where abundance decreases rapidly with length. Tangling percentages will also be lowest in mesh sizes from the middle of the range. In the present study, a selected number of mesh sizes per species yielded catch *LFD* that met with the above mentioned demands and could therefore be used to compare with estimated selection curves.

To compare selection curves with catch *LFD*, those two mesh sizes per species were used which represented the largest samples. The L_{opt}/m from the catch *LFD* was compared with the selection factor k or L_{opt}/m from selection curves. The coefficients of variation from selection curves and catch *LFD* were also compared.

Comparison of estimated selectivity with commercial catch LFD

Our experimental gillnets were made of monofilament twine. The commercial fishery uses nets made of the less expensive multifilament twine. Experimental fishing on *O. mossambicus* was carried out with commercially used red multifilament nets to enable extrapolation of selectivity estimates. A mesh size of 58 mm stretched mesh was used, which is below the range of commercially used mesh sizes. All vulnerable size classes of *O. mossambicus* were assumed equally available to this sampling gear. Catch *LFD* were accumulated for several months and the modus was used as an estimate for the optimum selection length. This estimated optimum selection length was compared with the estimated optimum length in monofilament nets.

Comparison of selectivity by species and estimation method

The selectivity to different species was compared by plotting estimated optimum sizes of selection per species on the mesh sizes as used in the present study. Optimum selection sizes were expressed both in total length and in girth at the common position of retention. Retention girths were calculated from optimum selection lengths using equation (7). Comparisons were made according to the extended Holt and Sechin models.

Hamley (1975) indicated the possibility of using a mean ratio of maximum body girth and mesh perimeter, to roughly estimate the modus of the selection curve independent of fish species.

$$G_{max} = 2 * m * K_{mn} \tag{16}$$

He noted a mean ratio K_{mn} of 1.25 at optimum selectivity over a range of species, ranging from 1.08 to 1.35 according to different authors. In this model the K_{mn} value is calculated for the maximum body girth, irrespective of the position of retention, and it is the inverse

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ratio of K values used in the present study.

Analogue to Hamley's method, an overall girth/perimeter ratio (K_{mn}) was calculated which could be used independent of fish species to calculate the optimum retention girth for a specific mesh size.

$$G_{pos} = 2 \ast m \ast K_{mn} \qquad (17)$$

The extended Holt and Sechin models were compared by plotting the estimated selection ranges (size ranges which are selected with 50% efficiency or more) according to each method on the mesh sizes. Consequences for the reconstruction of population structures were evaluated by means of the inverted selection curves for the total range of mesh sizes. The overal selection curves were calculated for both models as the sum of selection curves for individual mesh sizes with a maximum efficiency of 1. The inverted selection curves represent the required correction factors for reconstruction of the population structure from catch *LFD*.

Results

Estimation of gillnet selectivity

Plots of *-2a/b* on $(m_1 + m_2)$ show how the selection factor k in the Holt model can be calculated from catches in multiple mesh sizes (Fig. 4.1). The assumption of a constant coefficient of variation for selection curves estimated by the extended Holt model is validated by plots of $(\sigma_1 + \sigma_2)$ on $(L_{opt1} + L_{opt2})$, which approximate straight lines through the origin with overall coefficients of variation as the slopes (Fig. 4.2).

The assumption of a constant coefficient of variation in girth, in the extended Sechin model, is validated by plots of standard deviation on mean girth per length class, which approximate straight lines through the origin for at least six out of ten cases (Fig. 4.3). Coefficients of variation in girth show values between 5.78% and 10.32% (Table 4.3). The highest values were found for species with smallest maximum size.

All regressions of girth on length (Table 4.3) were significant ($\alpha < 0.001$) after natural log transformation. Most of the exponents in length-girth relationships were significantly ($\alpha < 0.05$) different from 1. All but one species obtained relatively larger girths with increasing length. The girth of *O. mossambicus* becomes relatively smaller with increasing length. Linear approximations of length-girth relationships (Table 4.4) show close fit with the data for all species (Fig. 4.4). The maximum relative deviation in predicted girth is always below 5% when the linear approximation is used (Table 4.3).

Plots of *2L/k* on G_{pos} show that the perimeter/girth ratio in the Sechin model can be estimated indirectly from individual girths and estimated optimum mesh sizes (Fig. 4.4). Perimeter/girth ratios are always smaller at maximum girth than at gill girth (Table 4.4).

All cyprinids, except *R. daniconius,* were commonly caught wedged with the mesh in between the maximum and gill girth (Table 4.4). *R. daniconius* was usually caught gilled. *G. giuris* and *H. gaimardi* were usually caught wedged with the mesh at maximum girth. Catfish (*Mystus* spp.) and tilapia (*Oreochromis* spp.) were commonly caught gilled.
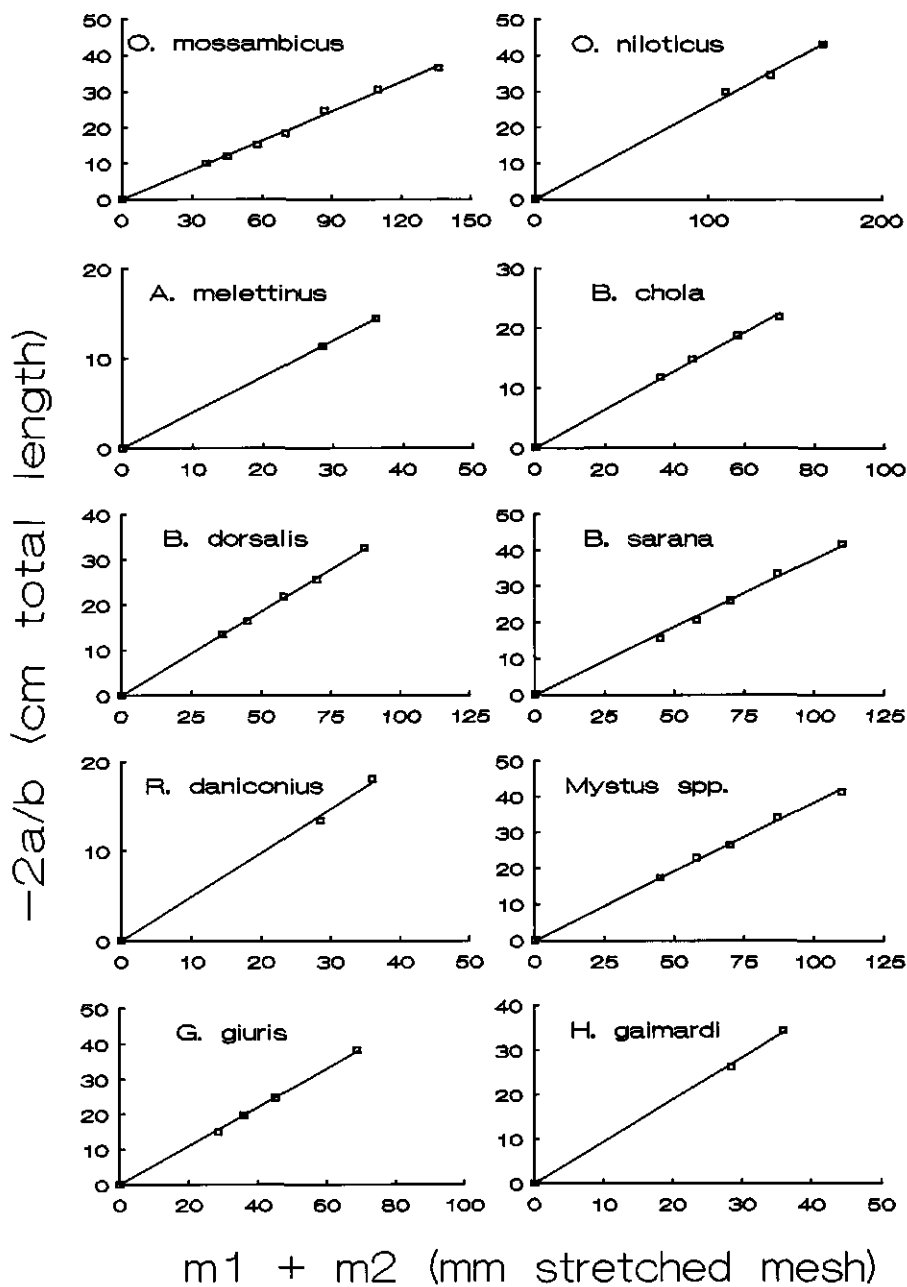
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Fig. 4.1. Plots of *-2a/b* on $(m_1 + m_2)$ per species, for the estimation of selection factors k according to the Holt model.
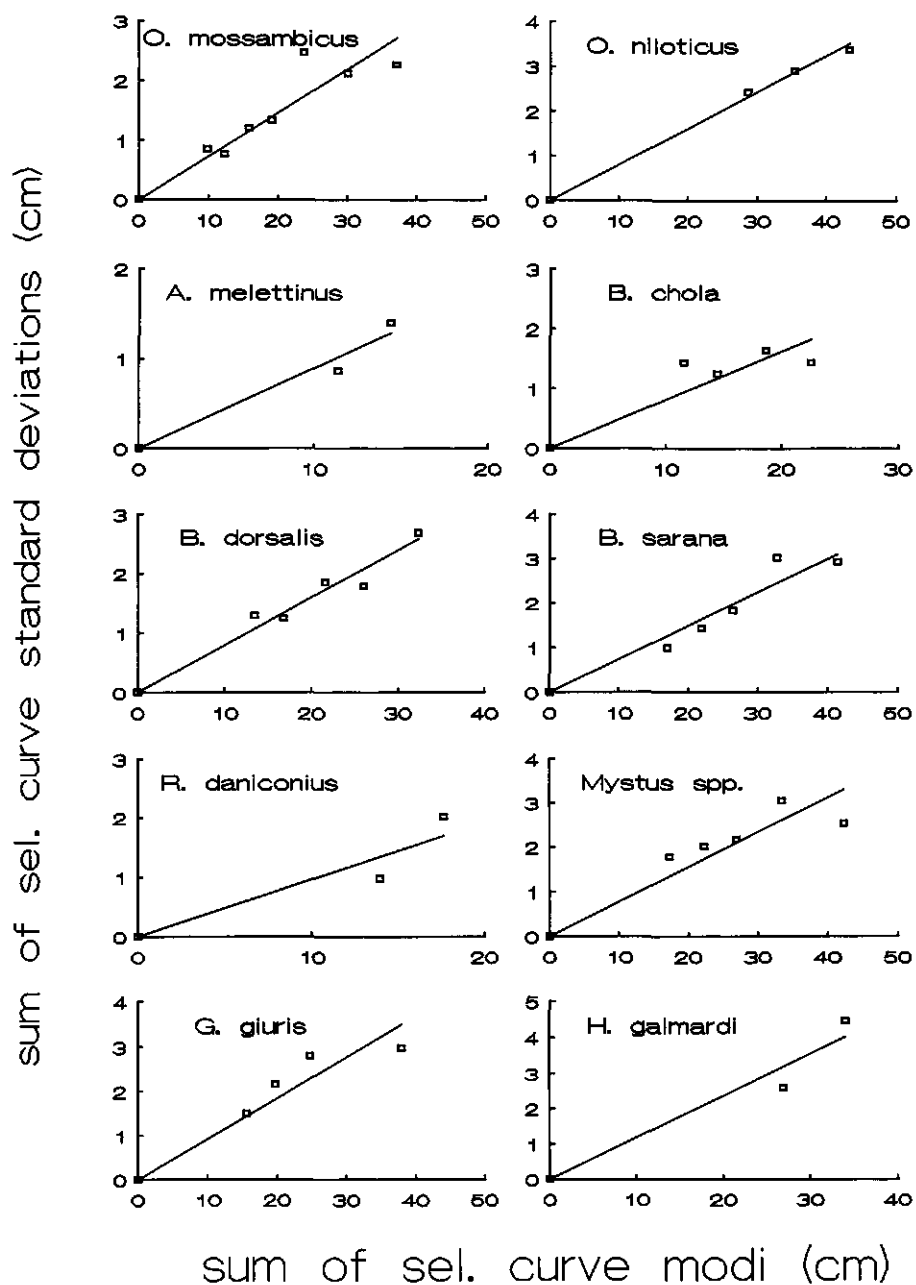
Fig. 4.2. Plots of $(\sigma_1 + \sigma_2)$ on $(L_{opt1} + L_{opt2})$, showing a constant coefficient of variation in Holt selectivity curves.
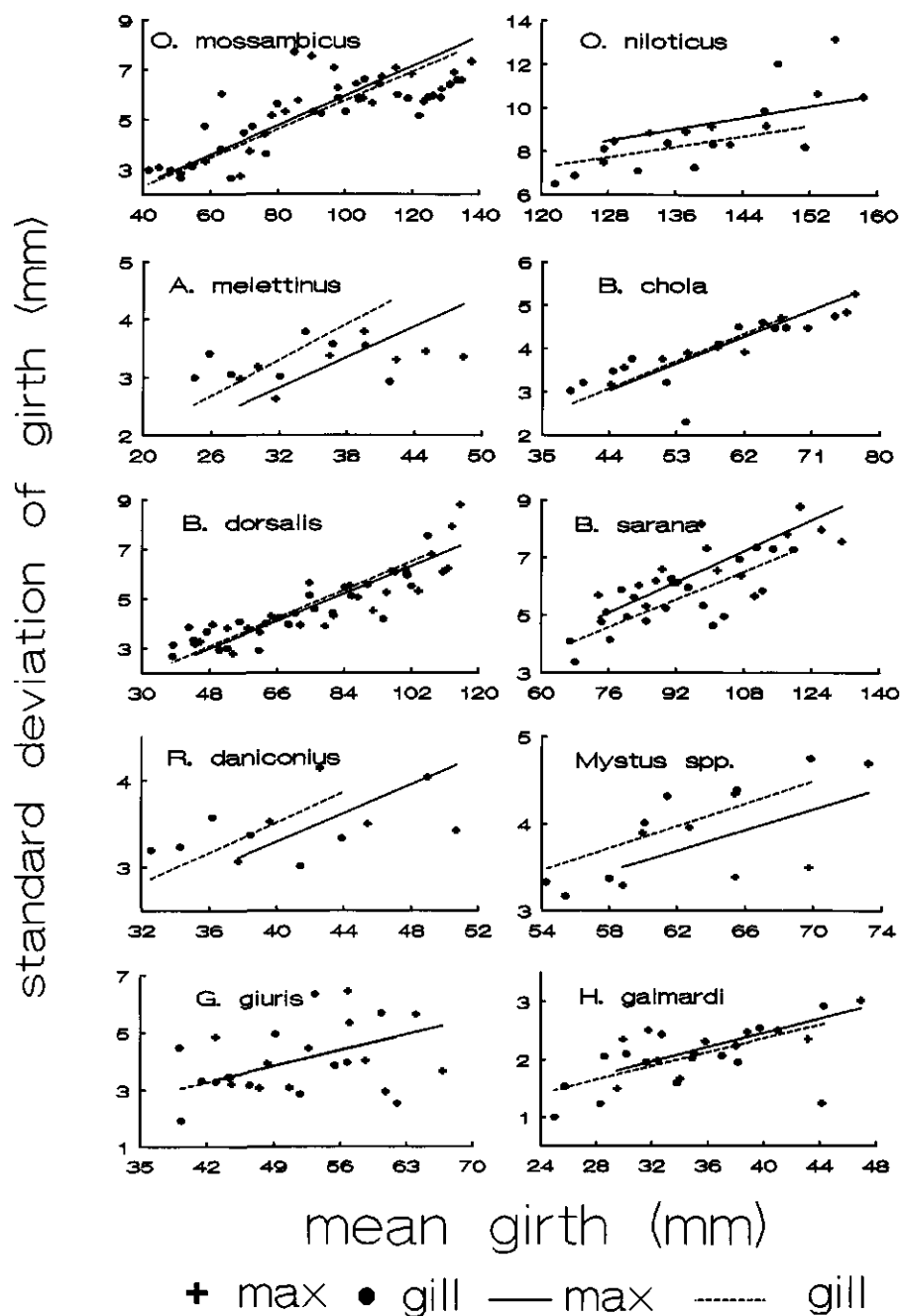
Fig. 4.3. Plots of recorded and estimated standard deviation on mean girth per length class for maximum and gill girth. Lines indicate the estimated standard deviation based on constant coefficients of variation in body girth.
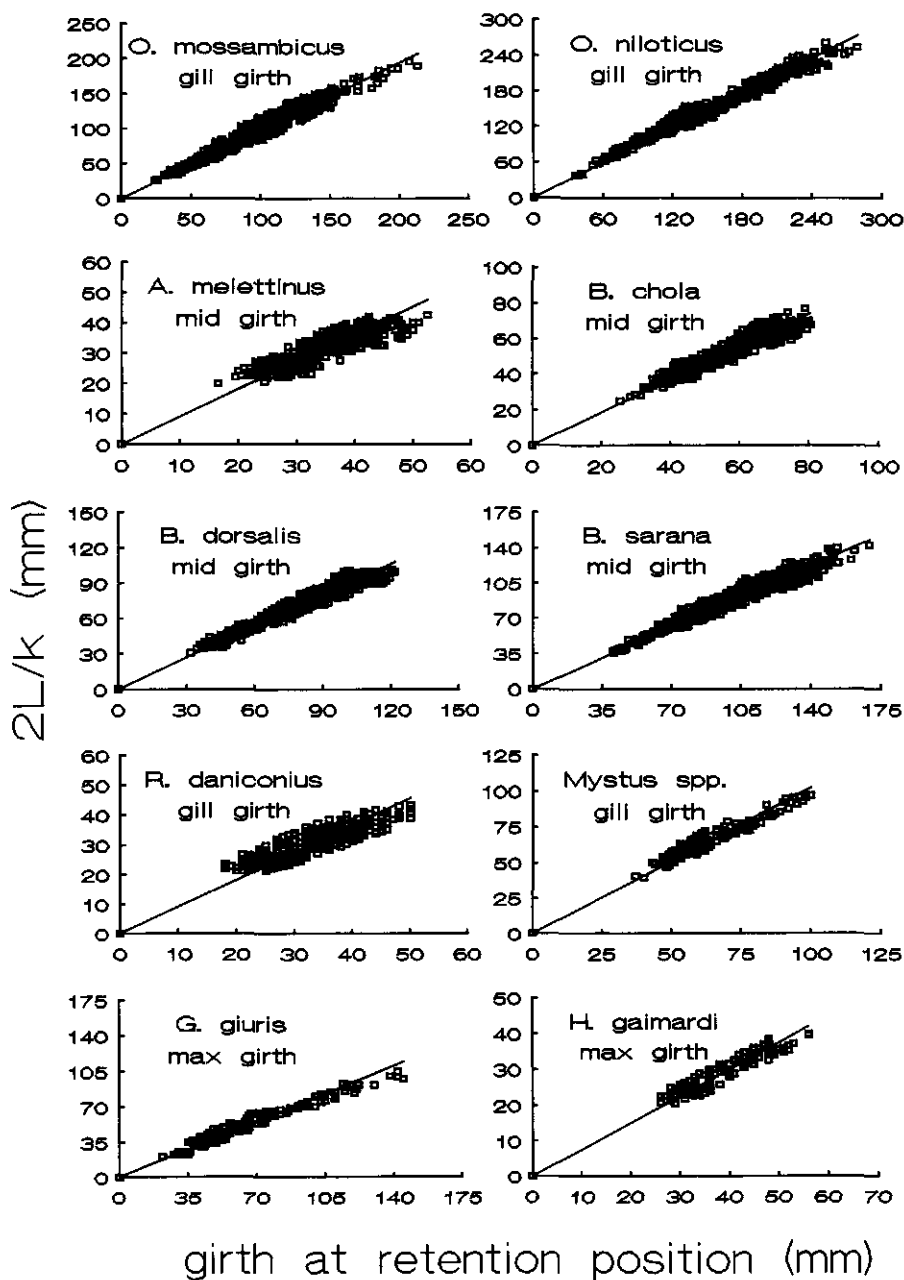
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Fig. 4.4. Plots of *2L/k* on girth at retention position. These plots are used to calculate ratios of mesh perimeter and body girth.

Table 4.3. Sample sizes, length-girth relationships and coefficients
of variation in girth per species.

species[*]	n	maximum girth			gill girth		
		a_{max}	b_{max}	cvG_m	a_{gil}	b_{gil}	cvG_g
OM	2192	9.073	0.944[s]	5.97	7.916	0.980[s]	5.78
ON	573	7.174	1.039[s]	6.63	6.653	1.050[s]	6.03
AM	537	5.662	1.017	8.82	4.347	1.083[s]	10.32
BC	553	6.651	1.032[s]	6.89	6.122	1.008	7.00
BD	945	6373	1.001	6.20	4.703	1.071[s]	6.38
BS	893	5.750	1.034[s]	6.68	5.340	1.027[s]	6.02
RD	496	4.124	1.109[s]	8.24	3.577	1.102[s]	8.79
MY	172	4.628	1.062[s]	5.95	3.968	1.095[s]	6.41
GG	196	4.072	1.036[s]	7.85	3.232	1.096[s]	7.81
HG	138	2.477	1.047	6.16	1.769	1.136[s]	5.92

[*]Species abbreviations as in Table 4.1, other abbreviations in Table 4.2. Girths in mm,
lengths in cm. [s]Exponent in length-girth relationship significantly ($\alpha < 0.05$) different
from 1.

Table 4.4. Common position of retention for non-tangled fish, tangling
percentages, perimeter/girth ratios and constant in linear
approximations of length-girth relationships with maximum
relative deviation (%) of the predicted girth.

species[*]	pos	tan%	K_{pos}	K_{max}	K_{gil}	c_{pos}	D_c
OM	gil	5.5	0.974	0.898	0.974	7.499	2.5
ON	gil	5.5	0.982	0.898	0.982	7.779	2.6
AM	mid	0.5	0.905	0.905	0.973	5.485	1.8
BC	mid	4.3	0.924	0.924	0.973	6.695	1.4
BD	mid	8.9	0.889	0.889	0.973	6.047	3.2
BS	mid	3.4	0.873	0.873	0.973	6.075	3.1
RD	gil	2.7	0.915	0.898	0.915	4.428	3.3
MY	gil	25.6	1.022	0.898	1.022	5.081	4.9
GG	max	48.6	0.790	0.790	0.973	4.572	4.9
HG	max	3.9	0.749	0.749	0.973	2.812	1.4

[*]Species abbreviations as in Table 4.1, other abbreviations in Table 4.2.

Tangling percentages were below 10%, except for gobies (*G. giuris)* and catfish (*Mystus*
spp.). They were lowest for mesh sizes which yielded the largest samples (Table 4.1) and
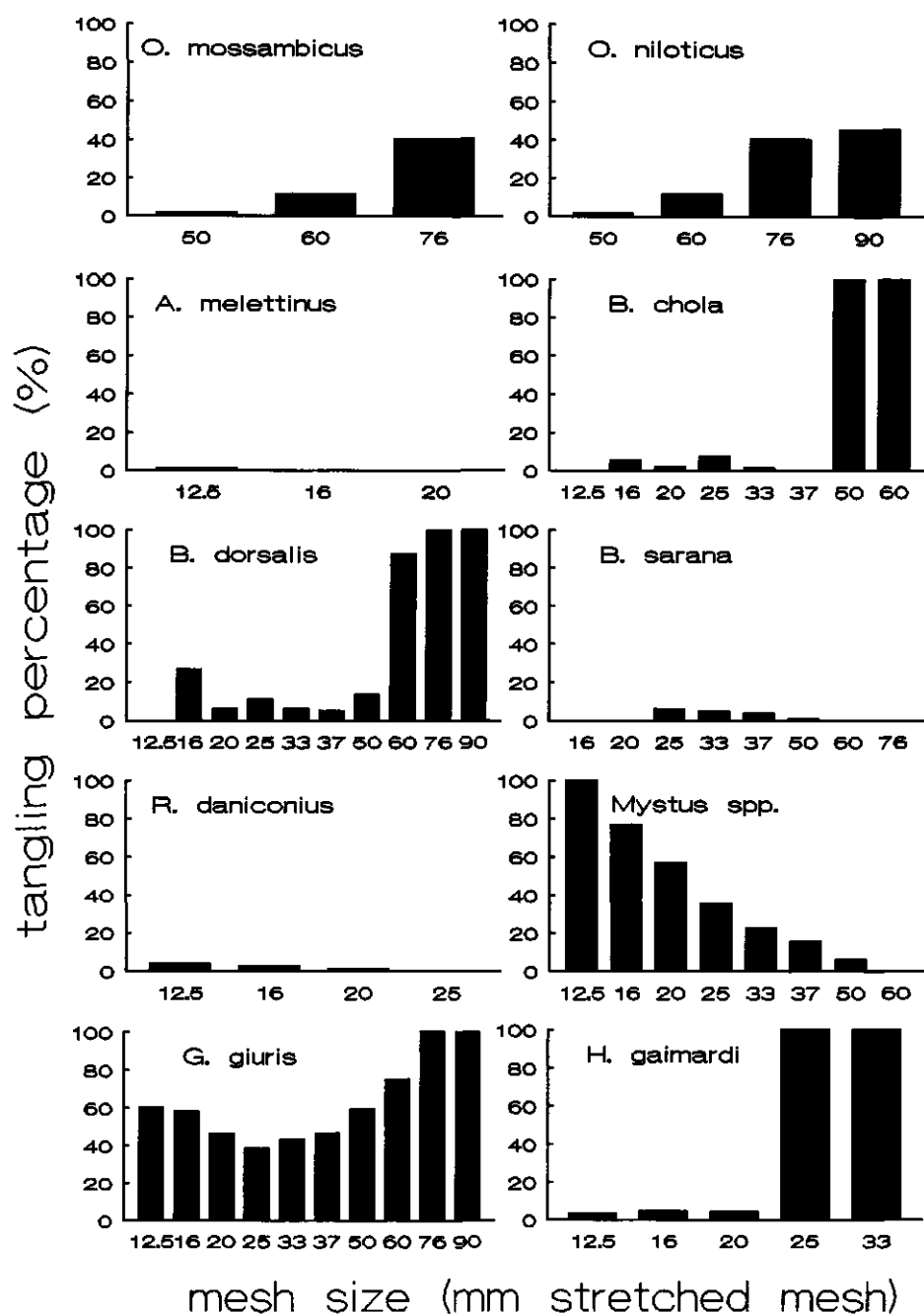for mesh sizes in the middle of the range (Fig. 4.5).

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Fig. 4.5. Tangling percentages per species and mesh size.

Comparison of selection curves with catch LFD

The results of the extended Holt and Sechin models were summarized and compared with *LFD* of catches for the two largest samples per species (Table 4.5). The estimated selection curves show close fit with recorded catch *LFD* (Fig. 4.6). The width of Holt curves and catch *LFD* are very similar in most cases and coefficients of variation are usually close to 9% of the optimum selection length. A similar relative width of indirectly estimated selection curves over ranges of species has been reported previously by Hamley (1975) and Jensen (1986). The Sechin curves are more narrow in general and show a slight positive skewness in a few cases. The catch *LFD* are not systematically positioned to the left or right of the selection curves. In most cases the Holt curves show the best fit with catch *LFD*, although the differences are small.

Table 4.5. Selection factor and coefficient of variation from selection curves compared with selection factor and coefficient of variation from the largest samples in the catch *LFD*.

species[*]	m	k Holt	L_{opt}/m S	L_{opt}/m C	cv H	cv S	cv C
OM	50	0.273	0.278	0.270	7.3	5.9	6.8
ON	50	0.261	0.272	0.270	8.1	5.8	6.8
AM	12.5	0.400	0.392	0.400	8.9	10.7	6.5
BC	25	0.322	0.316	0.300	8.1	7.8	10.5
BD	33	0.371	0.358	0.348	8.0	6.6	9.7
BS	50	0.376	0.356	0.370	7.5	6.1	7.9
RD	16	0.489	0.463	0.500	9.8	9.8	7.4
MY	33	0.384	0.397	0.379	7.8	5.3	7.4
GG	20	0.550	0.530	0.525	9.2	7.2	16.4
HG	12.5	0.945	0.880	0.800	11.8	5.3	10.1
mean					8.7	7.1	9.0

[*]Species abbreviations as in Table 4.1, other abbreviations in Table 4.2.

Catch *LFD* of the commercially important tilapia species are normally distributed for most mesh sizes, although the catch *LFD* of *O. mossambicus* in 37 mm stretched mesh shows some positive skewness. Catch *LFD* of cyprinid species were normally distributed for most mesh sizes. For *G. giuris*, which shows a very high tangling percentage, the catch *LFD* shows a clear positive skewness and the calculated coefficient of variation is much higher than in other species. Some of the cumulated catch *LFD* of *G. giuris* in the smallest mesh sizes appear to be bimodal (Fig. 4.7), where the second mode comprised fish which were caught by the teeth and maxillae.

