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REPORT OF THE WORKING GROUP ON ZOOPLANKTON ECOLOGY

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19-23 June 1995

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International Council for the Exploration of the Sea

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Activities underway on both sides of the North Atlantic have combined to constitute a full scale attack from now through at least 1998 on the biology of the region's dominant zooplankter, *Calanus finmarchicus*. In view of the importance of *C. finmarchicus* to fisheries and in the general ecology of the North Atlantic, the WG urges ICES and national agencies to support this effort.

.... 1997 has been designated the YEAR OF THE CALANUS ....

CONTENTS

1. Opening of the meeting

The meeting was held in the Carriage House at the Quissett Campus of the Woods Hole Oceanographic Institution and was opened at 9 am on Monday 19 June. The meeting was attended by 9 participants from 5 countries (Annex 1). The chairman Hein Rune Skjoldal noted in his opening remark that the WG was a continuation of the ICES Study Group of Zooplankton Production and represented an increased effort by the ICES in studies of zooplankton in relation to productivity and ecology of marine systems.

Associate Director of Research at WHOI, Dr. Jim Luyten, addressed the meeting and underlined the importance of international cooperation and exchange in marine research. He also noted the large complexity in issues involving interactions between ocean physics and biological processes.

Peter Wiebe gave a brief introduction to the WHOI campuses and laboratories and practical information about the meeting facilities.

Hein Rune Skjoldal referred to the terms of reference for the meeting (ICES C. Res. 1994/2:53) and noted that these arose partly from the former SGZP and partly from the ICES Workshop on Trans-latitudinal Studies of Calanus organized by Charles Miller and Kurt Tande in Oslo, April 1994. He noted that in addition to these tasks it would be of value if the WG could also consider other tasks which should be put on the future workprogramme of the WG.

2. Adoption of the agenda

The chairman presented a draft agenda which was adopted as the agenda for the meeting (Annex 2). The meeting agreed to the need for completing as much as possible of the drafting of chapters and standard protocols during the time the WG members were together, and that part of the meeting therefore needed to be spent in smaller drafting groups.

3. Review of progress on preparation of Zooplankton Methodology Manual and standard protocols

The chairman noted that the timetable agreed at the last meeting of the SG in Plymouth in March 1994 had not been kept and that there was a delay of approximately 6 mo relative to the plan. None of the drafts for the various chapters had been prepared and circulated in advance of this meeting. Detailed outlines or draft texts were brought to the meeting and it was agreed to use the time at this meeting to complete the drafting as far as possible.

The status of drafting of the various chapters differed, with some being not started and others brought as nearly completed drafts. The status of preparation of the different chapters is as follows:

- Chapters 1 (Introduction) and 2 (Sampling and experimental design) were not drafted yet. Outline of chapter 2 would be produced during the meeting.
- Chapter 3 - Sampling of zooplankton. Doug Sameoto had a draft text for much of the chapter but some parts were still missing. He would work on the draft with help from P. Wiebe and C. Miller. He would also produce a draft text for guidlines on sampling.
- Chapter 4 - Biomass and abundance. Lutz Postel had sent an outline for the chapter and draft text for a standard protocol for determination of biomass. Jürgen Lenz would work on this and suggest modifications if needed.
- Chapter 5 - Acoustical methods. P. Wiebe had draft text for part of the chapter. He and Ken Foote would produce a detailed outline for the chapter. Remaining parts of the chapter would be drafted with help from K. Foote and Tim Stanton.
- Chapter 6 - Optical methods. No text had been provided by Uwe Kils yet. Kils will be contacted to get his contribution.
- Chapter 7 - Feeding. Ulf Båmstedt had not produced any text yet but was to produce an outline during the meeting. JGOFS protocols on grazing should be consulted as before drafting standard protocols.
- Chapter 8 - Growth. Jeff Runge provided a fairly complete draft version of the chapter. He had also discussed and circulated among experts a survey of methods for egg production measurements. It was considered that the progress on this chapter was very good and that it could be used as a standard for other chapters.
- Chapter 9 - Metabolism. Tzutomu Ikeda sent a draft version of the chapter that reached the WG during the meeting.
- Chapter 10 - Behaviour. The suggested main author for this chapter could regretably not take this responsibility due to other duties. There was now some urgency to find a replacement as main author.
- Chapter 11 - Genetics. Ann Bucklin provided a detailed outline for the chapter during the meeting.
- Chapter 12 - Population dynamics. Dag Aksnes brought a fairly complete draft text for this chapter. He was to polish the text further with help from C. Miller.
- Chapter 13 - Modelling. The suggested main author for this chapter had also reclined the responsibility due to other obligations in the planned timeframe.

There was some discussion on chapters 10 and 13 that had not yet been planned with a responsible main author. There was concern that these chapters could delay the publication of the manual and that this could make other chapters that were nearly completed in need for a further update. It was agreed that an attempt should be made to have the chapters 10 and 13 drafted and included in the manual. One possibility was to restrict the content and level of ambition for these chapters and to focus on providing an introduction and overview to methodologies used for studies of behaviour and modelling of zooplankton. If these chapters cannot be completed within the 15 February deadline they are likely to be left out of the manual.

It was noted in relation to the chapter on sampling that video material to be included in the CD-ROM version need to be made and compiled. D. Sameoto was planning to have video recordings made during field work this summer. It was recommended that main authors and contributors should consider the possibility to have video recordings made in order to illustrate descriptions of methodologies. In making a video, commentary should not be made while doing the recording but added later on edited version of the video. Time marks should also not be included on the original video recordings. Wiebe commented that much illustrative material was already in existence that could be used as illustrating material to the manual.

4. Results from sea-going and laboratory workshops

A workshop on Calanus for intercomparison of methods for determination of growth was held in Bergen 19 April - 2 May 1994. A brief report from the workshop had been prepared for the ICES Science meeting last year (ICEC C.M. 1994/L:9).

H. R. Skjoldal gave a brief orientation about the workshop. The initial plan was to use developing cohorts of *Calanus finmarchicus* in mesocosms as the material to be applied for intercomparison of methods. This part failed, however, due to technical difficulties and a high demand of material for the various analyses. The plans were therefore changed to sampling of a field population in the fjord close to the field station of the University of Bergen at Espegrend. This made it difficult to have an accurate and precise estimate of the real growth rate to be used as a reference for comparison with results obtained with other methods.

The workshop was attended by researchers from several laboratories in France, Germany, Norway, Spain and the UK. Measurements and methods included stage and size analysis, feeding and metabolic rate, fecal pellet production, moulting and stage duration, direct measurement of growth as size increment, enzyme analyses (ETS and ATC), RNA, DNA, and C and N content. All results had not yet been compiled and compared, and only some preliminary results were available.

H. R. Skjoldal presented results on measurements of RNA and DNA in *Calanus* stages III-V. The RNA content and the RNA/DNA ratio showed trends with lower values in individuals kept in the laboratory without food addition than in individuals that were fed. A general experience was that the DNA content also varied and showed trends similar to that of the RNA content. It appears from this and other evidence that the DNA content can show rapid changes with changes in metabolic activity, and this may make the RNA/DNA-ratio less suitable as an indicator for growth activity than the RNA content normalized per unit biomass.

