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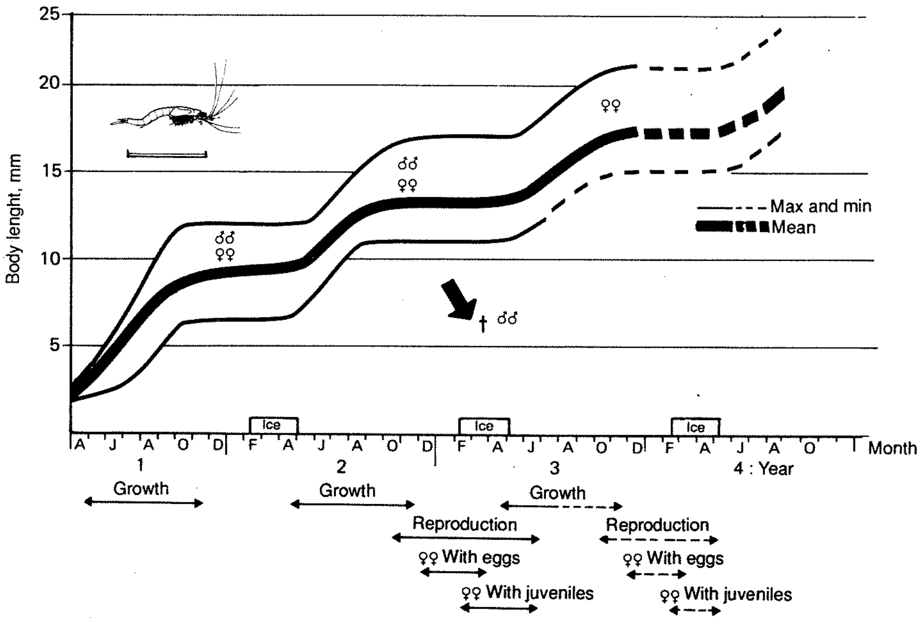
Mysis relicta i Mjøsa

Livshistorie og trofisk funksjon



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Ekstrakt:

Biologien hos krepsdyret Mysis relicta er undersøkt over en periode på 17 år i Mjøsa. Rapporten presenterer de viktigste data på fødevalg, vertikalutbredelse, livshistorietilpasning og diskuterer den trofiske rolle Mysis spiller i det pelagiske økosystem. Krøkle synes å være en nøkkelart i systemet, som i stor grad regulerer forekomsten av Mysis. Ubalanse i samspillet krøkle-Mysis-dyreplankton vil kunne få betydelige konsekvenser for næringsnettstrukturen i Mjøsa.

4 emneord, norske:
1. Mysis relicta
2. Fødevalg
3. Livshistorie
4. Trofisk funksjon

4 emneord, engelske:
1. Mysis relicta
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FORORD

Økologien til *Mysis relicta* i Mjøsa er undersøkt siden 1972 i forbindelse med Mjøsundersøkelsene og det pågående overvåkingsprogram. Deler av dette materialet er presentert i tidligere rapporter fra Mjøsundersøkelsen, men noen samlet presentasjon og vurdering av den trofiske funksjon *Mysis* innehar i sjøen finnes ikke. Sett på bakgrunn av de undersøkelser som er foretatt i sjøer hvor *Mysis* opptrer som en ny art i økosystemet (enten via utsetting eller naturlig spredning), er det et klart behov for dokumentasjon omkring økologien til denne organismen i sjøer hvor den er en naturlig del av økosystemet, og har tilpasset seg økosystemet gjennom flere tusen år. På denne bakgrunn bevilget Nasjonalkomiteen for Miljøforskning, ved Program for Fiskeforsterkningstiltak, midler for en supplerende undersøkelse omkring vandringsmønster og fødevalg hos *Mysis* i Mjøsa. Et videre siktemål var at dette materialet skulle integreres i øvrige studier, og ende opp i publisering basert på det omfattende materialet fra hele perioden 1972 - 89. Prosjektet ble også fulgt opp med feltundersøkelser i innsjøene Bjørkelangen og Rødnessjøen i Haldenvassdraget, begge sjøer med naturlige populasjoner av *Mysis*. Disse dataene er under bearbeidelse, og vil bli rapportert ved utgangen av 1991. I denne rapporten presenteres en generell oversikt over økologien til *Mysis relicta* i Mjøsa, fulgt av to publiseringsklare artikler som i større detalj beskriver og diskuterer de ulike aspekter som behandles i oversikten.

INNLEDNING

Mysis relicta er en stor (opptil 2.5 cm) pungreke som forekommer naturlig i en rekke innsjøer under marin grense på den nordlige halvkule. På grunn av artens potensielle rolle som fødekilde for fisk, har den blitt satt ut i en rekke innsjøer både i Nord-Amerika og Skandinavia med det formål å bedre fødegrunnlaget for naturlige fiskebestander (Lasenby et al. 1986). I perioden 1968-74 ble Mysis satt ut i ni av de største regulerte sjøene i Trøndelag, og har fra disse igjen spredd seg til nye sjøer i området. Mange av disse utsettingene, både i innland og utland, har klart demonstrert problemet med utsetting av arter som ikke er tilpasset det naturlige økosystem. Mysis ernærer seg i stor grad av dyreplankton, og har spesielt i røyevann framstått mer som konkurrent enn fødekilde, ofte med betydelige negative effekter på zooplankton og fiskefauna (Furst 1981, Langeland 1981, 1988, Lasenby et al. 1986). En stor epilimnetisk Mysispopulasjon kan gi en dramatisk reduksjon av viktige algebeitere blant zooplanktonet som Daphnia spp. og Bosmina spp., og en sekundæreffekt av dette blir redusert beitekontroll over planktonalgene. Lien m. fl.(1988) beregnet at den store Mysis-populasjonen i Snåsavann ga en økning i algebiomasse som tilsvarte ekstra fosforbelastning på 12 tonn pr. år. Til tross for en betydelige usikkerhet i slike beregninger, indikerer dette at i tillegg til en negativ effekt på fisket, kan Mysis også indirekte ha en negativ innvirkning på vannkvaliteten.

I de sjøer hvor Mysis forekommer "naturlig" (dvs. innvandret under siste istid), finner man ofte en helt annen romlig fordeling i sjøen, et helt annet mønster for predasjon, og en mindre dramatisk effekt på de øvrige komponenter i økosystemet. Viktigst er kanskje at det har innstilt seg en predator-kontroll med tettheten av Mysis, hvor ofte lake er viktig predator i bunnområdene, og krøkle og ørret er predatorer i de frie vannmasser. Spesielt krøkle synes å spille en viktig rolle når det gjelder å regulere både biomasse og vertikal utbredelse av Mysis i mange av de sjøer som har en naturlig Mysisbestand.

MYSIS I MJØSA

I likhet med andre innsjøer der Mysis forekommer i større bestander, utgjør den i Mjøsa et viktig ledd i innsjøens pelagiske næringskjede. Den utgjør et viktig fødeemne først og fremst for krøkle, men også for lake, hork, abbor og i noen grad sik, samt krepsdyret <u>Gammaracanthus loricatus</u>. Mysis innvandret antakelig til Mjøsa straks etter siste istid (for 8 - 10 000 år siden), og har derfor en livshistorie som er vel tilpasset den øvrige fauna i innsjøen.

<u>Utbredelse:</u>

Mysis forekommer i hele Mjøsa med størst individtetthet der innsjøen har større dyp enn 80 meter. Ved en regional inventering som ble foretatt i oktober 1980, ble det funnet størst forekomst i Mjøsas sentrale deler, inklusive Furnesfjorden. Senere enkeltprøver fra ulike deler av sjøen bekrefter dette inntrykket. I områder med større dyp enn 80 meter forekommer Mysis pelagisk hele døgnet, men med en hovedutbredelse i området 60 - 120 meter på dagtid. De yngre individene står da noe høyere i vannmassene enn de eldre. I områder grunnere enn 80 m står Mysis i eller nær sedimentet på dagtid. Om sommeren finnes Mysis sjelden grunnere enn 20 meter i littoralsonen, mens på vinteren kan den vandre helt inn i strandsonen.

<u>Mengde og biomasse:</u>

Individantall og biomasse av Mysis over Mjøsas sentrale områder viser betydelig variasjon både gjennom året og mellom de ulike år. Størst individtetthet finnes som regel på forsommeren da hunnene slipper ungene, men enkelte år kan også individtettheten øke utover høsten. På grunn av tilveksten finnes også den høyeste biomassen om høsten.

Laveste tetthet og biomasse, beregnet som middelverdi for perioden mai - oktober, ble funnet i 1989 (75 ind. og 100 mg tørrvekt m^{-2}), mens høyeste ble funnet i 1983 (> 400 ind. og 400 mg tørrvekt m^{-2}). Høyeste enkeltregistrering hadde over 1000 ind. m^{-2}, og den høyeste tørrvekten var 900 mg m^{-2}. Gjennomsnitt for hele perioden (1972-89) ligger noe over 200 ind. m^{-2} og 300 mg m^{-2} for individtall og biomasse. I grunnere områder (20-50 m) ligger individtettheten som regel i området 20 - 120 ind. m^{-2}.

<u>Produksjon:</u>

Produksjonsberegninger uttrykt som nettoproduksjon pr. m^2 ble beregnet for vekstsesongene 1976, 1978, 1979 og 1980. Hovedproduksjonen foregår i tidsperioden mai-oktober, men en viss tilvekst skjer også i november-desember. Beregningene er basert på inividenes kumulative biomasseøkning gjennom året. I tillegg skjer produksjon av egg og unger på senvinteren. Dette er ikke regnet med i disse produksjonsestimatene, slik at den totale årsproduksjon blir noe høyere enn det som her angis.

Den beregnede nettoproduksjon for de ulike årene varierte i området 0,5 - 0.7 gram tørrvekt m^{-2}. For alle årene var det 0+ som ga det største bidrag til totalproduksjonen, med en andel fra 0.63 til 0.89. For den totale populasjon av Mysis, ligger P/B-forholdet nær 2 (P uttrykker produksjon og B er gjennomsnittlig biomasse i perioden mai-oktober). Eldre individer (1+, 2+) hadde et P/B-forhold nær 1, og de yngre (0+) nær 3.

Livssyklus:

Hoveddelen av Mysispopulasjonen i Mjøsa har en toårig livssyklus, men en mindre del av bestanden, spesielt hannene, kan i visse år nå reproduserbar størrelse allerede i sitt første leveår og enkelte hunner lever i tre år. De hunnene som lever i tre år får som regel unger tidlig i sitt andre reproduksjonsår, og det er sannsynligvis ungene til disse som har mulighet til å nå reproduserbar størrelse allerede i sitt første leveår dersom tilvekstforholdene er gode.

En "normal" to-årig livssyklus i Mjøsa forløper som følger: første leveåret (0+) er en ren vekstperiode, der den hovedsakelige tilveksten skjer i perioden mai-oktober. Mysisen har da nådd en lengde på 7-10 mm, og en vekt på 1,7 - 2,7 mg tørrvekt. I løpet av vinteren skjer det liten eller ingen tilvekst. Året etter skjer en ny tilvekst, hovedsakelig i perioden mai-august. Individene utvikles da til kjønnsmodne hunner og hanner (1+), og har oppnådd en lengde på 11 - 15 mm og en vekt omkring 4 mg.

Reproduksjonen skjer i løpet av vinter og vår (november til begynnelsen av juni). Størst forekomst av hunner med egg finnes i desember til ut i mars og hunner med unger fra mars til begynnelsen av juli. Samtlige hanner dør etter sin første forplantning, mens en del av hunnene overlever og kan delta i en tredie tilvekstperiode (2+) og ytterligere en forplantning. De kan da nå lengder opp mot 20 mm og en vekt på 10 mg.

Vandringer:

Mysis foretar vertikale døgnvandringer med 30-40 m amplitude i Mjøsa. Vandringene utløses og styres av lysintensiteten, mens de bakenforliggende årsaker er predatorunnvikelse og næringssøk. Når lysintensiteten avtar om kvelden, forflytter Mysis seg gradvis oppover i vannmnassene, og når det er blitt mørkt skjer en rask oppvandring til 10 - 60 m dyp. Generelt vandrer Mysis høyere opp i vannmassene om vinteren enn om sommeren. Når det begynner å lysne, skjer en rask migrasjon ned til større dyp (60 - 120 m). Spesielt sommerstid kan oppholdet i de øvre vannlag være av meget kort varighet. Unger klekt i april utgjør et unntak, da disse kan påtreffes under isen hele døgnet. Som nevnt står de yngre (0+) individene noe høyere enn de eldre (1+, 2+), og dette mønsteret gjelder også under vandringen. Mysis oppholder seg i øvre vannlag bare under den mørkeste perioden av døgnet. Midt på sommeren er oppholdet i øvre vannlag begrenset til 1-2 timer, mens de om vinteren tilbringer en stor del av døgnet i øvre vannlag og strandnære gruntområder.

Fødevalg:

Næringsvalget hos Mysis i de pelagiske deler av Mjøsa, fordeler seg på fire hovedgrupper: planteplankton, pollen (først og fremst fra gran), hjuldyrplankton og krepsdyrplankton. Det er en viss forskjell i næringsvalget hos unge og eldre individer. For 0+ av Mysis var planteplankton, særlig monader og kiselalger, helt dominerende føde i juni og juli. Hos eldre individer var planteplankton og krepsdyr av omtrent like stor betydning på forsommeren. Fra og med august var krepsdyrplankton dominerende næring hos alle størrelsesgrupper. Av krepsdyrplanktonet dominerte cladocerene Bosmina longispina og Daphnia galeata i dietten. Det ble ikke påvist noen klar størrelsespreferanse for disse to artene.