The newly proposed method for rapid estimation was tested using data on Pacific herring (Kawamura, 1972), Atlantic herring (Clarke and King, 1986) and Spanish mackerel (Ehrhardt and Die, 1988).
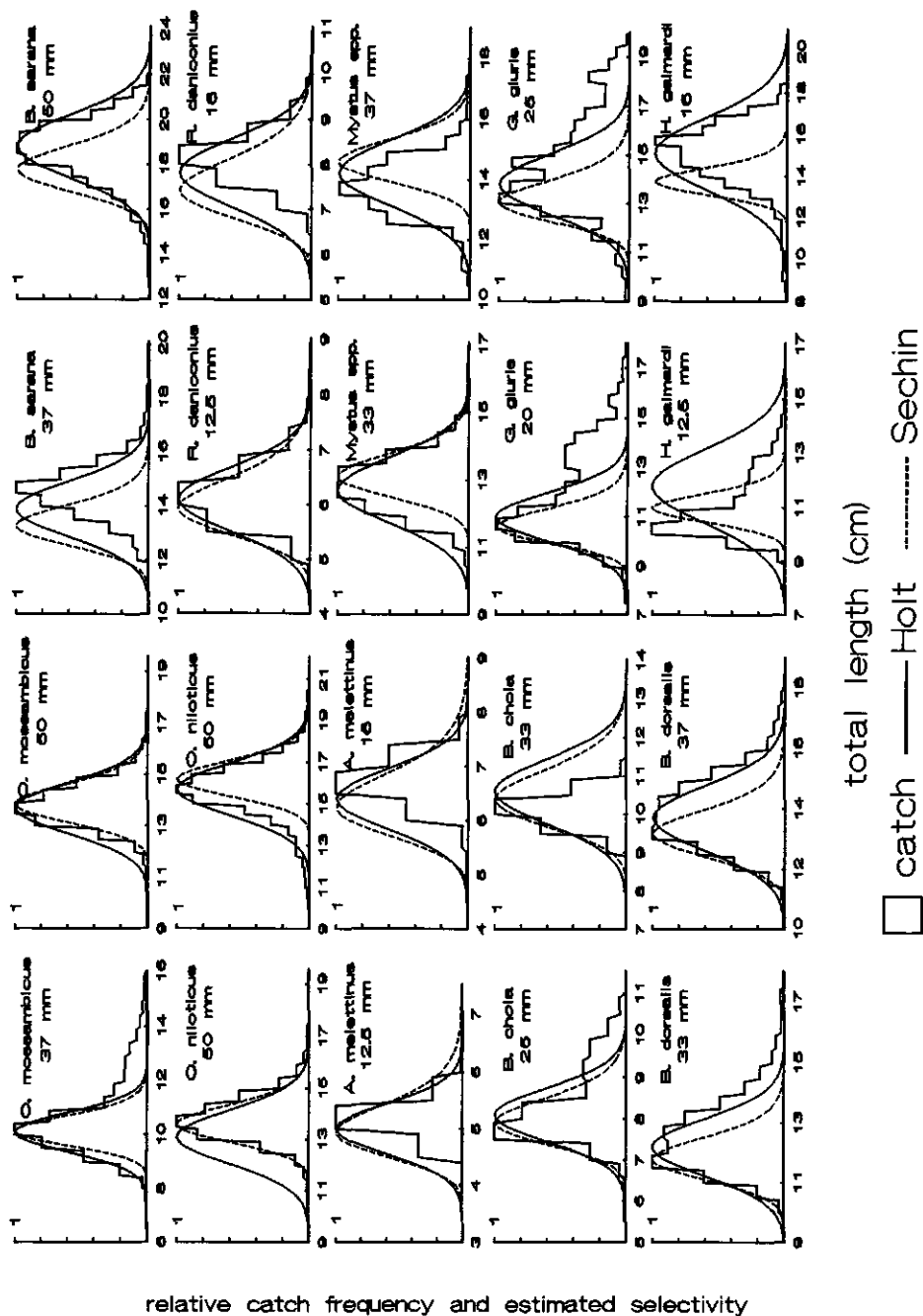
Fig. 4.6. Catch length frequency distributions compared with selectivity curves estimated with the extended models of Holt and Sechin.
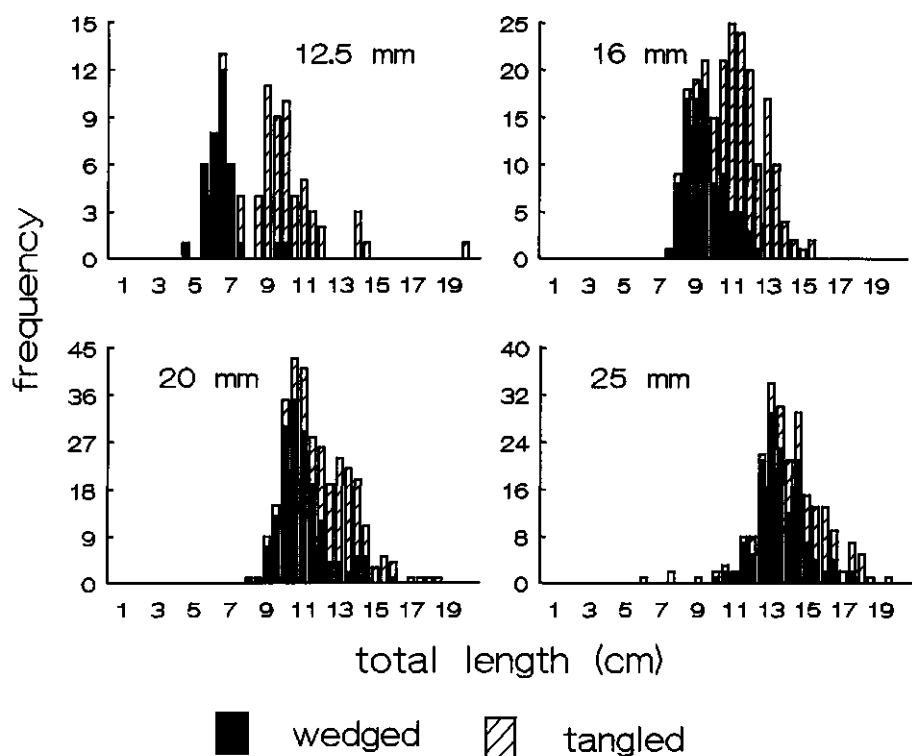
Fig. 4.7. Tangling percentages and bimodality in the catch length frequency distributions of *Glossogobius giuris* (Hamilton).

Table 4.6. Estimated length-girth relationships, perimeter/girth ratios and selection factors according to our new method compared with data from literature on herring and Spanish mackerel.

species[*]	sex	pos	c_{pos}	K_{pos}	k_{new}	L_{opt}/m
Pacific herring		mid	4.892	0.903	0.453	0.446-0.476
Atlantic herring	f	mid	4.184	0.947	0.505	0.505-0.506
	m	mid	4.208	0.950	0.500	0.500-0.501
Spanish mackerel		mid	4.220	0.975	0.486	0.484-0.500

[*]Authority: Pacific herring, Kawamura (1972); Atlantic herring, Clarke and King (1986); Spanish mackerel, Ehrhardt and Die (1988). Abbreviations in Table 4.2.

Above mentioned authors used the related methods of Sechin (1969a, b) and Kawamura (1972) to calculate the shape and position of the selection curves. Values for c_{pos}, K_{pos} and L_{opt}/m (Table 4.6) were calculated from the above mentioned data sets. K_{max} was used as

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a good estimate for K_{mid} (Clarke and King, 1986) when necessary. Estimated selection factors according to the proposed model were very similar to the values of L_{opt}/m from the respective data sets. Coefficients of variation in the selection curves from all above mentioned data sets were close to 9%.

Comparison of estimated selectivity with commercial catch LFD

The optimum selection length of *O. mossambicus* ($n = 61$) in the catch *LFD* of 58 mm stretched mesh multifilament nets was 14.0 cm. This is 10% below the estimated optimum length of 15.5 cm for monofilament nets, using a selection factor of 0.273.

Comparison of species and models

Grouping of species with comparable morphology was apparent when optimum selection lengths were plotted on mesh sizes (Fig. 4.8). All species came together when the girth at the common position of retention was used as the independent variable. A rough estimation of the retention girth could be calculated from equation (16), using a girth/perimeter ratio K_{mn} of 1.05, independent of fish species. This equation is an improvement compared to the method presented by Hamley (1975) for rough estimation of the selection curve optimum.
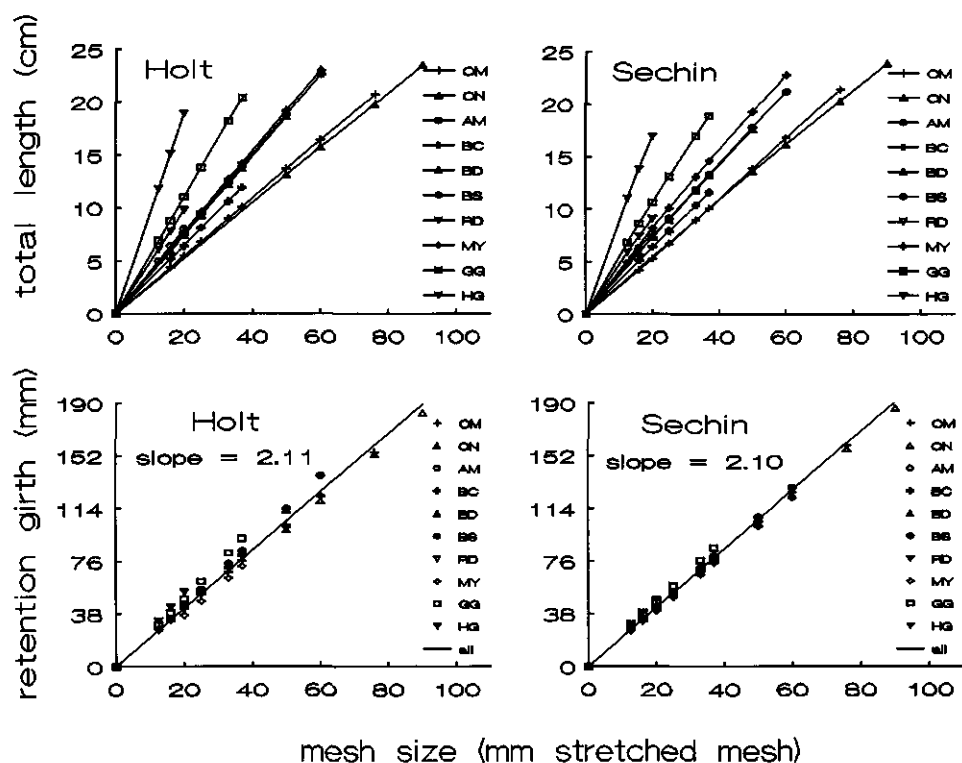

Fig. 4.8. Optimum selection lengths and girths at most common position of retention per mesh size.

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For most species the selection curves according to the Holt and Sechin models showed similar positions on the length axis (Fig. 4.6). The most evident difference between the two models was that Sechin selection ranges were more narrow than Holt ranges (Fig. 4.9). Sechin ranges were also more narrow than ranges in catch *LFD* and relative catch frequencies higher than 50% were recorded outside Sechin selection ranges in several cases. This had consequences for the reconstruction of population structures, when the inverse of the overall selection curve was used as a correction factor. The Sechin model resulted in an overestimation of correction factors since Sechin curves underestimated the selectivity in between two mesh sizes. Overall selection curves constructed from Sechin curves showed deeper and wider gaps than those constructed from Holt curves. For *O. mossambicus* the correction factor could differ a factor 5 between the two models (Fig. 4.10). A correct choice of mesh sizes minimized the required correction factors. Therefore some of the mesh sizes in the present study were changed after August 1992.

Discussion and conclusions

Factors affecting gillnet selectivity: 1. Morphology and compressibility

In the present study a range of morphologically different species has been studied with respect to the selectivity of gillnets. Variance in morphology within species should be taken into account when selection curves are estimated. Girths may vary among fish of the same length and species due to different condition, sex, stage of maturity and amount of food in the gut (McCombie and Berst, 1969; Hamley, 1975; Van Densen, 1987). In the present study, all data were pooled over a long period of time and different habitats. Coefficients of variation in girth may be overestimated in the smallest species since the relative error in girth measurement increases with decreasing length. This increasing relative error makes it difficult to observe a constant coefficient of variation in girth for small species.

Length-girth relationships and cumulated catch *LFD* changed only during extreme low water levels and very high fish density in August 1992. *O. mossambicus* showed a very poor condition in that month, which partly explains the positive skewness in the catch *LFD* of 37 mm stretched mesh (Fig. 4.6). A large number of fish were caught in that month, which all had a very small girth in relation to their length. This is regarded as an exceptional situation and the catch *LFD* of tilapia will be assumed to be normally distributed (Garrod, 1961). Condition may be of greater importance in systems where food availability is more variable (Van Densen, 1987; Winters and Wheeler, 1990).

The length-girth relationships resulting from the present study differ from those reported by De Silva and Sirisena (1987). For all species and length classes their results produced girths which were less than half the size observed in the present study. Therefore it was assumed that they describe maximum body depth instead of girth. Amarasinghe (1988) reports a relationship between length and maximum body depth of *O. mossambicus* which confirms this assumption.

All morphological features mentioned above were of minor importance compared to spines, teeth and other parts which cause high tangling percentages in gillnet catches.
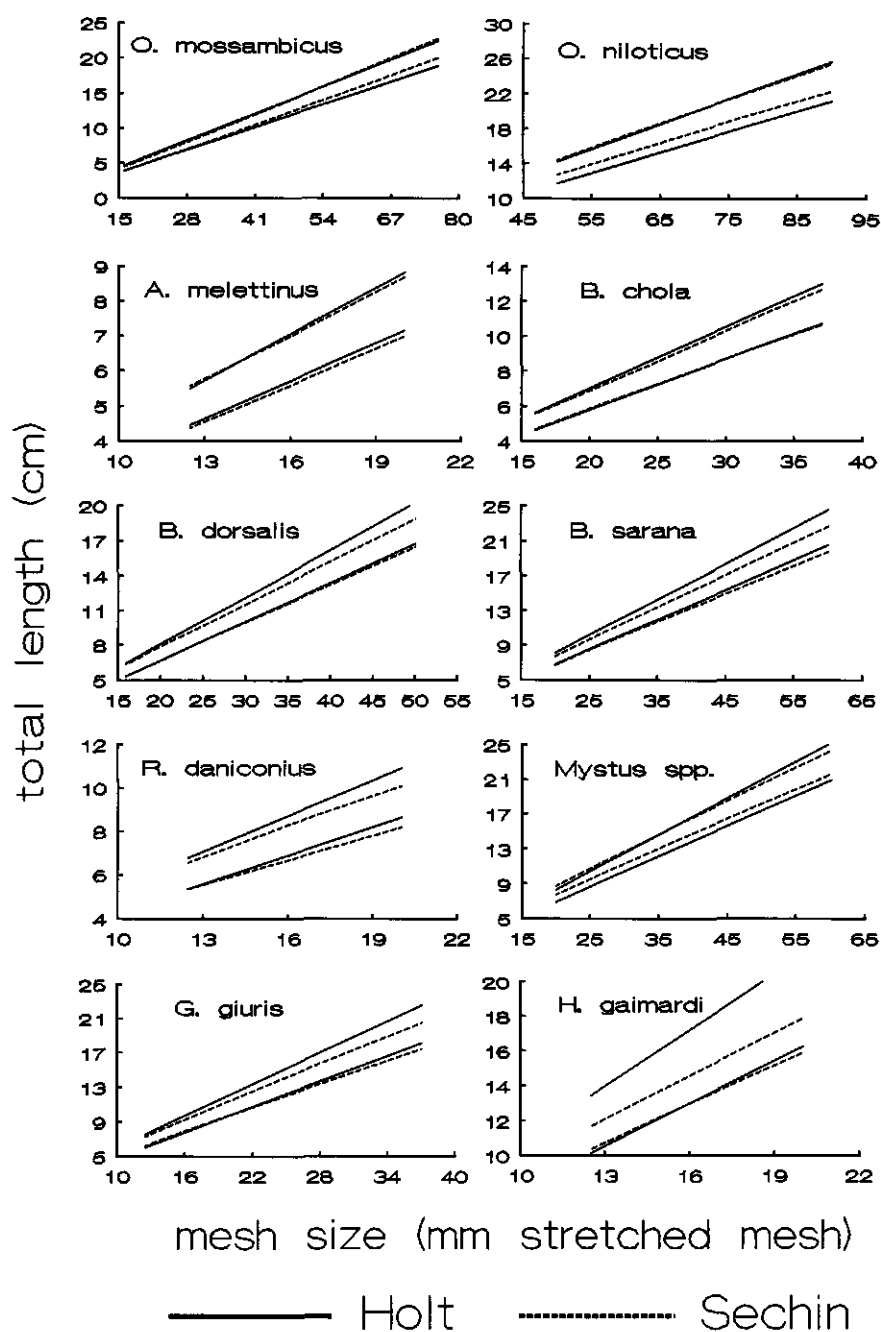
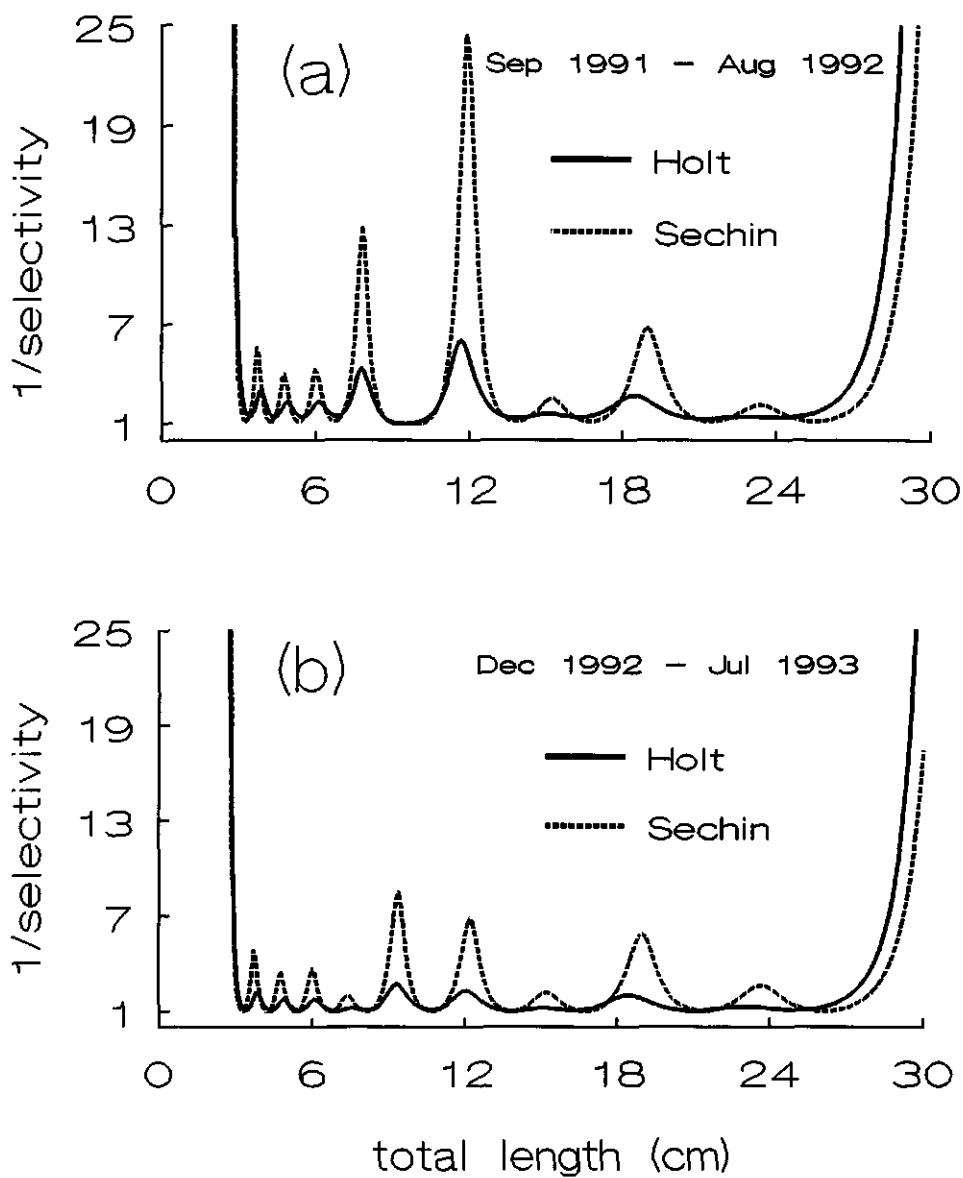Fig. 4.9. Selection ranges for all species in the present study.

Fig. 4.10. Inverted overall selection curves for *O. mossambicus* according to the extended Holt and Sechin models for two combinations of mesh sizes: (a); 12.5, 16, 20, 25, 33, 37, 50, 60, 76 and 90 mm stretched mesh, (b); 12.5, 16, 20, 25, 30, 39, 50, 60, 76 and 92 mm stretched mesh.

Bimodal catch *LFD* of small mesh sizes for spiny and toothy fish have been recorded in this study for *G. giuris* and were described earlier for walleye (Hamley and Regier, 1973) and pikeperch (Van Densen, 1987).

Coefficients of variation were expected to be higher in catch *LFD* than in estimated selection curves, due to the presence of tangled fish. This effect is limited in the samples used for comparison in the present study. For species which are not spiny or toothy, tangling is only important in the largest mesh sizes. The tangling percentage of *Mystus* spp. may be overestimated in the present study, since this spiny fish often becomes entangled in the net, even if it was initially caught gilled.

Each species of fish is retained in the net in a specific way, depending on its morphology. Elongated fish (*G. giuris* and *H. gaimardi*) are usually caught with the mesh around the maximum girth. Fish are caught gilled when deeper body shapes, bony structures or fat abdomens (*O. mossambicus, O. niloticus, M. gulio, M. vittatus* and *R. daniconius*) prevent the mesh to slip further over the body. Fish with medium tapered body shapes and/or large scales (*A. melettinus, B. chola, B. dorsalis* and *B. sarana*) are usually caught with the mesh in between the maximum and gill girth.

Differences between species are very small when the retention girth is chosen as the independent variable in gillnet selectivity. An estimation of the girth at the common position of retention, independent of fish species, could be obtained from the overall relationship with the mesh size.

$$G_{pos} = 2 * m * 1.05 \tag{18}$$

Sechin's method has sometimes been used with perimeter/girth ratios assumed equal to 1 (Reis and Pawson, 1992). In the present study length-girth measurements and optimum mesh sizes were used to calculate K_{pos} values. Clarke and King (1986) assumed K_{max} to be equal to K_{mid} and they estimated K_{gil} as $1-(1-K_{max})/5$. This method yields values close to the average values used in the present study (Table 4.4). The K_{gil} value for *Mystus* spp. is greater than 1. The girth just behind the wide and hard gills of this species is somewhat less then on top of the gills and a mesh size larger than the gill girth is needed to catch these fish in a gilled position. The *K* values in the present study were lower at maximum girth than at gill girth, which confirms earlier reports on this subject (Ehrhardt and Die, 1988; Winters and Wheeler, 1990). The estimation of selection curves according to the extended Sechin model was repeated with *K* values equal to 1. This resulted in a systematic decrease in the estimated optimum selection lengths with 3.9% to 12.0% over the range of species. The mean deviation of estimated optimum selection lengths with *K*=1 was -7.1%.

Factors affecting gillnet selectivity: 2. Behaviour

A constant maximum efficiency was assumed for all mesh sizes in the present study, although gillnet efficiency was reported to increase with the mesh size in direct estimations (Hamley and Regier, 1973; Hamley, 1975). Decreased efficiency with increasing mesh size was reported as a result of decreasing swimming distances with increasing size of brown trout (Borgström and Plahte, 1992). A correction method was proposed (Rudstam *et al.*,

1984), based on the assumption that net efficiency is a result of encounter probability which is a function of routine swimming speed. Swimming speed was expressed as a power function of fish length, L^n. The n values for species in the present study are not known. A 0.8% and 3.0% shift in k and a 0.4% and 1.6% increase in σ were found when selection curves for pikeperch were corrected using n values for cisco and walleye respectively (Van Densen, 1987).

A size-dependent habitat preference will have major effects on the catch LFD when only a limited part of the available habitats is covered in the sampling program. Size-dependent habitat preference was shown to exist for all species in the present study (Pet and Piet, 1993). All but one (the shallowest) habitat in the reservoir were fished with equal effort. Samples from small mesh sizes are absent when juvenile fish are absent or rare in those sampling sites (Table 4.1). For this same reason the catch LFD of *B. sarana* in 37 mm stretched mesh is positioned to the right in comparison to the selection curves.

Factors affecting gillnet selectivity: 3. Position of the net in the water column

When gillnets are not fully stretched, the amount of tangled fish will increase. This happened in August 1992, when water depth was less than net depth. Next to the above mentioned influence of lowered condition, this is probably a second reason for the positive skewness of the catch LFD of *O. mossambicus* in 37 mm stretched mesh. Catches during high water level showed normally distributed catch LFD and relatively few tangled fish.

Factors affecting gillnet selectivity: 4. Net material and hanging coefficient

The perimeter/girth ratio K and selection factor k are dependent on the elasticity of the net material. Relatively large fish are expected in nets with a small twine diameter (Hansen, 1972), which need less power to be stretched. Larger meshes are made of thicker twine with lower elasticity, but larger fish are caught which are assumed to be proportionally stronger. A small increase in perimeter/girth ratios with increasing mesh size was reported for Atlantic herring caught in multifilament gillnets (Winters and Wheeler, 1990). K values for Spanish mackerel did not show a clear trend with mesh size (Ehrhardt and Die, 1988). K values were assumed to be independent of mesh size in another study on Atlantic herring (Clarke and King, 1986) and in the present study.

Commercial multifilament nets were estimated to select 10% smaller fish than monofilament nets, which can be explained by a lower elasticity of multifilament nets. The mean length of cod in 159 mm multifilament nets was around 10% below the mean length in 151 mm monofilament nets (Stewart, 1987). Size distributions were similar for multi- and monofilament nets for a range of species when thick twine (0.23 mm) was used over a range of mesh sizes (Collins, 1979; Henderson and Nepszy, 1992).

A low hanging ratio of the gillnet was reported to result in a higher tangling percentage (Riedel, 1963; Mohr, 1965; Sparre *et al.*, 1989) and broader selection curves. This effect was also evident for bream (*Abramis brama* L.) but not for pikeperch (*Stizostedion lucioperca* L.) (Machiels et al., 1994).

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Comparison of methods for the estimation of gillnet selectivity

Selection curves derived by the extended Holt model showed closest resemblance with the catch *LFD*, where Sechin curves are more narrow. Reis and Pawson (1992) reported good fit of Sechin curves to catch *LFD* but they had no information on perimeter/girth ratios and assumed them equal to 1. They assumed gill girths to equal $0.75*G_{max}$, although a higher value for the proportionality factor is evident for many species (Table 4.3). Differences between G_{max} and G_{gil} are small in many species, also in *O. mossambicus* (Riedel, 1963; this study). This results in narrow Sechin curves. Catch *LFD* show that the actual selection curves are broader. Wider curves are expected for species with greater differences between G_{max} and G_{gil}, such as the bream (*Abramis brama*, L.) which Sechin used to test his model (Sechin, 1969b).

A rapid estimation of gillnet selectivity can be obtained from a small sample of fish with different lengths, caught with a single mesh size. Data required are common position of retention, a linear approximation of the length-girth relationship and perimeter/girth ratio at the position of retention. The selection curve is assumed to be shaped as a normal distribution and the standard deviation is estimated by taking a mean coefficient of variation of 9% over a number of species.

Optimum selection lengths were similar for the extended Holt and Sechin models but 10% to 20% lower than those reported by De Silva and Sirisena (1987). Both models are only suitable for species with tangling percentages below 10%. Selection ranges from Sechin curves were more narrow than those from Holt curves. The difference in selection range width results in an over-estimation of the required correction factors when population structures are reconstructed by means of inverted Sechin selection curves. Therefore Holt curves are more suitable for the reconstruction of population *LFD* than Sechin curves.

Acknowledgements

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Chapter 5

Management options for a more complete utilization of the biological fish production in Sri Lankan reservoirs

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Abstract

Stock dynamics of the introduced tilapia *Oreochromis mossambicus* and co-occurring indigenous cyprinids were studied in a typical lowland reservoir in Sri Lanka. All species exhibited recruitment peaks during the rainy seasons in November and May. *O. mossambicus* was estimated to grow to 14 cm in its first year and to 21 cm in its second. A high instantaneous natural mortality (M) was found for the cyprinids ($M = 1.3$ yr^{-1} to 4.7 yr^{-1} over a range of species) and for *O. mossambicus* ($M = 1.9$ yr^{-1} and 1.7 yr^{-1} for females and males respectively). The instantaneous fishing mortality (F) of *O. mossambicus*, estimated for the length range from 15.0 to 18.5 cm, was also high with $F = 5.5$ yr^{-1} for females and $F = 4.7$ yr^{-1} for males. The total fish biomass was estimated at 1 829 kg/ha, with 128 kg/ha *O. mossambicus* and 1 098 kg/ha small pelagic cyprinids, mainly *Amblypharyngodon melettinus*. The total biological fish production was around 5 400 kg/ha/yr, with *O. mossambicus* and the small pelagic cyprinids accounting for 400 kg/ha/yr and 3 600 kg/ha/yr respectively. The commercial fishery yielded 242 kg/ha/yr (mainly *O. mossambicus*), indicating an incomplete utilization of the total biological fish production. It was concluded that there is scope for an approximately 100% increase of this yield. Re-implementation of a 76 mm minimum mesh size, to prevent overfishing of *O. mossambicus*, should be the first priority measure. Additional options are direct exploitation of the untapped resource of small pelagic cyprinids, or indirect exploitation by means of a culture-based fishery on *Lates calcarifer*, a controllable predator.

Introduction

The fish communities in Sri Lankan reservoirs are characterized by small adult sizes of the most important species which largely feed directly on phytoplankton and detritus (De Silva, 1988; Schiemer & Duncan, 1988; Pet & Piet, 1993). The major groups in terms of biomass and numbers are the indigenous riverine cyprinids and the introduced lacustrine tilapia *Oreochromis mossambicus* (Peters). The commercial reservoir fishery targets mainly *O. mossambicus*, using 64 to 100 mm stretched mesh gillnets (De Silva, 1988). Mesh sizes have been declining in recent years, even below the minimum mesh size of 76 mm stretched mesh, with possibly growth overfishing as a result (Amarasinghe, 1988a; Pet *et al.*, in press a). The reservoir fishery presently yields around 270 to 300 kg/ha/yr (De Silva, 1988), which is high for this type of fishery in the tropical region (Oglesby, 1985). It has been suggested however, that yields can still be increased considerably by exploitation of presently untapped resources (De Silva & Sirisena, 1987, 1989; Sirisena & De Silva, 1988, 1989). Large stocks of small indigenous cyprinids are targeted in a proposed additional fishery with fine meshed gillnets. Detailed information on ecology and stock dynamics of all important species is needed before the results of any management measure can be predicted.