Santiago Hernandez-Léon presented results from the work of his group who participated in the *Calanus* workshop as well as from the previous workshop on *Acartia* in October 1993. Using a flow-through system they observed rapid increase in the rate of respiration following addition of food, followed by a reduction after some time. The range of respiration varied by a factor of 3 or more between individuals in starved and fed states. This was interpreted to reflect the increased metabolic rate associated with feeding activity and food processesing. ETS activity also showed considerable changes partly correlated to those in respiration. He considered the relationship between ETS activity and respiration to be complex, i.e. they are dependent on other factors such as the substrates in the organisms and whether they are at saturating levels or not.

Results on ATC (aspartate transcarbamylase) activity showed no clear relationship with other measures of metabolic activity.

The status of analysis of the results from the seagoing workshop on intercomparison of sampling gears in Norway in June 1993 was briefly considered. A quality controlled dataset on biomass and species composition was available and could be retrieved from Institute of Marine Research in Bergen by anonymous ftp. Preliminary analysis had showed no large differences in biomass of mesozooplankton caught by the different gears. The BIONESS with coarser mesh and operated at higher speed collected more macroplankton and micronekton (krill, shrimps, small fish) than did the MOCNESS. MOCNESS on the other hand, collected more in the smallest size fraction than BIONESS (with same mesh size in the two gears), probably reflecting more extrusion due to the higher speed.

Steve Coombs had reported a fairly good agreement in the results on number and size of zooplankton organisms obtained by manual examination of LHPR (Longhurst-Hardy Plankton Recorder) samples compared to results obtained in situ with an OPC (Optical Plankton Counter) mounted on the LHPR.

Further analysis were to be agreed and performed by D. Sameoto, P. Wiebe and H. R. Skjoldal, to be used as part of the basis for conclusions and recommendations on sampling. A 12 min video from the workshop had been made and this was shown during the meeting. The video shows operation of some of the sampling gears used at the workshop. It is available from the Institute of Marine Research in Bergen upon request.

5. Evaluation of methods and recommended standard protocols

The methods dealt with in each chapter of the manual were considered with emphasis on the detailed content of the chapters and issues related to standardization and improvements. At the previous meetings of the Study group on Zooplankton Production in Las Palmas (1993) and Plymouth (1994) a list of candidate methods for standardization and improvements had been made and drafting tasks for outlines of standard protocols or guidelines had been distributed.

An updated list of main and associate authors for the various chapters of the Zooplankton Methodology Manual is given in Annex 3. Detailed outlines of the chapters are given as Annex 4.

Some of the main points regarding evaluation of the methods and recommendations on standardization and improvements are given below for the main chapters of the Manual.

5.1 Sampling

The detailed outline for the chapter was considered to give an appropriate treatment of the various types of sampling gear and of the sources of error involved. Issues related to combined use of net sampling and acoustical and optical sampling systems will be dealt with in chapter 2 (Sampling and experimental design) and only a brief reference will be included in the chapter on sampling.

The WG make the following recommendations:

1. No specific sampling gear is recommended for sampling of mesozooplankton. The difference in sampling efficiency between commonly used nets is considered not to be large, and a flexibility in choice of net is therefore possible. Information on the vertical distribution of zooplankton is important for many purposes, and it is therefore recommended to use depth-stratified sampling with available multiple net sampling systems. If such systems are not available or can be operated for practical reasons, an alternative option is to use vertical or oblique net hauls. We recommend that the WP-2 net should still be used as a standard for vertical nets.

2. In order to obtain comparative data on mesozooplankton biomass and abundance across different ecosystems and ocean areas, we recommend that 200 μm mesh net be used as a standard whenever possible. The choice of 200 μm is a compromise between the wish to sample representatively the younger copepodite stages of medium-sized copepods (e.g. *Calanus finmarchicus*) and to reduce the likelihood of net clogging. 200 μm is also the lower size limit of mesozooplankton by definition. Specific research objectives in particular environments may dictate the choice of another mesh size. Choice of a lower mesh size may still give comparable data if the degree of net clogging is low and controlled. We recommend the use of flowmeters on a routine basis, preferably inside the net opening.

3. Two promising developments to reduce net avoidance and increase the sampling efficiency of macrozooplankton and micronekton are the use of flashing light to blind the individuals and transparent nose cone in front of the net to hinder escape by short distance response to the approacing net. We recommend that more research should be carried out to further document the efficiency of such measures and that they should be taken into use in further gear development and operation.

The WG aims at producing a short standard protocol or guidelines for mesozooplankton sampling as part of the Manual. D. Sameoto will produce the first draft text with help from P. Wiebe and H. R. Skjoldal.

5.2 Biomass and abundance

A modified outline for the content of Chapter 4 on Biomass and abundance was agreed as the basis for further drafting. L. Postel had provided a standard protocol for determination of mesozooplankton biomass in net samples. J. Lenz has made a second draft of this text for circulation and comments from experts.

The WG recommend that the following elements should be included in the standard protocol on determination of mesozooplankton biomass:

1. Where there is a need for splitting, it should be done on fresh samples shortly after capture using a Folsom splitter or similar splitting device. Large gelatinous organisms should preferably be removed from the sample prior to splitting, and their biomass determined separately.

2. Dry weight should be the standard unit for reporting mesozooplankton biomass. It is desirable also to measure ash-free dry weight for the whole or part of sample collection from a field study, particularly if there is a large proportion of gelatinous forms of zooplankton. For some research or monitoring purposes it may also be required to take subsamples from the dried biomass for determination of elemental and gross biochemical composition (e.g. C, N, P, protein, lipid). An alternative will be to use appropriate conversion factors to estimate C and N from dry weight biomass.

3. Size fractionation by wet sieving of fresh samples can be used to have information on size distribution of biomass. It is recommended to have the following standard set of mesh sizes in the screens for the wet sieving: 200, 500, 1000, 2000, 4000, 10000 μm. It may not be necessary or desirable to use all mesh sizes in a given study. We recommend that 1000 μm should be applied as a minimum in addition to 200 μm in order to separate between small and large mesozooplankton.

4. Estimation of biomass and abundance by use of silhoutte photography or video techniques with sufficient resolution can be used in addition or as an alternative to dry weight biomass determination for some purposes. The advantage of this method is that it provides more detailed information on size distribution and taxonomic composition which is important when the data are to be used in combination with acoustical data.

5.3 Acoustical methods

An outline of Chapter 5 on Acoustical methods was prepared by K. Foote, P. Wiebe and T. Stanton. This was considered a good basis for drafting the chapter. It was underlined that the chapter had to be written so that it would be readily understood by researchers with little background knowledge of acoustics.

The WG discussed the issue of the inverse or forward methods, and the difficulties and required steps in the further development and use of acoustics in data collection for studies of zooplankton. Use of multi-frequency acoustics to derive information on the size distribution and abundance of plankton by the so-called inverse method requires use of models and usually assumptions about physical properties of the organisms for the quantitative relationships between acoustic backscattering and the properties of the organisms. Different models exist, and the choice of model(s) for any given situation requires knowledge about the taxonomic composition of the plankton. Knowing the taxonomic composition, on the other hand, the acoustic backscattering can be calculated with the so-called forward method by applying the appropriate models for the different taxa. Extensive and representative sampling is therefore required in order to apply the forward method to verify the reliability of information that can be derived from acoustical data. This will be a necessary step before the inverse method can be applied with confidence in the future (see Annex 5 for further information and references).

