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International Council for the
Exploration of the Sea

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REPORT OF THE WORKSHOP ON THE TRANS-LATITUDINAL STUDY OF *CALANUS FINMARCHICUS* IN THE NORTH ATLANTIC

Oslo, Norway 6-8 April 1994

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1. SUMMARY

The Workshop held at the University of Oslo from 6-8 April 1994 reviewed the present status of our knowledge on *Calanus finmarchicus* in the North Atlantic. The meeting treated four separate scientific areas relevant for TransAtlantic Studies on *Calanus finmarchicus* (TASC): 1) The interplay between generation cycles and large scale circulation patterns in oceanic and shelf areas; 2) *Calanus finmarchicus*: strategies for diapause and reproduction; 3) Population coherence and latitudinal impact on growth patterns; 4) Trophic interactions and mortality. The topics covered the major facets in the population dynamics of the species, and emphasized how the physical and biological factors might control the observed range in generation cycle patterns of *C. finmarchicus* in the North Atlantic. The Workshop concluded on each topic by formulating **TASC recommendations** in order to focus on gaps in our knowledge and provide directional momentum for future studies on this species in the North Atlantic. These recommendations are building blocks for an implementation plan for a coherent study on the species in the North Atlantic.

2. SCIENTIFIC BACKGROUND FOR THE MEETING

The goal of GLOBEC is stated to be: "To understand the effects of physical processes on predator-prey interactions and population dynamics of zooplankton, and their relation to ocean ecosystems in the context of the global climate system and anthropogenic change".

In the Report of the First International GLOBEC Planning Meeting in Italy in 1992, the first step was taken towards development of the Globec Core Program (GCP). The GCP was intended to provide a common scientific focus and a means for communication and interaction among the diverse participants in GLOBEC. The goal of GCP is investigation of global-ocean issues in zooplankton dynamics. These include relations between zooplankton and phytoplankton and between fish production and zooplankton, both in the context of physical oceanographic processes.

In the developing the GCP, the Scientific Steering Committee (SSC) considered both region-specific and problem-oriented approaches. They noted that to maintain fidelity to the "global-change orientation" of GLOBEC, it was necessary to integrate the various ways of thinking peculiar to study of different regions, then to use the integrated view to reformulate region-specific problems in a global-change context. Following this reasoning, the SSC partitioned the development phase of the GCP into four problem-oriented working groups and two region specific studies. These last two address the Southern Ocean and the North Atlantic (Cod and Climate Change).

The ICES Study Group on Cod Stock Fluctuations pointed out in their documents, ICES CM/Gi 50, 1990 and ICES CM/Gi 78, 1991, the need to emphasize studies of copepod population dynamics to understand the recruitment processes of cod in the North Atlantic. In Globec Report no. 1, the specific central problems with respect to copepod dynamics were: 1) timing relations between cod spawning and zooplankton spawning (match-mismatch); 2) the local copepod production at the nursery ground of cod; 3) advection of copepods from their large scale habitat onto the cod nursery ground; 4) interannual variability of copepod production. The SSC invited ICES as a co-sponsor of GLOBEC to specify the components of a pan Atlantic program to link physical and biological studies in the North Atlantic and to serve as a coordinating mechanism in communications with the GLOBEC Secretariat and the GLOBEC SSC.

In the plans for following up the above initative for the North Atlantic (Working Group on Cod and Climate Change in Lowestoft, U.K. and a Symposium on Cod and Climate Change in Reykjavik), *Calanus finmarchicus* was highlighted as the key copepod species, due to its pivotal role in the pelagic food web of the North Atlantic ecosystem. Additionally, several nationally sponsored projects and programs around the North Atlantic were under development with emphasis on *C. finmarchicus*.

Recognizing this international concern with the population dynamics of *Calanus finmarchicus*, Kurt Tande and Charles Miller proposed to GLOBEC and ICES that it would be valuable to assemble workers on this key species from all along its range to discuss the future of our research. In their 1993 letter stating intent to hold a workshop, they set the goal of establishing an internationally cooperative program to be called "Trans-Latitudinal Study of *Calanus finmarchicus*"*. They argued that simultaneous work on stocks all along the range, together with direct, cooperative comparisons of results, would allow progress that no single, nationally-based program could achieve alone. The purpose of the proposed workshop was to critically address the status of knowledge of *C. finmarchicus* and to begin planning for cooperative work and information exchange. GLOBEC and ICES accepted the proposal for a workshop, and ICES provided the terms of reference reiterated next.