Quantitative predictions about the reactions of fish populations to alternative management options are the basic concern of fish stock assessment studies (Gulland, 1983; Sparre *et al.*, 1989; Hilborn & Walters, 1992). Analytical yield models are used to select management options which ensure maximum sustainable yield from fish stocks. Growth, recruitment and mortality are important input parameters in these models, but are often difficult to estimate for fish stocks from tropical regions (Pauly & Murphy, 1982; Sparre *et al.*, 1989) although length-based methods are available (Pauly & Morgan, 1987; Gulland & Rosenberg, 1992). Length-based methods however, should be supported with reliable information on recruitment patterns and, whenever possible, with some information on length at age (Macdonald & Pitcher, 1979).

Size distributions of commercial catches have been used in earlier studies to assess growth and mortality parameters of *O. mossambicus* in Sri Lankan reservoirs (Amarasinghe, 1987; De Silva *et al.*, 1988; Amarasinghe *et al.*, 1989) and recruitment peaks were reported to occur during the rainy seasons (De Silva & Chandrasoma, 1980; De Silva, 1983). Several cyprinid species were reported to migrate upstream from the reservoirs into the rivers for spawning (Silva & Davis, 1986) and reproduction periods have been reported to coincide with the rainy seasons (Chandrasoma & De Silva, 1981; De Silva, 1983; De Silva *et al.*, 1985). This kind of ecological information, however, has not been used as extra input in the assessment of stock dynamics. Recruitment patterns, in studies on growth and mortality, are usually presented as output of length-frequency analyses, instead of input parameters which can be used to define the starting points of growth curves. Fisheries mortality was commonly estimated after calculating the natural mortality with an empirical formula, without any consideration of the ecological characteristics of the system. The lack of integrated ecological information seems to be a general character of recent stock assessment studies from tropical regions (Yap, 1984; Amarasinghe, 1987; De Silva *et al.*, 1988;

Amarasinghe *et al.*, 1989; De Silva, 1991; Getabu, 1992).

In the present study, the scope for increased fisheries yield in a Sri Lankan reservoir is estimated on the basis of a length-based stock assessment, supported by ecological information and direct ageing. This ecological information consists of recruitment patterns on the basis of temporal dynamics in gonado-somatic index (*GSI*) and larval abundance, temporal patterns in juvenile abundance and direct estimates of natural mortality for unexploited species. Integration of the ecological information leads to an upgraded use of the length-based methods. The feasability of the proposed exploitation of minor cyprinids is discussed on the basis of estimated biomass and production of different species (-groups).

Materials and methods

Study area, fishery and data collection

Data for the present study were collected in Tissawewa during a two year period from September 1991 to July 1993. Tissawewa is a typical irrigation reservoir in the south eastern lowland of Sri Lanka, with a mean surface area of 195 ha and a mean maximum depth of 2.55 m since January 1987 (Pet *et al.*, in press a). Maximum depth and surface area fluctuations follow the patterns in rainfall. Two monsoon periods occur annually in the southern and eastern lowland of Sri Lanka. The major rainy season is during the north east monsoon around November and a minor peak in rainfall occurs during the south west monsoon around May (Fig. 5.1a).

Information from the first year (September 1991 to August 1992) was used to estimate growth, recruitment and mortality parameters. The situation had changed drastically after a drought in September 1992, which may have influenced growth, recruitment and/or distribution patterns. After the drought, the water had become very clear with Secchi disc depths of 150 to 200 cm compared 30 to 50 cm in the period before the drought. Secchi disc depths of 30 to 50 cm are normal for this type of reservoir. Immediately after water levels had risen in November 1992, there was a strong development of macrophytes which were not present before. The first year, September 1991 to August 1992, was a representative year in terms of environmental factors (Fig. 5.1a & 5.1b).

The commercial fishery in Tissawewa is typical for Sri Lankan reservoirs, with gillnets fished from outrigger canoes as the most important gear. A normal fishing trip includes one or two fishermen who are setting two gillnets of about 225 m long, usually during the night. The most common mesh sizes are 64, 70 and 76 mm stretched mesh, used in a ratio of 4:4:1. During the study period, the mean catch per trip (one night) was around 14 kg and the annual yield from this reservoir was 242 kg/ha with 65% contribution of *O. mossambicus* (Pet *et al.*, in press a). The commercial fisheries were sampled during 4 days each month in the first year and during 2 days per month in the second year.

The six species for which data were collected during the study period include one introduced tilapia, *O. mossambicus*, and five indigenous riverine cyprinids, *Amblypharyngodon melettinus* (Valenciennes), *Barbus chola* (Hamilton), *Barbus dorsalis* (Jerdon), *Barbus sarana* (Hamilton) and *Rasbora daniconius* (Hamilton).
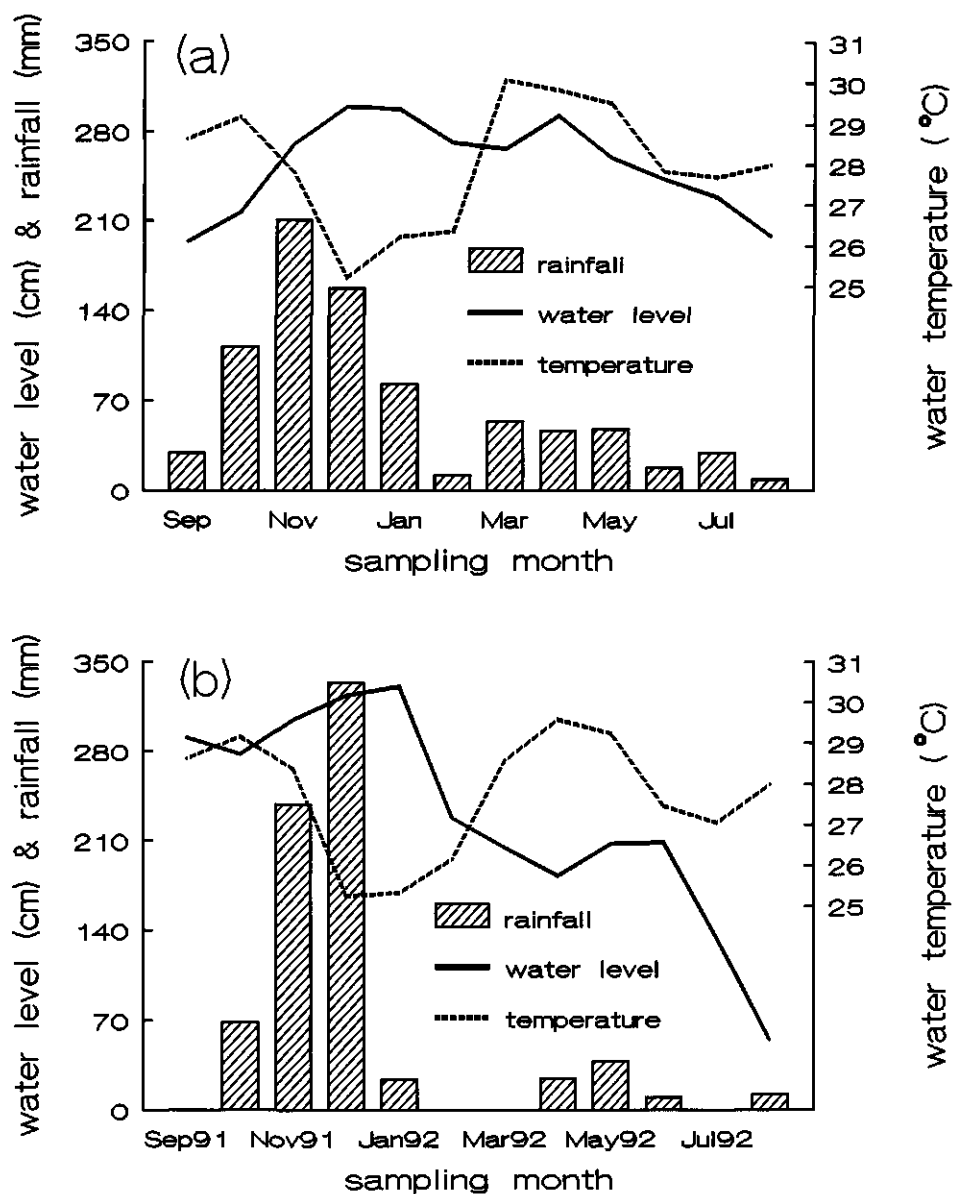
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Fig. 5.1. Mean water level and rainfall from January 1987 to August 1993 and mean water temperature from September 1991 to August 1993 (a). Water level, rainfall and water temperature from September 1991 to August 1992 (b).

Experimental fishing was carried out with 480 meters of gillnet, containing 10 different mesh sizes ranging from 12.5 to 90 mm stretched mesh (Pet & Piet, 1993; Pet *et al.*, in press b). The nets were set 4 times each month, twice during the day and twice at night, at 4 different stations. Nets with mesh sizes from 12.5 to 37 mm were set for 2 hours, while larger mesh sizes, up to 90 mm, were standing for 12 hours each setting. Additional fishing was carried out with a fine meshed scoop net to sample fish larvae.

All abbreviations used in the text, in tables and/or in figures are listed in Table 5.1.

Table 5.1. Abbreviations.

B	=	biomass (kg)
B_{mn}	=	mean biomass in the reservoir (ton)
f, m	=	female, male
F	=	instantaneous fishing mortality (yr^{-1})
FP, FY	=	biological fish production, fisheries yield
GSI	=	gonado-somatic index (%)
K	=	Von Bertalanffy growth constant (yr^{-1})
L	=	total length, length class (cm)
$LFD(A)$	=	length frequency distribution (analysis)
L_{inf}	=	theoretical length at infinite age (cm)
L_{mat}	=	length at which 95% of females (or 50% in case of *Oreochromis mossambicus*) reaches maturity stage 4
M, M_p	=	instantaneous natural mortality, M according to Pauly's empirical formula (yr^{-1})
n	=	sample size
N_C, N_{mn}	=	total number in catch, mean number in population
P	=	productivity (kg/ha/yr)
PG, PN	=	gross and net primary productivity (kgC/ha/yr)
R	=	starting date of growth curve in November & May
Sp	=	species
t	=	time (years)
W	=	weight of individual fish (g)
Y_{tot}	=	mean annual yield from the reservoir (ton/yr)
Z	=	instantaneous total mortality (yr^{-1})

Identification of recruitment patterns

Patterns in recruitment were identified on the basis of geometric mean *GSI*, gonad development stage and larvae abundance. A maximum of 24 fish per 0.5 cm length class per species was dissected during each fishery-independent (experimental fishery) sampling session. A sample of around 400 *O. mossambicus* and all available *B. sarana*, irrespective of size, were weighed and dissected during each fishery-dependent (commercial fishery) sampling session. These larger fish were not sufficiently available in fishery-independent samples. The gonads of each dissected fish were weighed and categorized according to their development stage (Tables 5.2 & 5.3). For cyprinid species, females were regarded mature above the length where at least 95% of the individuals had reached maturity stage 4 or higher. Stage 4 is the stage to which females return after spawning and it corresponds with

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Table 5.2. Maturity stages of female *Oreochromis mossambicus*.

1.	Immature, impossible to distinguish females from males. Gonads are a pair of transparant strings running along body cavity wall.
2.	Unmistakably female, ovary very small, transparant reddish, r und and thicker than in 1, eggs not visible.
3.	As 2, but small white eggs are visible in transparant matrix.
4.	Eggs larger and yellow, filling the ovary, ovary also larger.
5.	Eggs very large and yellow, still fixed in matrix. ovary covering ca. 25% of body cavity wall.
6.	As 5, but eggs loose in ovary. They can be extruded from the body by putting pressure on the abdomen.
7.	Spent. Wrinkled ovary, transparent-reddish, containing a few yellow eggs.

Table 5.3. Maturity stages of female cyprinids.

1.	Immature, impossible to distinguish females from males. Gonads are a pair of transparant strings running along body cavity wall.
2.	Unmistakably female, ovary very small, tube shaped and reddish, eggs not visible.
3.	Ovary somewhat larger and starting to flatten sideways, eggs visible but very small.
4	larger ovary, flattened sideways and almost covering body cavity wall, eggs yellowish.
5.	Large and full ovary, completely covering body cavity wall. Yellowish eggs run out when ovary is cut.
6.	Running, yellow eggs can be extruded by putting pressure on the abdomen.
7.	Spent. Wrinkled ovary, reddish, containing a few yellow eggs.

the development stage for which *Barbus* spp. in Sri Lanka were considered to reach maturity (De Silva *et al.*, 1985). For *O. mossambicus* females, the length at 50% stage 4 was used since insufficient numbers were available above 95%. Seasonal patterns in gonad development were described with the geometric mean *GSI* of mature females and the proportion of females in stage 6 (running). A specific site in the littoral zone was sampled biweekly with a scoop net to identify peaks in fish larvae abundance, a third indicator for reproductive activity. This sampling station was chosen after it was established that larvae were always present there, if anywhere in the reservoir.

Estimation of growth parameters

Growth parameters for *O. mossambicus* and other species were estimated from the temporal dynamics in length frequency distributions (*LFD* analysis or *LFDA*), which were obtained from fishery-independent sampling with gillnets. *LFD* from experimental gillnets were corrected for fishing effort (duration and panel length) and selectivity per mesh size. The extended Holt model (Pet *et al.*, in press b) was used for the estimation of gillnet

selectivity. Monthly *LFD* were split into sexes on the basis of monthly sex ratios per 0.5 cm length class. The patterns in sex ratios per length class were smoothed by taking the running average over 5 length classes, and used to establish differences in L_{inf} between sexes. Maximum sizes attained per species and per sex were used as a starting estimate for L_{inf} in the Von Bertalanffy growth curves. Peak spawning seasons were identified and used as the fixed starting points of growth curves. The growth constant K was estimated by forcing the curves through temporary peaks in absolute abundance of specific size classes and by following the shifts in peaks of relative abundance where possible. The ELEFAN (Gayanilo et al., 1989) and LFDA (Holden & Bravington, 1992) packages were used to fit growth curves under conditions as mentioned above. Dissection data from both fishery-independent and fishery-dependent surveys were used to calculate constants and coefficients in length weight relationships ($W=a*L^b$) for all species and both sexes.

Otoliths were taken from 10 female and 10 male *O. mossambicus* to use in a direct estimation of length at age. These otoliths were examined on daily growth rings (In 't Veld, 1993). Sagittal coups of 100 μm were obtained after grinding wax-embedded otoliths on 40, 15 and 5 μm grinding disks. After grinding, the otoliths were glued on glass slides, the wax was removed and the coups were polished with diamond paste of 10, 1 and 0.1 μm. The grinded and polished sagittal coups of otoliths were photographed (Kodak Technical Pan film) under a light microscope (20* magn.) and the total number of daily growth rings was counted from the photographs. Total ring counts were corrected for material loss at the margins due to grinding of the coups. Macro structures or annuli were not observed.

Estimation of mortality

LFD from experimental gillnets were used to apply length converted catch curve analysis (Pauly, 1983, 1984a, b) for all cyprinid species. For these species the estimated total mortality was equal to the natural mortality since they are not exploited, except for the largest size classes of female *B. sarana*. Natural mortality of female *B. sarana* was estimated from the value for males, based on differences in growth and mortality between sexes of the other cyprinids. Estimated natural mortality values for all species were compared with values computed from Pauly's empirical formula (Pauly, 1980), which relates natural mortality to the growth parameters in combination with water temperature for a large number of fish stocks.

Total mortality of *O. mossambicus* was estimated by means of catch curve analysis with fishery-dependent data. The catch *LFD* of the commercial fisheries was corrected for gillnet selectivity on the basis of mesh sizes used and their relative frequency of occurrence. The selection factor of commercial multifilament gillnets was assumed to be 10% below the estimated factor for experimental monofilament nets (Pet *et al.*, in press b).

A length dependent mechanism in natural mortality was assumed to exist for all species. The relation between mean adult fish length and natural mortality in unexploited cyprinid species was used to estimate natural mortality for the exploited size classes of *O. mossambicus*.

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Stock assessment and production

The estimates for the standing stock of *O. mossambicus* were based on length-based cohort analysis (Jones, 1984). The total catch *LFD* of the commercial fisheries was reconstructed for the first year of the present study. The mean biomass of 10 to 19 cm *O. mossambicus* was estimated separately for males and females. The starting value of F/Z in the cohort analysis was chosen at such a level that the mean F corresponded with the F as estimated for the length range analysed by means of catch curve analysis. The resulting pattern in F per length class was compared with the estimated overall selection curve.

The standing stock biomass of *O. mossambicus*, over the full size-range, was based on the estimated biomass for 10 to 19 cm fish from cohort analysis and the overall size composition and total weight in experimental gillnet catches, after correction for fishing effort and selectivity (Pet & Piet, 1993). The standing stock biomass of cyprinid species was calculated on the basis of species composition in experimental gillnet catches and estimated biomass for the full size range of *O. mossambicus*.

P/B ratios were estimated on the basis of fish yield and natural mortality for *O. mossambicus*, assuming a steady state situation where total mortality equals production. Natural mortality was assumed to equal production in a steady state situation for unexploited cyprinids. Mean adult sizes were used to estimate P/B ratios for the group of other species on the basis of calculated ratios for tilapia and cyprinids.

Results

Recruitment patterns

Data on *GSI* and percentage of running females show clear peaks in spawning activity for all species, except *R. daniconius*, around November and May (Fig. 5.2). The fixed starting points of the growth curves (dates in November and May, *R* in Table 5.4) were based on these results. The total number of mature female *B. sarana* in the commercial catch dropped with 80% during the spawning seasons in November and May, indicating an emigration from the reservoir in these months. Based on the monthly mean number per 15 minutes scoop net fishing, *O. mossambicus* larvae were present throughout the year (Fig. 5.3a) but peak abundance occurred around November and May. An additional peak was observed in March 1992 but this was the result of a single high catch, probably caused by decreasing water levels (Fig. 5.1b) which forced fish larvae out of the littoral vegetation.

Growth parameters

Juveniles of all species show temporal peaks in abundance in experimental gillnet catches (Fig. 5.3a & 5.3b), which indicates the formation of cohorts. Peaks of different size classes of *O. mossambicus* show a clear sequence in time. The peak abundance of 5 cm fish in February/March ($t=0.28$ yr) and the peaks of 13 cm fish around September/October ($t=0.88$ yr) and March/April (Fig. 5.3a) were used for calibration of growth curves. Peak abundance of 16 cm *O. mossambicus* in January/February ($t=1.21$ yr) and July/August, as well as peak abundance of 20 cm fish in February/March and August/September ($t=1.79$ yr),
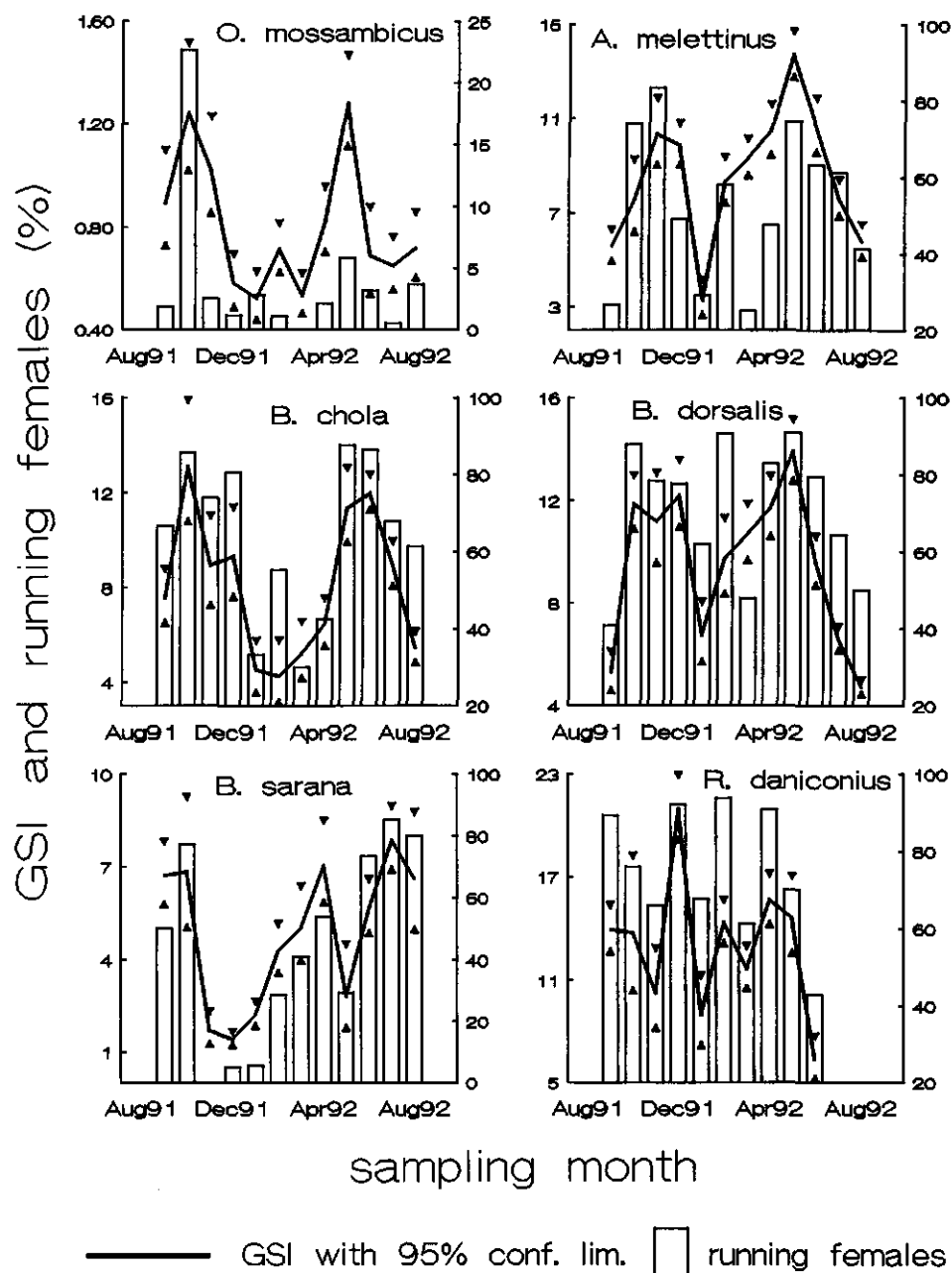
Fig. 5.2. Geometric mean gonado-somatic index (*GSI*) of females with 95% confidence limits and percentage of running females for *Oreochromis mossambicus* and five cyprinids from September 1991 to August 1992.
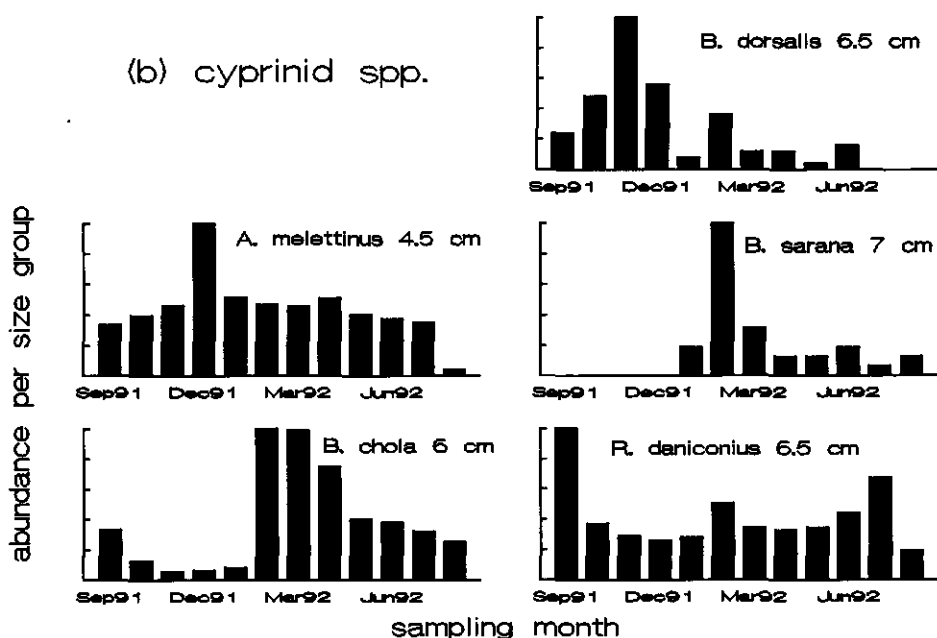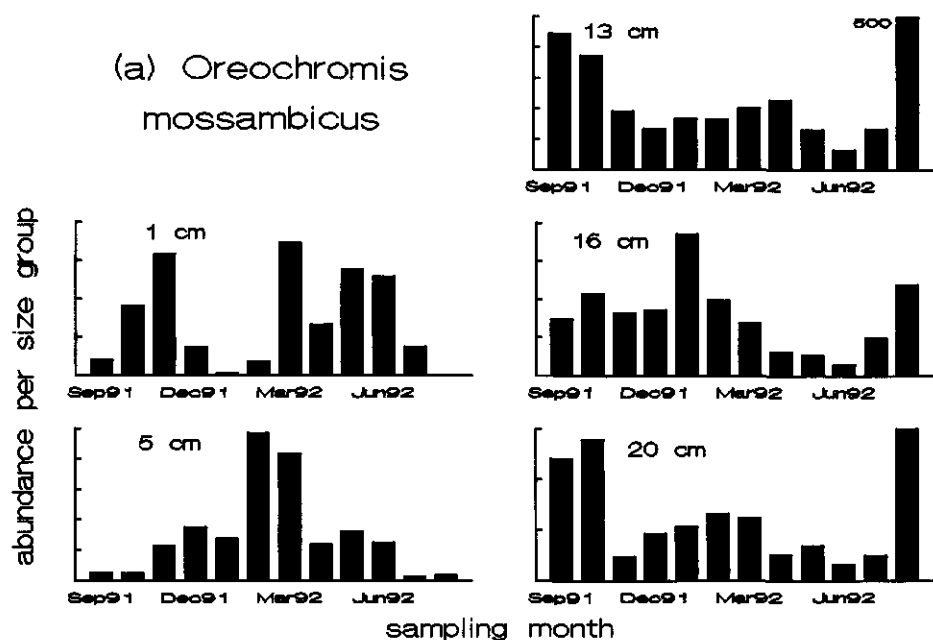
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Fig. 5.3. Temporal patterns in abundance of five size classes of *Oreochromis mossambicus* (a) and temporal patterns in fingerling abundance for five species of cyprinids (b).
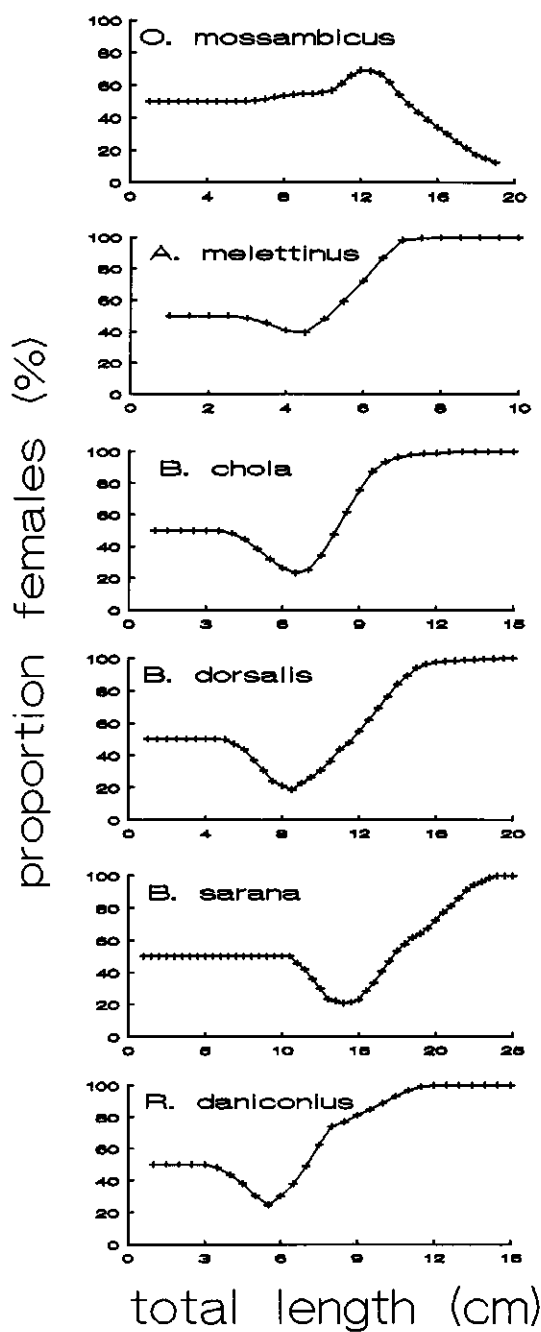
Fig. 5.4. Size-dependent mean sex ratios of *Oreochromis mossambicus* and five cyprinid species from Tissawewa.

were recorded from commercial catches (Fig. 5.3a). Sex ratios were length dependent for all species in the present study (Fig. 5.4). Male *O. mossambicus* reach larger sizes than females, with observed maximum sizes of 27 cm for females and 28.5 cm for males in Tissawewa. Shifting peaks of relative abundance in experimental gillnets were difficult to observe for *O. mossambicus* (Figs. 5.5a & 5.5b), probably due to prolonged spawning periods, but estimates for the parameters in Von Bertalanffy's growth equation could still be made (Table 5.4), using additional ecological information. *LFD* from commercial landings did not show shifting modes, as a result of a high fishing pressure, exerted with gillnets of similar mesh sizes (mainly 64 and 70 mm).