En grundig ernæringsstudie i 1979 ga følgende volummessig fordeling av føde i perioden juni-oktober: krepsdyrplankton 49%, planteplankton 33 %, hjuldyrplankton 12% og pollen 5%. Spesielt for de eldre individene er det uklart hvor mye av planteplanktonet som spises direkte, og hvor mye som kommer indirekte via spist dyreplankton. Mye tyder på at Mysis ofte selekterer de bløtere deler av dyreplanktonet, spesielt egg hos hoppekreps og mage/tarm-regionen hos vannlopper som Daphnia. Ut fra mageanalysene kan dette gi inntrykk av et høyere inntak av planteplankton, og et lavere inntak av dyreplankton enn hva som er tilfelle.

Trofisk rolle:

Det eksisterer i dag et balansert samspill mellom Mysis, byttedyr og predatorer i Mjøsa. I økologisk forstand er Mysis en utpreget omnivor, som ernærer seg på et vidt spekter av fødeemner og opptrer både som primær-, sekundær- og tertiærkonsument. Den spiller en dobbeltrolle både i forhold til planteplankton og fisk: den beiter direkte på fytoplanktonet, samtidig som den reduserer det totale beitetrykk ved å predatere effektive algebeitere som Daphnia og Bosmina og den er både næring og næringskonkurrent til fisk. Mysis' rolle som algebeiter er relativt beskjeden sammenliknet med det øvrige dyreplankton, og nettoeffekten av økt tetthet av Mysis blir redusert beitetrykk på planteplanktonet. Nettoeffekten i forhold til fisk er noe mer komplisert, men basert på situasjonen i Mjøsa synes Mysis primært å være (et viktig) fødeemne for krøkle.

Planteplanktonet i Mjøsa er fortsatt i betydelig grad regulert av tilførselen av næringssalter, særlig fosfor, i vekstsesongen. Begrenses fosfortilførselen, vil den relative effekten av dyreplanktonets beiting på planktonalgene øke. Biomasse av dyreplankton er primært regulert av næringstilgang og predasjon. Fiskepredasjon er i dagens situasjon klart viktigere enn predasjon fra Mysis. Et overslag basert på massebalansebetraktninger indikerer at fisken (primært lagesild, sik, krøkle og abbor) i dag står for 75% av den predatorinduserte dødelighet hos dyreplanktonet (Kjellberg og Sandlund 1983).

Tetthet og produksjon av Mysis synes i liten grad å være regulert av fødetilgang, og høyst sannsynlig er predatorkontroll viktig i Mjøsa. Forekomsten av krøkle og Mysis regulerer hverandre gjensidig, og krøkle avgjør sannsynligvis i stor grad både totalbiomasse og romlig fordeling av Mysis.

Vi vet lite om hva som primært regulerer krøklebestanden i Mjøsa, fødetilgang (dyreplankton, Mysis) eller predasjon (primært ørret). Ørreten som topp-predator kan imidlertid utgjøre et viktig regulerende ledd.

Det er vanskelig å si noe entydig om hvor stabilt det pelagiske økosystem i Mjøsa er. Et stort antall arter, og en komplisert næringsnettstruktur er ikke nødvendigvis ensbetydende med stabilitet (Pimm 1982), men de store årsklasse- og bestandssvingninger man finner blandt de pelagiske fiskeartene, indikerer at systemet kan svinge innenfor en betydelig ramme uten å bringes ut av likevekt. Næringsnettets nøkkelart synes å være krøkla, som i enhver forstand har en sentral posisjon i næringsnettet. En tenkt situasjon med redusert krøklebestand vil, i mangel på andre viktige pelagiske Mysis-predatorer, kunne gi en situasjon hvor Mysisbestanden øker, og hvor Mysis i større grad utnytter dyreplanktonet i de øvre vannlag gjennom en større del av døgnet. Mens det er vist at Mysis i betydelig grad kan utkonkurrere planktonpredatorer som røye, er det uklart hvordan en situasjon med økt konkurranse mellom Mysis, lagesild og sik vil slå ut. Det kan gi redusert biomasse og produksjon av pelagiske fiskearter, men totaleffekten vil med stor sannsynlighet bli redusert tetthet av de viktigste algebeiterne blant dyreplanktonet, redusert beitekontroll og økt algeutbytte per enhet av tilført fosfor.

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LIFE HISTORY, GROWTH AND PRODUCTION OF MYSIS RELICTA IN THE LARGE, FJORD-TYPE LAKE MJØSA, NORWAY.

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SUMMARY

1. Biomass, production and life history of Mysis relicta was studied in the large lake Mjøsa during the years 1976-80. Biomass fluctuations were large, but oscillated around 1 g WW m^{-2} or 200 ind m^{-2}. Cumulative net production during summer ranged from 1.6 to near 2.1 g DW m^{-2}. Mean population P/B-ratio was close to 2.

3. Production and biomass of Mysis were neither correlated to biomass of phytoplankton or main zooplankton prey species (Daphnia and Bosmina), suggesting a predominant "top down" control of Mysis in this lake.

3. The share of juveniles apparently increased upon years with strong fish predation pressure, and fish predation pressure was an important determinant to life history patterns.

4. Mysis had a predominant two-year life history, but a fraction of the population may reproduce after one or three years. Reproduction occur during winter. Even in such large and stable systems, where Mysis has coexisted with its main food items and predators for 8 - 10 000 years, a flexible life history is maintained and is probably an important buffer against year-to-year fluctuations in food and predator abundance

INTRODUCTION

The semi-planktonic glacial immigrant Mysis relicta is distributed over the northern Holarctic (Dadswell 1974), and is often considered a hypolimnetic, cold-water species. Although most common in relatively large, deep lakes, it is also frequently recorded in more shallow lakes, and the abiotic factor that severly limits its occurrence seem to be low levels of hypolimnetic oxygen (Dadswell 1974). Mysis is considered to be the most eutytopic of all glacial immigrants (Holmquist 1959, Dadswell 1974). The pronounced plasticity in life cycle strategies (Morgan 1980), spatial distribution and migration patters (Beeton and Bowers 1982, Moen and Langeland 1989) as well as its omnivorous mode of feeding (Bowers and Grossnickle 1978, Grossnickle 1982) makes Mysis an highly adaptive organism. Trough a number of recent introductions to new lakes, Mysis has further proven to be a competitively superior species, which readily adapt to new localities (Lasenby et al. 1986).

In many localities, Mysis plays a key role in the pelagic ecosystems. In localities where potential predators are absent, or not yet adapted to prey Mysis, its introduction may cause unbalanced ecosystems, and especially the negative impact on the zooplankton population may be pronounced (Furst 1981, Lasenby et al. 1986, Langeland 1988). This may severely affecty the native fish species adapted to a zooplankton diet (Langeland 1988). As Mysis in most localities prefer cladocerans, in particular Daphniids which are the most important phytoplankton grazers in most lakes, a secondary effect of Mysis introductions may be increased phytoplankton biomass. In systems with a native population of Mysis, a balance between Mysis, its main prey and predators has evolved for several thousand years. In such systems, the question is rather how "bottom-up" effect (e.g. eutrophication) or "top-down" effects (e.g. changes is fish stocks) may affect the Mysis population, and how this in turn affect zooplankton (and phytoplankton) biomass and composition. In some lakes, Mysis or single fish species may be key species, and changes in these populations may severely affect the whole ecosystem, while in other lakes more complex food web structures may buffer the effects from single-species changes.

In the well studied, large lake Mjøsa, Mysis is a natural inhabitant together with 20 fish species, and there is a very complex pelagic interplay between phytoplankton, zooplankton, Mysis and several pelagic fish species, feeding on both Mysis and zooplankton. During recent years, there has been a increased eutrophication, although the situations since the "Mjøsa Campaign" (1978 -81) has stabilized. The lake still receives "critical" loads of nutrients, and the food chain structure in the pelagic zone is considered important for the development of algal biomasses. Thus it is crucial to understand the trophic interplays in the lake. As Mysis appear as an important organism in the pelagic community of the lake, its ecology has been extensively studied for almost 20 years. We here present data from a long term study (1972-89) on feeding patterns, migrations and the overall trophic role of Mysis in the ecosystem of Lake Mjøsa.

MATERIAL AND METHODS

The study was performed in Lake Mjøsa, an oligo-mesotrophic, large fjord-type lake in S.E. Norway. The lake has a surface area of 362 km^2, max. depth of 449 m, mean depth of 153 m, and a volume of 56 244 mill. m^3. The lake has dense schools of pelagic fish species. The most important predator on Mysis is smelt (Osmerus eperlanus) and to some extent also whitefish (Coregonus lavaretus). Benthic predators are burbot (Lota lota), perch (Perca fluviatilis), ruffe (Acerinia cernua), as well as the glacial immigrant Gammaracanthus loricatus. Restricted information is available on biomass development of predator species on Mysis, but catch data indicate that fish numbers probably have been more or less constant within the last 100 years. Cladocera, the main food group for Mysis, have increased slightly during recent years following the eutrophication development (Rognerud and Kjellberg 1990).

Most samples were performed over the central, deepest part of the lake, but controls on regional variance in density and feeding patterns were performed. Sampling were performed by means of vertical net hauls. For the first years of this study (1972-80), samples were taken with a net opening of 30 cm and a mesh size of 200 µm. From 1981, a 100 cm diameter net was used (200 µm). Paralell control samples using both nets, revealed little difference in abundancy estimates. 12 - 18 samples were taken for biomass determination each year, and each sample consisted of ten parallel net hauls. Each pooled sample consisted of from 100 to 400 individuals. Samples for density estimates were usually taken during day-time, because Mysis show a more even distribution during day, compared to night when a more contagious distribution was recorded. Over more shallow areas, where Mysis is recorded in or close above the sediment surface, night samples were used for density estimates. In addition to net samples, an Ekman bottom sampler and a fine-netted trawl as well as data from fish-stomach analysis from smelt and roach have been used to gain information concerning habitat selection.

Zooplankton samples were taken with a 10 l Schindler trap at 2 m intervals down to 50 m. For determination of seasonal biomass, a mean of 12 - 18 samples (corresponding to the sampling dates for Mysis) were taken.

The material was preserved in 4% formalin added $CaCO_3$. Length measurements were performed in a stereomicroscope and total length includes the distance from tip of the rostrum to the telson bend. Wet and dry-weights were determined on a Sartorious microbalance to the nearest 0.01 mg, and a length-weight relationship was established for both wet and dry weights. Food analysis was performed on the total samples (all individuals) under a stereoscopic microscope, after dissecting the stomachs off and transferring the content to a wetted coverglass. As *Mysis* breaks larger food items (diatoms and zooplankton) into pieces, an accurate determination of food items eaten may be difficult to assess. Moreover, food remnants in the stomach may originate from food items ingested by zooplankton. *Mysis* seem to select the soft parts including the gut and postabdomen of species like *Daphnia*. We believe nevertheless that stomach analysis of *Mysis* tend to underestimate the consumption of zooplankton and possibly overestimate the importance of phytoplankton and detritus, especially during periods when cladocera make up the major food items. The rest of the body is rarely recovered from *Mysis* stomachs. We have therefore used numbers of postabdomens to assess abundance of *Bosmina* and *Daphnia*, and numbers of mouthparts to assess the abundance of copepods. Length of ingested individuals of *Bosmina* and *Daphnia* were calculated from length of the postabdominal claw. Total length - claw-length was established from 25 individuals of various size of each species, and described by the equations:

Bosmina longispina: $Lt = -\ 0.01 + 11.5\ Lp$ $R = 0.85$, $p < 0.001$
Daphnia galeata: $Lt = -\ 0.06 + 11.9\ Lp$ $R = 0.98$, $p < 0.001$
Daphnia cristata: $Lt = 0.06 + 11.1\ Lp$ $R = 0.86$, $p < 0.01$

where Lt is total length from top of head to base of spine, and Lp is length of the postabdominal claw.

RESULTS

Biomass:

During the period 1976-1989, biomass (mean of 12 -18 sampling dates) of Mysis ranged from 100 to 417 mg DW m^{-2} while the numerical density ranged from 75 to more than 400 ind m^{-2} (Fig. 1). The highest density recorded was more than 1000 ind m^{-2}. Biomass data from 1972-75 are not available due to infrequent sampling. These data are based on samples from the central station. A regional survey during 1980 showed that Mysis had a rather even distribution over most of the lake, however with somewhat lower densities in the northermost and shallower part of the lake (Fig. 2).

Spatial distribution and migration:

In central parts of the basin, Mysis lives pelagic at depths below 80 m, whereas in more shallow parts of the lake (< 40 m) it is found close to the sediment surface during day-time. During winter, Mysis is recorded in more shallow habitats, normally up to 20 m, but occationally even in near-shore, littoral areas. The immigration to more shallow areas during periods of ice-cover may partly be due to the lower ligth levels, lower temperature and thus a relaxed fish predation pressure. Higher food availability for Mysis in the upper littoral areas could be the ulitimate cause for this horizontal migration.