The use of ADCPs for measuring biological acoustic backscattering has become common in recent years due to the availability of user friendly software. A number of recent publications have suggested that the 150 kHz ADCP instruments were capable of providing a quantitative measure of backscatter from copepods, whereas other authors have questioned whether the scattering actually originates from copepods. Acoustic theory suggests that 150 kHz is too low a frequency to detect copepods at the levels of concentration reported in the literature. It is most likely the backscattering came from macrozooplankton or small fish associated with the copepod layers and that these larger organisms avoided the sampling nets when the copepods were caught at the depth of the acoustic backscattering layers. The ADCP is a very useful tool for mapping the patterns in macrozooplankton distribution, but the evidence that it detects copepod concentrations is not convincing. On the contrary, sampling for copepods at depths with no acoustic backscattering from 150 kHz ADCPs has revealed large concentrations of *Calanus* in the absence of macrozooplankton. The backscattering that was observed was consistently associated with the presence of macrozooplankton such as euphausiids, amphipods and pteropods (Sameoto personal communication). We encourage the use of ADCPs for biological studies, but caution the users to be aware of their limitations.

5.4 Optical methods

No outline for the chapter on Optical methods has been produced yet. Some text describing optical systems is available from previous meeting of the SG and this will be used along with additional text. Several recent reviews on optical methods are available (e.g. GLOBEC reports) to be used as references and background material. U. Kils had in a letter reported further development of his ecoSCOPE and use of CYBERSPACE technologies in studies of zooplankton and fish. Kils will be asked to produce text for the chapter of optical methods with input from associate authors.

5.5 Feeding

An outline for the chapter on feeding was provided during the meeting by U. Båmstedt. This will be used as the basis for drafting the chapter. The WG was informed by Roger Harris that JGOFS protocol for determination of mesozooplankton grazing had been discussed at a meeting during the ICES Zooplankton Symposium in August last year, but that no final agreement and adoption of this protocol had been made yet. Harris agreed to help with the production of a standard protocol on mesozooplankton grazing and to assure harmonisation with the JGOFS protocol.

5.6 Growth

Runge provided a detailed overview of the chapter on growth. The chapter focused on copepods but an attempt would be made to broaden the scope where possible and to seek assistance from experts on other groups of zooplankton if appropriate. Patricia Kremer would be asked to provide an input to the chapter on methods for determining growth of gelatinous zooplankton.

Runge is redrafting a standard protocol on egg production by *Calanus finmarchicus* and related *Calanus* species to be circulated for comments among experts. The intention is to include this as a standard protocol to be used in the TASC program and possibly other GLOBEC or ICES activities.

Michael Moore from WHOI attended the meeting at this agenda point to inform about some recent work using bichemical techniques to study rates of cell proliferation in fish larvae and copepods. PCNA (proliferating cell nuclear antigen) is a necessary cofactor for DNA polymerase delta. In simplistic terms, it can be described as the "grease that helps DNA polymerase run down the zipper". The quantity of PCNA can be determined by immunohistochemical methods using a commercially available antibody.

The hypothesis under investigation is that the quantity of PCNA in marine planktonic tissue is related to the rate of cell division and consequently can be used as an index of growth. Studies have been carried out on copepods during a GLOBEC workshop held in Hawaii and on ichthyoplankton reared in the laboratory at Woods Hole. Preliminary results do not show clear relationships between PCNA and reproductive activity in copepods. There is a need to have a better understanding of relationships between oogenesis, cell proliferation and actual egg production. Preliminary results of experiments on fish larvae do show a differences in PCNA levels between starved and fed groups. The rate of cell proliferation in fish larvae, as shown by PCNA analysis, is remarkably high. PCNA levels will be measured in zooplankton and ichthyoplankton from liquid nitrogen frozen samples collected on Georges Bank.

5.7 Metabolism

T. Ikeda provided an outline and draft text for the chapter on metabolism to the WG during the meeting. He has made a comprehensive review on problems and methods for determining rates of metabolism. The WG suggested that S. Hernandez-Léon should contribute to the chapter with additional inputs of biochemical methods.

The WG will consider further whether a standard protocol for determination of metabolic rate of zooplankton should be produced. A protocol in the form of general guidelines to the conduct of such measurements could of value. Also video sequences of handling of animals should be included as illustration in the CD-ROM part of the Manual.

5.8 Behaviour

No outline for the chapter is yet available. The chairman will discuss this with potential authors with the aim to have the chapter drafted during the autumn.

5.9 Genetics

A. Bucklin provided an outline for the content of the chapter on genetics. She will draft the chapter with input from associate authors.

5.10 Population dynamics

D. Aksnes has provided an outline and draft text with input from coauthors for the chapter on population dynamics. He will draft a shorter version as guidelines for studies of population dynamics of zooplankton.

5.11 Modelling

No outline of this chapter is available yet. Francois Carlotti and Jarl Giske have agreed to contribute to the chapter. The chairman will complete the author list with the aim to have the chapter produced over the next 4 months for inclusion in the Manual.

6. Actions to finalize preparations of the Zooplankton Methodology Manual including standard protocols and guidelines

The author list for the manual is now nearly complete. The outstanding questions regarding responsible main authors for chapters 10 (Behaviour) and 13 (Modelling) will be dealt with by the chairman. Inclusion of additional authors to some of the chapters is the responsibility of the respective main authors.

The time table for completion of the Manual is to have the drafting and internal review (circulation for comments from other experts and members of the WG) done by **1 November** this year. Harry Dooley at the ICES secretariat has set up a mailbox called «zoop@server.ices.inst.dk». Members of the WG and main authors and coauthors for the manual are requested to send their e-mail address to H. Dooley (harry@server.ices.inst.dk) so that they can be connected to the mailbox. Messages to the mailbox will then be distributed to all those connected. H. Dooley has also set up a directory on anonymous ftp called .zoop. Files containing versions of the chapters can be deposited and retrieved from there. The directory can be reached as follows by anonymous users with their user-name as password:

ftp ftp.ices.inst.dk
cd pub/.zoop
Files can be retrieved by the command
retrieve "filename".txt
quit/exit
Contact H. Dooley at ICES in case of difficulties or if further instructions are needed.

We intend to carry out an external review of the chapters by experts that have not taken directly part in the preparation of the Manual. The aim is to have this external review process and adjustment of the manuscripts completed by **15 February 1996**. The review process will be handled by the editors with assistance from the ICES secretariat.

The ICES secretariat has met with representatives from the EU/MAST-III program. There was an expressed interest from MAST to support the publication and distribution of the Manual. This option will be followed up by the ICES secretariat and the editor.

7. Report on progress from the Calanus TASC workshop in Oslo, April 1994

Calanus finmarchicus is a large copepod which is dominant in the plankton of the boreal North Atlantic from the Gulf Stream north to the southern edges of the Arctic Ocean. It is currently a target species for study programs based in Norway (Mare Cognitum program), the European Union (Mast supported ICOS program), and the U.S. (GLOBEC Georges Bank study). In addition, laboratories and investigators in Canada, Iceland, the Faroes, Sweden, Denmark, Germany, U.K. and France are engaged in *Calanus* studies. In order to foster communications among the scientists doing this work, they have formed a study group calling itself TASC: TransAtlantic Studies of *Calanus finmarchicus*.