Table 5.4. Estimated growth, recruitment and mortality parameters.

$Sp^\#$	sex	L_{mat}	R	K	L_{inf}	Z	M_p	F	L-range
		fishery-independent estimates (* = not used)							
OM	f	13.0	01	0.75	26.0	8.7*	1.5*	7.2*	12.5-18.5
OM	m		01	0.65	30.0	7.0*	1.3*	5.7*	14.0-19.5
AM	f	6.0	15	1.50	8.0	2.7	3.4*	0.0	6.0- 7.0
AM	m		15	1.60	7.0	3.8	3.6*	0.0	5.0- 6.0
BC	f	9.5	30	1.00	12.0	2.8	2.3*	0.0	9.5-11.0
BC	m		30	1.10	10.5	2.9	2.5*	0.0	7.0- 9.0
BD	f	13.0	15	0.85	19.0	2.3	1.8*	0.0	16.0-18.0
BD	m		15	0.95	17.0	2.5	2.0*	0.0	9.0-16.0
BS	f	20.0	01	0.40	26.0	1.7	1.0*	0.6	20.0-24.5
BS	m		01	0.45	22.0	1.3	1.2*	0.0	14.5-19.0
RD	f	7.5	15	1.10	11.0	4.7	2.5*	0.0	7.5-10.0
RD	m		15	1.20	10.0	4.0	2.7*	0.0	6.0- 9.0
		fishery-dependent estimates					M		
OM	f	13.0	01			7.4	1.9	5.5	15.0-18.5
OM	m		01			6.4	1.7	4.7	15.0-18.5
BS	f	20.0	01			1.9*	1.1	0.6	20.5-23.5
BS	m		01			7.1*	1.3	0.0	20.5-23.5

[#]Species: OM, *Oreochromis mossambicus*; AM, *Amblypharyngodon melettinus*; BC, *Barbus chola*;
BD, *Barbus dorsalis*; BS, *Barbus sarana*; RD, *Rasbora daniconius*.
For other abbreviations see Table 5.1.

Growth curves of cyprinids were fitted on the basis of fixed recruitment dates (Table 5.4), temporary abundance of fingerlings (Fig. 5.3b) and shifting peaks of relative abundance in experimental gillnet catches (Figs. 5.5c - 5.7l). For all cyprinid species in the present study, females attained larger sizes than males.

Estimated growth parameters for *O. mossambicus* indicated rapid growth during the first two years of life (Fig. 5.8a). The fish grow to about 14 cm in the first year. A "November cohort" has entered the fishery around January in its second year (ca. 15.5 cm), which was confirmed by a peak in numerical landings of tilapia in that period (Pet *et al.*, in press a).
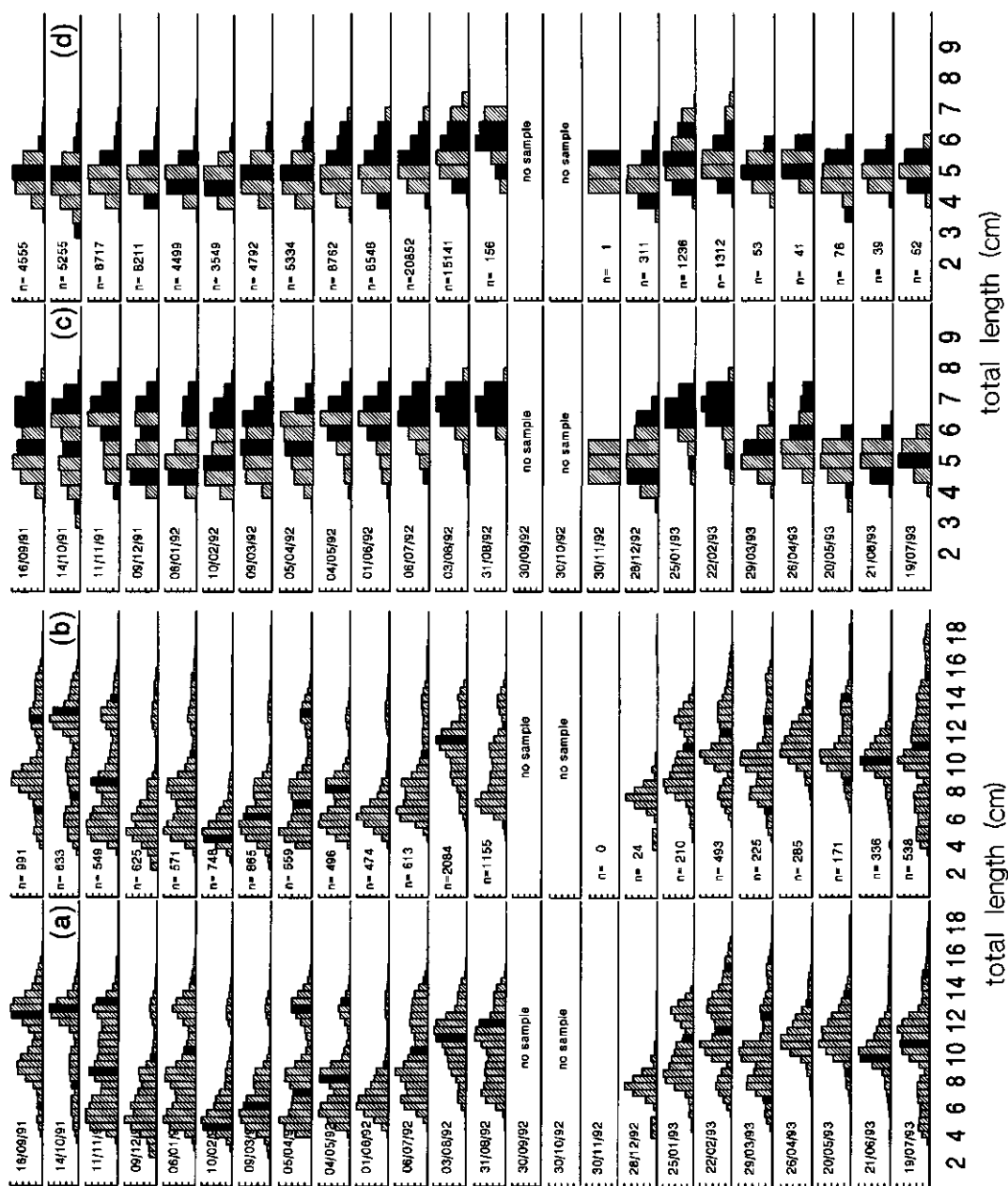
Fig. 5.5. Relative length frequency distributions of *Oreochromis mossambicus* females (a) and males (b) and *Amblypharyngodon melettinus* females (c) and males (d) in experimental gillnets. Total number (*n*) = females + males. Estimated growth curves are represented by black bars.
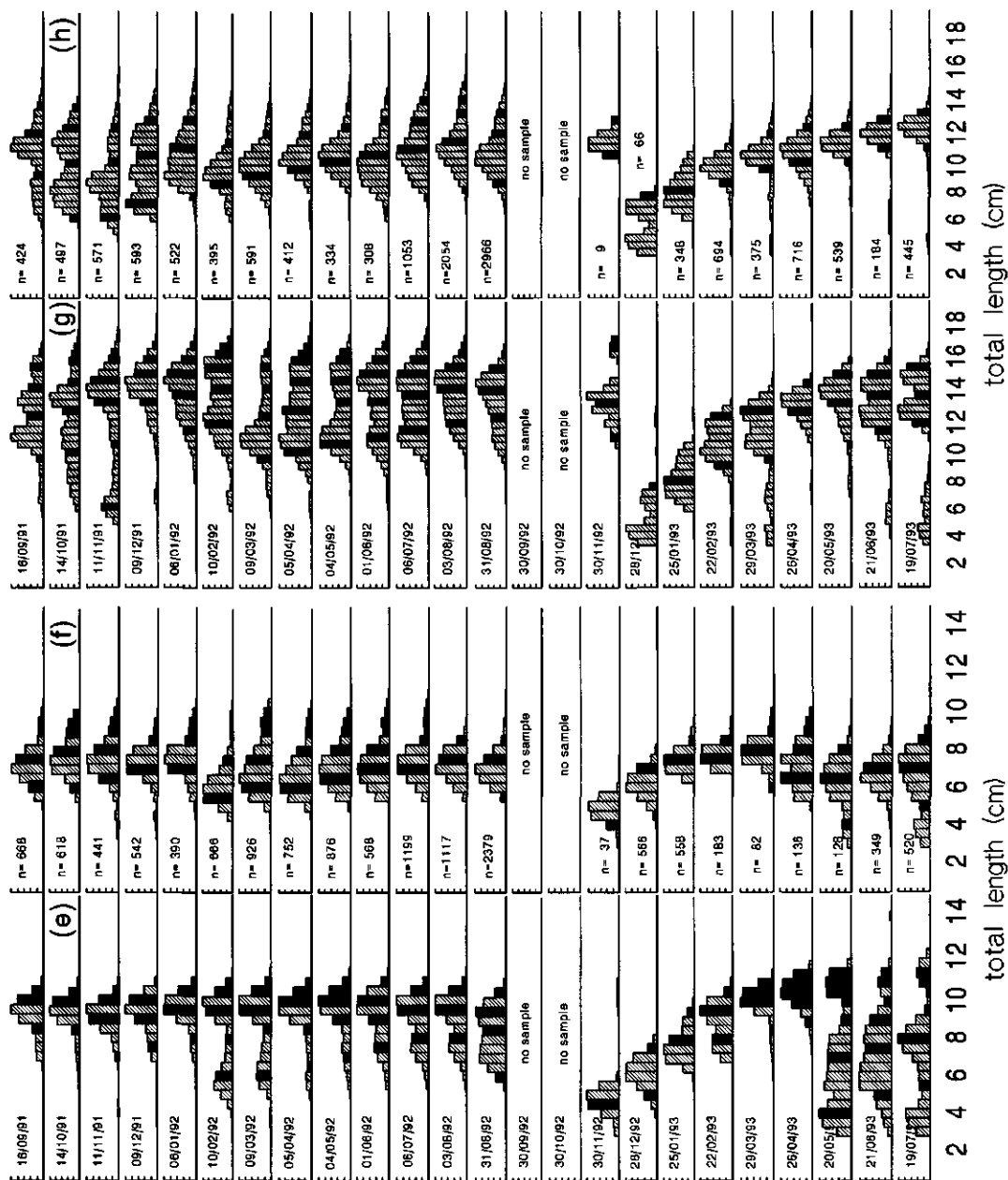
109

Fig. 5.6. Relative length frequency distributions of *Barbus chola* females (e) and males (f) and *Barbus dorsalis* females (g) and males (h) in experimental gillnets. Total number (*n*) = females + males. Estimated growth curves are represented by black bars.
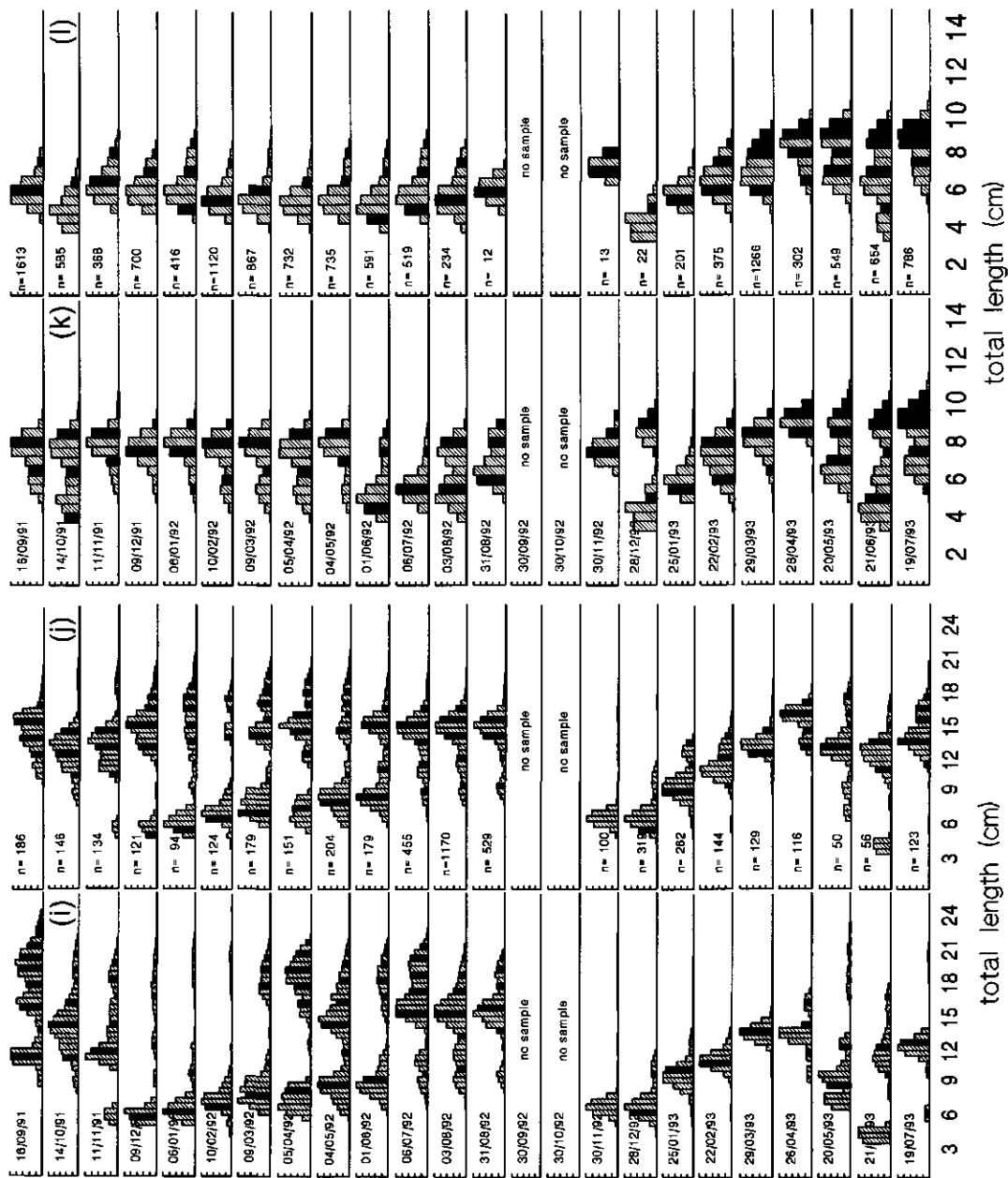
110

Fig. 5.7. Relative length frequency distributions of *Barbus sarana* females (i) and males (j) and *Rasbora daniconius* females (k) and males (l) in experimental gillnets. Total number (*n*) = females + males. Estimated growth curves are represented by black bars.
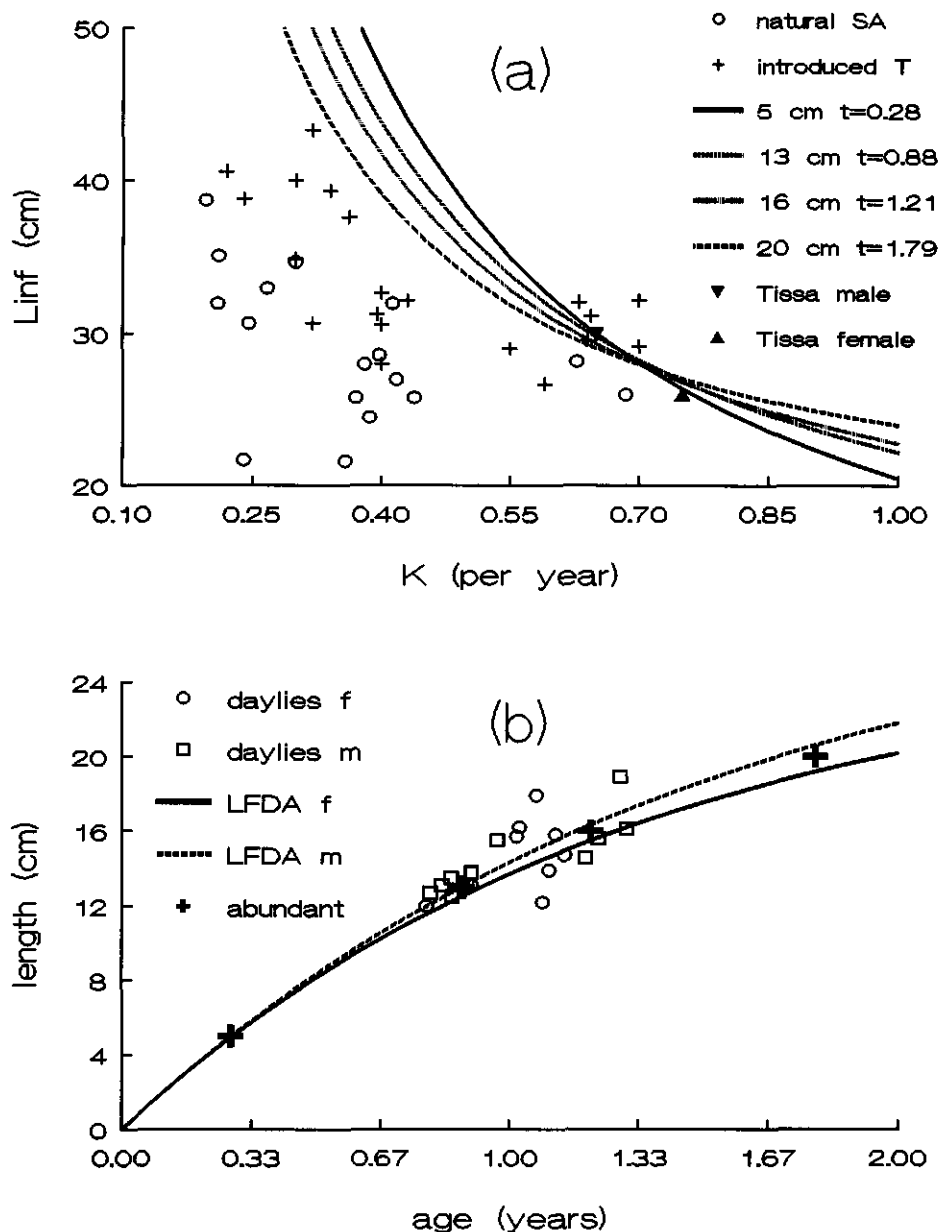
111

Fig. 5.8. Growth parameters of *Oreochromis mossambicus* from Tissawewa compared with literature data on natural populations in South Africa (*SA*) and introduced populations in tropical (*T*) regions (a). Estimated growth curves for *O. mossambicus* compared with temporary peaks in abundance for specific size classes and with length at age data based on daily growth rings in otoliths (b). For abbreviations see Table 5.1.

The results from readings of daily growth rings in otoliths of *O. mossambicus* confirmed estimated growth curves on the basis of *LFDA* (Fig. 5.8b), for this species. Grinded sagittal coups of otoliths showed 17% loss of material around the margins. Since the outer 17% of the coups contained an average of 22% of the remaining dailies, the total count was corrected with 22% for all otoliths.

Before the drought period in September 1992, the largest *Barbus* species (*B. sarana*) showed a slower initial growth (Table 5.4) than the second largest species (*B. dorsalis*). Growth was possibly faster after the drought period but catch *LFD* from that period were difficult to interpret due to a size-dependent immigration of fish into the reservoir (Figs. 5.5 - 5.7). The smallest cyprinid species, *A. melettinus* and *R. daniconius*, showed similar and rapid growth rates (Table 5.4) and reached mature sizes in about 1 year.

Mortality estimates

Total mortality rates for cyprinid species, estimated by catch curve analysis (Fig. 5.9), were assumed to be the best estimates for natural mortality in these unexploited species. These estimated natural mortalities where somewhat higher than values calculated with Pauly's empirical formula (Table 5.4).

Total mortality of *O. mossambicus*, based on commercial catch curve analysis, was high with 7.4 and 6.4 yr^{-1} for females and males respectively (Fig. 5.10a). The natural mortality of *O. mossambicus* was based on interpolation in the overall size-dependent natural mortality equation (Fig. 5.10b),

$$M = 17.99 * L^{-0.83}$$

where *M* is natural mortality and *L* is the mean of the length-range used in catch curve analyses. This resulted in higher values than the estimates based on Pauly's empirical formula. An input length of 17 cm, the mean length for which *Z* was calculated, resulted in an estimated natural mortality of 1.7 yr^{-1} for male *O. mossambicus*. Females of 17 cm are rare in Tissawewa and their natural mortality was estimated at 1.9 yr^{-1}, corresponding with an input length of 15 cm. Fishing mortality of female and male *O. mossambicus* was estimated at 5.5 and 4.7 yr^{-1} respectively, over the size range from 15.0 to 18.5 cm.

Commercial catch *LFD* were corrected for gillnet selectivity before application of catch curve analysis. An overall selection curve for the commercial fisheries was estimated from a 4:4:1 relative frequency of occurrence of 64, 70 and 76 mm gillnets respectively (Fig. 5.11a). A correction factor per length class, to reconstruct the population structure from commercial catch *LFD* of *O. mossambicus*, was calculated based on this overall selectivity estimate (Fig. 5.11b). The selection factor, relating fish size to mesh size, was estimated at 0.246 (Pet *et al.*, in press b) and the coefficient of variation in the selection curve was found to be 7.3% of the optimum selection length .
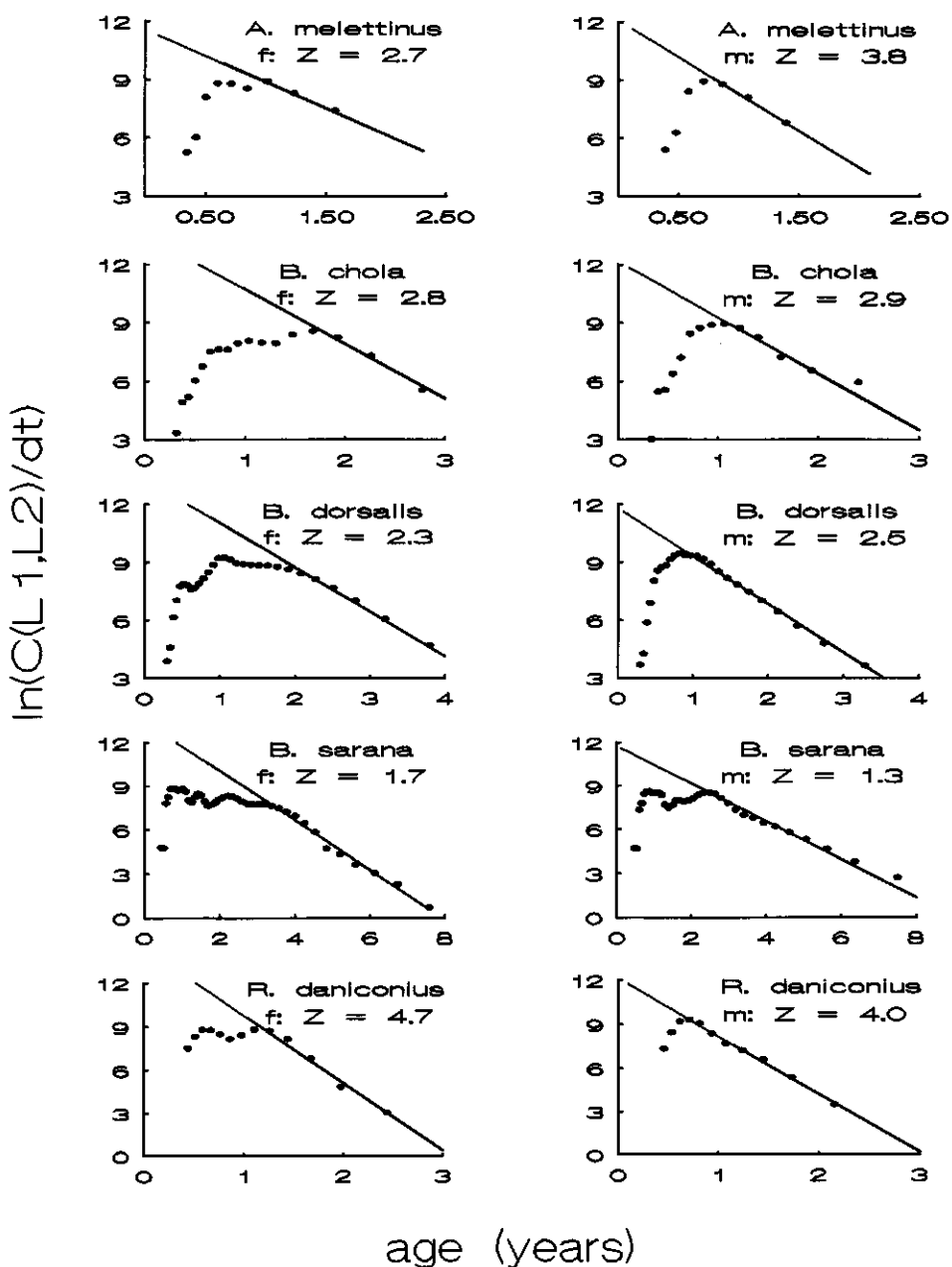
113

Fig. 5.9. Catch curve analysis plots, based on catch *LFD* from experimental gillnets, for five cyprinid species in Tissawewa. For abbreviations see Table 5.1.

114
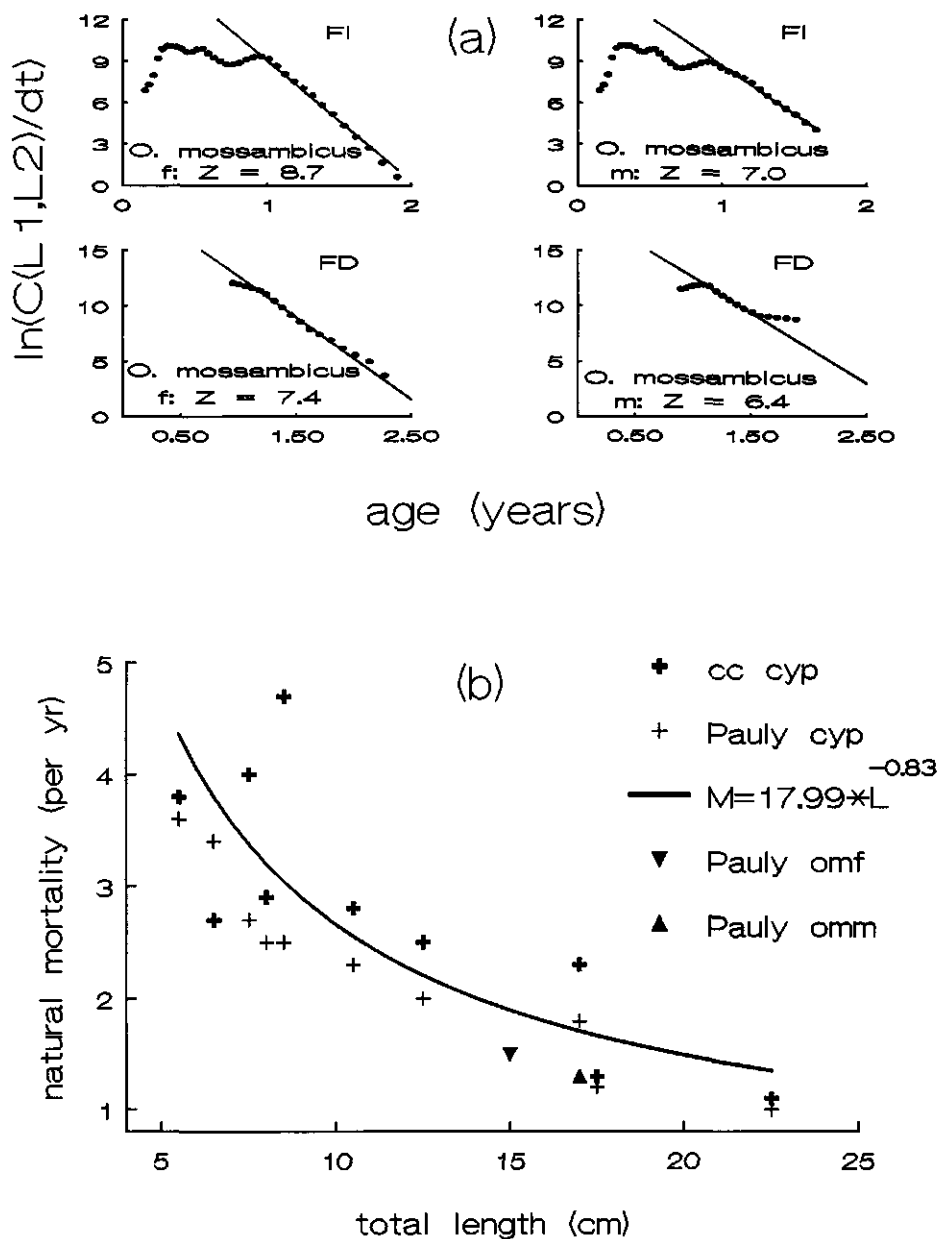
Fig. 5.10. Catch curve analysis plots, based on fishery-independent (*FI*) and fishery-dependent (*FD*) catch *LFD*, for *Oreochromis mossambicus* (a). Relationship between mean body length and estimated natural mortality, based on catch curve analysis, compared with natural mortality estimates based on Pauly's empirical formula (b). Abbreviations used: om, *Oreochromis mossambicus*; cyp, cyprinids; cc, catch curve. For other abbreviations see Table 5.1.