The Mysis population in Lake Mjøsa show a pronounced diurnal, vertical migration, with mean diurnal amplitudes of 40-80 m during the ice-free season. The main bulk of the planktonic population is during day-time distributed between 60 - 120 m over the central basin. The diurnal migration starts during dusk, when Mysis rapidly ascend to upper layers. During mid summer the diurnal migration starts during midnight, and the animals stay for a very short period of time (~ 1 h) in the upper layers. During winter, the ascend start much earlier, and the population remain in the upper water masses for several hours. During early spring (April), the 0+ remain in the upper layers troughout the day. While the proximate cause for migration obviously is light, predator avoidance and food search seem to be a major ultimate causes. During their stay in upper water masses, especially older individuals of Mysis, tend to aggregate. This swarming behaviour could be a further adaption to decrease exploitance from planktivorous fish. In general, the younger stages were observed above the advanced both during day and night (Fig. 3).

Food choice:

Food selection was studied during three periods; 1972-76, 1979-80 and 1989. The first period includes the peak eutrophication period, while 1979-80 and 1989 was periods of lower production. The periods thus represents periods of differing phyto- and zooplankton biomass and composition. In general, the food choice did not differ between these three periods.

Four principally different food items dominated in the diet of Mysis: Phytoplankton, zooplankton, pollen (mainly pine) and detritus. The share of phytoplankton in the diet is somewhat higher in the juveniles compared with the adults, but in general the seasonal patterns followed closely in adults and juveniles (Fig. 4). After the juveniles leave their mothers, they initially consume phytoplankton, mainly various monads. Later diatoms and rotifers show increasing proportions of the diet. Notably larger phytoplankton species are preferred among both juveniles and adults. Monads like Chromulina, Chrysococcus, and Chlamydomonas and diatoms like Asterionella, Tabellaria, Fragilaria and Staurastrum were preferred, although Mysis feed a wide variety of phytoplankton. At the end of July, the crustaceans Bosmina longispina and Daphnia galeata become abundant, and all size groups of Mysis gradually shift towards these food items which dominate the stomach content during summer and autumn. During winter and spring, cyclopoids, mainly Eudiaptomus gracilis, Limnocalanus macrurus and nauplii of Cyclops lacustris are consumed. During late winter, ovi-sacs and sperm-sacs of Eudiaptomus gracilis are common, and apparently these are selected prior to the individual itself. In general, the same food choice was recognized in the individuals from the main station, and individuals from more shallow areas, although the latter had a higher proportion of detritus in their diet. A regional survey on diet in different regions of the lake over the year is given in Fig. 5. This confirms that Mysis show no strong regional variation in food preference. While detritus dominates on all stations during winter, with copepods as the most common food item, there is a shift towards pine-pollen in spring before the diet from July onwards become dominated by cladocera.

During 1989, a more detailed study on seasonal and diurnal food selection was performed (Fig. 6). As for the previous year, the early summer situation was characterized by a total dominance of algae and detritus in the diet. During summer, zooplankton accounted in total for almost 75 % of ingested food, with a total dominance of cladocerans. The share of zooplankton increased during night, but even during day-time, zooplankton made up a considerable share of the gut content. This does not necessarily reflect the share of zooplankton consumed during day-time, but represent probably remains of zooplankton consumed during night, not yet defeacated. During autumn, no diurnal changes in gut content was recorded, in accordance with the high overlap between zooplankton and Mysis at that time. Gut content of juveniles and adults were basically identical in all samples.

In general, the zooplankton items ingested is strongly fragmented. This holds even for the rotifers Notolca and Kellicottia, while Keratella spp. is ingested without fragmentation. From the copepods, mainly appendages, antennae and the mandibulae are recorded, while dominating remains from cladocera are the postabdomen. Only occationally, complete (but still crushed) individuals are recorded. The frequent dominance of eggs and sperm-sacs from Eudiaptomus in the diet during winter, with no remains of the parent individual, strongly suggest that Mysis feed selectively on parts of the single prey. During parts of the year, Mysis may also show a strong selection on single prey-species.

No difference in preference in size of prey (Daphnia and Bosmina) could be detected between juvenile and adult individuals. Mysis consumes all size groups of Daphnia in the range 0.6 - 1.4 mm, but the size around 0.8 mm is dominating. All size classes of Bosmina is also consumed (0.25 - 0.8 mm), but the size range 0.4 - 0.5 mm is dominating. This holds both for 0+ and the larger individuals of Mysis, although the 0+ stick to Bosmina for a longer period in early summer, before starting to consume Daphnia. Although an exact size determination on the consumed prey is difficult based on the fragments, Mysis show apparently no preference for small or large individuals of cladocerans. This in opposite to the fish species of the lake, which in general prefer the larger individuals. Still, there is a pronounced overlap in food choice both with regard to species and sizes between Mysis and pelagic fish species like cisco, whitefish and smelt.

During the 1989 survey, vertical distribution and migrations of Mysis and its zooplankton prey items were recorded simultaneously during autumn (the period of peak zooplankton biomass). During august, the main food items Daphnia galeata and Daphnia cristata remained in the upper layers (above 15 m) even during daytime (Fig. 8). Bosmina were distributed down to 50 m during daytime, while during night, the main population was restricted to the upper 20 m. Thus, although running the risk of fish predation, the main bulk of the cladocera remained in the layers above the distribution of Mysis. During November, when the main density of Mysis remained in the deeper layers, this was reflected in the more relaxed depth distribution of the cladocera (Fig. 7).

DISCUSSION

The density of Mysis in lake Mjøsa is comparable to that of other large lakes, where normally 50 - 350 ind. m^{-2} are reported (Reynolds and DeGraeve 1972, Carpenter et al 1974, Morgan and Beeton 1978, Goldman et al. 1979, Lehman et al. 1990). Depending upon life history and shifts in habitat preferance, pelagic numbers of Mysis varies within seasons. In lake Michigan, the pelagic Mysis population changes from 54 ind m^{-2} in December to more than 1000 ind. m^{-2} in September when Mysis enter the pelagic zone from more shallow waters (Grossnickle and Morgan 1979). The corresponding within-year changes in pelagic density in lake Mjøsa reflects these horizontal migrations. The reason for the migration towards the shallow profundal after ice laying may be interpreted as an active food search, at food availability in the pelagic is scarce during winter. During summer and autumn, the pelagic offers both food and is the most profitable habitat with regard to predator avoidance. The between-year variations in density is also pronounced, but is scarcely understood. As no clearcut pattern arise when comparing abundance of Mysis with density of food (phyto- and zooplankton biomass) (Fig. 8), it is reason to believe that Mysis may be "top-down" regulated by abundance of fish predators (see below). This cannot be verified, however, due to insufficient data on year-to-year variance in fish biomass.

The depth distribution of Mysis in other lakes is also comparable to that of lake Mjøsa (Cf. Beeton and Bowers 1982). It seems to be a common feature that Mysis is benthic down to a specific depth, below which it is mainly pelagic. This depth amounts to 200 m in the very transparent lake Tahoe (Morgan et al. 1978) and only about 20 m in the colored, humic lake Paajarvi (Hakkala 1979). The proximate factor for vertical and horizontal migrations seems to be light (Beeton and Bowers 1982, Moen and Langeland 1989), while the ultimate factors most probably are predator avoidance and food search combined (Grossnickle and Morgan 1979, Beeton and Bowers 1982). The pronounced migration in lake Mjøsa even during periods with none or only weak thermal stratification, suggest that metabolic gain due to temperature gradients (Cf. McLaren 1963) may not be an important cue in lake Mjøsa. The size dependent migration, with the juveniles beeing distributed in more shallow areas during both day and night fit other observations (Morgan and Threlkeld 1982) and support the hypothesis of a predator induced migration.

Smelt, the main predator of Mysis in lake Mjøsa, has a depth distribution below that of the other pelagic fish species (Sandlund et al. 1980 a). In the benthic habitat, the smelt has its main distribution in a rather narrow zone around 30 m (20-40 m), whereas in the pelagic the main distribution was above 10 m (Sandlund et al. 1980 a,b). Thus, in the pelagic the vertical migration of Mysis would promote a spatial segregation from smelt even during night. On the other hand, as the main distribution of the most vulnerable zooplankton prey also are above 10-15 m even during night, Mysis must choose between the conflicting strategies of food accessability and predation risk, and consequently, a certain overlap between smelt, Mysis and cladocera is observed during night, whereas they are more separated during day. The nighttime vertical distribution of Mysis and its main zooplankton prey fits well with the observations of Lehman et al. (1990) from Lake Michigan. Parallel to this, the zooplankton prey are forced to chooce between conflicting strategies. Distribution in the deeper layers will increase the risk of predation by Mysis, while a distribution in the upper layer increase their vulnerability to fish predators. The distribution of cladocera in the upper layers, even during daytime, support other studies on zooplankton distribution in lake Mjøsa (Kjellberg unpubl.), and suggest that Mysis avoidance is a main selective force with regard to vertical distribution of the cladocera.

Based on an detailed seasonal survey (1979), Kjellberg and Sandlund (1983) made an integrated estimate on the food web dynamics of the pelagic ecosystem in lake Mjøsa. On a seasonal average, the phytoplankton production was balanced by zooplankton grazing, thus zooplankton act as an important top-down regulator on phytoplankton biomass. Less than 10 % of total zooplankton production was diverted to higher trophic levels, although this fraction is probably far higher for important prey species like Daphnia and Bosmina, which account for a small fraction of the whole zooplankton community, but a major fraction of food items for Mysis and fish. While mean seasonal biomass of total zooplankton was positively related to phytoplankton ($P < 0.001$, $r = 0.73$), no significant correlation was found between the individual Daphnia species or Bosmina and phytoplankton biomass ($p > 0.1$) (Table 1). This further indicate a "bottom-up" regulation of total zooplankton biomass while a "top-down" regulation of these most predation vulnerable species. No significant correlations were detected between seasonal mean of biomass between Mysis and its main prey species, however (Table 1), indicating that Mysis was not a main contributor to this top-down regulation. A corresponding analysis on fish/zooplankton correlations was not possible due to lack of sufficient data on fish biomass. These conclusions fit well with the previous study of Kjellberg and Sandlund (1983), where pelagic fish species was found to account for 75 % of zooplankton consumed, and Mysis for the remaining 25 %. It also supports the findings of Lehman et al. (1990) from Lake Michigan, suggesting that in lakes with dense stochs of planktivorous fish, including predators on Mysis, the Mysis contribution to total zooplankton consumption is relatively modest due to a vertical separation between Mysis and its prey.

Smelt is the only important pelagic predator on Mysis, and probably the main determinant to vertical distribution of Mysis, although it does not constitute any important part of the smelts' diet until autumn (Sandlund et al. 1980 b). Although 75 % of predator induced zooplankton mortality is caused by fish, Mysis represents a great potential consumer of the cladoceran populations. The lack of a regulating key species as smelt would allow a more intense foraging by Mysis also in the epilimnetic layer of lake Mjøsa, probably followed by an increased population density (cf. Rognerud and Kjellberg 1990). The primary effect would be reduced biomass of cladocera, parallel to what observed from numerous lakes where Mysis has been artificially introduced (Richards et al. 1975, Threlkeld et al. 1980, Cooper and Goldman 1980, Langeland 1981, 1988, Grossnickle 1982). The competitive outcome between Mysis and planktivorous fish is not straightforward, but probably secondary effects from a Mysis expansion would be reduced production and catches of pelagic fish species, and at least temporarily increased phytoplankton biomass due to reduced zooplankton grazing.

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Table 1. Correlations, estimated by least square regressions, between mean seasonal biomass of various plankton categories in Lake Mjøsa for the years 1972 - 1989 (1976 - 1989 for Mysis). Levels of significans (p) is given. Where $p < 0.5$, positive (+), or negative (-) correlation is indicated.

	Mysis	Tot zoo.	D. gal.	D. cris.	B. lon.
Phyto.	.271(+)	.001(+)	.179(+)	.787	.118
Mysis	-	.941	.990	.707	.624

LEGEND TO FIGURES

Fig. 1. Numerical density (black bars, ind m^{-2}) and biomass (white bars, mg DW m^{-2}) of _Mysis_ during 1976-89. SD as vertical lines. Each year represent means of 12-15 samples over the central station.

Fig. 2. Regional distribution of _Mysis_ in lake Mjøsa during October, 1980.

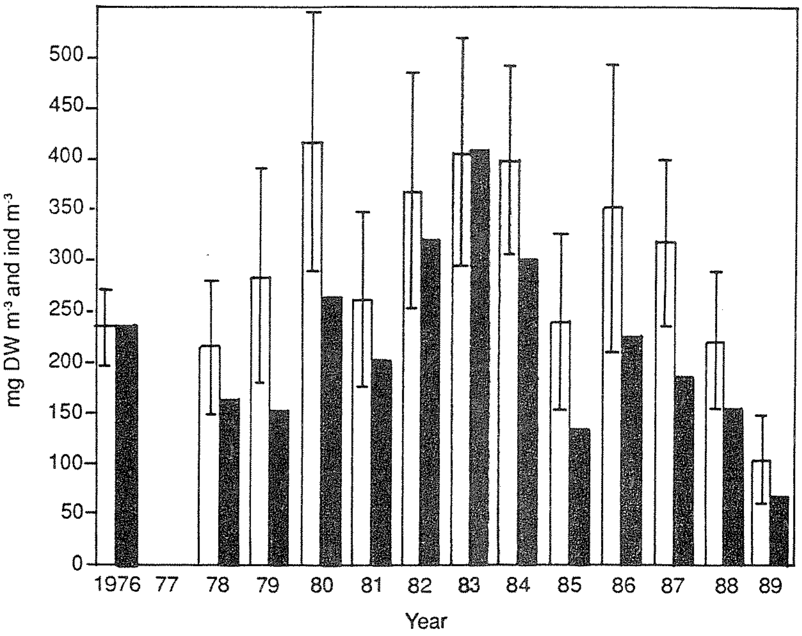
Fig. 3. Diurnal distribution of juvenile (0+) and adult (1+ and 2+) _Mysis_ during season.