TASC was founded at a workshop convened with Norwegian, EU and US GLOBEC support and ICES terms of reference in April 1994 in Oslo. Many laboratories provided support for individual scientists to attend. The convener of the workshop was K. Tande of the University of Tromsø, and about 30 planktologists attended. During its first year

of activities TASC has:
(1) prepared working documents from the Oslo workshop for publication in *Ophelia* (delayed at the journal); (2) published a newsletter (C. Miller, editor, No. 4 is currently in preparation); and (3) sought and received recognition as an official ICES activity for which purpose it reports to the ICES Working Group on Zooplankton Ecology chaired by H. R. Skjoldal. TASC is also reporting its efforts and activities to the International GLOBEC Committee.

Finally, (4) the European members of TASC prepared and submitted, under the leadership of K. Tande, a joint proposal from 18 European laboratories seeking support from the EU-MAST program for an ambitious 3-year program of *Calanus* field studies from Iceland to North Cape and also incorporating laboratory and modelling efforts. This program is also called TASC, and it is expressly formulated to include comparisons between results to be generated in Icelandic and European waters and results from studies on the North American side. Review of MAST-III proposals is now complete, and the preliminary indications from Brussels are that the MAST-TASC program will be funded.

8. Implementation plan for Trans-Atlantic Studies of *Calanus finmarchicus* in the framework of ICES-GLOBEC North Atlantic Programme

Activities underway on both sides of the North Atlantic have combined to constitute a full scale attack from now through at least 1998 on the biology of the region's dominant zooplankter, *Calanus finmarchicus*. In view of the importance of C. finmarchicus to fisheries and in the general ecology of the North Atlantic, the WG urges ICES and national agencies to support this effort, and specific suggestions are detailed in this report.

With the implementation of MAST-TASC (18 laboratories) there will be a total of over 30 laboratories cooperatively studying *C. finmarchicus*. Studies include field sampling work on distribution, life history dynamics (particularly resting phase onset and termination), vertical migration (both diel and ontogenetic), growth, lipid storage, egg production, and most particularly interaction of life history processes with advection between shelf and oceanic areas. Laboratory rearing studies are included on both western and eastern shores to examine feeding rate processes and nutritional issues, the response of growth rate to temperature, and induction of diapause. Programs of modelling are active in MAST-TASC and in the U.S. GLOBEC Georges Bank study that aim to couple spatial models of ocean physics with *C. finmarchicus* life history events and population dynamics. The goal on both sides is to understand and predict the distributional patterns at different seasons and life history stages and to generate a basis for analyzing and predicting the responses of *C. finmarchius* stocks to regional and global climate change.

Both the MAST-TASC program and the U.S. GLOBEC Georges Bank study plan major field efforts in the winter-spring-summer season of 1997. The European program was planned to match the published intention of the ongoing Georges Bank program for an intense program of distributed sampling and field experimental work in that year. It is at least partly this international coordination that has made the MAST-TASC program attractive for support. Therefore, the WG urges that ICES support the resolve of all parties involved in these research efforts to sustain their commitment to studies of *C. finmarchicus* in 1997. We also urge that this commitment must extend through a data analysis phase lasting at least to the end of 1998.

The WG also recognizes a major geographic gap in the program of North Atlantic *Calanus* studies. There does not appear to be a complete spatial link between west Atlantic and east Atlantic studies, in that no study is planned for the major stock living in the large subpolar gyre south and east of Greenland. The only plankton program that will be studying this region during the peak of scientific activity will be the Z-line of the Continuous Plankton Recorder survey. Therefore, the WG recommends that every effort be made to continue this CPR run. In addition, the North Atlantic WOCE program will be studying the subpolar gyre in 1996-1997. While we recognize that WOCE desires maximum speed in its field operations, which may limit participation by biologists, efforts should be made to include sampling for *Calanus* in WOCE expeditions crossing the subpolar gyre. In general, the more completely sampling and dynamical observations of *Calanus* stocks can cover its entire range in 1997, the better we will come to understand its population processes on the scale of its entire range. This is most strongly emphasized for studies of population genetics, which can now be approached in species like *Calanus* thanks to molecular genetic techniques (PCR, economical gene sequencing).

The WG recognizes the value of *Calanus finmarchicus* studies, which may be partly because we all are professionally interested in zooplankton. It may be that other marine scientists may not immediately recognize the value and importance of such studies. Therefore, we recommend that TASC scientists put substantial effort into demonstrating the importance of *Calanus* to fisheries. The key issue is to demonstrate that variability in *Calanus* stocks is coupled to variability in fish stock success. To an extent this can be done by review of existant information. For example, a study by J. Runge (in litt.) demonstrates a relation between Mackeral year class strength and *Calanus* abundance during the Mackeral larval phase on the Scotian Shelf. This and similar examples need to be collated and published. Further, we recommend (1) that the suite of *Calanus* studies now in progress should attend directly to the importance of *Calanus* stocks to fish populations whenever possible, and (2) that long term time series of samples be maintained or established so that causal links can eventually be identified.

Linkages of *C. finmarchicus* population processes to local and regional physics are key issues in all of the studies of TASC scientists. Therefore, WG recommends that ICES and national agencies do everything possible to foster cooperation between those engaged in *Calanus* research and physical oceanographic programs. This is in the spirit of all GLOBEC activities, but it is not likely to happen without active support from funding agencies and research directors throughout the North Atlantic region.

9. New issues to the future workprogramme of the WGZE

The WG discussed new issues which could be on the agenda for its future work. The WG recognized the ongoing discussion within ICES to work towards a more holistic and ecosystem oriented basis for fishery management. We welcome a development where knowledge on environmental factors are used along with knowledge on size and state of fish stocks to characterize the current state of the ecosystems and to predict likely developments in recruitment patterns and interactions among stocks in the systems.

Based on theoretical and empirical evidence, the WG expressed the firm view that interactions between zooplankton populations and fish populations are important for the dynamics of the fish stocks. This fact needs to be generally recognized and data and knowledge about population structure and dynamics of zooplankton stocks needs to be incorporated in the information basis for fishery management. Two important issues in this respect are:

1) strategies and methodologies for monitoring zooplankton stocks and their dynamics, and
2) ways and methods for expressing and conveying information on the state of zooplankton stocks.

Monitoring of zooplankton stocks requires a combination of broad scale surveys and time series observations. Long time series are particularly important to assess long term changes and how these are related across ecosystems and oceans in the ICES area. The WG was informed of the possibility that Canada will withdraw its support of the Continuous Plankton Recorder Survey lines Z, which traverses the North Atlantic from Iceland to Newfoundland, and E, which samples in the Atlantic coastal region of Canada from Newfoundland to the Gulf of Maine and Georges Bank. The CPR Survey measures changes in the abundance and species composition of zooplankton and phytoplankton species on a monthly basis throughout the year and is part of a world wide series of surveys monitoring long term changes in zooplankton populations related to ocean climate change.

The northwest Atlantic survey lines Z and E ran from 1960 to 1976, when they were discontinued. Operation was restarted in 1991 and continues to this date. In hindsight it was recognized that stopping the Z and E lines in 1976 was a serious miscalculation. Had the survey continued uninterrupted, there would now exist a time series of zooplankton composition and abundance during the period of collapse of the Canadian east coast groundfish stocks. This would have been useful for either implicating or ruling out the contribution of fluctuations in zooplankton to the weaker-than-average recruitment levels observed in many of these stocks. The planktonic copepod,*Calanus finmarchicus*, dominates the zooplankton across a large area of the North Atlantic serviced by the Z and E lines. There is mounting evidence that variability in productivity of *Calanus finmarchicus* influences growth and survival of larvae, and in some cases juveniles, of fish stocks, such as redfish, arcto-norwegian cod, herring, and capelin that depend in large part on *Calanus* for food. The health of larval fish and the possible year class size of some species of fish may therefore depend on the size and health of the *Calanus* populations.