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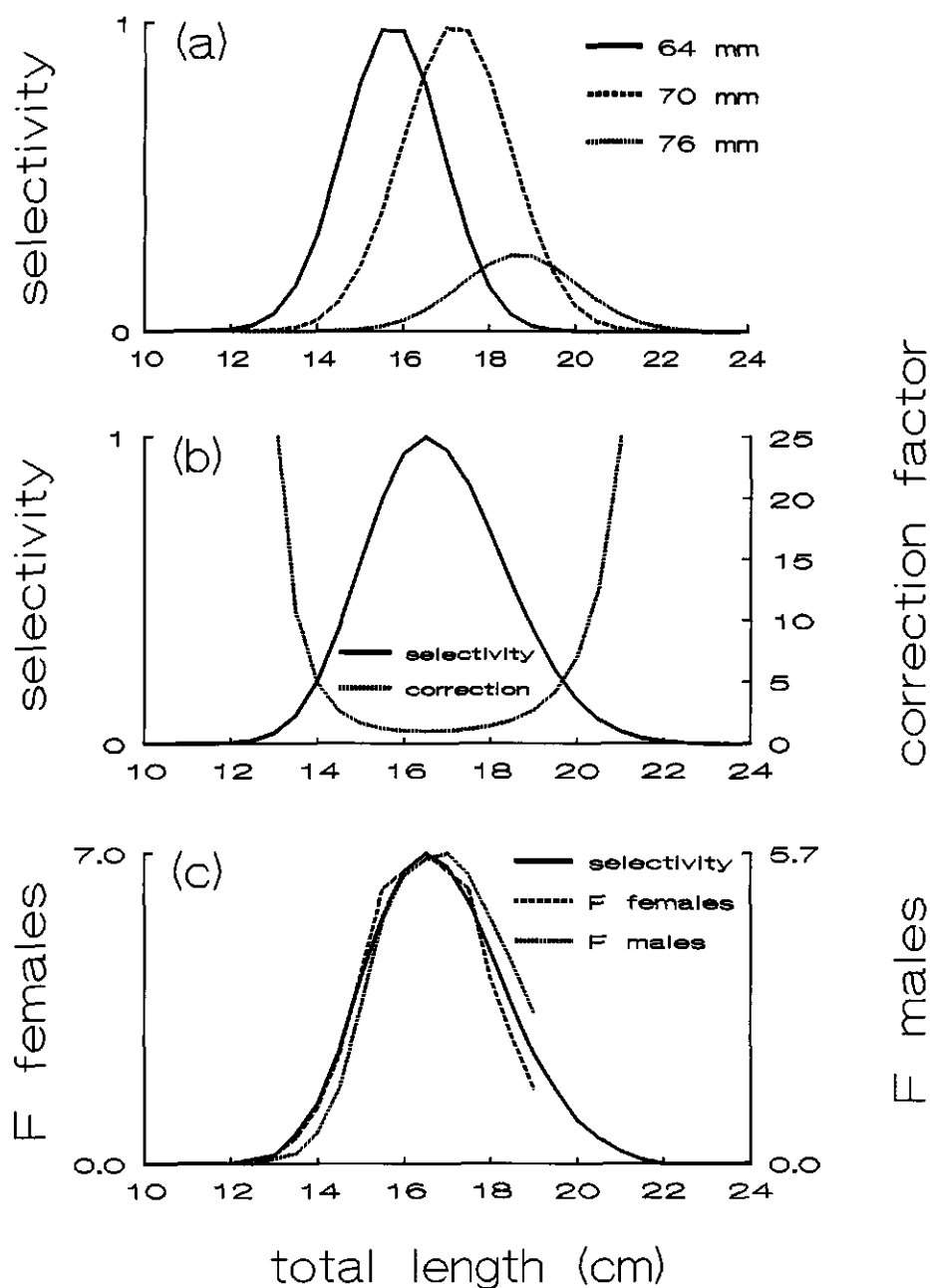Fig. 5.11. Gillnet selection curves for the most important mesh sizes in the commercial fishery for *Oreochromis mossambicus* in Tissawewa between September 1991 and August 1992 (a). Overall selection curve with correction factor per length class (b). Overall selection curve compared with size-dependent patterns in fishing mortality for female and male *O. mossambicus* (c). Abbreviations in Table 5.1.

Table 5.5. Sample sizes and length-weight relationships.

$Sp^{\#}$	sex	n	length-weight relationship	r squared
OM	f	3813	$W = 1.877 * 10^{-2} * L^{2.986}$	0.99
OM	m	3824	$W = 1.942 * 10^{-2} * L^{2.971}$	0.99
AM	f	1455	$W = 8.171 * 10^{-3} * L^{3.109}$	0.95
AM	m	616	$W = 2.203 * 10^{-2} * L^{2.493}$	0.77
BC	f	1150	$W = 1.331 * 10^{-2} * L^{3.042}$	0.97
BC	m	840	$W = 1.343 * 10^{-2} * L^{3.023}$	0.96
BD	f	1820	$W = 1.241 * 10^{-2} * L^{3.010}$	0.97
BD	m	1153	$W = 1.283 * 10^{-2} * L^{2.984}$	0.97
BS	f	1265	$W = 1.143 * 10^{-2} * L^{3.045}$	0.96
BS	m	1226	$W = 1.268 * 10^{-2} * L^{3.014}$	0.98
RD	f	869	$W = 9.302 * 10^{-3} * L^{3.006}$	0.95
RD	m	794	$W = 8.541 * 10^{-3} * L^{3.027}$	0.95

[#]Species: OM, *Oreochromis mossambicus*; AM, *Amblypharyngodon melettinus*; BC, *Barbus chola*;
BD, *Barbus dorsalis*; BS, *Barbus sarana*; RD, *Rasbora daniconius*.
For other abbreviations see Table 5.1.

Standing stock biomass and production

Length-weight relationships for all species and sexes (Table 5.5) were used to calculate the mean body weight of fish in each size class. The initial value of F/Z in the cohort analysis of *O. mossambicus* was chosen at such a level that the mean F over the size interval from 15.0 to 18.5 cm was 5.5 and 4.7 yr^{-1} for female and male *O. mossambicus* respectively (Tables 5.6 & 5.7). The resulting patterns in F for both females and males showed similar shape and position on the length axis as the estimated selection curve, with maximum fishery mortalities of 7.0 yr^{-1} for females of 16.5 cm and 5.7 yr^{-1} for males of 17.0 cm (Fig. 5.11c).

The estimated mean number of *O. mossambicus* in the range of 10.0 to 19.0 cm, between September 1991 and August 1992, was 169.494 females and 256.348 males in a reservoir with an average surface area of 175 ha during that time interval. This results in a density of 0.24 m^{-2} and a mean total biomass of 100 kg/ha for *O. mossambicus* larger than 10 cm. The contribution of *O. mossambicus* smaller than 10 cm was 22.4% of the weight of the full size range in experimental gillnet catches after correction for fishing effort and selectivity. The biomass of the full size-range of *O. mossambicus* in Tissawewa was calculated at 128 kg/ha and the biomass of fish vulnerable to the fishery (above 14.0 cm) at 45 kg/ha.

The species composition in terms of biomass in experimental gillnet catches, after correction for effort and selectivity, was 7% *O. mossambicus*, 60% pelagic minor cyprinids (54% *A. melettinus* and 6% *R. daniconius*), 25% benthic *Barbus* spp. and 8% other species. The total fish biomass, calculated on the basis of these percentages, was 1 829 kg/ha, including 128 kg/ha *O. mossambicus*, 1 098 kg/ha small pelagic cyprinids, 457 kg/ha *Barbus* spp. and 146 kg/ha other species. Over 60% of the total fish biomass was formed by two herbivorous species, *O. mossambicus* and *A. melettinus*.

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Table 5.6. Cohort analysis for female *Oreochromis mossambicus*.

$L^{\#}$	N_C	F/Z	F	Z	N_{mn}	B_{mn}	Y_{tot}
10.0	5	0.00	0.0	1.9	19451	0.39	0.00
10.5	14	0.00	0.0	1.9	18512	0.43	0.00
11.0	30	0.00	0.0	1.9	17588	0.47	0.00
11.5	76	0.00	0.0	1.9	16680	0.50	0.00
12.0	370	0.01	0.0	1.9	15781	0.54	0.01
12.5	1075	0.04	0.1	2.0	14874	0.57	0.04
13.0	3112	0.11	0.2	2.1	13917	0.60	0.13
13.5	7568	0.24	0.6	2.5	12810	0.62	0.36
14.0	15105	0.41	1.3	3.2	11401	0.61	0.81
14.5	23545	0.56	2.5	4.4	9576	0.57	1.40
15.0	31165	0.69	4.3	6.2	7323	0.48	2.04
15.5	30518	0.77	6.2	8.1	4919	0.36	2.20
16.0	19635	0.78	6.6	8.5	2958	0.23	1.56
16.5	11707	0.79	7.0	8.9	1680	0.15	1.02
17.0	6079	0.78	6.6	8.5	919	0.09	0.58
17.5	3090	0.77	6.2	8.1	500	0.05	0.32
18.0	1199	0.69	4.2	6.1	286	0.03	0.13
18.5	542	0.61	2.9	4.8	186	0.02	0.07
19.0	225	0.47	1.7	3.6	133	0.02	0.03
					169494	6.73	10.70

#Abbreviations in Table 5.1.

Table 5.7. Cohort analysis for male *Oreochromis mossambicus*.

$L^{\#}$	N_C	F/Z	F	Z	N_{mn}	B_{mn}	Y_{tot}
10.0	3	0.00	0.0	1.7	25773	0.50	0.00
10.5	12	0.00	0.0	1.7	24727	0.56	0.00
11.0	19	0.00	0.0	1.7	23697	0.61	0.00
11.5	30	0.00	0.0	1.7	22684	0.67	0.00
12.0	131	0.00	0.0	1.7	21685	0.72	0.00
12.5	422	0.01	0.0	1.7	20695	0.77	0.02
13.0	1310	0.04	0.1	1.8	19696	0.83	0.05
13.5	3865	0.11	0.2	1.9	18636	0.87	0.18
14.0	10287	0.26	0.6	2.3	17384	0.90	0.54
14.5	21958	0.45	1.4	3.1	15716	0.91	1.27
15.0	39083	0.63	2.9	4.6	13359	0.85	2.49
15.5	47178	0.73	4.5	6.2	10404	0.73	3.31
16.0	40049	0.76	5.3	7.0	7497	0.58	3.08
16.5	28948	0.77	5.6	7.3	5161	0.43	2.43
17.0	19627	0.77	5.7	7.4	3463	0.32	1.80
17.5	12198	0.76	5.3	7.0	2304	0.23	1.22
18.0	7044	0.73	4.5	6.2	1562	0.17	0.76
18.5	4108	0.69	3.7	5.4	1098	0.13	0.48
19.0	2265	0.62	2.8	4.5	807	0.10	0.29
					256348	10.88	17.92

#Abbreviations in Table 5.1.

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The dominance of small pelagic cyprinids was confirmed by the species composition in trawl net catches (Pet & Piet, 1993). *P/B* ratios were estimated at 3.1 for *O. mossambicus*, 3.3 for the small pelagic cyprinids, 2.4 for *Barbus* spp. and 2.0 for other species. With these ratios and the estimated biomass values for each group, a total *FP* of 5 400 kg/ha/yr or 540 kgC/ha/yr was estimated for Tissawewa. The production per species (-group) was 400 kg/ha/yr *O. mossambicus*, 3 600 kg/ha/yr small pelagic cyprinids, 1 100 kg/ha/yr *Barbus* spp. and 300 kg/ha/yr other species. The *P/B* ratio for the entire fish stock was estimated at 3.0.

Discussion and conclusions

Recruitment patterns

The size at maturity for *O. mossambicus* was reported to range from 15.5 to 21.0 cm in previous studies on Sri Lankan reservoir populations (De Silva, 1986; De Silva *et al.*, 1988; Amarasinghe, 1988a). The low size at maturity (13 cm) for *O. mossambicus* in Tissawewa, in the present study, may be attributed to a high fishing pressure with selective gillnets (Amarasinghe, 1988a; Pet *et al.*, in press a), causing stunting of the overfished population (Lowe-McConnell, 1982). Stunting, in this case, is caused by selectively fishing out the larger and faster growing individuals, resulting in a positive selection of smaller and slower growing fish (Rowell *et al.*, 1989; Smith *et al.*, 1991; McAllister & Peterman, 1992; McAllister *et al.*, 1992; Chambers, 1993). On the other hand, rapid growth, low maximum size and low size at maturity are life history traits which may be advantageous in a small water body exhibiting erratic fluctuations of water levels and periodic droughts (Noakes & Balon, 1982; Cambray & Bruton, 1984; Cambray & Bruton, 1985; James & Bruton, 1992).

The reproductive biology of *O. mossambicus* and cyprinids in Sri Lankan reservoirs is strongly influenced by the rainy seasons (De Silva & Chandrasoma, 1980; Chandrasoma & De Silva, 1981). *O. mossambicus* is spawning continuously, but shows peaks in reproductive activity during the rainy season. These peaks in spawning activity do not exclude continuous spawning throughout the year, whenever environmental factors are favourable. Survival of *O. mossambicus* larvae probably increases when the littoral zones are flooded and provide high quality food (Bowen, 1979) and shelter against predators (Werner et al., 1983; Savino & Stein, 1989). A littoral zone with vegetation is absent during low water levels and survival of fry is probably low during the dry seasons. The increased survival of larvae during the rainy seasons will enhance the formation of cohorts. Cyprinids, except perhaps for *R. daniconius*, also show spawning peaks during the rainy seasons. In case of *B. dorsalis* this result differs from findings in wet-zone rivers where this species was shown to spread its reproductive effort evenly throughout the year (De Silva *et al.*, 1985). Breeding of *O. mossambicus* and probably also of *A. melettinus*, takes place inside the reservoir (Pet & Piet, 1993) whereas *Barbus* spp. are migrating upstream to spawn (Silva & Davis, 1986).

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Growth estimates

The growth curves for *O. mossambicus*, as estimated in the present study, were similar to estimates for the first two years of life in an earlier study on the same population (De Silva *et al.*, 1988). A new batch of *O. mossambicus* grows to 14 cm during its first year and starts reproducing during the next rainy season. In their second year they reach a size which makes them vulnerable to the fishery. From a length of 14 cm they are harvested and the batch is eliminated in the first half of its second year, before the fish can reach lengths above 20 cm.

For older fish the growth in Tissawewa seems to be slower than literature data on Sri Lankan populations suggest. Compared to other populations (Moreau *et al.*, 1986; De Silva *et al.*, 1988; Amarasinghe *et al.*, 1989), the estimate for the growth constant K was relatively high in the present study (Fig. 5.8a), whereas the estimate of L_{inf} was low compared to most introduced populations in the tropics and similar to estimates for natural populations in South Africa. For several reservoirs in Sri Lanka, values of L_{inf} were reported to be well above values from natural populations in South Africa and also above the estimated value for Tissawewa (Fig. 5.8a). The growth of larger (>15.5 cm) *O. mossambicus* in Tissawewa may be under-estimated due to the impact of the gillnet fishery on the size distribution in the population (Ricker, 1969), although this effect was limited by the method used to estimate K and L_{inf}. Other explanations for growth differences could be stunting, the occurrence of different strains, the effect of environmental factors like size of the water body, food availability and/or quality (Bowen, 1979) or even hybridisation (Trewavas, 1983) with *Oreochromis niloticus* (L.) in reservoirs where this species is relatively abundant.

Cohorts of cyprinids, except of *R. daniconius*, can be followed in relative catch *LFD* due to regular recruitment patterns with two clear peaks each year around May and November. The size distribution in cyprinid populations is not disturbed by the fisheries. The slow growth of *B. sarana*, in the period before the drought, may be explained by the fact that periods of rising water levels are needed to maintain growth rates in omnivorous floodplain species (Bayley, 1988). Juvenile growth and body condition of *B. sarana*, an omnivore among *Barbus* spp., increased during the rising water levels immediately after the drought, when macrofauna was abundant.

Mortality

Natural mortality estimates for Tissawewa fishes appear rather high compared to estimates based on Pauly's empirical formula. This may partly be due to the fact that the larger mesh sizes of our experimental gillnets were longer in the water and catches were corrected with a proportionally higher fishing effort. This may have caused an underestimation of abundance of larger fish in the population, when catch per unit of effort decreased with increased set time, as was shown for walleye and yellow perch in Lake Ontario (Minns & Hurley, 1988). On the other hand, the catch per unit of effort increased with set time for white perch in the same study. The effect is attributed to fluctuating activity patterns which were not very pronounced in the turbid conditions before the drought of September 1992 (Pet & Piet, 1993). Differences in activity, based on catch per

unit of effort, became much more pronounced in the clear water conditions after the drought but this period was not used for the mortality estimates. In addition it should be noted that the full size range of most cyprinid species, except for *B. sarana*, was covered by the smaller mesh sizes and total mortality for *O. mossambicus* was estimated from commercial catch length frequency distributions. This means that over- or under-estimation of total mortality, by comparison of catches from nets with different set time, can only be serious for *B. sarana*.

The high estimates for natural mortality in a Sri Lankan reservoir can most likely be explained by a high predation pressure from birds, although the balance of immigration and emigration is also likely to be negative in an irrigation reservoir. Cormorants in Parakrama Samudra, a large lowland reservoir in eastern Sri Lanka, were reported to consume 183 kg/ha/yr (Winkler, 1983) of fish, with a strong preference for cichlids. This figure corresponds by approximation with the total yield of the commercial fisheries of Parakrama Samudra (Schiemer & Duncan, 1988) and with the total yield of tilapia in Tissawewa (Pet *et al.*, in press a). Such a predation pressure by cormorants could explain 80% of total losses through natural mortality of *O. mossambicus* in Tissawewa, assuming cormorants took only this species. Cormorants form only a portion of all birds observed daily to feed on fish in Tissawewa. Many other species of fish eating birds like herons, storks, pelicans, egrets, sterns and gulls are present, often in high densities.

Ecological efficiencies and utilization of the fish production

The total fish biomass in Tissawewa was estimated at 182.9 kgC/ha and the total fish production (*FP*) at 540 kgC/ha/yr (Fig. 5.12). The total fish yield (*FY*) was 242 kg/ha/yr or 24.2 kgC/ha/yr in the study period (Pet *et al.*, in press a). The estimated gross and net primary productivity (*PG* and *PN* respectively) were 10 500 kgC/ha/yr and 4 000 kgC/ha/yr (Amarasinghe, in prep.). The utilization percentages of *PG* and *PN*, in terms of *FY*, were 0.23% and 0.61% respectively. The efficiencies of *FP* over *PG* and *PN* were 5.1% and 13.5% respectively, and the utilization of *FP* in terms of *FY* was 4.5%.

The estimated efficiency of *FP* (5.1% of *PG*) in Tissawewa is high, compared to a range of 0.2% to 1.6% of *PG*, reported for a range of lakes and reservoirs and comparable to the efficiency (up to 8.0% of *PG*) reported for fish ponds with herbivorous fish (Morgan *et al.*, 1980). This can be explained by the fact that more than 60% of the fish biomass (mainly *O. mossambicus* and *A. melettinus*) feeds directly on phytoplankton and detritus. Especially the availability of detritus is important in a reservoir like Tissawewa. *O. mossambicus* is able to assimilate about 60% of ingested detrital aggregate (Bowen, 1980), which forms an important part of its diet. Detritus is an even more important source of energy for *A. melettinus*, since this stomachless fish can utilize only a small part of ingested algae (Bitterlich, 1985).

The amount of particulate organic matter (*POM*) in Tissawewa is around 20 times higher than the total phytoplankton biomass (Amarasinghe, in prep.). Most reservoirs in Sri Lanka have a high turnover rate, due to their relatively small size, and input of allochthonous material is therefore important (Wetzel, 1990).
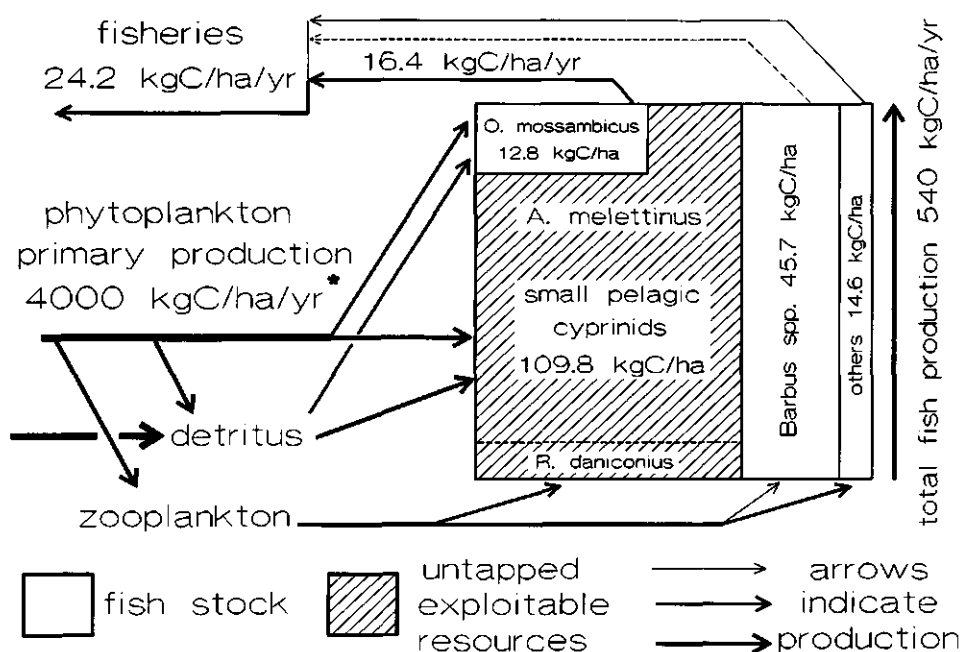
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Fig. 5.12. Estimated distribution of biomass in Tissawewa fish stocks with the availability of untapped resources and estimated input, output and fish production rates for this ecosystem.
*Data on primary production from Amarasinghe (in prep.).

The small reservoirs may be comparable to rivers, where inflowing detritus is an important source of food for secondary producers (Burgis & Dunn, 1978; Mann, 1988). The 'apparent' efficiency of fish production over gross primary production is higher in systems with a large inflow of foreign material than in stagnant lakes.

Utilization of PN in terms of FY was reported to range from 0.10 to 0.72% for 9 African lakes (Melack, 1976), with a mean of 0.35%. This utilization was reported to be as high as 1.2% in the fishery for *Saratherodon melanotheron* (Rüppel), a detritivorous tilapia in the Sakumo lagoon in Ghana, West Africa (Pauly *et al.*, 1988). It has been shown that man normally utilizes up to 0.2% of PG in lakes and reservoirs as fish yield (Blazka *et al.*, 1980; Morgan *et al.*, 1980). The utilization of primary production by the fisheries in Tissawewa (0.61% of PN and 0.23% of PG in terms of FY) is at a normal level by these standards. This utilization is still low, however, when the relatively high production of unexploited cyprinids is taken into account. The dominance of unexploited cyprinids, especially of *A. melettinus*, is evident for the lowland reservoirs which were studied in detail in Sri Lanka (Schiemer & Duncan, 1988; Sirisena & De Silva, 1989).

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Although the biological fish production is highly efficient in Tissawewa, the utilization of FP (5 400 kg/ha/yr) in terms of FY (242 kg/ha/yr) is only 4.5%, although 10% can normally be obtained from lakes and reservoirs (Blazka et al., 1980). One explanation could be that biomass and production of small fish was under-estimated in previous studies (Le Cren & Lowe-McConnell, 1980). A second possibility is that biological fish production was more completely utilized in other lakes and reservoirs, like for example in Lake George, Uganda. This equatorial Lake is comparable to Sri Lankan lowland reservoirs with a mean depth of 2.5 m, a transparency of 0.35 m and a net primary productivity of 5 500 kgC/ha/yr (Lowe-McConnell, 1982; Hecky, 1984). The main differences are that Lake George (25 000 ha) is much larger than Tissawewa and lies at an altitude of 914 m. Herbivorous cichlids (mainly *O. niloticus* and *Haplochromis nigrippinis* (Regan)) form 60% of the fish biomass. The fish yield in Lake George is estimated at 137 kg/ha/yr, with 111 kg/ha/yr *O. niloticus*. The estimated fish biomass is only 220 kg/ha, ranging from 60 kg/ha in open water to 900 kg/ha inshore.

At an assumed P/B ratio of 3.0, equal to the overall P/B ratio of the fish stocks in Tissawewa, the biological fish production in Lake George would still not be more than 660 kg/ha/yr. The estimated utilization of FP in terms of FY would be around 20%, four to five times higher than in Tissawewa. The utilization of PG was estimated at 0.4% for Lake George (Morgan et al., 1980), and also for the more oligotrophic Lake Tanganyika (Hecky et al., 1981). This is twice as high as what was normally obtained from a range of lakes and reservoirs (Morgan et al., 1980). The more complete utilization of FP in Lake George results in an annual fish yield in the same order of size as in Tissawewa, in spite of the fact that the efficiency from primary production to total secondary production is estimated to be low in Lake George, at only 3% (Burgis & Dunn, 1978; Hecky, 1984).

Management options

Conservation of the existing fisheries resources should be the primary concern for managers of the Sri Lankan reservoir fishery, which presently yields around 30 000 tonnes annually (De Silva, 1988), 20% of the national fish production. One of the major problems at the moment is the use of mesh sizes below the legal minimum of 76 mm stretched mesh (Amarasinghe, 1988a) and the lack of enforcement. A danger of over-exploitation exists in a situation where 64 and 70 mm are the most common mesh sizes used to catch *O. mossambicus*. The legal minimum seems to be more appropriate although its choice was not based on scientific research (Amarasinghe, 1992). Introduction of an increased minimum mesh size as high 100 mm has been suggested (Amarasinghe, 1988a; Amarasinghe, 1992) to catch *O. mossambicus* with a mean size above 20 cm. The estimation of the growth potential for *O. mossambicus* will have an important influence on the choice of a desirable mesh size. Re-implementation of the minimum mesh size of 76 mm is likely to succeed since fishermen societies are willing to cooperate when they are involved in the planning and when minimum mesh sizes are strictly enforced on all fishermen (Amarasinghe, 1988b; Pet-Soede, 1993).

The possibility to reach a utilization of 10% of FP in terms of FY (Blazka et al., 1980) indicates a large scope for improvement of the yield to at least 500 kg/ha. This is a 100%

increase of the present annual yield, which could be obtained by exploitation of the presently untapped resources of small pelagic cyprinids, especially *A. melettinus* (Fig. 5.12). This may be possible without doing major damage to the existing fishery for tilapia (De Silva & Sirisena, 1987; Sirisena & De Silva, 1989; Pet & Piet, 1993). *Barbus* spp. are not exploitable with gillnets without harming the existing fishery for tilapia, since adult specimen share their preferred habitat with juvenile tilapia and both are vulnerable to 30 mm gillnets (Pet & Piet, 1993). An annual yield of 250 kg/ha of small pelagic cyprinids is only 7% of the presently estimated biological production of 3 600 kg/ha/yr. At present a part of this production ends up as dead fish in the irrigation canals (Pet, pers. obs.) and another part is utilized by birds.

Forecasted yields of a subsidiary (small meshed) gillnet fishery for the combined minor cyprinids were estimated to be as high as 900 kg/ha/yr (De Silva & Sirisena, 1989). This figure is probably an overestimation since it is based on the catch per unit of effort in experimental gillnets of unexploited cyprinids compared to the exploited *O. mossambicus* (Amarasinghe, 1992). The exploited standing stock biomass of *A. melettinus* will be at least 50% below the unexploited biomass, when specimen larger than 5 cm become rare in a heavily exploited situation with 15 mm stretched mesh. A declining biomass of mature females may cause a further decrease in stock biomass. Still the yield of a subsidiary fishery with 15 mm stretched mesh drifting gillnets and/or lift nets, targeting mainly *A. melettinus*, may equal the present yield of *O. mossambicus* and result in a 100% increase of the total catch.

An alternative management option would be the indirect exploitation of small cyprinids by means of a culture-based fishery on large non-reproducing predators with high commercial value. Recent stocking of Sri lankan reservoirs with major Indian carps showed that culture-based fisheries have a future in Sri Lanka. Local fishermen were able to catch and sell large fish, using 202 and 254 mm gillnets, but poor returns of Indian carps left this stocking program open to criticism (De Silva, 1989; Amarasinghe, 1992), and it is uncertain whether Indian carps are competing for food with *O. mossambicus* and/or indigenous cyprinids.

An introduction of predators in reservoirs with large stocks of small fish was mentioned before as a management option (Schiemer & Duncan, 1988) but was viewed with alarm. Such an introduction must be carried out stepwise, with care and only when the predator population is fully controllable. The effect of the predators on the existing fishery must be carefully examined in isolated situations because large predators are hardly present in Sri Lankan reservoirs, except for low densities of *Channa striata* (Bloch). Small predators like *Glossogobius giuris* (Hamilton) and *Mystus* spp., are present but they do not seem to be able to control the large stocks of minor cyprinids. Piscivorous fish represented less than 5% of the weight in experimental gillnet catches (Pet & Piet, 1993). The small indigenous predators are not preferred by local consumers.

The best candidate for a stocking program in Sri Lankan lowland reservoirs seems 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). *L. calcarifer* is a prized consumption fish all over south east Asia. Pond

experiments show that predation by *Lates niloticus* (L.), a close relative of *L. calcarifer*, has a positive effect on stunted tilapia populations (Ofori, 1988). Due to food conversion, the resulting increase in catch from this third option will be a size-order lower than in the case of direct exploitation of small cyprinids, but the product will be of a much higher quality.