Fig. 4. Seasonal and diurnal variance in food choice in juvenile and adult _Mysis_. A/D: algae/detritus, B: _Bosmina_, C: copepods, D: _Daphnia_, P: pollen and R: rotifers.

Fig. 5. Regional and seasonal variance in food choice of _Mysis_. All size groups pooled.

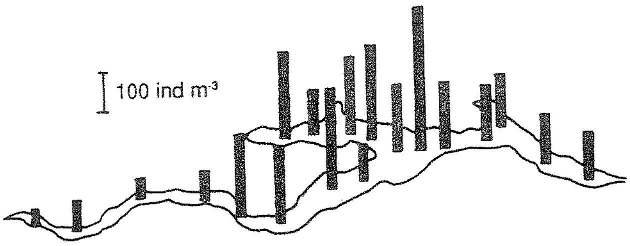
Fig. 6. Diurnal, vertical migration of _Mysis_ and its main zooplankton food items.

Fig. 7. Year-to-year variation in biomass of phytoplankton, total zooplankton, main cladocera and _Mysis_ during 1972-89.



mg DW m-3 and ind m-3
0
50
100
150
200
250
300
350
400
450
500
1976
77
78
79
80
81
82
83
84
85
86
87
88
89
Year

Fig. 1



100 ind m-3

Fig. 2

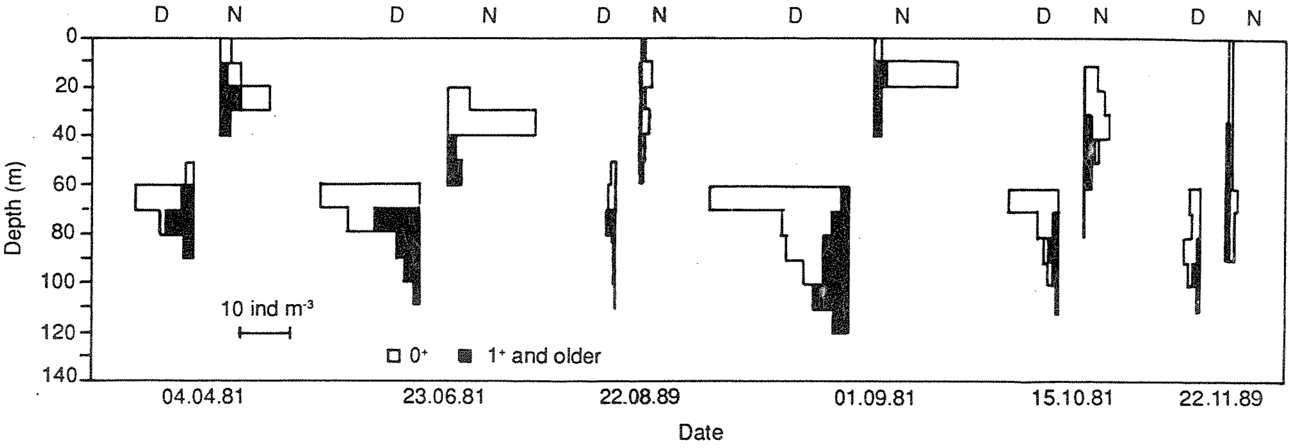

D
N
D
N
D
N
D
N
D
N
D
N
0
20
40
60
80
100
120
140
Depth (m)
10 ind m-3
☐ 0+
■ 1+ and older
04.04.81
23.06.81
22.08.89
01.09.81
15.10.81
22.11.89
Date

Fig. 3

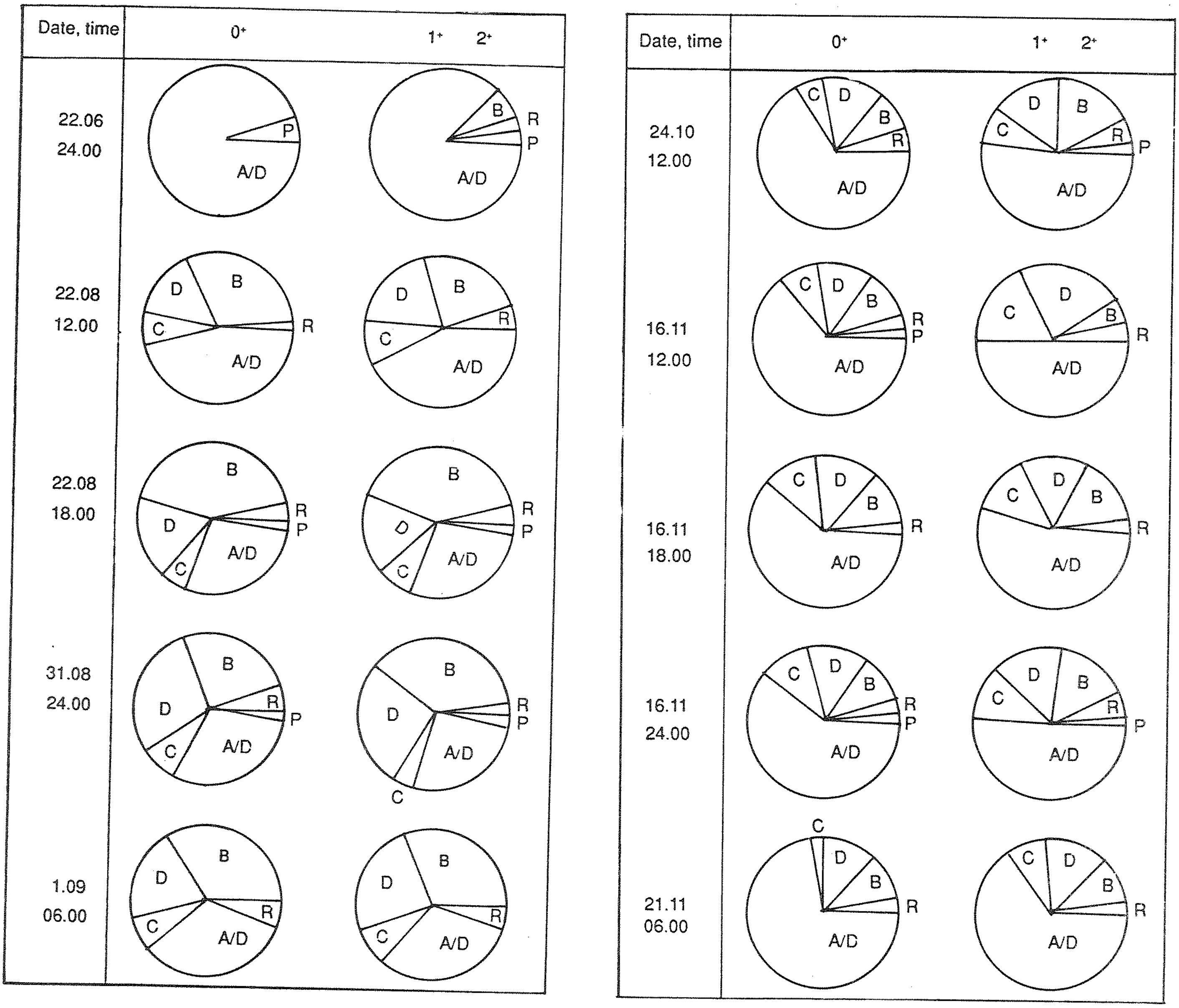

Date, time
0+
1+
2+
22.06 24.00
22.08 12.00
22.08 18.00
31.08 24.00
1.09 06.00
24.10 12.00
16.11 12.00
16.11 18.00
16.11 24.00
21.11 06.00
A/D
B
C
D
R
P

Fig. 4

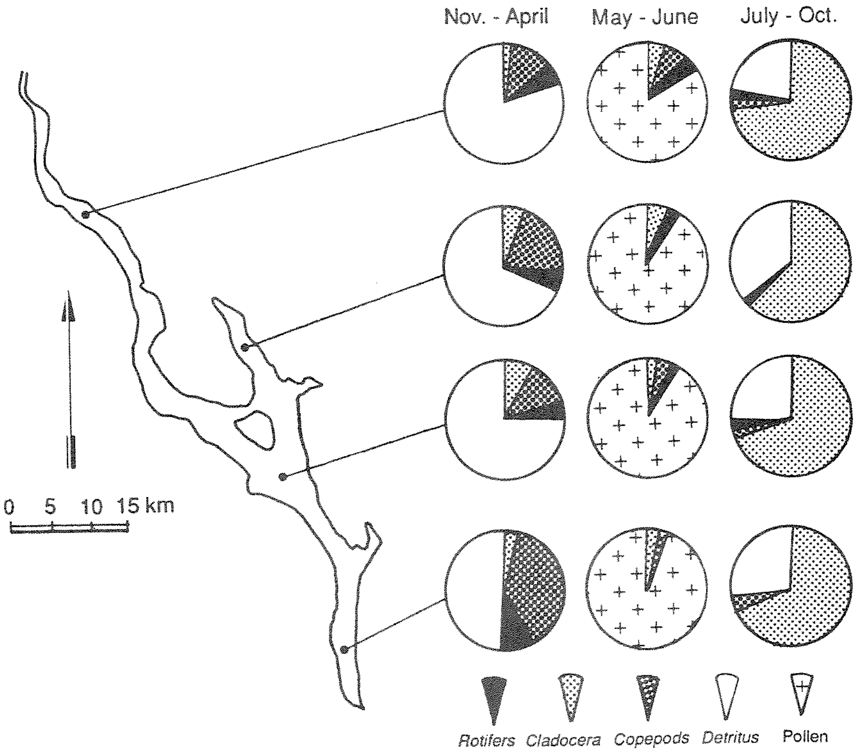

Nov. - April
May - June
July - Oct.
0 5 10 15 km
Rotifers
Cladocera
Copepods
Detritus
Pollen

Fig. 5

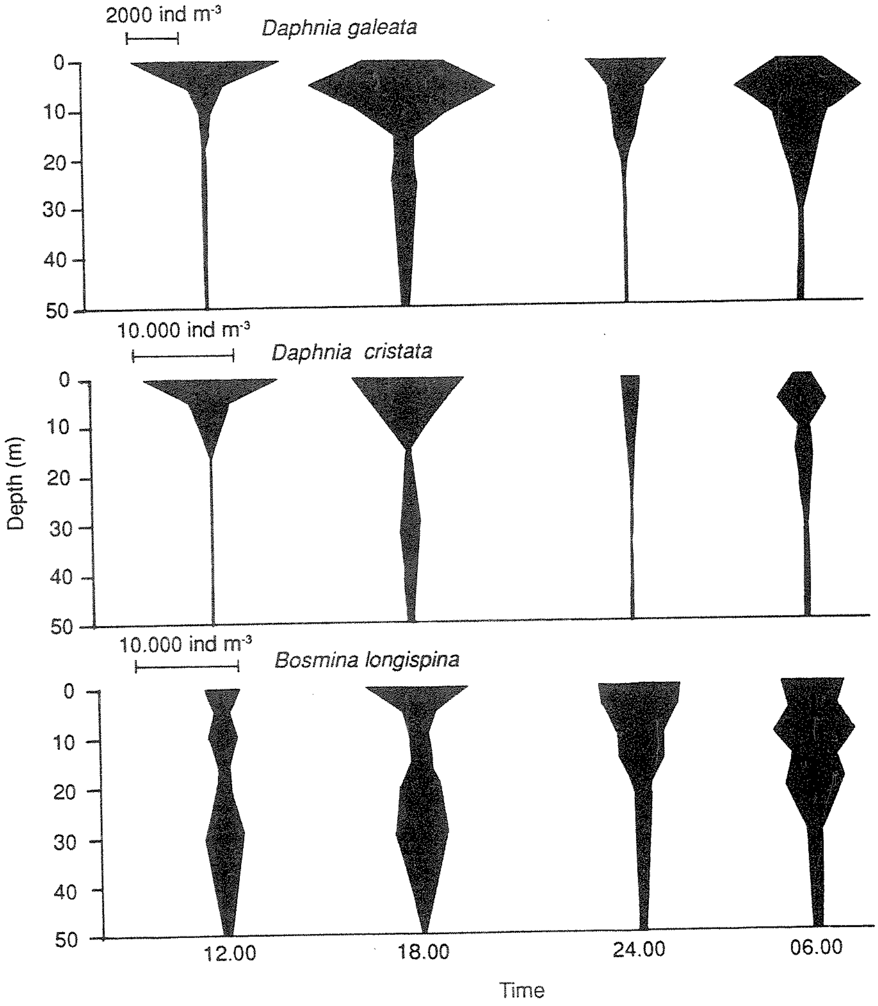

2000 ind m-3
Daphnia galeata
10.000 ind m-3
Daphnia cristata
10.000 ind m-3
Bosmina longispina
Depth (m)
0
10
20
30
40
50
12.00
18.00
24.00
06.00
Time