*This was changed to TransAtlantic Studies of *Calanus finmarchicus (TASC).*

3. TERMS OF REFERENCE

The terms of reference for the Workshop are contained in Council Resolution 1993/2:53 which was adopted at the 1993 Statutory Meeting in Dublin. A Workshop on Trans-Latitudinal Study of *Calanus finmarchicus* in the North Atlantic will be held in order to:

a) critically survey present knowledge of *Calanus finmarchicus*;

b) discuss the role of the population dynamics of this dominant copepod species in the North Atlantic in relation to latitudinal variation, hydrography, and fish recruitment;

c) prepare the outline for an implementation plan for a programme of research.

The result from the Workshop (by the Co-Chairmanship of Dr. K. Tande (Norway) and Dr. C. B. Miller (USA)) will be reported to the Biological Oceanography Committee before the 1994 Statutory Meeting.

The Workshop was organized around four topics, each covered by several position papers (see Section 10). After a short presentation of the 12 papers in plenum, the participants were grouped in four theme groups. These Working groups at the TASC Workshop considered specific themes in the ecology of <u>Calanus finmarchicus</u>. Each working group prepared a report, and these are presented here after some editing. The contributions to the Workshop will be published in one volume in Ophelia in 1995.

4. *THEME I: THE INTERPLAY BETWEEN GENERATION CYCLES AND LARGE SCALE CIRCULATION PATTERNS IN OCEANIC AND SHELF AREAS.*

4.1. Domain characters

The group working on Theme I highlighted a question concerning the basic character of *C. finmarchicus* stocks which should eventually be answerable. It is widely observed that large stocks of *C. finmarchicus* develop over continental shelves during late winter and spring, while diapause stocks typically inhabit deep layers in the oceanic waters farther out. At many shelf sites dominated by *Calanus* in spring, there are none whatever from summer's end to December. Are developing shelf stocks, then, dependent upon oceanic production in the previous generation, or are they mostly self-generated with only the resting phase offshore in deep water? Are oceanic resting stocks derived primarily from reproduction and development over the shelf, or are they derived from production locally? The working group report spells out these questions and also rephrases them as hypotheses:

The group began by reviewing both the collective knowledge of the participants and the new information reported in the position papers in order to deduce the main features of *C. finmarchicus* population processes as they vary across the North Atlantic. Four basic features emerged:

a) There seem to be two main groups of *C. finmarchicus*, discriminated on the basis of genetics and distribution. One is based in the NW Atlantic gyre, and the other in the Norwegian Sea/Greenland Sea basin. This division was originally proposed by Matthews (1969) and Jashnov (1970), and more recently reinforced by the genetic analysis of Bucklin et al. (this meeting).

b) Wherever *C. finmarchicus* stocks occur in shelf waters during summer months, there is almost always a nearby deep water area to which the species is confined during the winter. This is true on the European side of the Atlantic, for Norwegian fjords, in the Skaggerak, and in the northern North Sea. On the American side of the Atlantic it is true for the Gulf of St. Lawrence, the Nova Scotian shelf, and Georges Bank.

c) In some areas there are evidence for a response by shelf stocks of *C. finmarchicus* to large scale oceanographic forcing. Examples are the changes in abundance of total zooplankton (with dominant contribution from *C. finmarchicus*) northeast of Iceland in response to shifts of the polar front, and the relationships between *C. finmarchicus* recruitment and temperature in the NE Norwegian Sea. In the latter case, temperature is almost certainly a signature of some change in circulation rather than the causal factor itself.

d) There are marked inter-regional variations in the number of complete generations (CV-adult-egg-CV) of *C. finmarchicus* within an annual cycle.

4.2. Large scale circulation and control of generation cycles.

On the basis of the above gross properties of *C. finmarchicus*, a number of questions were posed relating to large scale circulation and the control of generation cycles. These are led by a single overarching question:

> * Is *C. finmarchicus* an oceanic species which overspills onto the continental shelves during summer ?

In order to clarify this in more details, a series of second order questions were posed:

> * What are the ocean circulation features which link or isolate the two main groups of *C. finmarchicus* in the North Atlantic?
>
> * *Thinking about the basin scale population as a whole,*
>
> a) is the primary production sustaining the basin scale population mainly consumed on the continental shelves fringing the ocean basin or in the surface waters of the open ocean itself?
>
> b) does the main population production of viable eggs take place - on the continental shelves or in the open ocean?
>
> c) could the basin scale population survive if it were denied access to the fringing shelf seas during spring and summer months?
>
> * On which geographic scale can we expect the on-shelf production of *C. finmarchicus* to show a coherent time series response to climatic forcing?