Acknowledgements

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Chapter 6

A size-structured simulation model for evaluating management strategies in gillnet fisheries exploiting spatially differentiated populations

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Abstract

A length-structured simulation model is presented as a tool in decision making for gillnet fisheries management. The analytical model simulates the fish population dynamics and impact of the fisheries, taking into account size-dependent spatial distribution patterns and migration of the fish. The daily recruitment of fish, at a theoretical starting length of 0 cm, is simulated with a variable temporal pattern, giving the model a high degree of generality and making it applicable to tropical situations where recruitment is not restricted to a short period in time. The model is sex-differentiated, the growth of the fish is determined by their length and the dispersion over the length-classes is controlled by the 'fractional boxcar train method'. Natural mortality is assumed constant for all exploited size classes. Fishing mortality is a function of fish length, based on a combination of gillnet selectivity curves for various mesh sizes. The fishing mortality for the most vulnerable size class is calibrated using estimates for the fishing mortality per length-class from length-based cohort analysis. Spatial distribution of the fish over different habitats is based on observed patterns in size-dependent habitat occupation. The realistic model provides predictions on the progressive effects of management regulations on numbers, size distributions and total biomass of the population and the catch in the various habitats. The commercial gillnet fishery for *Oreochromis mossambicus* (Cichlidae) in Tissawewa, a Sri Lankan reservoir, is used as an example. Simulation results correspond with independently estimated values for output parameters. Conclusions with respect to the fisheries management of this specific reservoir are put in a country-wide perspective, using data sets from the literature. Based on model predictions, conservation of this fishery is recommended by re-enforcement of the legal minimum mesh size of 76 mm stretched mesh, and a limitation of fishing effort to the present level. The model also provides predictions on the effects of subsidiary small-meshed fisheries for minor cyprinids on the existing fishery for *O. mossambicus*. Model predictions take into account the size-dependent spatial distribution patterns of the fish and the spatial

allocation of the fishing effort. A fishery with 30 mm stretched mesh for *Barbus* spp. (Cyprinidae) is predicted to cause major damage to the existing fishery for *O. mossambicus*. A fishery with smaller meshes of 15 mm stretched mesh, for *Amblypharyngodon melettinus* (Cyprinidae), is predicted to be less harmful.

Introduction

Predicting the results of different management alternatives is essential for fisheries management (Gulland, 1983; Hilborn and Walters, 1992) and simulation models are important tools to obtain such predictions (Jørgensen, 1994). For fish stocks in temperate regions these predictions were traditionally obtained from classical yield models (Beverton and Holt, 1957; Ricker, 1958), which were based on the concept of age-structured populations. These early analytical models assumed constant fishing mortality after knife-edge recruitment to the fishery. This is not realistic in case of gillnet fisheries with their gradual size-selective impact on the fish stocks. The realism of predictive models was improved by more modern age-structured models which include a gradual recruitment to the fishery (Pitcher and Hart, 1982; Jacobsen and Taylor, 1985) and by which one can predict the progressive effects of management regulations (Hightower and Grossman, 1987). However, the selection of fish by gillnets is through size and not through age. Moreover, age-structured models are difficult to apply in tropical situations where reproduction shows variable temporal patterns and where estimates of age are hard to obtain (Pauly and Murphy, 1982).

Various methods are available to estimate population parameters from size-structured information on fish stocks from tropical regions (Pauly and Morgan, 1987; Sparre *et al.*, 1989; Gulland and Rosenberg, 1992). To generate predictions on the effects of management regulations in gillnet fisheries, however, these parameters should be used as input in a size-structured model and not in traditional models which are only age-structured. A size-structured dynamic simulation model is particularly needed for gillnet fisheries which heavily exploit short-lived tropical species. Such a model will predict the effects of optional management measures in terms of length-frequency distributions of population and catch, in addition to predictions in terms of catch levels. Such a model will also show the consequences of management regulations more precisely, and with more detail than models which are only age-structured (Sissenwine, 1977; Schnute et al., 1989a, 1989b; Buijse *et al.*, 1992). Moreover, a size-structured model has the advantage that it can be validated by comparison of the size-structured output with independently obtained length-frequency distributions of the catch.

Static size-structured models (Berkes and Gönenc, 1982; Staub *et al.*, 1987) have the disadvantage that they cannot take into account the progressive change in population length-frequency distributions caused by a size-selective fishing mortality. A dynamic simulation model allows evaluation of the gradual size-selective impact on fish stocks. Information on the dispersion of abundant age- or size-groups (over length or time respectively) can be obtained directly from field observations and can be used to simulate the variation in

growth within these groups. The probability distributions of growth parameters, which are needed for stochastic individual-based models (Hampton and Majkowski, 1987), are harder to obtain. These individual based models possess a high level of resolution which is not needed to understand the essential features of a gillnet fishery in relation to its management.

The age- and size-structured simulation model which we developed earlier for the Lake IJssel fishery (Buijse et al., 1992), lacked generality since it could not be used with variable recruitment patterns as encountered in tropical situations. Furthermore it lacked realism since it did not account for spatial effects, which are known to be important in reservoir fisheries (Siler et al., 1986; Amarasinghe et al., 1989; Pet and Piet, 1993). Finally it lacked precision in the simulated dispersion of cohorts over the length-classes in the model, which was correct over time intervals of one year, but not over shorter time or length intervals.

In the present study, a simulation model is developed which is generally applicable in situations with variable recruitment patterns in both temperate and tropical situations. The importance of a spatial dimension (Renshaw, 1991) is recognized by accounting for size-dependent spatial distribution patterns of the fish, and their consequences for fisheries management. The gillnet fishery for *Oreochromis mossambicus* (Peters) in Sri Lankan reservoirs is used as an example to show the possibilities of this model.

The inland capture fisheries of Sri Lanka, contributing 20% to total fish production in this country (Jayasekera, 1990), is characterized by its small-scale gear, mainly outrigger canoes and multifilament gillnets. The introduced tilapia *O. mossambicus* accounts for 80% of the total annual catch of 27 000 to 30 000 tonnes from inland waters (De Silva, 1988). The most important water bodies for this fishery are man-made reservoirs, covering a total surface area of around 100 000 ha. The mean annual yield of 270 to 300 kg/ha/yr is high for tropical lacustrine fisheries (Oglesby, 1985) and conservation of this fishery should therefore be a first priority for fisheries management (Pet et al., submitted). Several stocks of *O. mossambicus* in Sri Lankan reservoirs have been reported to be subject to growth overfishing (Amarasinghe, 1988a; Amarasinghe, 1992). An alarming downward trend in mesh sizes and sizes of landed fish has been recorded, with mesh sizes in operation below the legal minimum of 76 mm stretched mesh (Pet et al., in press a). Neither the present legal minimum mesh size nor the recently proposed increase to 100 mm (Amarasinghe, 1992) were based on scientific research and feasability studies with analytical models.

Subsidiary fisheries for presently unexploited minor cyprinids, using small-meshed gillnets, have been proposed to improve inland fisheries production (De Silva and Sirisena, 1987; 1989; Sirisena and De Silva, 1988; 1989). The cyprinid resources would be exploitable with 15 and 30 mm gillnets, without any detrimental effect on the existing fishery for *O. mossambicus*, since juveniles of *O. mossambicus* would be spatially segregated from adult minor cyprinids. Adult stages of both minor cyprinids and *O. mossambicus* were assumed to occupy the open water zone, whereas juveniles of both species (-groups) would stay in the littoral areas. This hypothesis presumes spatially differentiated effects of optional mesh size regulations for the Sri Lankan reservoir fisheries. These effects are predicted in the present study, using a size-structured simulation model which takes into account the size-dependent spatial distribution patterns of the fish in combination with the spatial allocation of the fishing effort.

Materials and methods

The Tissawewa fisheries

The annual yield of *O. mossambicus* from Tissawewa (175 ha) in the period 1991-1992 was around 160 kg/ha, accounting for 65% of the total fish production (Pet *et al.*, in press a). Gillnets are the most important gear and the daily fishing effort is around 9 fishing trips, as long as the maximum depth in the reservoir remains above 2 m. Each fishing trip includes 2 gillnets of about 225 m long which are set during the night by one or two fishermen. The mean catch per trip is around 14 kg. The most common mesh sizes are 64, 70 and 76 mm stretched mesh, used in a ratio of 4:4:1 in terms of numbers of nets in operation.

O. mossambicus in Tissawewa are growing to about 14 cm in their first year and are caught in gillnets during their second year of life (Pet *et al.*, submitted). The modal length in catch length-frequency distributions is invariably found at 15.5 cm. The mean instantaneous fishing mortality (F) for the length range of 15.0 to 18.5 cm is high, with F = 4.7 yr^{-1} and F = 5.5 yr^{-1} for males and females respectively (Pet *et al.*, submitted). The instantaneous natural mortality (M), for length classes from 10 cm upwards, is also high, with M = 1.7 yr^{-1} and M = 1.9 yr^{-1} for males and females respectively. Due to the high fishing pressure, specimen of *O. mossambicus* larger then 19 cm are rare in Tissawewa, although estimates of potential growth indicate that lengths above 25 cm can be reached. Due to the use of mesh sizes smaller than 76 mm stretched mesh, the size at maturity of female *O. mossambicus* has decreased from 16 to 13 cm during recent years, which indicates a potential danger of growth overfishing.

Model structure, parameter estimation and calibration

The relational diagram (Fig. 6.1) represents the general structure of the model and all symbols used in this diagram are listed in Table 6.1. The model is written in Turbo Pascal, version 7.0 (Borland International, 1992). Growth, recruitment and mortality estimates for the Tissawewa stock of *O. mossambicus* (Pet *et al.*, submitted) are used as input parameters (Table 6.2) in a version which consists of 2 sexes and 36 length-classes (0 - 35 cm) and which uses a time step of one day.

Growth in length class L_n is simulated according to the von Bertalanffy growth function (abbreviations in Table 6.1).

$$(\frac{dL}{dt})_n = K * (L_\infty - L_n)$$

Growth of the fish depends on their individual length, in contrast to the model we developed earlier for the Lake IJssel fisheries (Buijse *et al.*, 1992), where growth depended on the mean length of the age group that individual fish belonged to. Female and male *O. mossambicus* grow to a mean length of 14 cm in their first year and to mean lengths of 20 and 22 cm respectively in their second year (Fig. 6.2). A power function is used to describe the relation between body length L (cm) and body weight W (g) for both sexes of *O. mossambicus*. The relation for females is $W = 0.01877 * L^{2.986}$ and for males this is
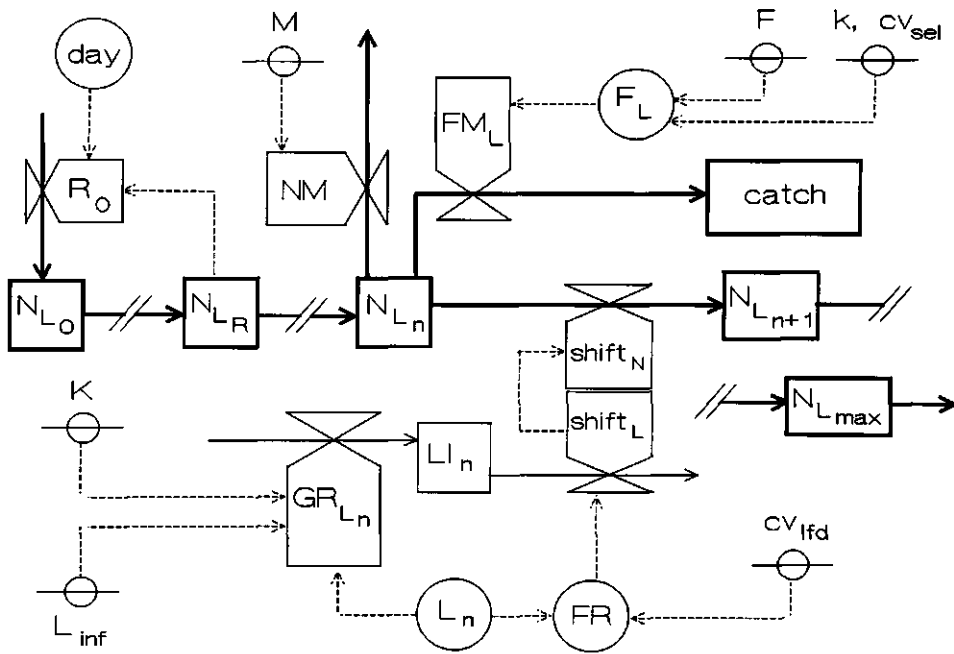
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Fig. 6.1. Relational diagram according to Forrester's conventions (De Wit and Goudriaan, 1978). State variables are presented by rectangles, rates of changes by valves, auxiliary variables by circles and parameters by circles with cross bars. The flow of material is represented by solid arrows and the flow of information by dotted arrows. The information flow from $N_{l,R}$ to R_0 represents a calibration of the model. Abbreviations are explained in Table 6.1.

$W = 0.01942 * L^{2.971}$. These relations are used in combination with simulated length-frequency distributions to calculate the biomass of the population and the weight of the catch. The female spawning stock biomass (FSSB) of O. mossambicus is calculated using the length at maturity of 13 cm (Pet et al., submitted) as a lower limit.

The dispersion of fish born on a single day, over the length-classes in the model (Fig. 6.3a), is simulated with the 'fractional boxcar train method' (Goudriaan and Van Roermund, 1989; Buijse et al., 1992), which controls the transfer of fish from one length-class to the next. This method for controlled dispersion prevents size distributions to accumulate in single size classes in situations where small fish grow faster than larger ones (Fig. 6.3b & 6.3c) and disperses the fish, born on a single day, over a size distribution with a defined standard deviation. A fraction FR of the number of fish in a length-class is transferred to the next as soon as their increase in length since the last transfer equals a proportion FR of the width of the length-class.

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Table 6.1. Abbreviations, parameters and variables.

cv_{lfd}	coefficient of variation in l-f distribution
cv_{sel}	coefficient of variation in selectivity curve
day	day number of the year
F	maximum instantaneous fishing mortality rate (day^{-1})
F_L	fishing mortality rate per length-class (day^{-1})
FM_L	fishing mortality per length-class (numbers per day)
FR	fraction shifted (controlling the dispersion)
GR_{Ln}	growth rate in length-class n (cm per day)
K	von Bertalanffy growth constant (day^{-1})
k	gillnet selectivity factor
LI_n	length increment in L_n since last shift (cm)
L_{inf}	theoretical (von Bertalanffy) maximum length (cm)
L_n	total length in length-class n (cm)
M	instantaneous natural mortality rate (day^{-1})
N_{L0}	number of 0 cm recruits
N_{Lmax}	number of fish in largest length-class
N_{Ln}	number of fish in length-class n
N_{LR}	number of recruits in L_R (the smallest length-class for which absolute numbers can be estimated)
NM	natural mortality (numbers per day)
R_0	recruitment of 0 cm fish (numbers per day)
$shift_L$	reduction of length increment LI_n with fraction FR
$shift_N$	transfer of fraction FR from length-class L_n to L_{n+1}

Table 6.2. Estimated values of input parameters and model output compared with simulation results for the gillnet fishery on *Oreochromis mossambicus* in Tissawewa.

input parameters[*]		model output[#]	estimated	simulated
N_{LR} 13 cm fish	65 000	POP	425 800	430 000
K males	0.65 yr^{-1}	POP_{males}	256 300	238 000
K females	0.75 yr^{-1}	$POP_{females}$	169 500	192 000
L_{inf} males	30 cm	BIOM	17.6 ton	19.1 ton
L_{inf} females	26 cm	FSSB	3.8 ton	4.7 ton
cv_{lfd}	0.1	CATCH	28.6 ton	29.7 ton
M males	1.7 yr^{-1}	L_{mn}	15.3 cm	15.5 cm
M females	1.9 yr^{-1}	sd_{lfc}	1.6 cm	1.7 cm
k	0.246	peak catch	Jan/Jul	Dec/Jun
cv_{sel}	0.073			
F males	5.7 yr^{-1}			
F females	7.0 yr^{-1}			

[*]Input parameter abbreviations in Table 6.1. [#]Model output abbreviations:
POP, number in population (≥ 10 cm); *BIOM*, biomass in population (≥ 10 cm); *FSSB*, female spawning stock biomass; *CATCH*, total annual catch; L_{mn}, mean length of the fish in the catch; sd_{lfc} standard deviation of the catch length-frequency distribution.
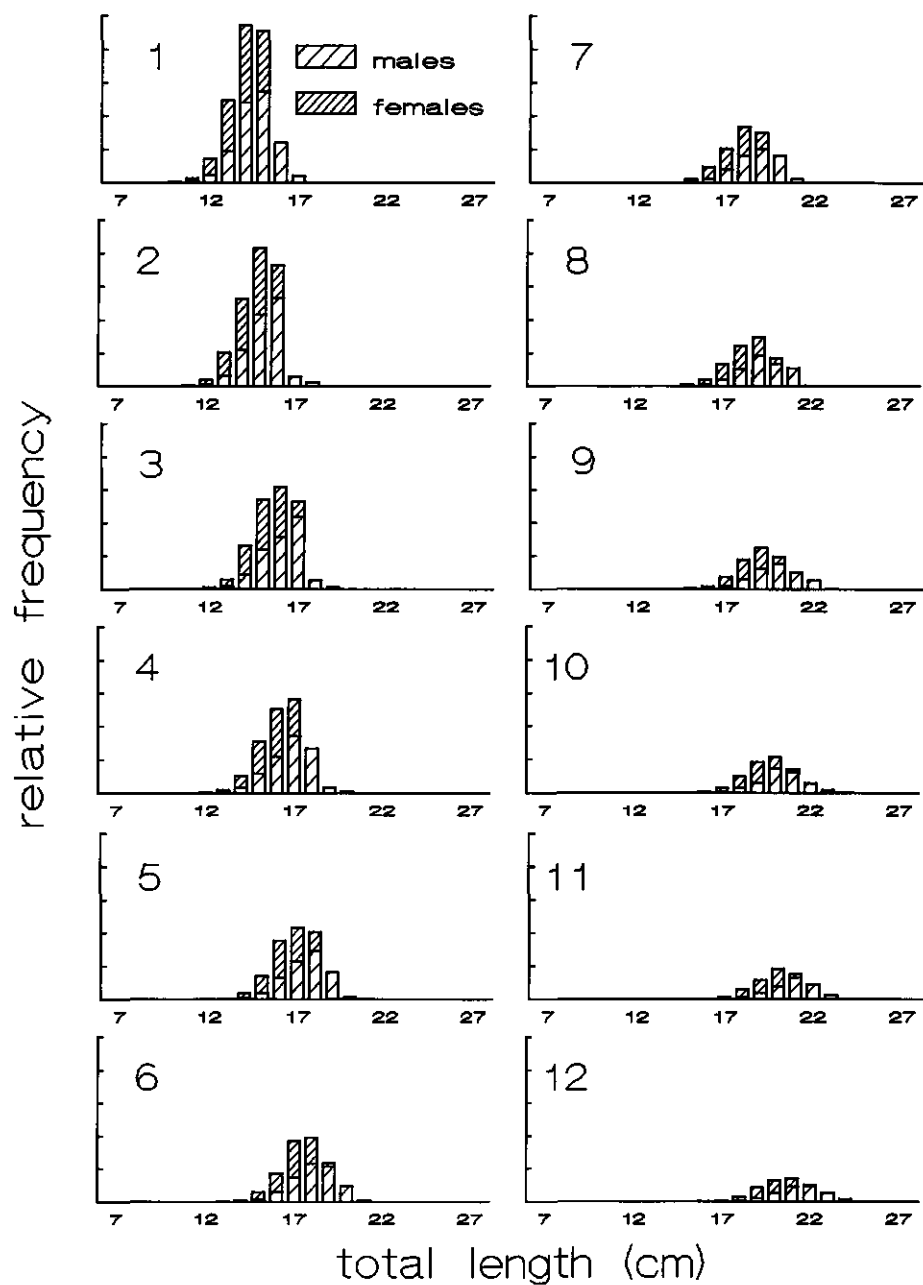
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Fig. 6.2. Simulated development of the length-frequency distribution of an unexploited batch of *O. mossambicus*, born on a single day in Tissawewa, during the twelve months of its second year.
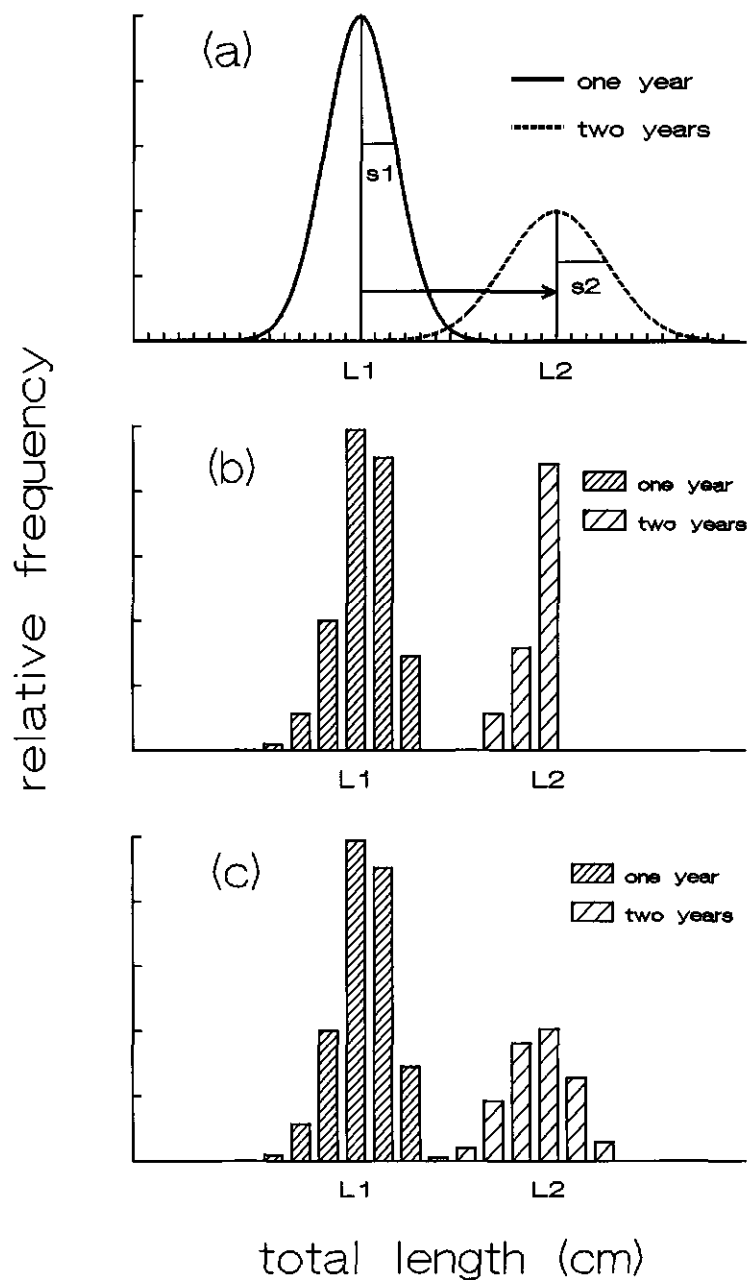
Fig. 6.3. Arbitrary length-frequency distributions of one and two year old fish with mean lengths *L1* and *L2* and standard deviations *s1* and *s2* (a). Simulated development of distribution with 100% shifted to next length-class after length increment reaches length-class width (b) and with controlled dispersion using the 'fractional boxcar train method' (c).

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In our previous model (Buijse *et al.*, 1992), the fraction *FR* was calculated using differences in mean lengths and standard deviations of consecutive age groups,

$$FR = 1 - \frac{(s_{A+1}^2 - s_A^2)}{L_{A+1} - L_A}$$

where L_A and L_{A+1} are the mean lengths at age A and age $A+1$ and s_A and s_{A+1} are the standard deviations of the length-frequency distributions at age A and age $A+1$. This resulted in a constant fraction FR_A for age A (years) in the life of a cohort. Herewith, the development of a cohort's length-frequency distribution was correctly simulated from year to year, but not over shorter time periods. When age in years is used as a class interval, the number of classes is too small for a precise simulation of the dispersion, especially for short lived tropical species.

This problem is solved in the present model, by calculating the fraction *FR* for the time period that a batch of fish, born on a single day, needs to grow through a single length-class L_n.

$$FR = 1 - \frac{(s_{n+1}^2 - s_n^2)}{L_{n+1} - L_n}$$

L_n and L_{n+1} are the lower and upper limits of length class L_n and s_n and s_{n+1} are the standard deviations of the length-frequency distributions at L_n and L_{n+1}.

Recruitment is simulated by a daily recruitment rate to length class L_0. Recorded recruitment pulses around May and November, based on temporal patterns in mean *GSI* (Fig. 6.4a) and larvae abundance (Fig. 6.4b), are well separated in time. Temporary peaks in abundance, originating from distinct recruitment pulses, can be observed for single length-classes in the catch from experimental gillnets (Fig. 6.4c - 6.4d).

The recorded dispersion of specific length-classes over time (Fig. 6.4b - 6.4d) is used to calibrate the dispersion of fish, over the length-classes in the model. This recorded dispersion is not affected by the correction of length-frequency distributions for effort and selectivity of the sampling gear. Time-frequency distributions for single length-classes show considerable overlap when the fish have reached a length of 13 cm (Fig. 6.4d). The recorded dispersion is calibrated assuming a constant coefficient of variation, cv_{lfd}, for the length-frequency distribution of fish born on a single day. With this assumption, the equation for the fraction *FR* can be re-written as

$$FR = 1 - cv_{lfd}^2 * (L_n + L_{n+1})$$

where cv_{lfd} is the coefficient of variation of the length-frequency distribution. The increasing overlap of simulated time-frequency distributions corresponds with recorded patterns when cv_{lfd} is calibrated at 0.1. With this coefficient of variation, the fraction *FR* for length class L_n, from L_n to L_{n+1}, is calculated directly from L_n and cv_{lfd}.

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$$FR = 1 - cv_{ifd}^2 * 2 * L_n$$

Negative fractions would be obtained if more than 50 classes were used in combination with a coefficient of variation of 0.1. Therefore length classes larger than 1 cm are needed to calculate the fraction FR for fish species which grow larger than 50 cm, when the coefficient of variation equals 0.1.
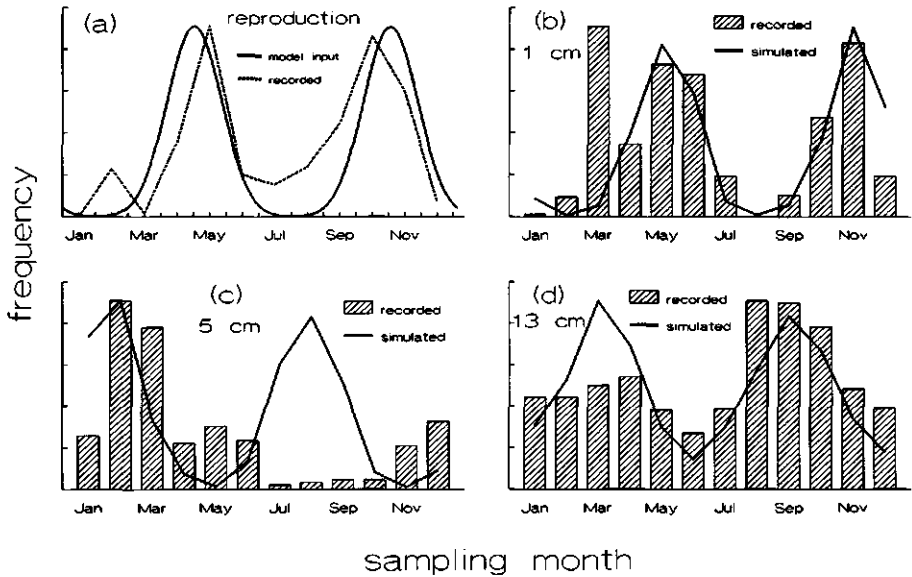

Fig. 6.4. Recorded and simulated reproduction pulses (a) and recorded and simulated temporal patterns in peak abundance of specific length-classes (b, c & d) of *O. mossambicus* in Tissawewa. The dispersion over time of specific length-classes, originating from distinct recruitment pulses (b, c & d), is used to calibrate the simulated dispersion of fish over the length-classes in the model.

The fishing mortality per length-class is a function of length-dependent gillnet selectivity and the estimated maximum fishing mortality for the most vulnerable size class. The model simulates a situation with three simultaneously operated mesh sizes in a variable ratio in terms of nets in operation. Gillnets of 64, 70 and 76 mm stretched mesh are operated in a ratio of 4:4:1 in the commercial fishery for *O. mossambicus* in Tissawewa.

The gillnet selectivity is simulated using the extended Holt model with constant coefficient of variation (Hamley, 1975; Pet *et al.*, in press b),

$$S = EXP \left(- (L - L_{opt})^2 / (2 * \sigma^2) \right)$$

where S is selectivity, L_{opt} is optimum selected length class calculated with $L_{opt} = k*m$, k is

selection factor, m is mesh size in mm stretched mesh and σ is standard deviation of selection curve calculated with $\sigma = cv_{sel} * L_{opt}$. The selection factor k and coefficient of variation cv_{sel} (Table 6.2) for *O. mossambicus* in multifilament gillnets were estimated at 0.246 and 0.073 respectively (Pet *et al.*, in press b).

The pattern in length-dependent fishery mortality, estimated with length-based cohort analysis, follows the shape of the combined selectivity curves (Pet *et al.*, submitted). The maximum fishing mortality, for the most vulnerable length-classes per sexe, was estimated with length-based cohort analysis at 5.7 yr^{-1} and 7.0 yr^{-1} year for males and females of 17 and 16.5 cm total length respectively (Pet *et al.*, submitted). This mortality is assumed constant throughout the year, since the fishing effort was also observed to remain constant (Pet *et al.*, in press a).

Total mortality was estimated by means of length converted catch curve analysis and natural mortality rates were estimated from data on unexploited species (Pet *et al.*, submitted) at 1.7 yr^{-1} and 1.9 yr^{-1} for males and females respectively. Natural mortality is assumed to be constant for all exploited length-classes. The smallest length class in the catch length-frequency distribution of *O. mossambicus* is 10 cm for the fishery in Tissawewa. The natural mortality for smaller length-classes is not known, but is also kept constant at the same level. This implies that absolute numbers per length-class are only valid above the length of first recruitment to the fishery (10 cm). The shape of the length-frequency distribution, in terms of peaks in abundance for certain length-classes, is expected to be valid at all times over the full size range from 0 to 35 cm.