Fig. 6

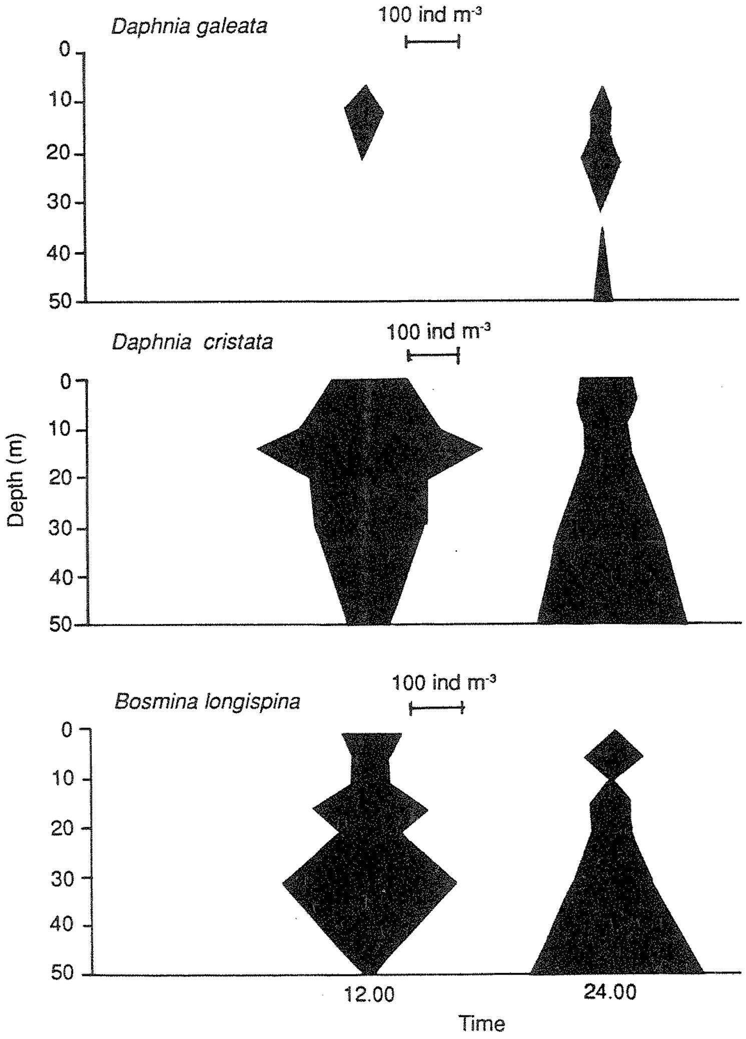
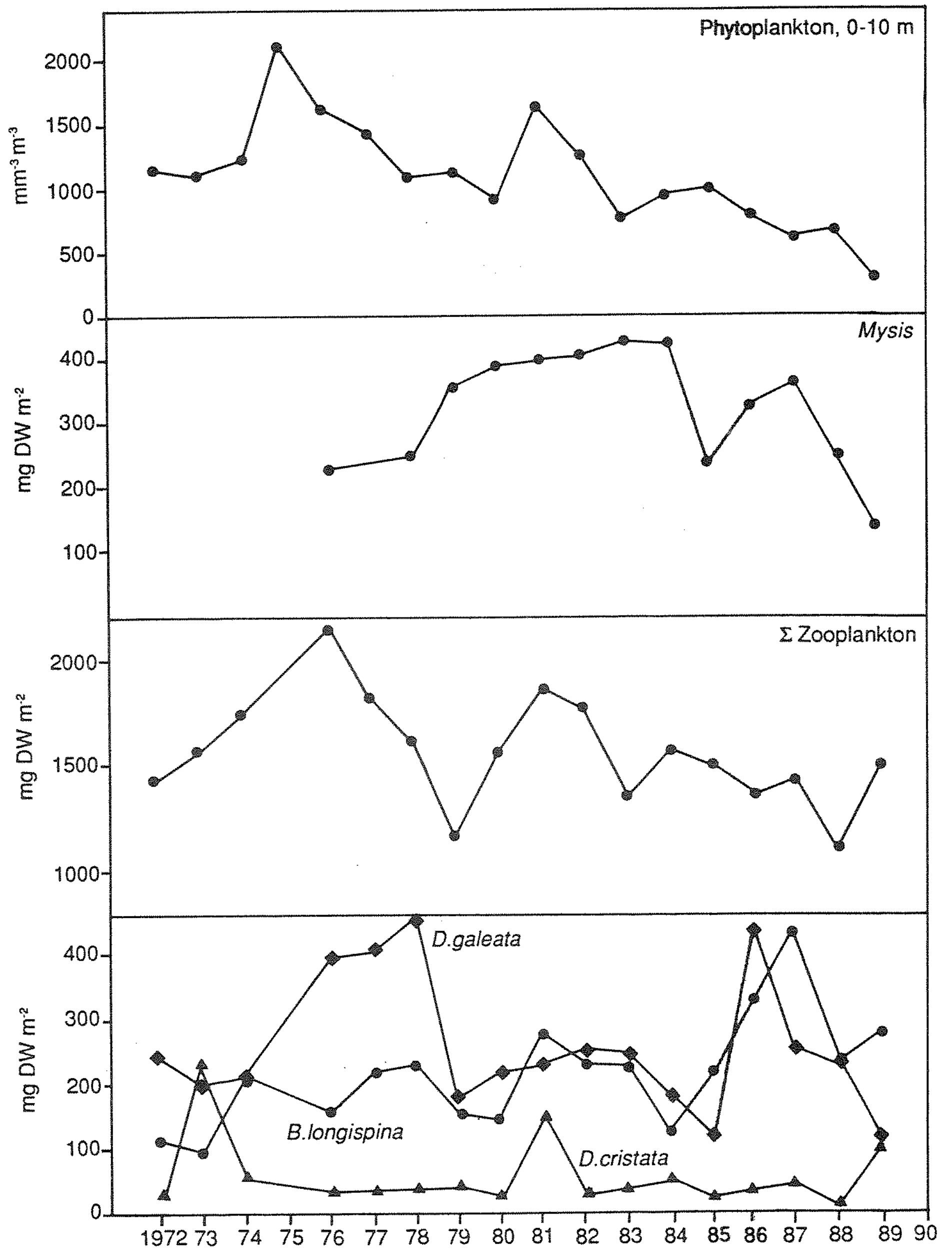


Fig. 6 continued...



Phytoplankton, 0-10 m
mm⁻³ m⁻³
2000
1500
1000
500
0
Mysis
mg DW m⁻²
400
300
200
100
Σ Zooplankton
mg DW m⁻²
2000
1500
1000
D.galeata
B.longispina
D.cristata
mg DW m⁻²
400
300
200
100
0
1972 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89 90

Fig. 7

BIOMASS, DISTRIBUTION, FOOD SELECTION AND TROPHIC ROLE OF *MYSIS RELICTA* IN THE LARGE FJORD-LAKE MJØSA, NORWAY.

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ABSTRACT

Biomass, vertical and horizontal distribution, food selection and the overall trophic role of the glacial immigrant Mysis relicta in the large lake Mjøsa was evaluated during a 17 year study (1972-89). Mean seasonal biomass ranged between 100-420 mg DW m^{-2} during this period. Diurnal migration was conspicous, with amplitudes of 40-80 m. The migration was considered a compromise between predator avoidance and food search. Mysis consumed mainly detritus and algae during winter and spring. During summer, the proportion of zooplankton, mainly cladocera, increased to more than 50 % of the diet. In general, small or negligible regional, diurnal, or age-specific differences were recorded in food choice. Neither was found any preference for prey size of zooplankton; size distribution of Bosmina and Daphnia in the guts corresponded to that of the lake. Mysis contribute to less than 30 % of total zooplankton predation in the lake, this was mainly due to depth segregation between Mysis and its main zooplankton prey. Smelt is the main predator of Mysis in Lake Mjøsa. It was concluded that the smelt/Mysis interaction is a key for maintenance of the balanced situation in the lake. A reduced smelt population would give increased abundance of Mysis in the upper layer over a larger period of the day. A primary consequence of this would be reduced biomass of important herbivores like Daphnia and Bosmina. An important secondary effect could be reduced grazing control and increased phytoplankton biomass and eventually reduced catches of pelagic zooplanktivore fish species.

INTRODUCTION

Animals adapt their life cycles to their environment to optimize survival and production. Species inhabiting narrow niches or inhabit localities with high stability may exhibit more or less fixed life cycle strategies, whereas other may have a pronounced geno- and phenotypic variability (including life cycles) to buffer against a fluctuating milieu.

Some freshwater planktonic crustaceans show a remarkable life cycle plasticity, although inhabiting localities with a rather predictable seasonality. Often these species have a wide geographical as well as a habitat-type range of distribution, indicating that the "cost" of maintaining a high variability is compensated for by a pronounced dispersal capacity and ability to establish populations in new localities. Prolonged life histories are well known from freshwater copepods in the temperate region (Elgmork, 1965, 1981; Nilssen, 1980) For the circumpolar cyclopoid copepod Cyclops scutifer a variety of life cycles have been detected, with great both inter- and intrapopulation variability (Elgmork, 1981). The ultimate reasons for this variability is apparently local, seasonal timing and/or predator avoidance. For the larger Mysidacea Mysis relicta, a number of local life cycle adaptations have been described (Furst, 1972; Morgan, 1981), the most common beeing a one or two year life history, but three year and even four year life histories may be recorded (Morgan, 1980). Following transplantations, Mysis may show rapid changes in its life history (Furst, 1972; Olsen, 1980), suggesting a strong phenotypic component inherited in the life history. Support for this was given by Morgan (1980), concluding that the life history traits of Mysis in lake Tahoe might represent phenotypic and not evolutionary life history adaptations. Changes in lake trophy (food abundance) and changes in temperature regime (by spending more time in the epilimneon) have been suggested as the main ultimate causes for such rapid changes in life history (Lasenby et al., 1986). Life history will naturally affect total production and production/biomass (P/B)-ratios, as well as the overall trophic role of Mysis in the ecosystem.

In lake Mjøsa, Mysis plays an important role in the pelagic ecosystem of the lake, both as a zooplankton predator and as a prey species for fish (Kjellberg et al., in ms.). It has coexisted with its prey and predators for 8 - 10 000 years, and would be expected to have adapted its life history to facilitate coexistence with prey and predators. The aim of this paper is to report on the production and life history tactics of Mysis in a lake with high system stability and complex biotic interactions.

MATERIALS AND METHODS

The ecology of the Mysis-population in Lake Mjøsa has been studied since 1972, including data on population density, vertical migration, and food choice (Kjellberg et al., in ms). During the years 1976-1980, a more thorough analysis on population dynamics and production was performed. The majority of the material was collected over the central, deepest part of the lake by means of vertical net hauls. Nets with 30 and 100 cm aperture was used, both with mesh size 200 µm. Parallel net hauls with the two types of nets, gave less than 10% variance between the estimated population densities. The two net types also captured the various size groups of Mysis with the same efficiency. At 12-18 sampling dates over each year, ten parallel net hauls were performed for estimating population density, and usually a total of 100 - 400 individuals were sampled on each date. The samples were usually taken during day-time, because Mysis then showed a more even distribution compared with night. During migration towards upper water layers during night, the distribution become more contagoius. To obtain more thorough data on habitat selection and feeding, additional samples were taken with an Ekman bottom sampler and a fine-netted trawl. The individuals were preserved in 4% formaline added $CaCO_3$. Length measurements were performed on all sampled individuals in a stereomicroscope, and total length includes the distance from the tip of the rostrum to the telson bend. Fresh-weight (FW) and dry-weight (DW) was measured on a Sartorious microbalance to the nearest 0.01 mg, and a length-weight relationship was established for both (Fig.1). DW was measured after 24 h at 60 °C.

Mean seasonal biomass of zooplankton was estimated from 12- 18 sampling dates (the same as for Mysis) with a 25 l Schindler trap. For each date, biomass was integrated over 0 - 50 m (9 samples: 0.5, 2, 5, 8, 12, 16, 20, 30 and 50 m). Phytoplankton biomass was given as Chlorophyll a, based on 12 - 18 mixed samples over 0 - 10 meters.

The life cycle determinations is based upon the different stages after differential sexual development according to Furst (1972). The production estimates are constructed from curves on number of individuals and biomass per square meter and time, the so called Allen curves, based on the method introduced by (Allen, 1951) for estimating fish production.

RESULTS

Mean density of Mysis over the central, station for the years 1976, 1978, 1979 and 1980 was close to 200 ind m^{-2}, with a corresponding biomass of near 1 g WW (Fig. 2). Numerical and biomass fluctuations was conspicous during all years, partly reflecting a contageous distribution but also the horizontal migrations of Mysis over the season. The contribution of preceeding year-classes showed great variablity, but in general decreased over season as the 0+ increased numerically.

During their first year, Mysis reach a weight of 5.5 - 8 mg WW/ind (Fig. 3). Adults show a mean weigth increase of almost 50 % (to 14-15 mg WW/ind during one year. In general 25 % of the 0+ survive their first year (Fig. 4). Growth- and survivalship curves for the different years (Figs. 3 and 4) show rather high similarity, but variations may be related to various predation pressure and food availability (see discussion).