Broad scale surveys of zooplankton stocks are carried out to support the fishery management system in Canada (Gulf of St. Lawrence) and Norway (Barents Sea). There is a large potential to improve such monitoring by use and further development of new technologies, combining the powers of acoustic registrations to survey large volumes and areas with that of video systems to identify the zooplankton in situ in near real time. The aim should be to develop methodologies which provide cost-efficient data collection that is compatible with the data collection in fish stock assessment.

Data on zooplankton stocks need to be made available in a form which is useful to the fishery managers. This will usually require geographically distributed data that are compatible with hydrographical data and physical modelling results and with data on distribution and abundance of fish stocks. Averaging and indexing the data for defined areas and regions are also ways which need to be explored to convey information on zooplankton into management models.

The chairperson of the WG on Harmful algal bloom had requested assistance from zooplankton ecologists to consider the role of zooplankton grazing for the dynamics of harmful algal blooms. Some harmful algae are characterized by slow growth rates and their ecological success is therefore likely to depend more on survival properties. Various defence mechanisms against zooplankton grazing could be important in this respect. The WG consider this to be an important issue which it could address at future meetings.

10. Conclusions and recommendations

The main part of the report from the meeting was completed in draft form. The report was approved with some minor amendments that were to be incorporated by the chairman. The final report was to be finished over the next few days for submission to ICES and distribution to WG members and authors of the Manual.

The WG made the following points of conclusion and recommendation:

1. The WG recommends that the further work on reviewing and completing the Zooplankton Methodology Manual should be carried out by correspondence under the

responsibility of the main editor H. R. Skjoldal and with assistance from the ICES secretariat. The Manual should be finalized by 15 February 1996 and published thereafter with no delay for low-cost distribution to the scientific community.

2. The WG appreciates the effort by C. Miller in chairing the informal TASC study group and distributing information about its activities in the TASC Newsletter. The WG welcomes the further assistance from C. Miller and the TASC group in the coordination and conduct of the research activities on *Calanus finmarchicus* in the northern North Atlantic.

The WG recommends that a coordinated field program on broad scale distribution and temporal dynamics of Calanus finmarchicus be carried out in 1997 within the framework of existing national and international ICES/GLOBEC programs and in cooperation with other programs such as JGOFS and WOCE.

3. The CPR Survey is the only sampling program that provides standardized time series data over ocean scale distances. The WG strongly urges Canada and other countries to continue support of CPR Survey lines. They serve both as a means for long-term, basin-scale monitoring of the zooplankton community and as a vital source of information for evaluation of the impact of fluctuations in zooplankton abundance and composition on commercial fish species.

4. The WG recommends that it should meet in spring 1996 in conjunction with the WG on Cod and Climate Change to:

a) review and develop detailed plans for a coordinated field program on *Calanus finmarchicus* in 1997,

b) consider further coordination and cooperation of experimental studies of *Calanus finmarchicus*,

c) review evidence for interactions between zooplankton populations and fish stocks in marine ecosystems and consider the implication with regard to fishery managment,

d) consider methods and technologies for monitoring zooplankton populations in a cost-efficient manner, and consider means of expressing and exchanging such information in ways which are useful to fishery managers,

e) review evidence for the regulatory role of zooplankton grazing on population dynamics and blooms of harmful algae, and suggest research activities to fill gaps in knowledge.

11. Closing of the meeting

The meeting was closed at 11 am on Friday 23 June. The chairman thanked Peter Wiebe for the hospitality and good working facilities provided for the WG. He also thanked the participants to the meeting for their effort.

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ICES WG on Zooplankton Ecology
Woods Hole, USA, 19-23 June 1995

ANNEX 2

AGENDA

1. Opening of the meeting

2. Adoption of the agenda

3. Review of progress on preparation of Zooplankton Methodology Manual and standard protocols

4. Results from sea-going and laboratory workshops

5. Evaluation of methods and recommended standard protocols

    1. sampling
    2. biomass and abundance
    3. acoustical methods
    4. optical methods
    5. feeding
    6. growth
    7. metabolism
    8. behaviour
    9. genetics
    10. population dynamics
    11. modelling

6. Actions to finalize preparations of the ZMM including standard protocols and guidelines

7. Report on progress from the Calanus TASC workshop in Oslo, April 1994

8. Implementation plan for Trans-Atlantic Studies of Calanus finmarchicus in the framework of ICES-GLOBEC North Atlantic Programme

9. New issues to the future workprogramme of the WGZE

10. Conclusions and recommendations

11. Closing of the meeting

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ANNEX 3

LIST OF AUTHORS FOR THE CHAPTERS OF THE ZOOPLANKTON METHODOLOGY MANUAL

Chapter	*Main author*	*Associate authors*
1. Introduction	Lenz	Huntley, Skjoldal
2. Sampling and experimental design	Skjoldal	Wiebe, Huntley, Foote
3. Collecting zooplankton	Sameoto	Wiebe, Miller, Runge, Kremer
4. Biomass and abundance	Postel	Lenz, Wiebe
5. Acoustical methods	Wiebe	Foote, Stanton
6. Optical methods	Kils	Herman
7. Feeding	Båmstedt	Harris, Gifford
8. Growth	Runge	Roff, Huntley, Kremer
9. Metabolism	Ikeda	Torres, Hernadez-Léon
10. Behaviour		Kaartvedt
11. Genetics	Bucklin	Boyd, Buckley, Clarke, Crawford,Dahle, Sundt
12. Population dynamics	Aksnes	Caswell, Miller, Ohman, Woods
13. Modelling		Carlotti, Giske, Slagstad

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ANNEX 4

OUTLINES OF CHAPTERS OF THE ZOOPLANKTON METHODOLOGY MANUAL

CHAPTER 2 - SAMPLING AND EXPERIMENTAL DESIGN

Outline of Chapter 2

Introduction

Research issues

- Pelagic habitats, life cycles and distribution patterns
- Zooplankton stocks and feeding conditons for pelagic fish stocks in LMEs
- Role of zooplankton grazing in regulating vertical flux
- Zooplankton grazing in relation to harmful algal blooms
- Integration needed: observe, describe, quantify, explain

Integration of disiplines: Zooplankton, between physics and fish

- Physics: effects on population dynamics, life cycles and distribution
- Phytoplankton: food and feeding conditions
- Predators: effects on behaviour and population dynamics
- Bottom-up and top-down at the same time

Integration of scales: from turbulence to climate

- Scales of physical processes
- Scales of biological processes
- Linking different scales

Integration of approaches: from theory to field

- Theory and modelling
    - What should be measured from theory and modelling points of view?
- Experimental work: lab, mesocosms and ship
- Field observations
- Theory and observations: hand in hand

Integration of technologies and methods

- Nets, pumps, acoustics, optics
- Representativeness in sampling and observations