The simulated population size is calibrated in the smallest length-class (L_R) for which the fishing mortality is higher than 0.1 yr^{-1}. It is assumed that absolute numbers for this length class, which is 13 cm for the fishery in Tissawewa, can be estimated accurately by means of length-based cohort analysis. The calibration is done by setting the maximum daily number of 0 cm recruits at such a level that the annual mean number of fish in L_R (13 cm) corresponds with the estimated number from cohort analysis. The estimated mean number of 13 cm fish was 65 000 individuals for the Tissawewa population, and this number is regarded as an input parameter.

The total number of fish in the model is spatially distributed over three areas (Fig. 6.5), representing habitats in the reservoir (Pet and Piet, 1993). The migration rate from area i to area j (V_{ij}) is calculated on the basis of numbers per size class in area i (N_{Ln})$_i$ and an instantaneous migration rate (*migrat*). The migration rate is corrected for densities by taking into account the size (*area$_i$*) of area i in relation to the total size of the reservoir ($\Sigma area$).

$$V_{ij} = migrat * (N_{Ln})_i * \frac{\Sigma\ area}{3 * area_i}$$

Based on the observed patterns in size-dependent habitat occupation (Pet and Piet, 1993), it is assumed that all fish in length class L_0 recruit to the population in one area, the littoral zone or area D. From here the fish start to spread out with migration rate V_{ij}, over the intermediate zone, area C, and the open water zone, area AB (Fig. 6.6a). At intermediate water levels, the surface areas of AB, C and D are 59, 73 and 46 ha respectively (Pet and Piet, 1993).
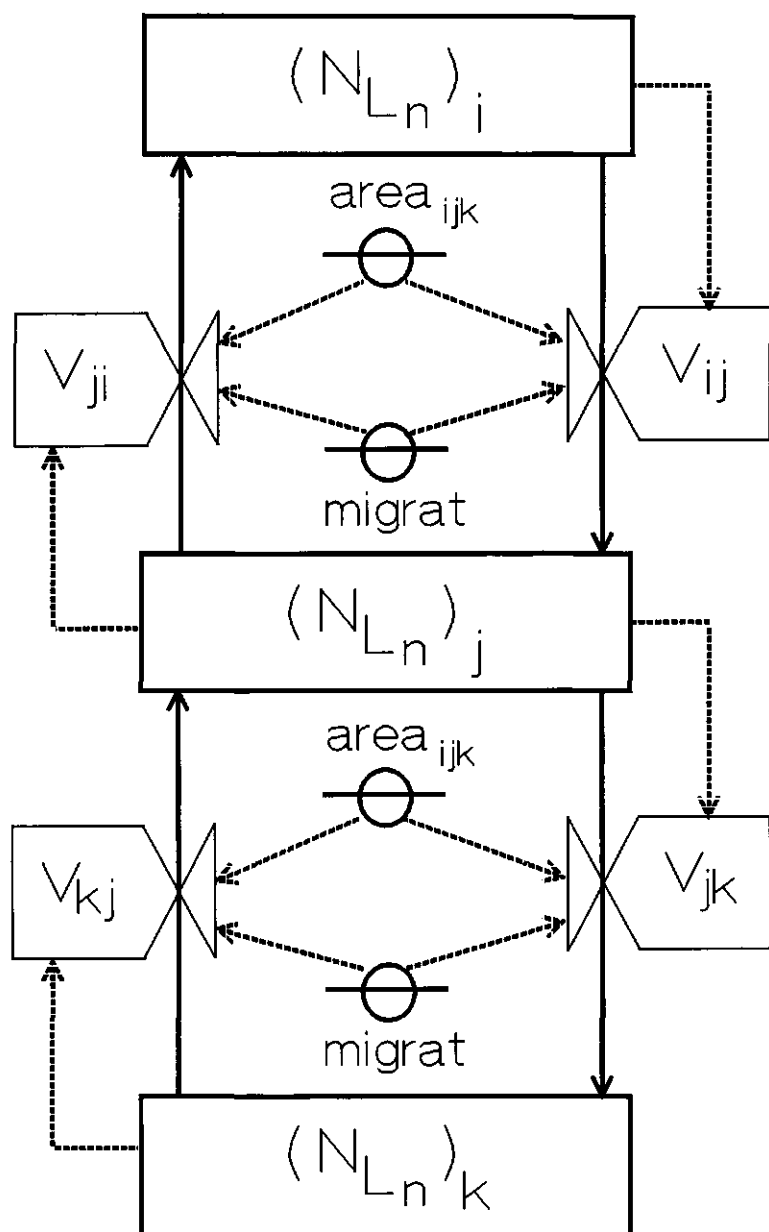
Fig. 6.5. Relational diagram of spatial distribution and migration in the model. Notations according to the conventions of Forrester (De Wit and Goudriaan, 1978) as in Fig. 6.1. $Area_i$ is the surface area (m^2) of area i, one of three areas in the reservoir. $Migrat$ is the instantaneous migration rate (day^{-1}) and $(N_{l,n})_i$ is the number of fish in length-class n in area i. V_{ij} is the migration rate of fish from area i to area j (numbers per day).
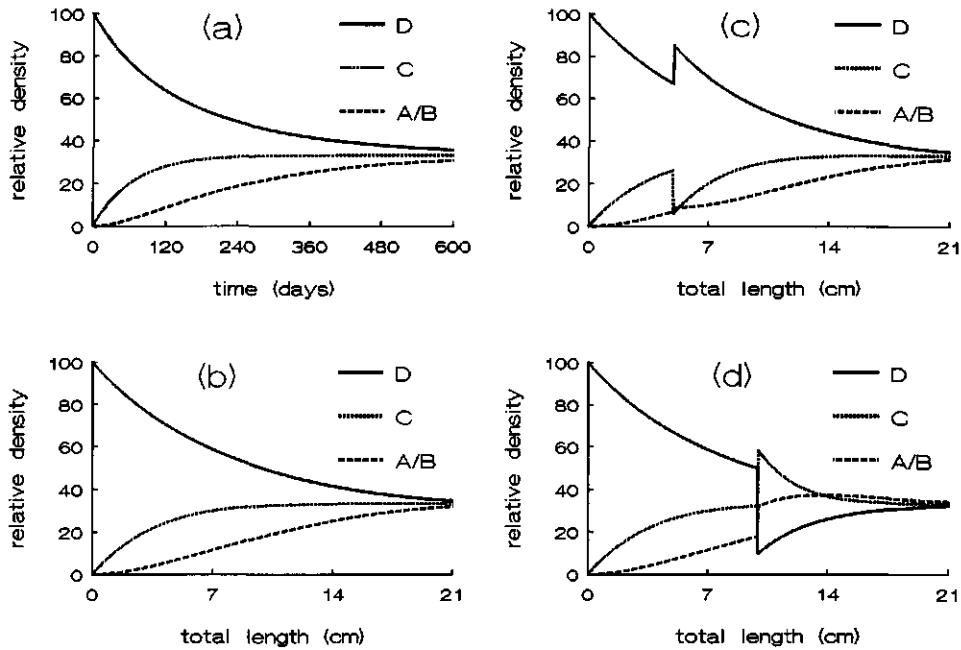
Fig. 6.6. Simulated spatial distribution patterns of the fish over three areas, with increasing age (a) and length (b). All fish in the simulation model are born in area D and the instantaneous migration rate (*migrat*) is equal for all length classes. Reaction of the simulated population to arbitrary disturbances of the distribution patterns. Removal of 20% of the fish at a length of 5 cm, all taken from area C (c). Removal of 40% of the fish at a length of 10 cm, all taken from area D (d).

Size-dependent habitat occupation results from the combination of migration rates between areas and the increase in length of the fish over time (Fig. 6.6b). The simulated distribution pattern continuously develops towards equal densities per size class for all areas. An equilibrium is only reached for larger size-classes (Pet and Piet, 1993), since fish of the smallest size class continuously recruit to the population in area D. The equilibrium in densities is regained following a disturbance by the fisheries (Fig. 6.6c & 6.6d). The simulated habitat occupation corresponds with recorded patterns when the instantaneous migration rate is calibrated at 0.005 day^{-1} (Fig. 6.7a & 6.7b). After calibration, a linear regression of simulated relative densities (sum of relative densities is 100) on observed relative densities showed a regression coefficient of 0.98 and an r^2 of 0.82 (30 observations).
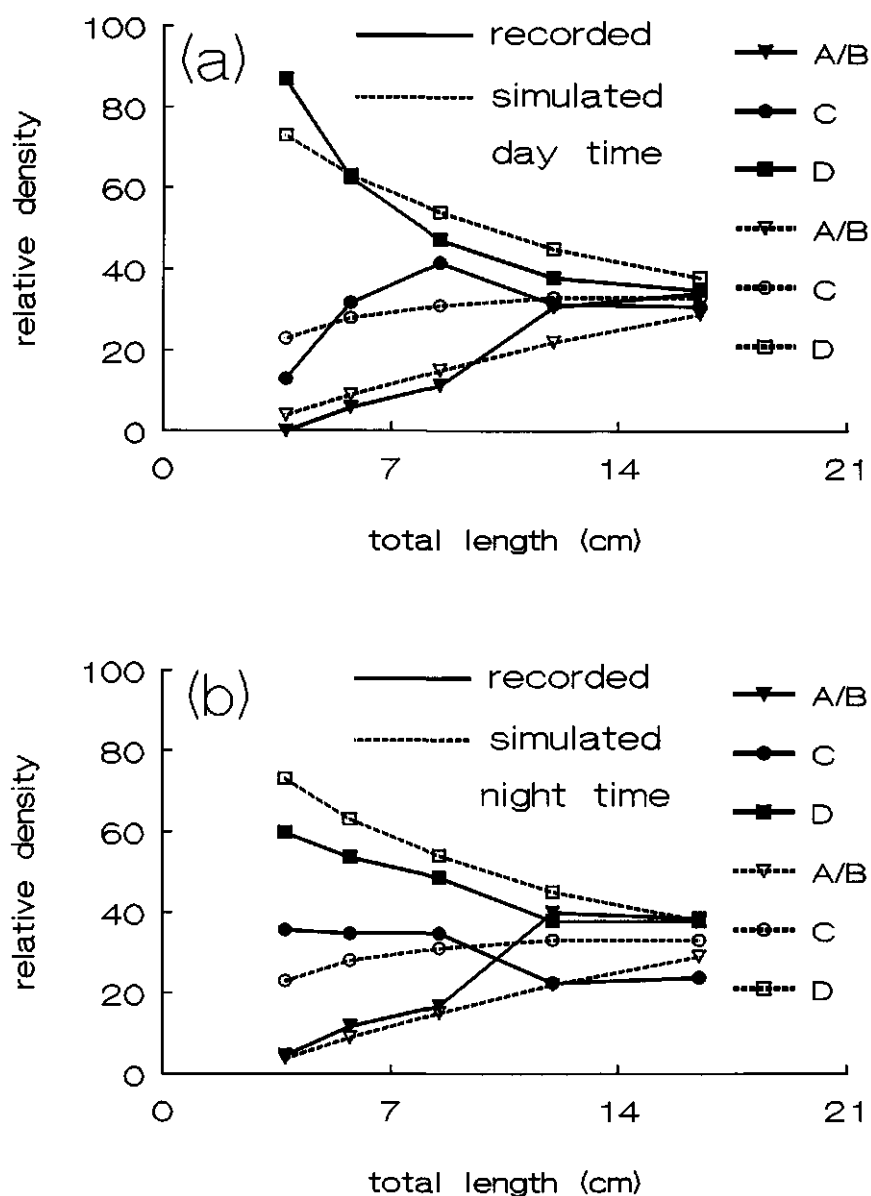
Fig. 6.7. Simulated and recorded spatial distribution patterns during day time (a) and at night (b). The simulated instantaneous migration rate (*migrat*) is 0.005 day^{-1} for all length classes. Data on size-dependent distribution from Pet and Piet (1993).

Results

Model validation

The population length-frequency distribution in an unexploited situation (Fig. 6.8a & 6.8b) is altered completely at sizes above 15 cm when the length-dependent fishing mortality is taken into account (Fig. 6.8c). The simulated catch length-frequency distributions compare well with distributions recorded on the landing sites during 1991 - 1992 (Fig. 6.8d) and mean lengths and standard deviations are almost identical (Table 6.2). The simulated size of the population above 10 cm total length, in numbers and biomass, is similar to the estimated size from length-based cohort analysis (Table 6.2). The sex ratio is slightly different at 1 : 0.8 (males : females) in the simulated population compared to 1 : 0.7 in the samples from experimental and commercial catches. This also has effect on the simulated biomass of the female spawning stock. The simulated annual catch (Table 6.2) of 29.7 tonnes corresponds with the estimated value of 28.6 tonnes from length-weight conversion of the total annual catch length-frequency distribution (Pet *et al.*, submitted).

The simulated population of fish above 10 cm total length fluctuates slightly with peak abundance and biomass in January and July (Fig. 6.9a). The simulated monthly catch fluctuates more with peak catches in December and June (Fig. 6.9b). This is 1-2 months earlier than the recorded peaks in catch per unit of effort (*CpUE*), which fell in January and August 1992 (Fig. 6.9c). Information obtained outside the regular sampling program indicated that the actual second peak in *CpUE* probably occurred in July 1992 (Pet *et al.*, in press a).

Sensitivity analysis for input parameters and time step

The sensitivity of the model for changes of 10% in input parameters is tested for factors controlling growth and mortality. The recruitment of 13 cm fish is regarded as an input parameter which does not affect the conclusions on management options and is kept constant at a mean of 65 000 individuals. The sensitivity analysis shows that the model is especially sensitive for the estimate of L_{inf} which controls the scope for growth (Table 6.3). Sensitivity for K, controlling the rate of growth, is also clear but only half as strong. The sensitivity for mortality parameters is not as strong as for growth parameters. The sensitivity for the selection factor k is evident but the effect can more easily be explained and validated by comparison of simulated and recorded catch length-frequency distributions. The choice of a time step of one day appears to be a conservative one since the output does not change materially when this time step is doubled (Table 6.3).

Management options for the fishery on O. mossambicus in Tissawewa

The model is used to evaluate management options for the improvement of catches in the gillnet fishery for *O. mossambicus* in Tissawewa. A range of mesh sizes in combination with different levels of fishing effort is tested with respect to the effects on the total catch (after stabilization) and the *CpUE* (Fig. 6.10). The maximum fishing mortality F for the most vulnerable length-class is assumed to be linearly related to the fishing effort. Each time three mesh sizes are used in a ratio of 4:4:1 in terms of numbers of nets in operation.
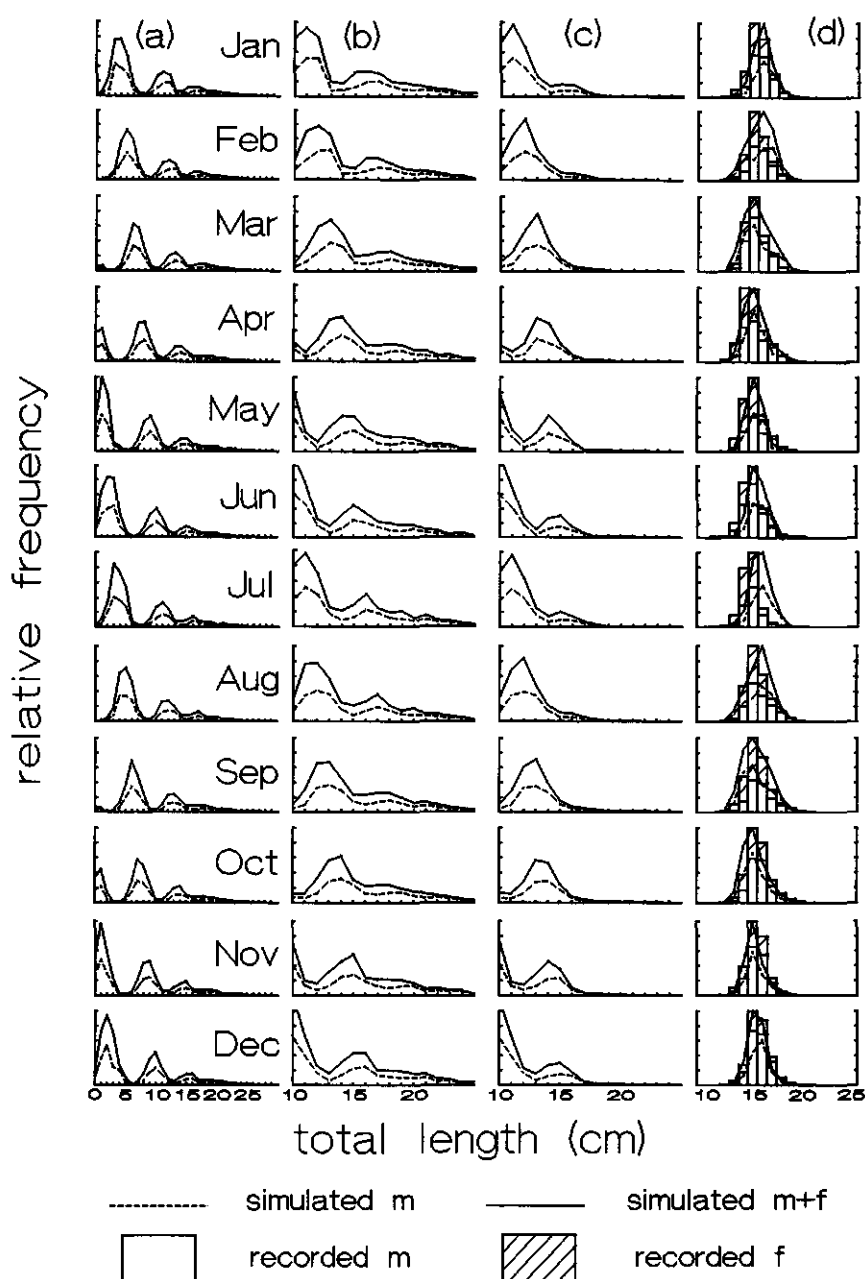
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Fig. 6.8. Simulated relative length-frequency distributions of male and female *O. mossambicus* in an unexploited population in Tissawewa (a) with details for the larger size classes (b) and the simulated impact of the gillnet fishery (c). Comparison of recorded and simulated relative length-frequency distributions of the catch of male and female *O. mossambicus* from Tissawewa (d).
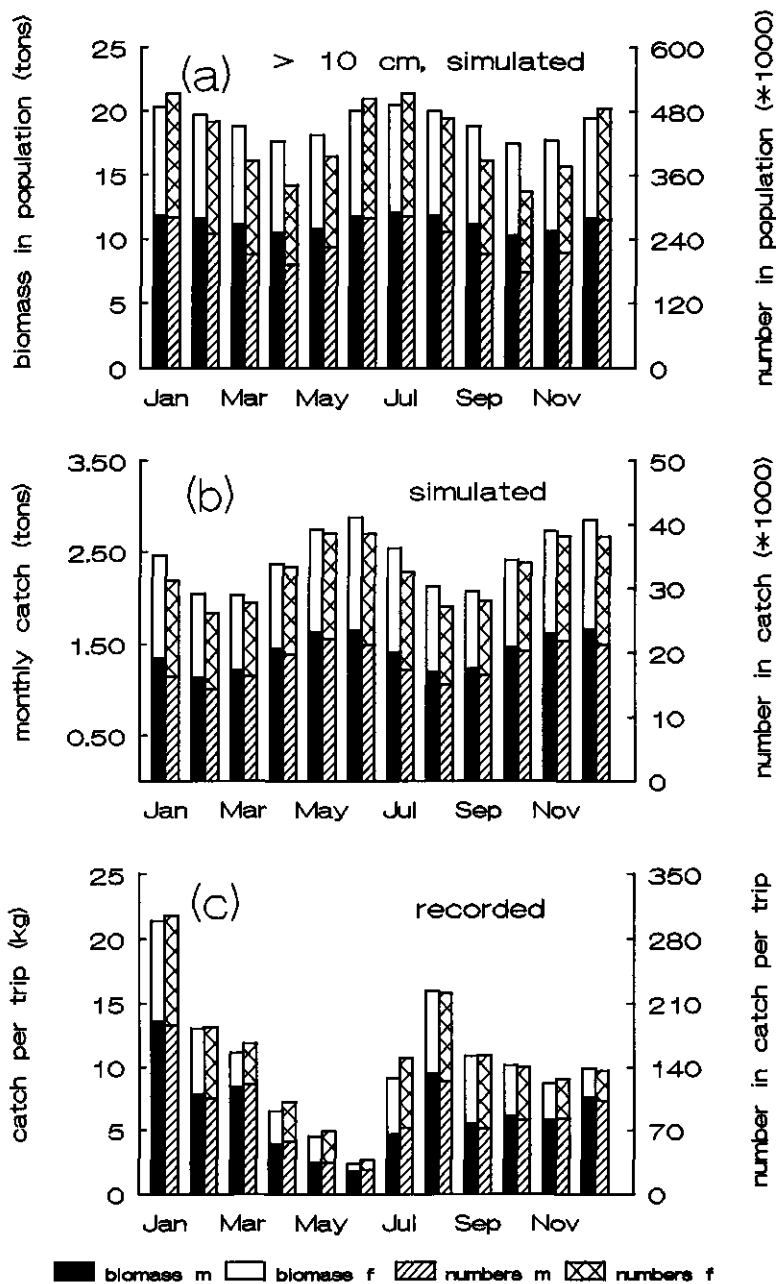
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Fig. 6.9. Simulated fluctuations in the biomass and numbers in the Tissawewa population (a) and catch (b) of *O. mossambicus*. Recorded fluctuations in the catch per unit of effort for *O. mossambicus* in Tissawewa between September 1991 and August 1992 (c).

Table 6.3. Sensitivity analysis for input parameters and time step.

relative change (%) in output[*]		POP	BIOM	FSSB	CATCH	L_c
input parameters[#]:	K	0	-6	-10	-12	0
- 10%	L_{inf}	-2	-12	-19	-25	0
	CV_{lfd}	-0	-1	-2	-1	0
	M	-0	2	6	5	0
	k	1	-1	-23	13	-7
	CV_{sel}	2	5	6	-3	0
	F	2	5	6	-2	0
input parameters[#]:	K	3	9	12	14	0
+ 10%	L_{inf}	5	20	25	26	0
	CV_{lfd}	1	1	2	1	0
	M	1	-2	-6	-5	0
	k	10	18	38	-5	13
	CV_{sel}	-1	-4	-6	3	0
	F	-1	-4	-6	2	0
increased time	2	0	0	0	2	0
step in days	3	0	1	2	5	0
(from 1)	5	1	3	4	10	0
	10	3	10	8	26	0

[*]Abbreviations of model output listed in Table 6.2. L_c, modal length in catch.
[#]Abbreviations of input parameters listed in Table 6.1.

The sequence of mesh sizes always has intervals of 6 mm, which means that '64 mm' in the isopleth diagrams stands for a combination of 64, 70 and 76 mm in a ratio of 4:4:1 (the present situation in Tissawewa). The effect of changes in fishing effort is tested for different fractions of the present level, which is 2677 trips per year (Pet *et al.*, in press a). The present situation in Fig. 6.10 is found at fishing effort = 1 and mesh size = 64 mm.

The catch-isopleth diagram (Fig. 6.10a) shows that any reduction of fishing effort or increase in mesh sizes, or any combination of these measures, would lead to a lower total catch. An increase of 50% in fishing effort would lead to a slight (5%) increase in the total catch but the *CpUE* would drop by 30%. The *CpUE*, which is to be considered as a return on inputs, would increase considerably (60%) when the fishing effort would be reduced by 50% (Fig. 6.10b) and total catches would decrease by only 20% in this case.

More detailed predictions, in terms of lag-times, initial losses and population parameters, are given for a range of mesh sizes in different ratios, both at the present level of exploitation and with a 50% reduction of fishing effort (Table 6.4). As in the catch-isopleth diagram for mesh sizes in constant ratios, the most striking result is that no combination of mesh sizes, ratios and/or reduction of fishing effort would lead to increased catches in the long term. An initial increase in catches (6%) is predicted to follow a reduction in mesh sizes from the present combination of 64, 70 and 76 mm, to a combination of 58, 64, and 70 mm in a ratio of 4:4:1. The catch would stabilize 2% below the present level, after a lag-time of two years. The total biomass of the population would decrease by 17% and the
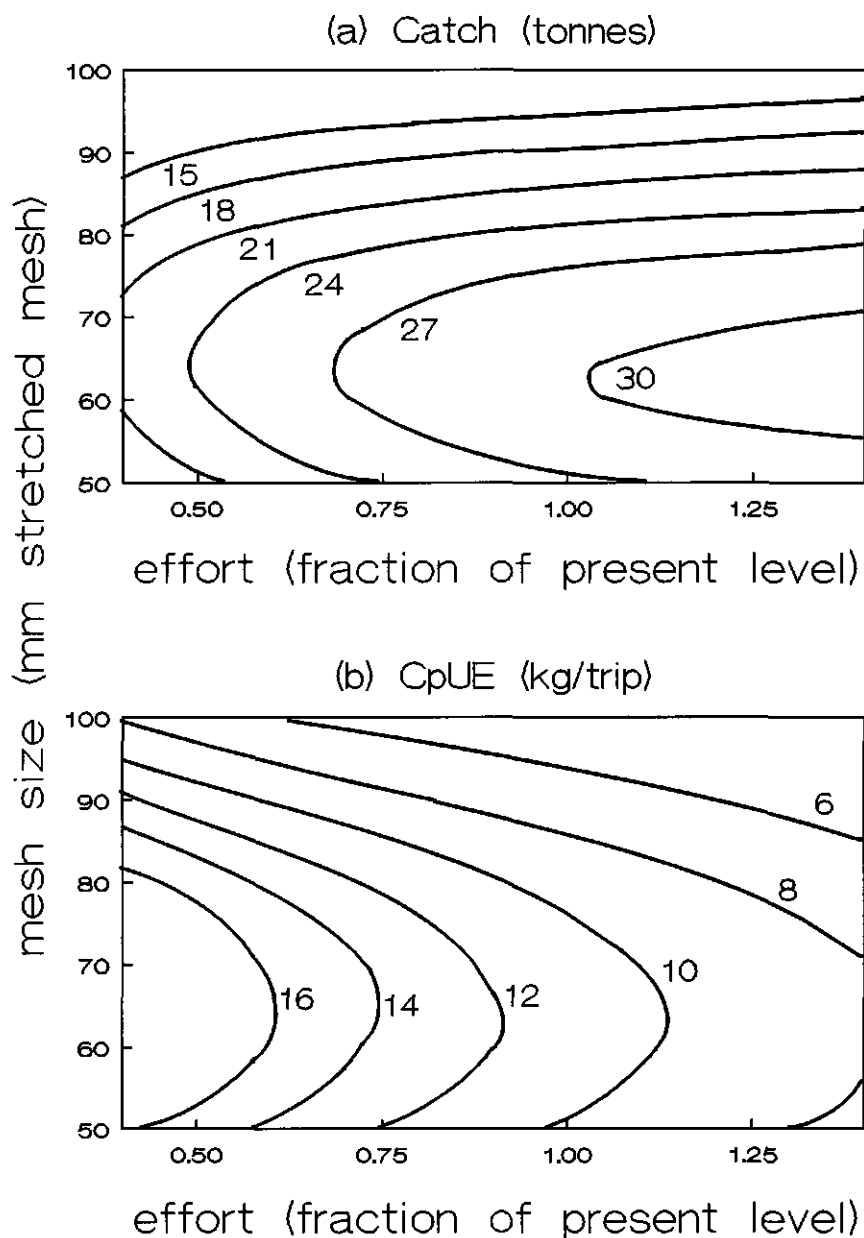
Fig. 6.10. Isopleth diagrams for total catch (a) and catch per unit of effort (*CpUE*) (b) in the gillnet fishery for *O. mossambicus* in Tissawewa. Each figure on the Y-axis represents a combination of three mesh sizes in a ratio of 4:4:1 in terms of nets in operation. The sequence of mesh sizes has intervals of 6 mm, therefore '64 mm' in the isopleth diagrams represents a combination of 64, 70 and 76 mm in a ratio of 4:4:1 (the present situation). The present level of fishing effort is 2677 trips/yr (Pet *et al.*, in press a).

Table 6.4. Effects of management regulations in terms of mesh size and fishing effort on relative yield and biomass of *Oreochromis mossambicus*, based on population parameters from Tissawewa.

m_a	m_b	m_c	r_a	r_b	r_c	F	C_1	C_2	C_3	BIOM	FSSB
64	70	76	1	1	0.25	100	100	100	100	100	100
58	64	70	1	1	0.25	"	106	98	98	83	65
"	"	"	1	0	0	"	89	85	85	100	79
64	70	76	1	0	0	"	94	92	92	107	100
"	"	"	0	1	0	"	84	94	94	120	131
"	"	"	0	0	1	"	69	91	91	137	167
70	76	82	1	1	0.25	"	84	97	97	120	137
"	"	"	0	0	1	"	52	82	82	157	202
76	82	88	1	1	0.25	"	65	90	90	140	177
"	"	"	0	0	1	"	34	70	70	178	238
64	70	76	1	1	0.25	50	73	80	80	138	146
"	"	"	1	0	0	"	65	67	67	152	160
"	"	"	0	1	0	"	60	71	71	158	177
"	"	"	0	0	1	"	49	71	71	168	200
70	76	82	1	1	0.25	"	61	79	79	151	175
"	"	"	0	0	1	"	36	65	65	181	229
76	72	88	1	1	0.25	"	47	73	74	166	206
"	"	"	0	0	1	"	23	55	57	196	258

Abbreviations: m, mesh size (mm); r, ratio per mesh size; F, fishing mortality (% of initial situation); C_n, annual catch after n years (%); BIOM, population biomass (%); FSSB, female spawning stock biomass (%).

female spawning stock by 35%, following such a reduction in mesh sizes. If only 58 mm is used, without additional larger meshes, the catch would drop by 15% within two years.