Based on Allen curves, cumulative net production of the different year-classes of Mysis was calculated for four various years (Fig. 5). Considerable differences were observed for the various year-classes for the different years, which would also be expected due to variable year-classes of the main predator smelt (Osmerus eperlanus), and variable food-availability. Total production between the four years came out rather close, however. During all years, the production/biomass (P/B)-ratio for the younger stages (0+) was near 3, whereas for the older it was around 1. For the population as a whole, P/B-ratio was close to 2. Production, biomass and P/B-ratio for the various year were tested against seasonal, epilimnetic (0-10 m) means of phytoplankton biomass, total zooplankton biomass, biomass of the dominant zooplankton prey Daphnia galeata and Bosmina longispina and mean water temperature. As given by the matrix in table 1, no clearcut relationships could be detected. The only significant correlation at a 5 % level, based on least square regressions, were the negative relationship between accumulated production of 0+ and total zooplankton biomass. In general, total production of Mysis were negatively (however insignificant) related to the other biotic parameters, while P/B-ratios gave a slightly positive (but again insignificant) correlation with the same parameters.

A generalized scheme of the life history of Mysis from lake Mjøsa is shown in Fig. 6. The reproductive period lasts from November - June, with the main bulk of ovigerous females recorded in December - March. Hatching normally occur in March, and the juveniles are attached until late June. The majority of the population show a two-year life cycle, but a fraction of the population may reproduce after the first year, and another fraction of the females may produce offspring after three years. All males die after their first copulation after one or two years. Within one year, the three and two year fractions reproduce first. As egg number is closely correlated to body-length (Fig. 7), the two-year (and eventually three-year) fraction also have larger clutch-size compared to the one-year fraction. Thus the proportion of small individuals in the breeding population may determine the size of the year-class the following year. Only the earliest offpring (from two- or three-year mothers) may complete their life-cycle within one year. Thus offspring from individuals having a one-year cycle will always have a two-or three year cycle, whereas offspring from individuals having two- or three-year life cycles may exhibit both one-, two- or three-year life cycles.

DISCUSSION

The density of Mysis relicta in lake Mjøsa is comparable to that of other large lakes (Reynolds & DeGraeve, 1972; Carpenter et al., 1974; Morgan & Beeton, 1978; Goldman et al., 1979). Although considerable year to year fluctuations were recorded, the four years of investigation fall well within the total biomass fluctuations over the last 14 years however (Kjellberg et al., in ms.) Depending on life history and habitat selection, pelagic numbers of Mysis varies with season. Similar to the situation in Mjøsa, in Lake Michigan the pelagic Mysis-population increase from 54 ind m^2 during December to more than 1000 ind m^2 in September when Mysis enter the pelagic zone from more shallow waters (Grossnickle & Morgan, 1979). In Lake Mjøsa, Mysis seem to accumulate in the pelagial during late autumn, before they migrate towards the shallow littoral during winter. This may explain the numerical increase during late autumn.

The rather pronounced differences in production of the different year-classes could be a combination of predatory activity of smelt and food availability for the young-of-the-year. The dominating proportion of 0+ in 1978 fit well with strong classes of smelt the previous years (Sandlund et al., 1980), feeding mainly upon the more advanced stages. This is supported by the high death rates of adults relative to juveniles this year (Fig. 3). As revealed by table 1, no obvious "bottom up" regulation of Mysis production could be detected by single factor analysis. One should keep in mind, however, that this is based upon seasonal means of four years only. The lack of quantitative fish data for all four years does not permit a corresponding analysis of the possible "top-down" effects on Mysis. The apparent lack of "bottom up" control suggest, however, that fish predation plays an important role in regulating biomass and total production of Mysis in Lake Mjøsa, analogous to what McDonald et al. (1990) suggested for Lake Michigan.

Mysis from Lake Mjøsa, as well as other lakes, seem to have a very flexible life cycle strategy. This phenotypic trait is seen even in this stable, old (8-10 000 year) Mysis population, but is clearly expressed when populations are introduced to new habitats. Three types of life histories have been recorded from Scandinavian lakes: one-year life cycle with winter breeding, two-year life cycle with winter breeding and finally summer breeding and winter breeding populations living sympatrically (Furst, 1972). It is generally believed that low temperature and shortage of food promote slow growth and lead to a two-year life history, or even four-year life history as observed in lake Tahoe (Morgan, 1980). This also reduce the P/B-ratio. In lake Paajarvi, where Mysis show a predominant one-year life cycle, P/B-ratio was near 3 (Hakala, 1978), in lake Mjøsa with a predominant two-year life cycle P/B-ratio was around 2, whereas only 0.5 in lake Tahoe where Mysis had a four-year life cycle (Morgan, 1980).

In some populations of Mysis, life history is difficult to elucidate due to overlapping sympatric cohorts with slightly different life histories (cf. Morgan & Beeton, 1978). The life history described for such Mysis-populations may be more common that hitherto recorded, but there are great differences concerned with the analysis of populations with such overlapping cohorts (cf. Carpenter et al., 1974; Hakala, 1978). In lake Mjøsa, breeding ocurred exclusively during winter.

The prolonged life-history of Mysis from Mjøsa is probably mainly governed by low temperature, although low food availability during parts of the year may also contribute to this. No changes is life history have been detected in recent years as due to changing food abundance in the lake (unpubl. data). Prolonged life histories are well known from freshwater copepods in the temperate region (Elgmork, 1965, 1981; Nilssen, 1980), and an unifying explanation for these life histories may be low temperature. Arctic and temperate populations of Mysis differed in generation lengths (two and one year, respectively), but M. relicta demonstrated no metabolic compensation over its environmental temperature range (Lasenby & Langford, 1972). Variable life cycle strategies seem to be an adaption to buffer against environmental fluctuations, and improve dispersal and establishment of populations in new habitats. Moreover, the fractionation of the deme results in a finer adaption to prevailing food abundance and predator activity in the immediate environment (cf. Nilssen, 1980).

The main release of juveniles in spring seem well correlated to the spring burst of phytoplankton, and the development and shifts in diet from phytoplankton via rotifers to cladocera is closely correlated to the biomass development of these groups (Kjellberg et al., in ms.). As indicated by our studies, also predator patterns may determine the life history, and the distribution between the different fractions and cohorts. A high biomass of smelt in 1977 (Sandlund et al., 1980) seemingly gave a high proportion of 0+, and a virtually extinction of two year and older Mysis. The following year (1978), the population experienced a predominant one-year life history.

An important question remains as to the genetic basis of the life history of Mysis. Through a number of tranplantation experiments, a better understanding of factors governing life history may be obtained. For a short period of time, it would be expected that a given population would show the life history exhibited in its original site, if genotypic determinants were most important, since alteratios of life cycle by selection would take some time (or generations) to occur. During transplantation studies, the opposite may be observed (e.g. Olsen, 1980): the population changes its life history within the very first year, and after 2-4 years the population changed back to a two-year life history as exhibited at its original site. This show the strong phenotypic component inherited in the life history of *Mysis*. The rapid change to a one-year life cycle would be a natural consequence of high food abundance and low predation pressure in a new environment. For the first years, *Mysis* may exploitate resources in the upper, warm layer (Langeland, 1981), until food abundance declines and a more *Mysis*-oriented predator community has evolved. Probably, all (or most) *Mysis* populations have the genetic base for the full range of life cycle strategies (cf. Morgan, 1980). The actual life history capacity may be largely hidden, since the selective forces in a specific environment does not select for all combinations of life histories.

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Table 1. Correlations based on least square regressions, between production and biomass of *Mysis* against environmental parameters. Positive (+) or negative correlation indicated when $p < 0.5$. D. gal.: *Daphnia galeata*, B. lon.: *Bosmina longispina*. Determinations are based on seasonal means for each parameter from the four years.

	Prod.0+	Prod.1+,2+	Tot. prod.	Tot. biom.	P/B
Phyto.	.248(-)	.456(+)	.616	.423(-)	.612
Tot. zoo.	.014(-)	.751	.179(-)	.664	.946
D. gal.	.447(-)	.511	.108(-)	.278(-)	.628
B. lon.	.822	.109(-)	.567	.334(-)	.441(+)
Temp.	.767	.843	.873	.091(-)	.112(+)

FIGURE LEGEND

Fig. 1. Fresh-weight (FW) and dry-weight (DW) as a function of body-length for Mysis relicta in Lake Mjøsa.

Fig. 2. Relative numbers (ind. m^{-2}) of Mysis relicta over the central parts of lake Mjøsa for 1976, 1978, 1979 and 1980.

Fig. 3. Seasonal growth curves for 0+ and 1+ Mysis in lake Mjøsa for the four years of survey.

Fig. 4. Survivalship-curve for Mysis in lake Mjøsa for the four years of survey.

Fig. 5. Net production (mg WW m^{-2}) for the various size groups of Mysis in lake Mjøsa, basaed on Allen curves.

Fig. 6. Generalized life scheme for the life history of Mysis in lake Mjøsa. Mean individual length increment with 95% confidence limits indicated.

Fig. 7. Relationship between body-length and mean no. of offspring for Mysis in lake Mjøsa.

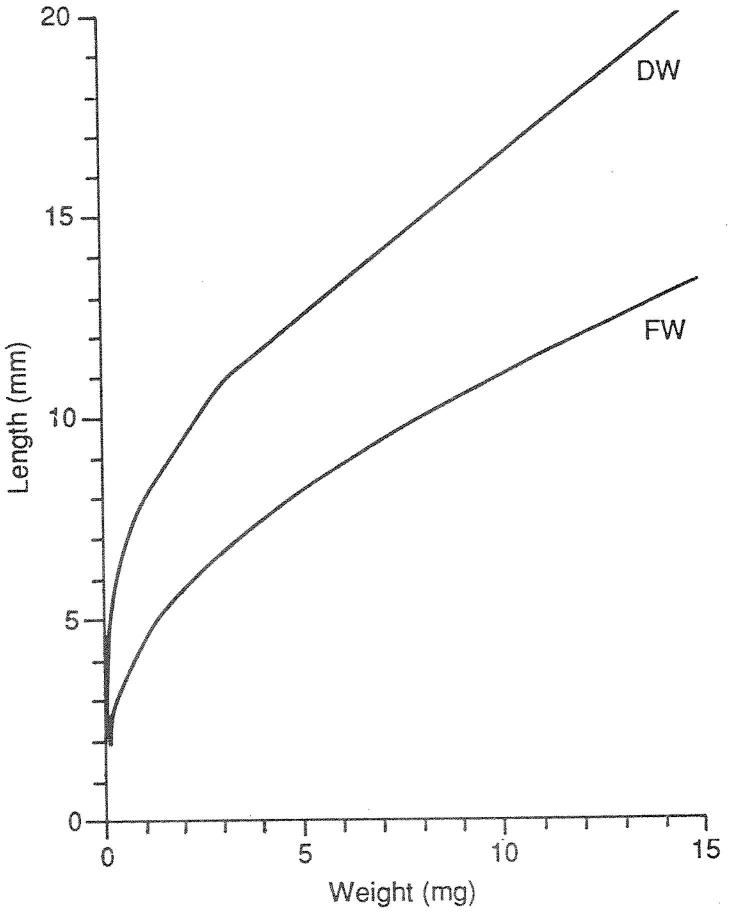
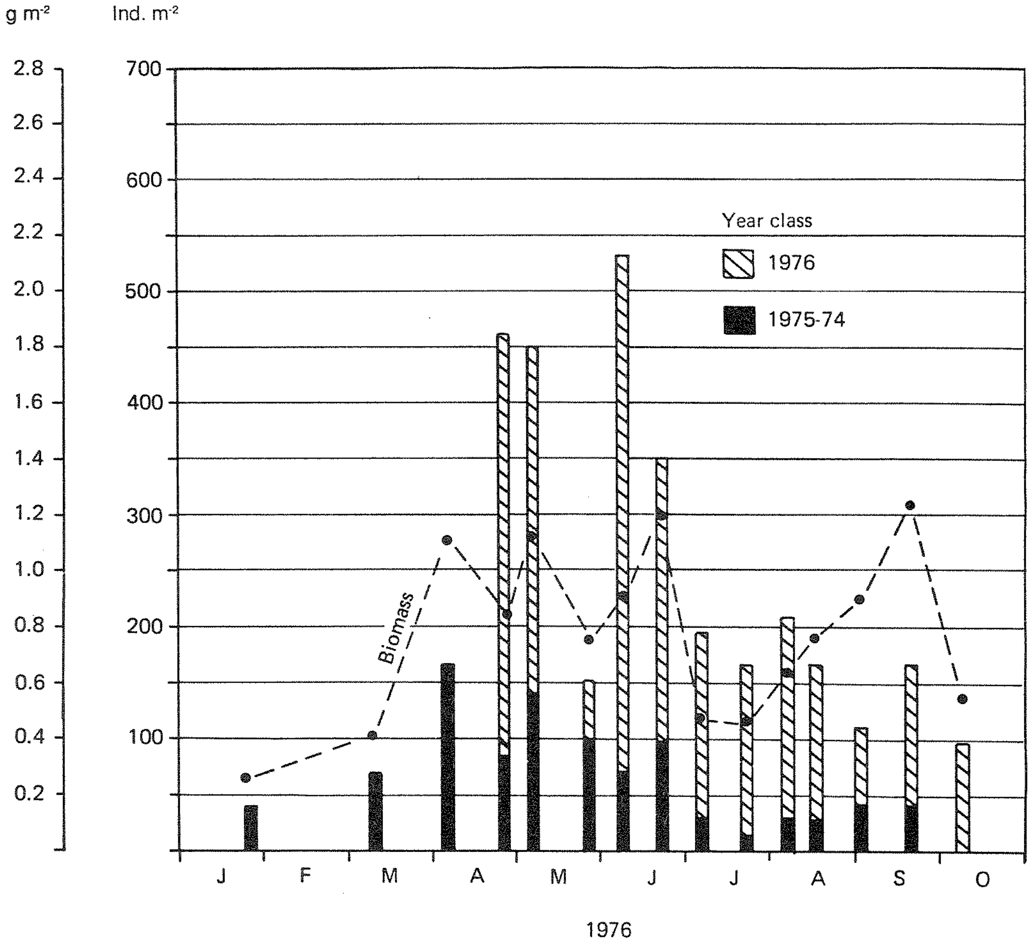