Integration of measurements of rates and abundances

- Consideration of variability
- Causal relationships

Design of oceanographic cruises and surveys

- Sampling stations
  - Station representation: linking observations in space and time
- Design considerations
  - Objectives
    - Mapping distribution patterns
    - Estimation of abundance and stocks size
    - Estimation of production
    - Process studies
  - Sea area to be covered
  - Vessel availability
  - Prior knowledge
    - Hydrographic structures and flow field
    - Animal distribution
  - Use of models in planning surveys
- Survey design types
  - Systematic
  - Random
  - Stratified random
  - Preferential
  - Other combinations
- Examples of field programs
  - standardized, time series (e.g. CALCOFI, MARMAP, CPR/UOR)
  - sampling in relation to physics (e.g. US GLOBEC Georges Bank, Calanus/ICOS/TASC)
  - sampling in relation to fish (e.g. Norwegian Sea/MARE COGNITUM)

Laboratory experiments

- Introduction to facilities and good laboratory practices
- Types of lab. experiments
- Factorial design and statistical considerations
- Extrapolation from lab. to nature

Mesocosm experiments

Between beakers and bays
Complexity and naturalness vs. experimental control and replicability

Outlook

CHAPTER 3 - COLLECTING OF ZOOPLANKTON

Outline of chapter 3 " Collecting zooplankton"

1. Introduction
   -Type of sampler used is dictated by program requirements and target species of zooplankton to be collected

2. Net Samplers
   a. Mesh and frame colour
   b. mesh size and size of organisms caught (John Nicols)
      -extrusion through mesh
   c. Speed of net
   d. R-ratio of net
   e. Net bridle effects
      -best use net without bridle (ie. bongo)or crossbow
   f. Measurement of flow through net
   g. Calibration of meters
      -calibration tanks
      -series of vertical tows without net
      -horizontal tow using ships log for speed and distance
   h. Net mouth area
      -effect of size on catches of animals
   i. Effect of ambient light
      -best to sample at night
      -no ship's light
   j. Use of artificial light to reduce avoidance
      -continuous light
      -strobe light
   k. Nose cones to reduce avoidance

3. Single net samplers (advantages and disadvantages)
    a. ring net
    b. bongo
    c. other types of nets

4. Multi-net samplers
    a. CPR
    b. LHPR
    c. BIONESS
    d. MOCNESS
    e. Multinet
    f. RMT-1 and 8
    g. Gulf 3 (Mike Heath)

5. Method of towing nets
    a. Vertical tows
    b. Oblique tows
    c. Stratified tows

6. Handling actively towed nets
    a. Load compensating winches
    b. Shock cords
    c. Types of tow cables
    d. Handling and care of cables

7. Handling samples
    a. Proper washing of net
    b. Preserving samples
        -formalin
        - other types of preservatives

8. Pumps (C. Miller)

9. Water bottles

10. Sampling live animals for experimental studies (Jeff Runge)

11. Methods of sampling gelatinous animals (Pat Kramer)

12. Microzooplankton sampling (name??)

13. Non-Net Zooplankton Samplers used in conjunction with nets
    a. Optical Plankton Counter
    b. Video Camera Samplers

1. Video Plankton Profiler
2. The Ichthyplankton Recorder

14. Acoustic Systems
    a. General advantages of using acoustics
    b. Direction of acoustic research for zooplankton
    c. Types of acoustic systems used
        1. Single beam transducers
        2. Multi-frequency single beam transducers
        3. Dual beam systems
        4. Multi-beam systems
    d. Target strength problem
    e. Application of acoustic systems to zooplankton research

15. Integration of different methods in sampling programs
    a. Acoustics
    b. Optical instruments
    c. Nets

CHAPTER 4 - BIOMASS AND ABUNDANCE

Proposed outline of Chapter 4 "Biomass and abundance" by L. Postel et al.

4.1 Introduction
4.2 Sampling and preparation of samples
4.3 Biomass estimation
    4.3. Volumetric methods
        4.3.1.1 Settling volume
        4.3.1.2 Displacement volume
    4.3.2 Gravimetric methods
        4.3.2.1 Wet weight
        4.3.2.2 Dry weight
        4.3.2.3 Ash-free dry weight
    4.3.3 Biochemical methods
        4.3.3.1 Carbon content
        4.3.3.2 Nitrogen content

4.3.3.3 Protein content
4.3.3.4 Lipid content
4.3.3.5 Carbohydrate content
4.3.4 Caloric method
4.3.4.1 Energy content
4.3.5 Conversion factors
4.4 Abundance and species composition
4.4.1 Counting methods
4.4.1.1 Microscopical counting
4.4.1.2 Electronic counting
4.4.1.3 Optical counting
4.4.1.4 Silhouette photography
4.4.2 Establishing size/weight relationships
4.4.3 Calculation of biomass
4.4.4 Analysis of community structure
4.4.4.1 Presence and dominance
4.4.4.2 Diversity indices
4.4.4.3 Eveness index
4.4.4.4 Similarity index
4.4.4.5 Principal component analysis

CHAPTER 5 - ACOUSTICAL METHODS

Chapter 5 Acoustical methods

5.1 Introduction
Scenario: Example illustrating arbitrary variability in species content and size distribution of zooplankton in vicinity of a station
Scenario: Comparison of sampling volumes of pumps and optical recorders when detecting copepods
5.1.1Motivation for acoustical sampling
5.1.1.1Achieve essentially spatial continuity in observations
5.1.1.2Increase sampling volume
5.1.2Specific aims of acoustic measurement
5.1.2.1Species classification
5.1.2.2Sizing
5.1.2.3Determination of number density
5.1.2.4Observation of animal behavior, as in process studies
5.1.3Qualifications
5.1.3.1Interpretation of echoes subject to ambiguity

5.1.3.2Fisheries acoustics methods have particular applicability
5.1.3.3Need for reference to scattering models in order to interpret measurement
5.1.4Organization of materials

5.2 Background
5.2.1Acoustic scattering in general: origin of echoes from underwater bodies
5.2.2Basic terminology
5.2.2.1Beam Pattern
5.2.2.2Echo amplitude
5.2.2.3Backscattering cross section
5.2.2.4Target Strength
5.2.2.5Volume backscattering coefficient and strength
5.2.2.6Area backscattering coefficient
5.2.3Zooplankton as acoustic scatterers
5.2.3.1Classification of types through acoustic boundary condition
5.2.3.2Fluid-like bodies e.g., krill, salps, copepods
5.2.3.3Hard-shelled bodies, e.g., pteropods
5.2.3.4Gas-bearing animals, e.g., siphonophores
5.2.4Scatterer identification
5.2.4.1Physical capture by nets, pumps
5.2.4.2Optical registration by video plankton recorder
5.2.4.3Mismatch events
Elusive organisms
Physical (non-biological) structures
5.2.5Elements of scattering theory (described qualitatively)
5.2.5.1Wave equation
5.2.5.2Summation of echo energy
5.2.5.3Forward and inverse problems
5.2.6Scattering models
5.2.6.1Shapes
Deformed sphere
Deformed cylinder
5.2.6.2Boundary conditions
Fluid-like bodies
Hard-shelled bodies
Gas-bearing animals
5.2.6.3Examples by species
Krill: deformed fluid-like cylinder
Copepod: deformed fluid-like sphere
Pteropod: deformed elastic shelled sphere
Siphonophore: composite body with fluid-like tissue and spherical gas bubble

5.3 Methods
5.3.1Primary data display

5.3.1.1Echogram
5.3.2Echo integration
5.3.2.1Fundamental equation
5.3.2.2Mathematical operation
5.3.2.3Process of determining abundance from local measurements of density
5.3.3Target strength determination
5.3.3.1Dependencies of target strength
5.3.3.2Stochastic nature of target strength
5.3.3.3Classification of methods
5.3.3.4Summary of major methods
5.3.4Postprocessing and data analysis
5.3.4.1Echogram interpretation
5.3.4.2Target tracking
5.3.4.3Bottom detection
5.3.4.4Bottom organism discrimination
5.3.4.5Echo classification
5.3.5Advanced data visualization including GIS