Combinations of mesh sizes only result in larger catches, compared to situations where all effort is concentrated in a single mesh sizes, when the smallest mesh size is less than 76 mm (Table 6.4). The small fish, which are caught in mesh sizes below 76 mm, grow fast and spend relatively little time in the vulnerable size classes. Combination of 76 mm with larger mesh sizes is not effective due to the slower growth of larger fish. In this case, the fish which do not die of natural causes are all caught in the 76 mm nets before they are large enough to become vulnerable to 82 mm nets.

Under a strict enforcement of the legal minimum mesh size of 76 mm stretched mesh, the population above 10 cm total length would increase by 19% to 511 400 and the sex ratio for fish in length classes above 15 cm would shift to a higher percentage of females (Fig. 6.11a). The biomass would increase by 37% to 26.2 tonnes and the female spawning stock biomass by 67% to a mean of 7.8 tonnes with peaks of almost 9 tonnes during the spawning seasons. The modal length of the fish in the catch would increase to 17-18 cm (Fig. 6.11b) and peak catches are expected around February and August, two months later than simulated peaks in the present situation. The total catch is predicted to decrease by 31% in the first year after enforcement of the '76 mm option'. The catch would stabilize at 26.9 tonnes, 9% below the initial level (Fig. 6.12a), already in the second year after implementation.
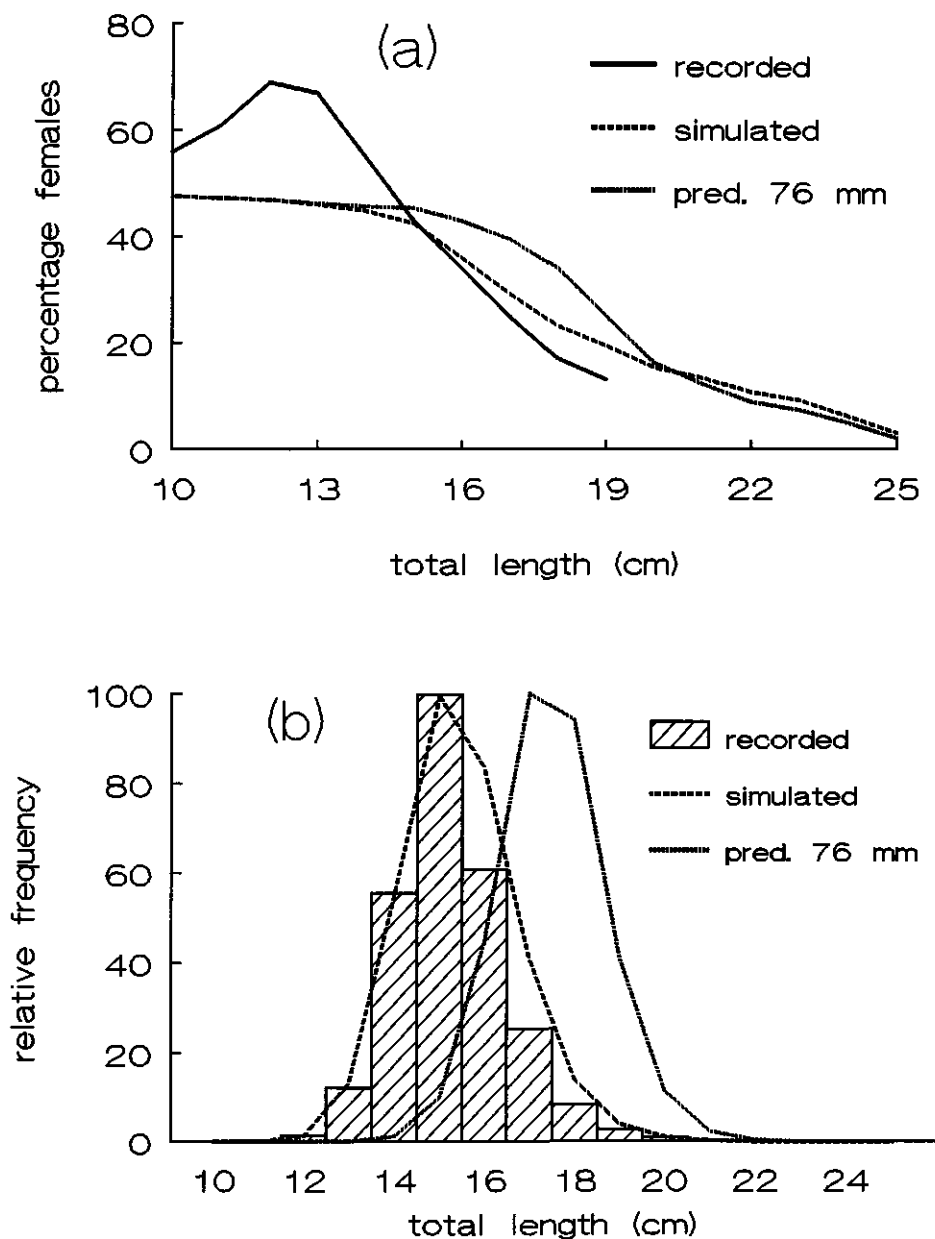
Fig. 6.11. Recorded and simulated length-dependent sex ratios of *O. mossambicus* in Tissawewa (present situation) and the predicted change (pred. 76) after introducing a minimum mesh size of 76 mm stretched mesh (a). Recorded and simulated length-frequency distribution of the catch (present situation with 64, 70 and 76 mm meshes in 4:4:1 ratio) with predicted change (pred. 76) after introducing a minimum mesh size of 76 mm (c).
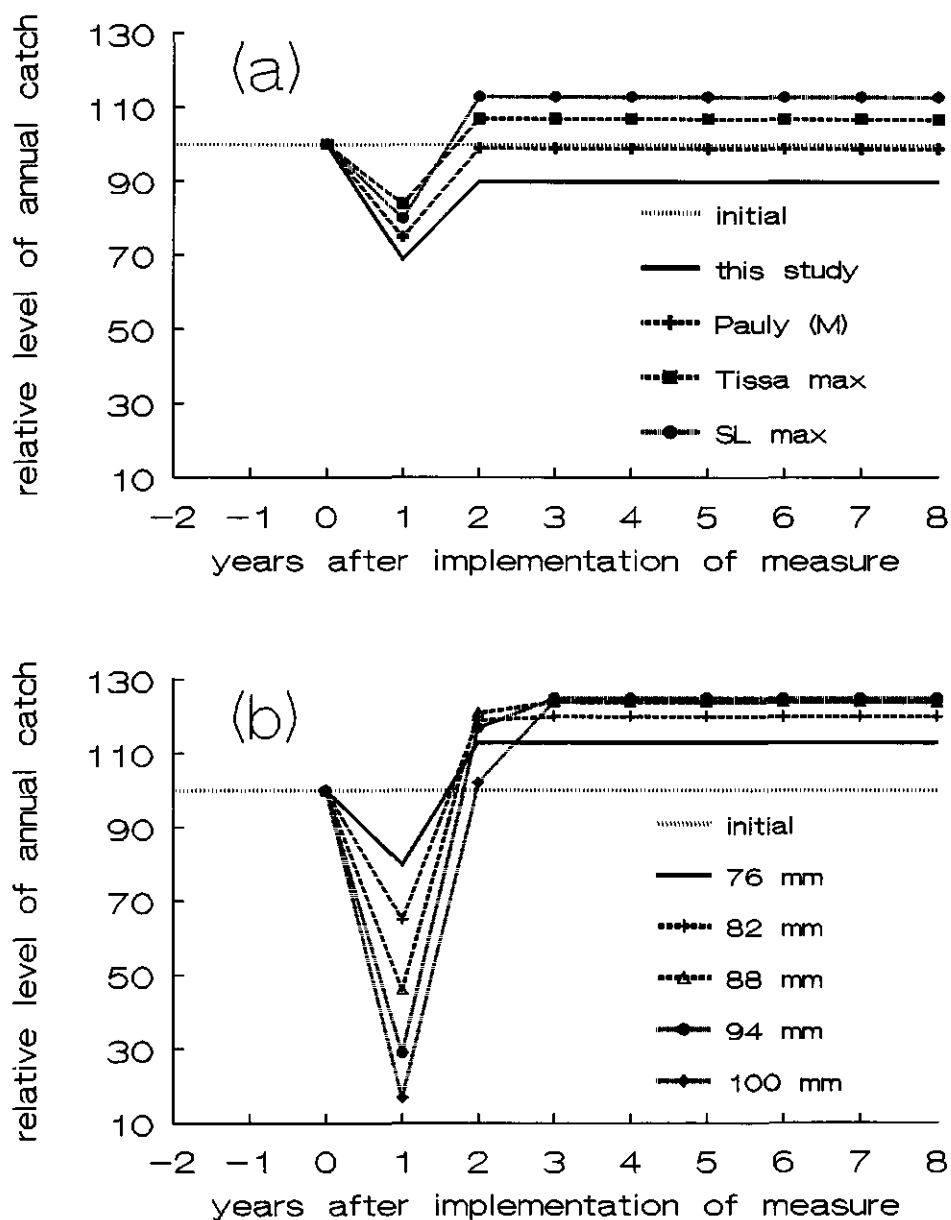
Fig. 6.12. Predicted catch levels (76 mm mesh) of *O. mossambicus*, for different parameter values and *Z* as recorded for Tissawewa (a). Pauly (M), *M* with Pauly's (1980) empirical formula; Tissa max, maximum L_{inf} and *K* and minimum *M* as reported for Tissawewa; SL max, maximum L_{inf} and *K* and minimum *M* as reported for Sri Lanka. Effects of different mesh size regulations under conditions of maximum growth ($L_{inf} = 40$ cm, $K = 0.3$ yr^{-1}) and minimum natural mortality ($M = 0.8$ yr^{-1}) with total mortality as recorded for Tissawewa (b).

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Model predictions in a country-wide perspective

The simulated effects of management regulations depend on the values of input parameters, especially for growth and mortality, which may differ between reservoirs or between estimation methods. Therefore, predictions for the total Sri Lankan reservoir fishery can only be made after reconsideration of the parameter values for growth and mortality, using the available literature on Sri Lankan reservoir fisheries. The '76 mm option' is reconsidered below, using various alternative estimates, or combinations of estimates, for growth and mortality parameters from the literature. The total mortality is kept constant at the level as estimated for the Tissawewa fishery and the fishing mortality changes with changing estimates for the natural mortality.

Estimates for the length-dependent patterns in fishing mortality over the exploited size range of *O. mossambicus* are not available for other reservoir fisheries in Sri Lanka. The maximum fishing mortality for male and female *O. mossambicus*, estimated with length based cohort analysis, was 5.7 yr^{-1} and 7.0 yr^{-1} for males and females of 17.0 and 16.5 cm respectively. This estimate is only valid for these length-classes and the corresponding time intervals of less than 1 month. The mean fishing mortality is lower when it is calculated over a wider size range or longer time interval. The mean values for males and females of 15.0 to 18.5 cm, estimated with length converted catch curve analysis are 4.7 yr^{-1} and 5.5 yr^{-1} for a corresponding time interval of 5 months. The mean fishing mortality over the exploited size range of 10 to 19 cm, corresponding with a time interval of one year, is calculated from the yield of 28.6 tonnes divided by the biomass of 17.6 tonnes. This mean fishing mortality is 1.6 yr^{-1}, which corresponds with the mean fishing mortality, over a period of one year, estimated in a study on the gillnet fishery for *O. mossambicus* in another man-made lake in Sri Lanka (Amarasinghe, 1987).

The natural mortality in the population of *O. mossambicus* in Tissawewa was estimated from data on unexploited species (Pet *et al.*, submitted) and the estimate is relatively high (1.7 yr^{-1} - 1.9 yr^{-1}) compared to literature data. Pauly's empirical formula for the estimation of natural mortality (Pauly, 1980; Sparre *et al.*, 1989) was used in previous studies on populations of *O. mossambicus* in Sri Lankan reservoirs (Amarasinghe, 1987; Amarasinghe *et al.*, 1989; De Silva, 1991). This formula relates natural mortality to the growth parameters and water temperature, on the basis of estimates for a large number of different fish stocks. An estimation according to this formula leads to a lower natural mortality of 1.3 yr^{-1} for males and 1.5 yr^{-1} for females and to a higher fishing mortality of 6.1 yr^{-1} for males and 7.4 yr^{-1} for females. With this lower estimate of natural mortality, the predicted dip in the catch of O. mossambicus, in the first year after implementation of the '76 mm option', would be 25%. The stabilized catch after 2 years would be 1% below the present level (Fig. 6.12a).

With respect to growth, it should be noted that the population of *O. mossambicus* in Tissawewa may be stunted due to heavy exploitation with small-meshed gillnets (Amarasinghe, 1988a; Pet et al., in press a). Stunting, in this case, would be caused by selectively fishing out the larger and faster growing individuals, resulting in a positive selection of smaller and slower growing fish (Rowell *et al.*, 1989; Smith et al., 1991; McAllister et al., 1992; McAllister and Peterman, 1992; Chambers, 1993). If stunting has

indeed occurred in Tissawewa, the mean growth potential of *O. mossambicus* may have decreased during recent years and may therefore be different in other Sri Lankan reservoirs.

The combined effect of a lower natural mortality and a higher growth potential of *O. mossambicus* in Tissawewa is evaluated, using growth parameters from an earlier study (De Silva *et al.*, 1988) on the same population. In this earlier study, the values of K and L_{inf} were estimated at 0.63 yr^{-1} and 32 cm respectively, without differentiation between sexes. Using Pauly's (1980) formula, the estimated mean natural mortality is 1.3 yr^{-1}, resulting in a mean fishing mortality of 6.8 yr^{-1}. With these values for growth and mortality parameters the dip in the catch of *O. mossambicus*, in the first year after implementation of the '76 mm option', would be only 16% and the catch would stabilize after two years at 7% above the initial level (Fig. 6.12a).

The best simulation result, in terms of ultimate catch levels, from the '76 mm option' is obtained using the mean of the most optimistic estimates reported on potential growth and natural mortality for Sri Lankan reservoirs (De Silva *et al.*, 1988; Amarasinghe *et al.*, 1989). These mean values are 0.3 yr^{-1} and 40 cm for K and L_{inf} respectively, irrespective of sex. With a natural mortality of 0.8 yr^{-1} the fishing mortality is estimated at 7.3 yr^{-1}. The most optimistic prediction for the '76 mm option' is an increase of catches by 13% after two years, following a dip of 20% in the first year (Fig. 6.12a).

Mesh size regulations for Sri Lankan reservoirs were recently proposed with minimum mesh sizes as high as 100 mm (Amarasinghe, 1992). Therefore mesh sizes in the model are enlarged further than 76 mm, to evaluate the effects of such measures. Using the most optimistic estimates for input parameter values, in terms of high growth potential and low natural mortality, the catches are predicted to increase up to a maximum of about 25% above the initial level for 88, 94 and 100 mm (Fig. 6.12b).

Effects of an additional small-meshed fishery for minor cyprinids on the existing fishery for O. mossambicus.

The model is also used to evaluate spatial differences in the effects of subsidiary small-meshed fisheries, for other (smaller) species, on the existing fishery for *O. mossambicus*. Gillnet fisheries with mesh sizes of 30 and 15 mm stretched mesh were proposed, targeting *Barbus* spp. and *Amblypharyngodon melettinus* (Valenciennes) respectively (Pet and Piet, 1993; Pet *et al.*, submitted).

The effects of the proposed mesh sizes on the catch of *O. mossambicus* are evaluated separately for all three habitats in the reservoir: the open water (area *AB*), the intermediate zone (area *C*), and the littoral zone (area *D*). The size distribution of *O. mossambicus* differs between habitats, with the smallest fish concentrated in area *D* and the largest fish evenly distributed over the reservoir. The maximum fisheries mortality in a subsidiary fishery is assumed to equal the mortality in the existing fishery, based on the assumption that the fishing efforts in both fisheries will be equal. The losses to a fishery with 76 mm stretched mesh for *O. mossambicus* are calculated in terms of the weight of the catch of fish above 13 cm total length. The length class of 13 cm is the smallest one in the catch length frequency distribution of 76 mm gillnets. Losses are calculated separately for the two proposed additional fisheries with 30 and 15 mm stretched mesh respectively. Predicted

losses, in terms of weight of the catch of *O. mossambicus* larger than 13 cm, are 12, 32 and 46% following introduction of 30 mm stretched mesh in area *AB*, *C* and *D* respectively (Table 6.5). These predicted losses are 3, 12 and 36% following introduction of 15 mm stretched mesh in the same areas.

Table 6.5. Effects on the existing fishery of introduction of small-meshed gillnets in different areas of the reservoir.

tilapia[*]	76	76	76	76	76	76	76
cyprinids[#]		30 *AB*	30 *C*	30 *D*	15 *AB*	15 *C*	15 *D*
Population	511	450	347	276	499	449	328
Biomass	26.2	23.0	17.8	14.2	25.6	23.0	16.8
FSSB	7.8	6.8	5.1	4.1	7.6	6.8	4.8
Catch	26.9	25.3	22.7	20.6	26.3	24.0	18.5
Catch ≥ 13	26.9	23.8	18.3	14.6	26.2	23.7	17.3
Loss (%)		12	32	46	3	12	36

[*]Mesh size used (mm) in the existing fishery. [#]Mesh size used (mm) and fishing area in the introduced fishery. Population numbers are divided by 1 000. Biomass, female spawning stock biomass (*FSSB*) and catch are given in tonnes. Losses in the existing fishery are calculated from the catch of tilapia larger than 13 cm (Catch ≥ 13).

Discussion and conclusions

Evaluation of the model

After calibration of the model with input parameters as estimated for the population of *O. mossambicus* in Tissawewa, the simulation results of the model are in agreement with independent estimates for the output parameters. Besides a good precision, the model possesses a high degree of realism when simulating size-structured processes in gillnet fisheries, especially when compared to the more traditional and widely accepted yield models (Beverton and Holt, 1957). The simulation of length-dependent fishery mortality is the only realistic option in situations where short-lived tropical species are exploited with size-selective gear over short length- and time-intervals. The estimation of a mean fishing mortality for complete age-groups is not very meaningful in these situations, unless age is expressed in time units much shorter than one year. In a combined study on 52 different species of fish from Indonesian waters, the age of full recruitment to the fisheries was below one year in 67% of the cases, below 2 years in 96% of the cases and below 3 years in all cases (Dwiponggo et al., 1986).

The model is also realistic in the simulation of size-dependent spatial distribution patterns of the fish and can therefore differentiate between various habitats with respect to the effects of optional management measures. Model predictions can be specified for various spatial allocation patterns of fishing effort per mesh size. This is essential in multi-species gillnet fisheries exploiting species with various size-dependent spatial distribution patterns, but the spatial allocation of the fishing effort may also be important in many other types

of fisheries (Fletcher, 1992; Gillis *et al.*, 1993).

Another feature of the present version of the model is the high degree of generality. The flexibility in simulation of various temporal patterns in recruitment makes this model a useful management tool for both temperate and tropical gillnet fisheries. The model resolution is at the population level, which is sufficient to simulate the variation in growth with the "fractional boxcar train method". Description of processes on the level of individual fish (Hampton and Majkowski, 1987; Madenjian, 1991) would not contribute much to the understanding of the most essential features of gillnet fisheries.

The model provides detailed predictions (per sex) on the developments in population and catch after implementation of a management measure. The output shows the temporal patterns in population-size, spawning stock and catch in numbers and weight. Developments in length-frequency distributions and length-dependent sex ratios are given for population and catch. The model not only predicts the ultimate levels of population size and catch, but also the lag-time to stabilization. In case of a temporary loss, for example after implementation of a mesh size enlargement (Fig. 6.12), the model provides information on the maximum temporary loss per year and the total temporary loss until the initial level of catch is regained. The model also predicts the time needed to regain this initial level of catch, and the time needed to compensate the temporary loss (time until 'break-even point'). This information on temporary losses and various lag-times is needed to facilitate decision making and planning in fisheries management (Buijse *et al.*, 1992).

The stock recruitment relationship and management objectives.

An important addition to the present version of this model would be the inclusion of a stock-recruitment relationship (Gulland, 1983; Rothschild and Mullen, 1985; Hilborn and Walters, 1992). Density dependent effects on recruitment have not been quantified for *O. mossambicus* in Sri Lankan reservoirs. Therefore the present version of the model does not include such effects as has been done, for example, in population models for the north American walleye (Shuter & Koonce, 1977; Jensen, 1989; Jensen 1991) and southern New England yellowtail flounder (Sissenwine, 1977). The present model does provide an assessment of the female spawning stock biomass, which can be evaluated by itself.

Environmental factors are known to affect recruitment in many fish stocks (Swartzman *et al.*, 1983; Henderson and Nepszy, 1988; Buijse and Houthuijzen, 1992; Cowan *et al.*, 1993). Although the rainy seasons are known to induce increased spawning activity in *O. mossambicus* populations in Sri Lankan reservoirs (De Silva and Chandrasoma, 1980; De Silva, 1983; Pet *et al.*, submitted), little is known about the effects of environmental factors on the survival of *O. mossambicus* larvae. The preferred habitat of *O. mossambicus* larvae in Tissawewa is the shallowest part of the littoral zone (Pet and Piet, 1993), especially those parts with vegetation and a detritus layer on the bottom. During the rainy seasons most reservoirs have large areas of this habitat available and hardly any other fish are present here. Only a minor part of the available habitat is occupied by *O. mossambicus* larvae in Tissawewa and the carrying capacity of the littoral habitat may therefore not be fully utilized by these larvae.

The carrying capacity of the Sri Lankan reservoirs for larger size-classes of *O.*

mossambicus also remains to be assessed, but competition for food with *A. melettinus* is likely to occur (Pet and Piet, 1993). The spawning habitat in the reservoirs may be almost fully occupied, based on the densities of nesting sites which can be observed during low water levels (De Silva and Sirisena, 1988; Pet, pers. obs.). These observations would lead to the hypothesis that recruitment of *O. mossambicus* in Sri lankan reservoirs is presently not limited by the carrying capacity for larvae but rather by the size of the niche available to the adult stages. This niche may be almost fully utilized at present and model predictions of an increased population and female spawning stock biomass should be interpreted in this light.

Sri Lankan reservoirs show little variation in *CpUE* between reservoirs. Moreover, reservoirs with lower fishing pressure do not show significantly higher *CpUE* values (De Silva, 1985; De Silva et al., 1991), and may therefore not have a higher fish density. This may confirm the hypothesis that populations of *O. mossambicus* are close to their maximum density in most reservoirs, since these reservoirs are considered very similar in terms of carrying capacity per unit surface (De Silva, 1985). Based on the limited inter-year variation in the *CpUE* of *O. mossambicus* in Sri Lankan reservoirs (De Silva *et al.*, 1991), the recruitment seems to be quite constant in this fishery.

The variation in recruitment and related problems of yield-stabilization can be major issues in fisheries management (Silvert, 1982; Buijse et al., 1994), but apparently not in the Sri Lankan reservoir fisheries. More important issues are the returns on effort and the maintenance of the overall level of the catch which together determine the socio-economic position of the fishermen (Amarasinghe, 1988b; De Silva, 1988). The total catch is also increasingly important as a source of high-protein food for the rural population (De Silva, 1988).

Recommendation of management regulations

Based on model predictions, a conservation of the existing fishery by re-enforcement of the minimum mesh size of 76 mm stretched mesh is recommended for Sri Lankan reservoirs. This mesh size would reduce the chance of stunting in *O. mossambicus* populations, since the peak in the length frequency distribution of the catch would shift from 15 to 17-18 cm, leaving fish of 16 cm a chance to reproduce. The size at maturity for *O. mossambicus* was reported to range from 15.5 to 21.0 cm in previous studies on Sri Lankan reservoir populations (De Silva, 1986; De Silva et al., 1988; Amarasinghe, 1988a). A stabilization level around or just above the present level of catch is expected from this measure, after a short lag-time of two years and a relatively small temporary loss (less than one third of the annual catch) in the first year. Lag times will be short in general for fast growing, short lived and early maturing species in tropical situations, especially when compared to fisheries for large size classes of percids in temperate climates (Buijse *et al.*, 1992).

The results of the '76 mm option' should be monitored through catch and effort data recording (Pet *et al.*, in press a), and evaluation of the catch and its size-structure, after several years, should lead to further decision making. If catch levels increase with more than 10% and fish of 18 cm become dominant in the catch, the minimum mesh size may

be enlarged some more to 82 mm. A reduction of growth overfishing, through an increased minimum mesh size, will not lead to a large (> 25%) increase in the annual catch of *O. mossambicus*. Minimum mesh sizes above 88 mm will lead to great losses during the first year, longer periods for catches to return to their initial level and longer periods to regain losses and reach stability. Mesh sizes above 88 mm stretched mesh will not lead to a further increase of catches and should therefore not be considered.

Fishermen societies in Sri Lanka are willing to accept management regulations if these would be agreed upon unanimously and would be strictly enforced on all fishermen (Amarasinghe, 1988b; Pet-Soede, 1993). The fishing effort in terms of active fishermen should be limited to the present level. This is possible in cooperation with the fishermen's societies, which practice a limited access to the fishery. A reduction of the fishing effort in terms of nets per fisherman is not recommended, since a decrease in the total catch of each fisherman is predicted to follow such a measure. The costs of fishing are very low in this fishery (Pet-Soede, 1993) and the fishermen are therefore more interested in their total catch than in the catch per net. A reduction of the total number of fishermen is also not recommended since there is no alternative employment for them. Moreover, a reduction of the total catch should be prevented, since *O. mossambicus* is an important source of cheap high-protein food for the rural population.

If the legal minimum is not strictly enforced, the fishermen may start using mesh sizes below 64 mm since the model predicted an initial increase of catches when mesh sizes are lowered to 58 mm in combination with 64 and 70 mm (Table 6.4). The increase in catch with this combination will only be temporary, since the available fish of 14 cm will soon be decimated. The catch will stabilize at the present level but small fish (< 15 cm) will be caught and the female spawning stock biomass will decline by 35%, probably resulting in decreased recruitment and even greater losses in the long term, when we assume a relation between stock and recruitment (Sissenwine, 1977; Jensen, 1982; Cook & Armstrong, 1986). On the other hand, the loss of female spawning stock biomass may be overestimated here, since the length at maturity may become even smaller following a lowering of mesh sizes. Small fish from 58 mm gillnets, with a mean length of 14 cm, can still be sold at the markets, as shown by fishermen sporadically using this mesh size at present and selling fish as small as 13 cm.

An introduction of 30 mm stretched mesh, for the exploitation of *Barbus* spp., is predicted to lead to serious losses in the fishery for *O. mossambicus*. The *Barbus* spp. are concentrated in the intermediate zone and the littoral zone of the reservoir (Pet and Piet, 1993), and the vulnerable size classes of *O. mossambicus* (7-10 cm) are also abundant in these two areas. The fishery for these species is expected to concentrate in the same two areas, since observations on the spatial allocation of fishing effort indicated that fishermen follow concentrations of fish, even into the littoral zone of the reservoir (Pet et al., in press a). The predicted losses, following introduction of the *Barbus* fishery, are 32 to 46% of the catch (Table 6.5) in terms of weight of *O. mossambicus* above 13 cm total length. The actual losses may turn out even higher in the long term, since the female spawning stock will be reduced by 35 to 47%.

The losses in the tilapia fishery are expected to be less heavy following introduction of

a fishery with 15 mm stretched mesh, since the vulnerable size-classes of *O. mossambicus* (< 4.5 cm) are only abundant in the shallowest parts of the littoral zone. This fishery would mainly be targeting *A. melettinus*, a small pelagic cyprinid which is abundant in the intermediate and open water zone of the reservoir. It is therefore expected that a fishery for *A. melettinus* will concentrate in these two areas of the reservoir. The predicted losses after introduction of 15 mm gillnets are 3 to 12% of the catch in terms of weight of *O. mossambicus* above 13 cm total length. The reduction of the female spawning stock biomass of *O. mossambicus* will be only 3 to 13%. The gain from this fishery is expected to be relatively high since the biomass of *A. melettinus* is an order of magnitude higher than the biomass of *O. mossambicus* (Pet et al., submitted).

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Curriculum vitae

Jos Pet werd op 26 oktober 1962 in Leiderdorp geboren. In 1981 behaalde hij het VWO-diploma aan het Christelijk Lyceum Visser 't Hoofd in Leiden. In 1983 behaalde hij het Propedeuse diploma aan Technische Universiteit in Delft en in 1984 werd begonnen met de studie Zootechniek aan de Landbouwuniversiteit in Wageningen. In 1989 studeerde hij daar af (met lof) als Ingenieur in de Landbouwwetenschappen met als hoofdvakken Visserijkunde, Visteelt en Theoretische Productie Ecologie en stages voor Visserijkunde en Visteelt. Van 1989 tot 1991 is hij als wetenschappelijk projekt medewerker van de vakgroep Visteelt en Visserij werkzaam geweest op het NUFFIC/UNIBRAW/LUW visserij-projekt aan de Faculty of Fisheries van de Brawijaya University in Malang, Indonesia. Gedurende 1991 is hij als onderzoeker in opleiding in dienst geweest bij NWO en werd hij gestationeerd op het RU/WOTRO/NIE/WAU visserij-projekt bij het Department of Zoology van de Ruhuna University in Matara, Sri Lanka. Tijdens deze periode werd het in dit proefschrift beschreven onderzoek opgestart. Van eind 1991 tot begin 1995 is hij, tot en met 1993 gestationeerd bij de Ruhuna University in Sri Lanka, als assistent in opleiding werkzaam geweest bij de vakgroep Visteelt en Visserij waar dit proefschrift werd afgerond.