Fig. 1


g m⁻²
Ind. m⁻²
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
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0.8
0.6
0.4
0.2
700
600
500
400
300
200
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1975-74
Biomass
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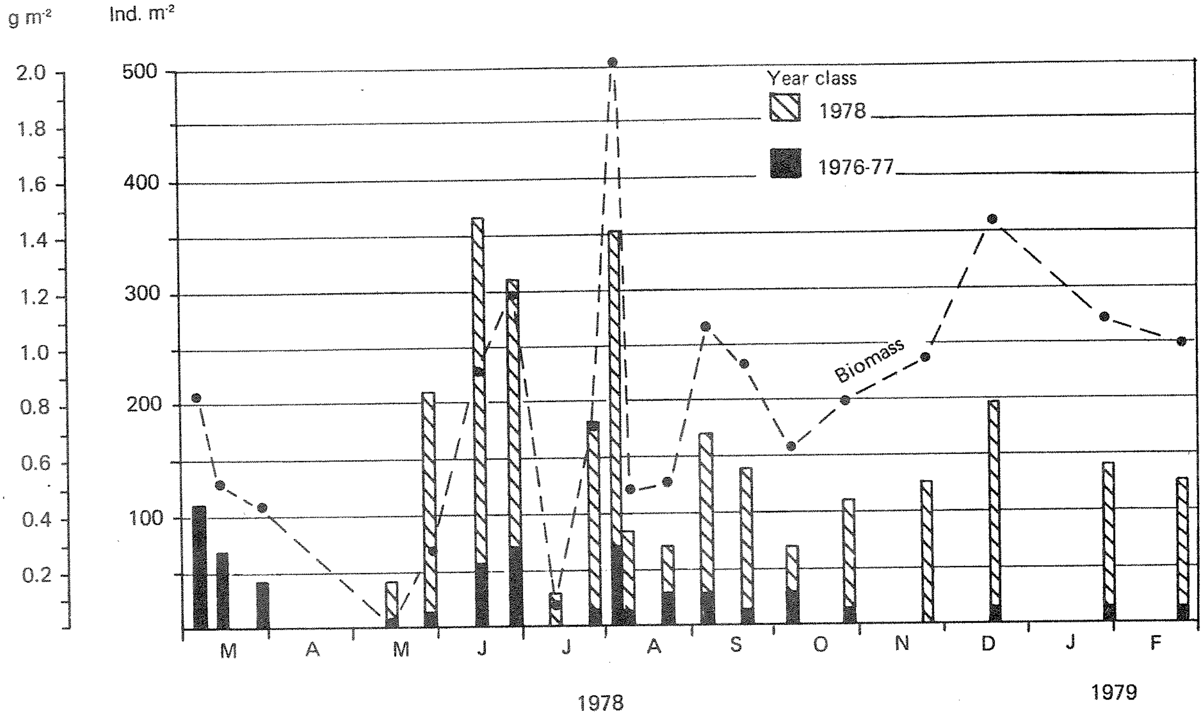
Fig. 2



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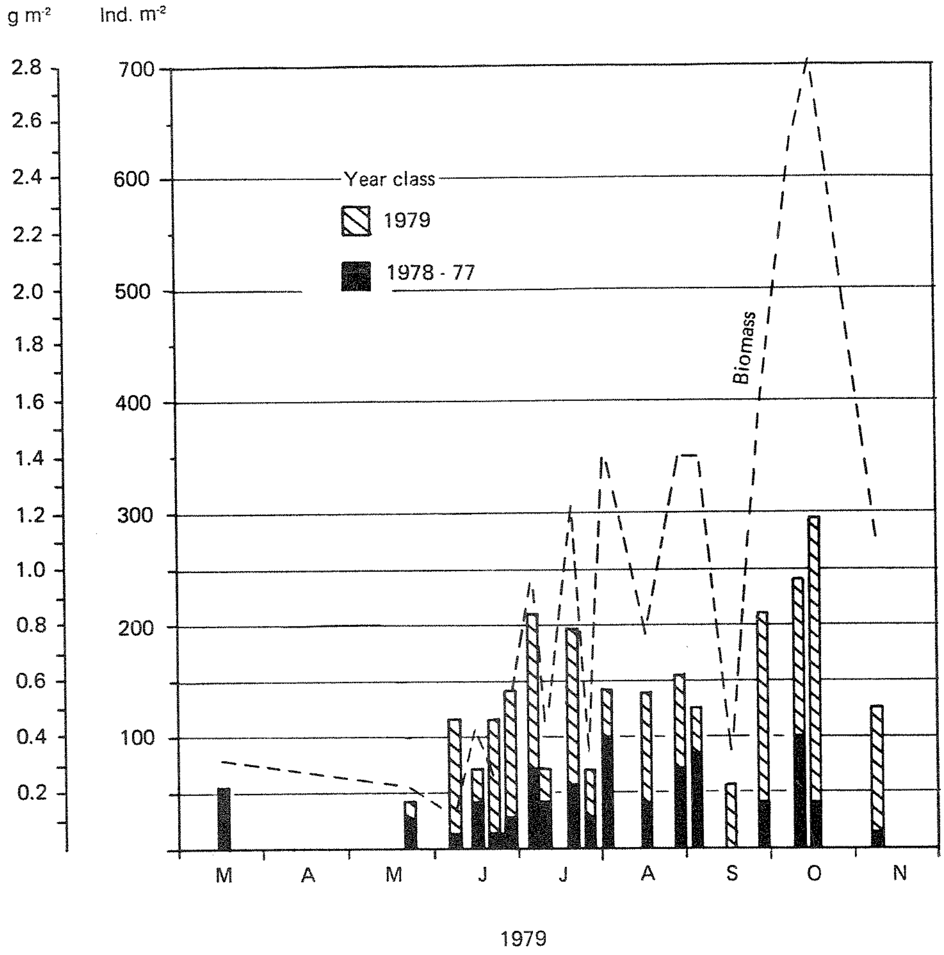

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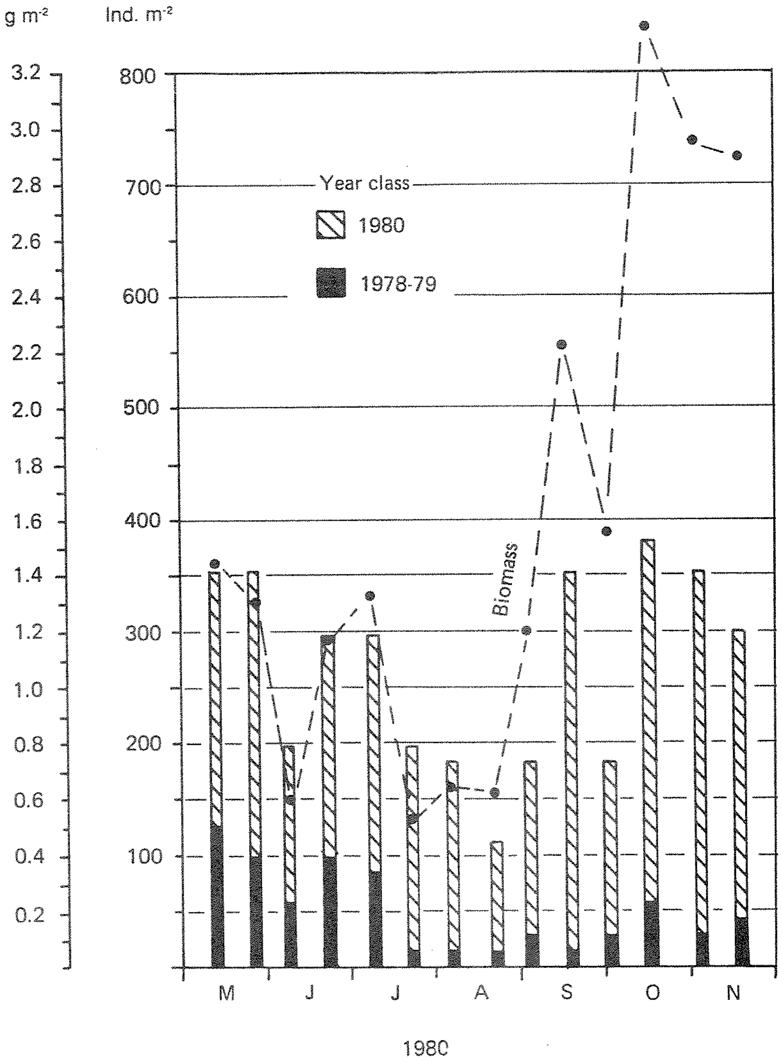

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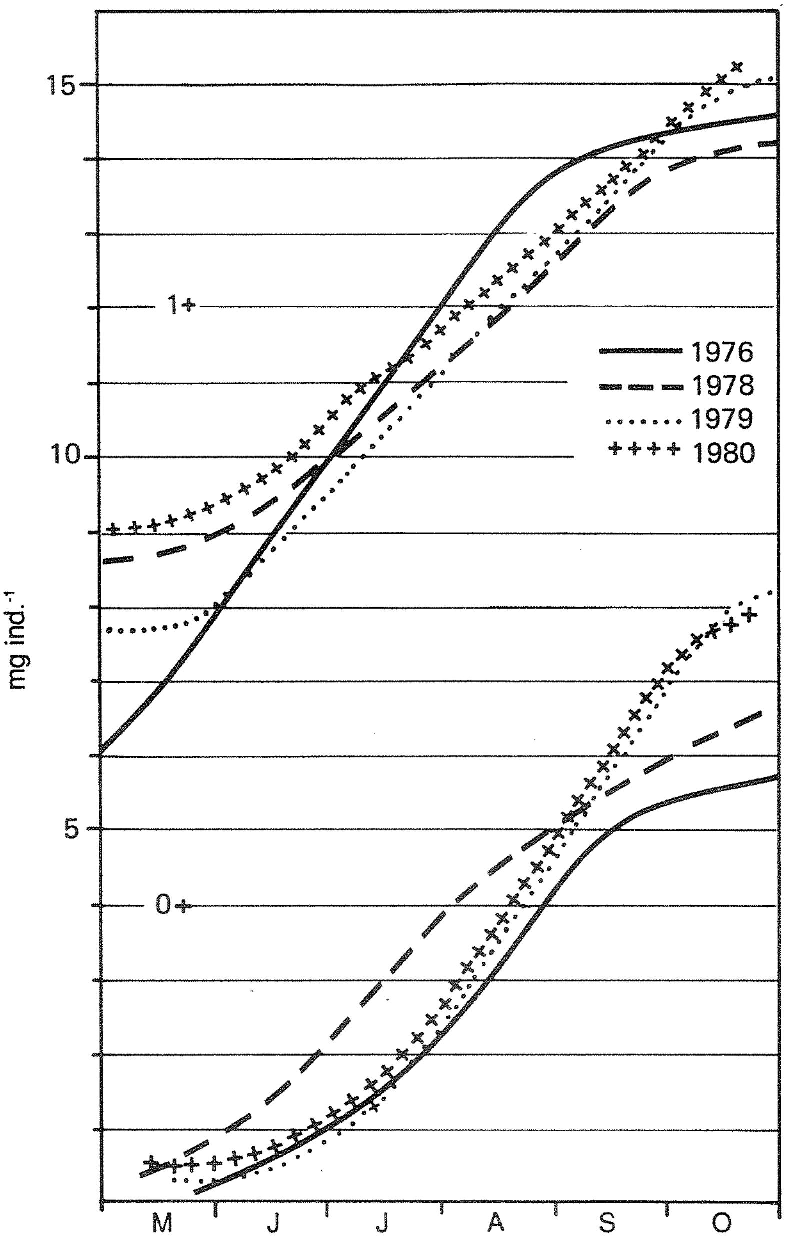