5.4 Instruments

5.4.1Terminology
5.4.1.1Blurred distinction between echo sounder and echo sounder system
5.4.1.2Ambiguity in describing multiple-beam multiple-frequency systems and techniques
5.4.2Basic limitations
5.4.2.1Definition through active sonar equation
5.4.2.2Numerical examples
5.4.3Scientific echo sounder
5.4.3.1Single beam
5.4.3.2Dual beams
5.4.3.3Split beams
5.4.3.4Multiple frequencies
MAPS
TAPS
Hybrid systems
5.4.4Acoustic Doppler Current Profiler
5.4.5Sonar (for volume imaging)
5.4.6Echo integrator
5.4.7Postprocessing systems
5.4.7.1Bergen Echo Integrator
5.4.7.2British Antarctic Survey Shareware system

5.5 Calibration

5.5.1Aims
5.5.1.1Ensure stability in operation

5.5.1.2Enable absolute measurement
5.5.2Standard-target method (for low frequencies)
5.5.3Reciprocity (for high frequencies)

5.6 Platforms
5.6.1Vessels: hull-mounted, retractable-keel-mounted, suspended (cast), towed
5.6.2Buoys: drifting, moored
5.6.3ROVs:
5.6.4AUVs:
5.6.5Net-mounted: fixed, vertically migrating
5.6.6Seabed-mounted
5.6.7Rotary mounting

5.7 .Exemplary applications
5.7.1Mono-specific assemblage
5.7.1.1Example:Abundance estimation of Antarctic krill (*Euphausia superba*) in the Southern Ocean
5.7.2Multiple-species assemblages
5.7.2.1Example:Density measurement of animals diversely distributed with respect to species and size as encountered by a moored- buoy-mounted or towed hybrid echo sounder system
5.7.2.2Example:Monitoring zooplankton with a bottom-mounted ADCP (Cochrane et al. 1994)

5.8 Current issues
5.8.1Introduction
5.8.1.1Rapid developments in instruments and techniques
5.8.2Transducer deployment
5.8.3Detection range
5.8.3.1Study system performance through active sonar equation
5.8.4Animal orientation
5.8.4.1Sensitivity of high-frequency measurements
5.8.4.2Inference through multiple-frequency measurements
5.8.5Physical properties of animal
5.8.5.1Sensitivity of target strength to physical properties
5.8.5.2Variations in target strength with changes in life stage, e.g., as due to molting
5.8.6Chronic need for measurements
5.8.7Morphometry
5.8.8Frequency diversity
5.8.8.1Requirement to achieve specific aims: recommendations given animal types, which frequencies should be used?
5.8.9Broadband technology
5.8.9.1Performance of genuinely broadband transducers

CHAPTER 6 - OPTICAL METHODS

No outline is available yet.

CHAPTER 7 - FEEDING

No outline is available yet

CHAPTER 8 - GROWTH

Chapter 8: Determination of rates of growth and reproduction in planktonic copepods

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J.C. Roff, Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1

Other contributers to follow.

I. Introduction and approaches to the study of growth and reproduction

Theoretical context:

a) Factors controlling the dynamics of copepod populations.

b) The influence of food availability on growth and egg laying rates, including the linkage between copepod spawning and primary production cycles.

c) Variability in the production of the prey field for fish larvae.

II. Models of fecundity and growth

A. The physiological or laboratory-derived budgetary models

B. Temperature-dependent model: Huntley and Lopez (1992).

III. Direct determination of growth

A. Estimates from preserved samples

1. Cohort analysis (not discussed in detail here)
2. Estimation of growth rate from weight increments of successive stages and development time (field or laboratory estimate): e.g. McLaren et al.(1989).

B. Incubation methods

1. Capture techniques
2. Sorted copepods:

a. Molting rates; growth rate from intermolt duration and weight increment of successive copepodite stages: e.g. Peterson et al. (1991).

b. Direct estimate of growth rates in mesocosms (e.g. Durbin, U.S. Globec)

3. Artificial cohorts by gentle size fractionation with screens (e.g.: Kimmerer and McKinnon 1987; Peterson et al. 1991).

IV. Direct determination of egg production rate

A. History of egg production rate measurement in the marine environment

B. The basic method for broadcast spawners

1. The underlying assumption: egg laying in first 24 h reflects egg laying in situ.
2. Capture techniques
3. Sources of error

a. Stress of capture

b. Cannabilism

c. Incubation conditions: containers, duration of incubation, temperature, light, food.

d. Stage structure and mortality rate of females

4. Estimation of egg production rates from preserved samples.
5. Calculation of egg production rate and statistics

C. The estimation of hatching success: recent methods and results of Ianora, Poulet and coworkers.

D. The method for egg carrying species.

1. The egg ratio method.
2. The incubation method for estimation of egg extrusion rate.

V. Biochemical and radiochemical methods

Potential uses include identification of situations where food is limiting growth. Possibility to sample at high frequency, allowing investigation of small-scale variability in growth indices. Note, however that most methods yield indices or measure correlates of growth rather than growth rates per se.

A. Ratios of biochemical quantities: RNA/DNA ratio
B. Hormones and growth factors
  1. Ecdysteroids
  2. Other bioregulators: e.g. telomerase and other cell regulation factors in protists.
C. Enzyme activities
  1. The limitations of enzyme activity indices
  2. Citrate synthase
  3. Aspartate transcarbamylase
  4. Chitobiase activity
D. Radiochemical methods: isotope methods can provide direct estimate of growth rate.
  1. *in vitro* rate of incorporation or production of label using whole body homogenates or body tissues.
  2. *in vivo* uptake of labelled compounds from the environment.
  3. *in vivo* infusion, perfusion or flooding dose injection of labelled compound
  4. *in vivo* ingestion of labelled food: chitin synthesis method.

CHAPTER 9 - METABOLISM

Contents

CHAPTER 10 - BEHAVIOUR

No outline available yet.

CHAPTER 11 - GENETICS

Chapter 11: Methods for Population Genetic Analysis of Zooplankton

Author: Ann Bucklin (University of New Hampshire, Durham, NH)

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Geir Dahle (Institute of Marine Research, Bergen, Norway)
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Review of methods to assess genetic diversity and population structure.

11.1. Introduction - Why are genetic assessments of zooplankton important? What ecological and evolutionary questions can be addressed using genetic approaches? This introduction will provide some perspective on: why study the genetics of zooplankton?

11.2. Technical approaches to determining genetic diversity - This section will provide a brief general overview of the principles behind each approach to assaying genetic diversity in natural populations. The technical approach will be sketched out. Advantages and disadvantages of each technique will be discussed in relation to solving ecological and evolutionary questions.

11.2.1. allozymes (R. Sundt)
11.2.2. mtDNA restriction fragment length polymorphisms (G. Dahle)
11.2.3. DNA sequence analysis (A. Bucklin)
11.2.4. microsatellite DNA (G.Dahle and A. Bucklin)
11.2.5. mRNA concentrations (L. Buckley and D. Crawford)
11.2.6. techniques in development

11.3 Statistical approaches to assessing genetic diversity and structure - This section will briefly review the suite of population genetic tools used to evaluate spatial and temporal patterns of genetic diversity and structure in natural populations.

11.3.1. Statistical measures of genetic diversity
11.3.1.1. Number of alleles
11.3.1.2. Genotype / haplotype diversity
11.3.1.3. Nucleotide diversity

11.3.2. Statistical measures of genetic structure
11.3.2.1. Genotype (haplotype) frequency differences
11.3.2.2. Chi square tests of heterogeneity
11.3.2.3. F-statistics; hierarchical F-statistics
11.3.2.4. Multivariate approaches
11.3.2.5. Spatial autocorrelation

11.3.3. Statistical analysis of gene flow (dispersal)
11.3.3.1. Estimates based on F-statistics
11.3.3.2. Phylogeographic approaches
11.3.3.3. Other methods (minimum dispersal steps)

11.3.4. Computer methods and software sources for molecular population genetic analysis
11.3.4.1. Commercial software and sources for purchase
11.3.4.2. Access to free-ware

11.4. Application of genetic analysis to ecological studies. What can population genetics tell us about biological processes in the ocean ?
11.4.1. Population parameters (birth, death, immigration, emigration)
11.4.2. Dispersal and gene flow
11.4.3. Zooplankton responses to ocean circulation
11.4.4. Effective population size; reproductive variance
11.4.5. Molecular systematics: species identification and biogeography.

11.4.6. Molecular assessment of condition and growth
11.4.7. Molecular probes for gut content analysis and trophic assessments.

11.5. Strategies for preservation of samples for genetic analysis
11.5.1. Enabling multiple uses of samples.
11.5.2. Planning for the development of new techniques in the future.
11.5.3. Selection of appropriate preservatives for genetic analyses.
11.5.3.1. Optimal preservation: ethanol (DNA) and freezing (DNA and proteins).
11.5.3.2. New approaches: buffers (S. Boyd)
11.5.3.3. Formalin, glutaraldehyde, and other bad things.
11.5.3.4. Dehydration

11.6. New directions in the genetics of zooplankton populations.
11.6.1. Molecular analysis of existing collections: museum specimens and formalin-preserved samples.
11.6.2. The role of population genetics in studies of marine biodiversity.
11.6.3. Global climate change issues.
11.6.4. Pollution assessments
11.6.5. New and emerging technical approaches

CHAPTER 12 - POPULATION DYNAMICS

CONTENTS OF CHAPTER 12 - POPULATION DYNAMICS

I Introduction

II Sampling considerations
Advection
Biased stage composition

III The population parameters and the possibility of direct measurements
Measures of birth rate
Egg carrying life histories
Broadcast spawning life histories
Influence of mortality on birth rate measurements
Measures of development rate, stage durations and generations
Measurements of mortality in periods with no recruitment

IV Parameter estimation from census data

The vertical approach
The horizontal approach
Cohort methods
Estimation models assuming negligible mortality
Estimation models including mortality
Temporal sampling coverage
Methods involving fitting of models to census data
Models
Matrix models
Partial differential models
Delay differential equation models
Dormancy and model specification
Fitting

V Recommendations

VI References

CHAPTER 13 - MODELLING

No outline is available yet.

On the use of Inverse/Forward Methods to study zooplankton spatial pattern and abundance. Peter Wiebe

High frequency echo sounders (12 kHz and higher) have long been used to qualitatively and quantitatively study the abundance of nekton. More recently, precision echo sounders operating at frequencies up to 10 MHZ have made it possible to study zooplankton (Holliday et al, 1989; Genin et al., 1994; Greene et al., 1994; Wiebe and Greene, 1994). The use of acoustical data to estimate the biological properties of nekton and zooplankton (i.e. biomass, numbers of individuals, size distribution of individuals, and taxonomic composition) in the volume of water ensonified is in essence an "Inverse Problem". The solution relies upon a knowledge of the quantitative relationship between acoustic backscattering and the biological properties (Holliday et al., 1989; Stanton, 1989; Chu, et al. 1992, Wiebe et al., 1990). Although the fluid sphere model has been used as a "first approximation" in representing the scattering of sound by zooplankton (Anderson, 1950; Greenlaw, 1979; Holliday, 1980), recent work has demonstrated substantial differences in acoustic scattering properties of zooplankton comprising different anatomical classes (Stanton et al., 1994). This has led to the development of new models which account for the acoustic scattering of groups thus far studied (Stanton et al., 1994). Fundamental to the acceptance and application of these new models is their application in controlled field experiments in which biological information on the numerical abundance and size of individuals plankton in combination with the appropriate model(s) are used to estimate the acoustic backscattering in a given volume of water. Solving this "Forward Problem" and comparing the result to in situ measurements can be used to test the robustness of the scattering models and to verify their use in field applications (Stanton, et al., 1987). Solving the foward problem is an essential first step towards using acoustical measurements to solve the inverse problem.

REFERENCES

Anderson, V.C. 1950. Sound scattering from a fluid sphere. Journal of the Acoustical Society of America. 22: 426-431.

Chu, D., T.K. Stanton, and P.H. Wiebe. 1992. Frequency dependence of sound backscattering from live individual zooplankton. ICES Journal of Marine Science. 49: 97-106.

C. Greene, L. Haury, P. Wiebe, G. Gal, S. Kaartvedt, E. Meir, C. Fey, and J. Dawson. 1994. Zooplankton patch dynamics: Daily gap formation over abrupt topography. Deep-Sea Research 41: 941-951.

Greene, C.H., P.H. Wiebe, and J.E. Zamon. 1994. Acoustic visualization of patch

dynamics in oceanic ecosystems. Oceanography 7(1): 4-12.
Greenlaw, C.F. 1979. Acoustical estimation of zooplankton populations. Limnology and Oceanography 24: 226-242.
Holliday, D.V. 1980. Use of acoustic frequency diversity for marine biological measurements. In "Advanced Concepts in Ocean Measurements for Marine Biology". F.P. Diemer, F.J. Vernberg, and D.Z. Mirkes [eds]. Belle W. Baruch Library in Marine Science # 10, University of South Carolina Press, Columbia, S.C. pps: 423-460.
Holliday, D.V., R.E. Pieper, and G.S Kleppel. 1989. Determination of zooplankton size and distribution with multi-frequency acoustic technology. J. Cons. int. Explor. Mer 41, 226-238.
Stanton, T.K., R.D.M. Nash, R.L. Eastwood, and R.W. Nero. 1987. A field examination of acoustical scattering from marine organisms at 70 kHz. IEEE Journal of Oceanic engineering. OE_12(2): 339-348.
Stanton, T.K.1989. Simple approximate formulas for backscattering of sound by spherical and elongated objects. Journal of the Acoustical Society of America.. 86: 1499-1510.
Stanton, T.K., P.H. Wiebe, D. Chu, M. Benfield, L. Scanlon, L. Martin, and R.L. Eastwood, 1994. On acoustic estimates of zooplankton biomass. ICES Jouranl of Marine Science. 51: 505-512.
Wiebe, P.H., C.H. Greene, T. Stanton, and J. Burczynski. 1990. Sound scattering by live zooplankton and micronekton: empirical studies with a dual-beam acoustical system. Journal of the Acoustical Society of America. 88: 2346-2360.
Wiebe, P.H. and C.H. Greene. 1994. The use of high frequency acoustics in the study of zooplankton spatial and temporal patterns. Proceedings of the NIPR Symposium on Polar Biology, No. 7:133-157.