Fig. 3

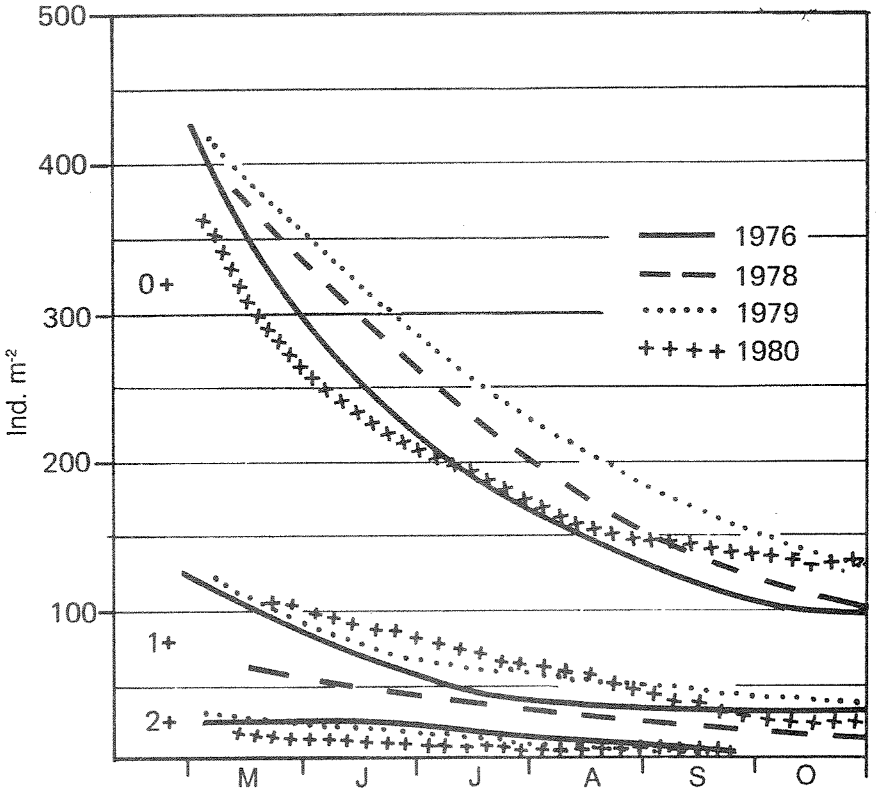
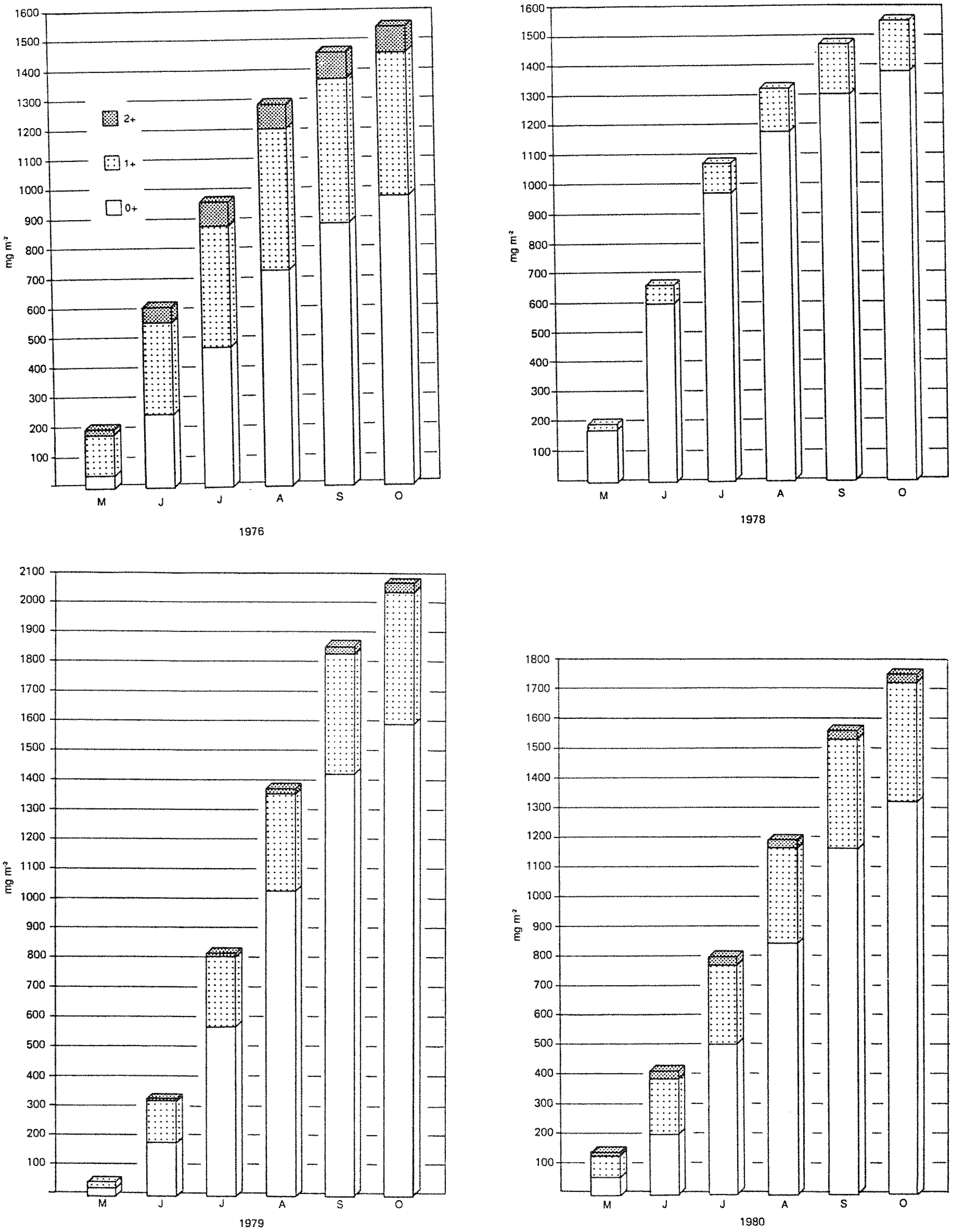


Fig. 4


2+
1+
0+
mg m²
1600
1500
1400
1300
1200
1100
1000
900
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700
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500
400
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M
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A
S
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1976
1978
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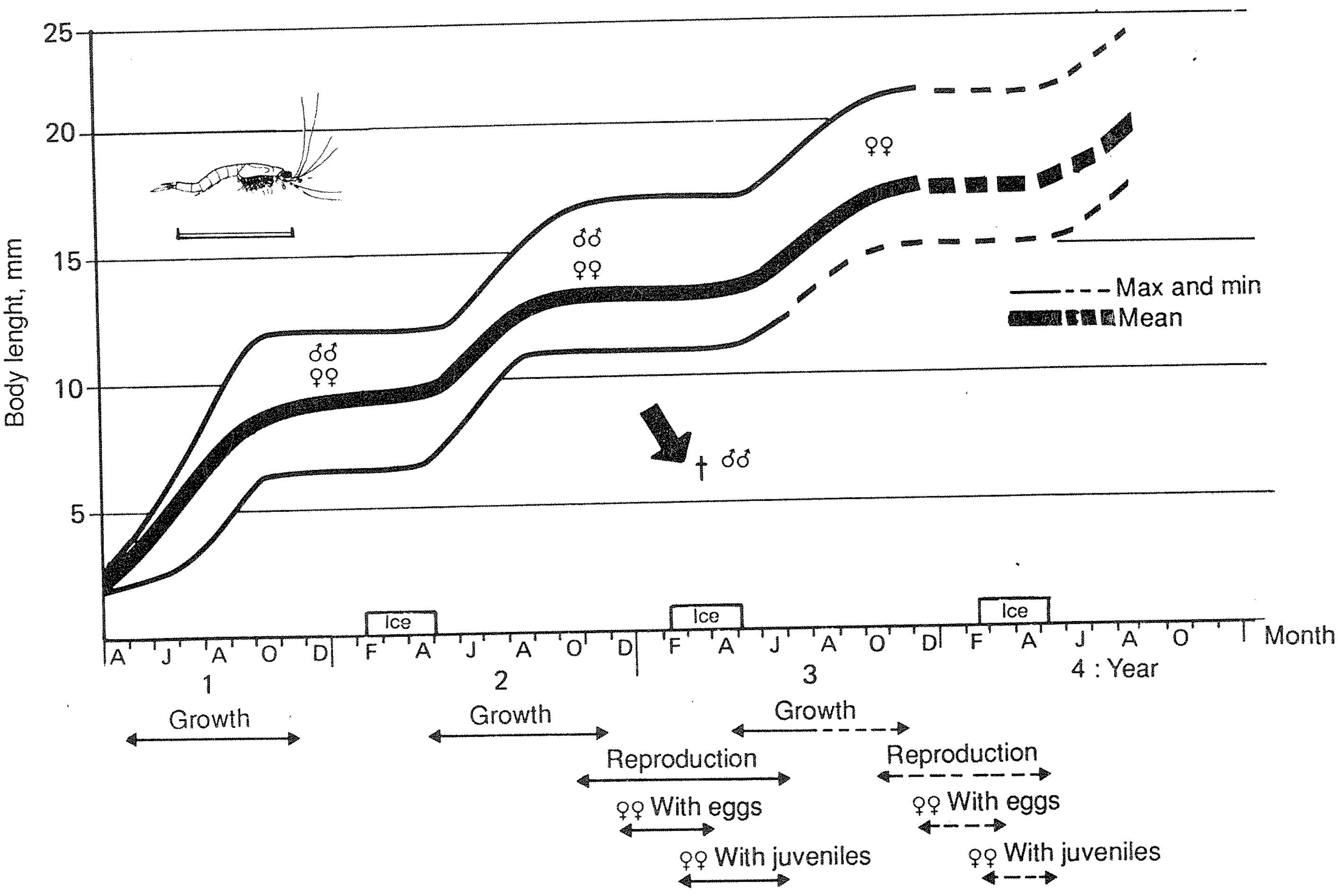
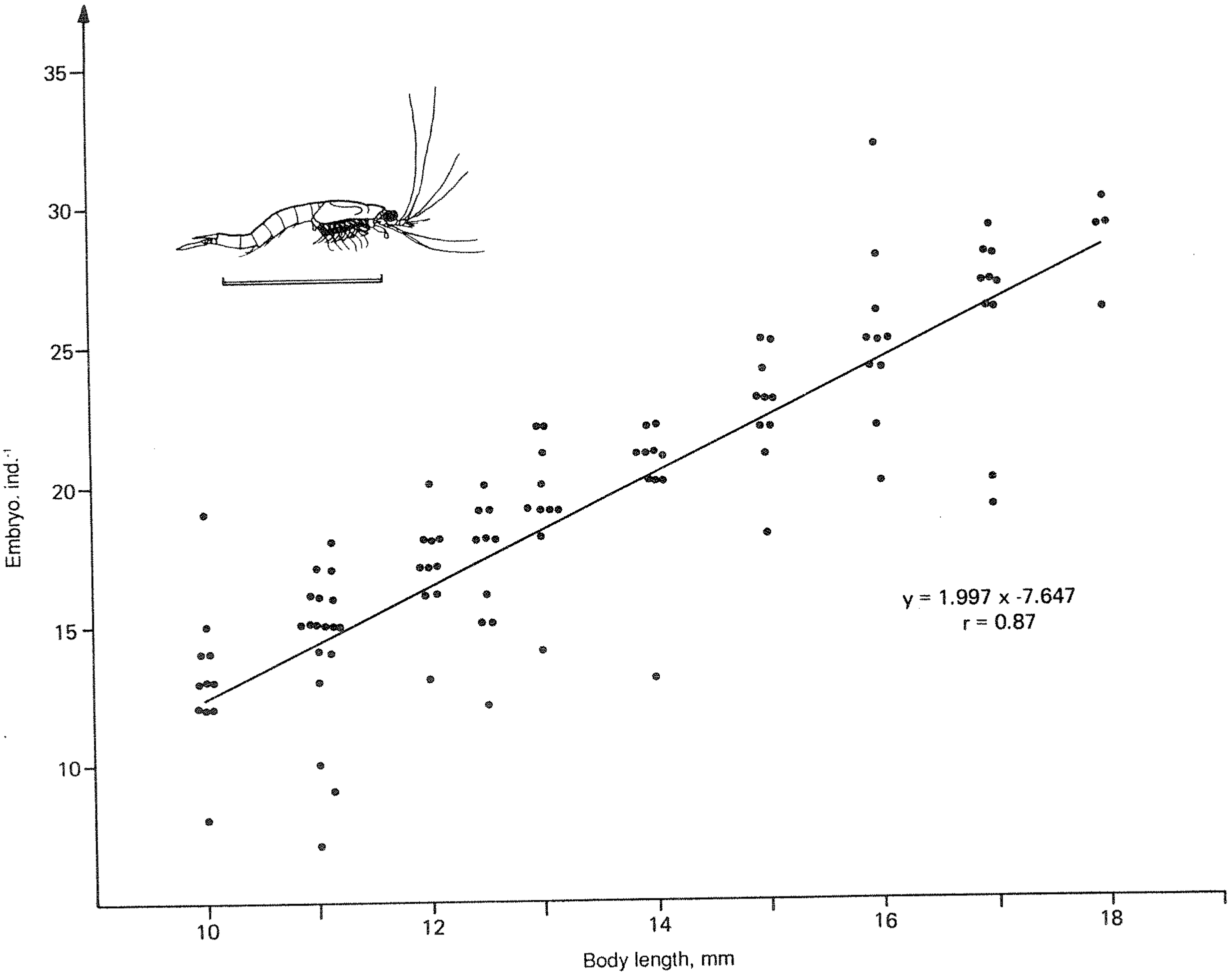
1800
1979
1980

Fig. 5



25
20
15
10
5
Body lenght, mm
♂♂
♀♀
♂♂
♀♀
♀♀
† ♂♂
Max and min
Mean
Ice
Ice
Ice
A J A O D F A J A O D F A J A O D F A J A O
Month
1
2
3
4 : Year
Growth
Growth
Growth
Reproduction
Reproduction
♀♀ With eggs
♀♀ With eggs
♀♀ With juveniles
♀♀ With juveniles

Fig. 6


35
30
25
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15
10
Embryo. ind.⁻¹
10
12
14
16
18
Body length, mm
y = 1.997 x -7.647
r = 0.87

Fig. 7

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