With these questions as a set of broad objectives for further study of the linkage of *C. finmarchicus* population processes to ocean-climate, we proposed general hypotheses which we suggest should become a recurrent theme in regional studies of *C. finmarchicus* around the North Atlantic rim:

Hypothesis 1: Interactions between physical oceanographic processes and behavioral features of *C. finmarchicus* control a) a seasonal invasion of the shallow shelf waters in the spring and b) a retreat in the autumn.

Hypothesis 2: The seasonal invasion of shallow continental shelves by *C. finmarchicus* is critical both for a) the maintenance of the basin scale population and b) as a contribution to secondary production in shelf waters.

Hypothesis 3: Annual production of *C. finmarchicus* in the shelf seas is forced by the dynamics of the basin scale population.

Hypotheses 2b is in harmony with 3, but represent uncertainties about the dominance of events over shelves or in oceanic waters for the maintenance of the *C. finmarchicus* stock in the North Atlantic. The following recommendation is given:

> ***TASC projects should provide a combined budget for population development and advective transfer to establish whether individuals entering the deep-water resting habitat have grown primarily over the shelves or in the open oceanic.***

The above statement was further substantiated by reviewing the major data required to obtain answers to the questions set out above:

In the Northeast Atlantic *C. finmarchicus* overwinters in the basin of the Norwegian Sea below 500 m depth. When the overwintering population surfaces in late winter/early spring to spawn, parts of the new generation are advected onto the surrounding shelves where they are fed upon by larval fish.

A comparable process occurs over Georges Bank, where the population sequestered for the autumn and early winter in deep basins of the Gulf of Maine and offshore in North Atlantic Slope water to the south emerges to repopulate the bank. These deep stocks also repopulate Narragansett shoals and the entire shelf of the New York bight.

The number of *C. finmarchicus* generations per year most probably varies with the temperature. In the northern Norwegian Sea *C. finmarchicus* may have problems to produce one generation per year, while in the southern Norwegian Sea there are most probably 2 generations per year. What is the maximum number of generations per year? Is this purely a function of the temperature or is it also influenced by the feeding conditions? Are specific factors involved in the induction of the diapause phase important in setting the number of generations and causing this number to vary among regions? Recommendation:

> ***TASC projects should study what determines whether a given generation matures and reproduces or enters diapause.***

In order to describe the transport and dispersion of a generation from the egg stage to the overwintering stage, the details of diapause ascent and descent and the vertical deistribution of developmental stages should be included in modelling, together with the representation of circulation features. The numerical model has to resolve the bottom topography steering on the shelves in order to describe properly the advection onto and later away from the shelf. Recommendation:

TASC projects should favor models which aim to fully specify both population processes (growth, reproduction, mortality, behavior) and regional advection.

5. *THEME II: CALANUS FINMARCHICUS: STRATEGIES OF DIAPAUSE AND REPRODUCTION.*

5.1. Phenology of C. finmarchicus.

5.1.1. Diapause: general problem and research goals

Several of the position papers (e.g. Kaartvedt, Hirche, Miller) review the knowledge related to overwintering of *C. finmarchicus*. In general, there appears to be a flexibility in the programming for overwintering/diapause. The working group considered that better and more comprehensive sets of observations from different regions are needed to respond to fundamental questions about the behavior of *Calanus* when it is not actively feeding and growing in the upper water column.

For each region, these questions may be stated as follows:

1) What is the depth distribution of the overwintering stages. Are overwintering populations maintaining the same depths over time. In Northwest Atlantic Slope Water the answer is clearly yes. Is that generally the case? A finer resolution of distribution is required.

2) What is the relation of the depth distribution to topography and hydrography?

3) What are the mortality rates during the overwintering period? Are they due mostely to predators and do predators effect the overwintering depth?

4) When does the downward overwintering migration begin? To what habitat factors is it a response?

5) When do overwintering stages commence upward migration in late winter-spring? Over how long a period? Do populations in different regions ascend at very nearly the same time as implied by Marshall and Orr (1955)? How fast is the upward migration?

6) What are the timing cues for diapause?

Observations to date suggest two generally-stated hypotheses to explain variability in overwintering depth distribution across different regions: a) That the depth distribution is driven by the predator field, and b) that it is related to the nutritional status (as measured by the quantity of depot lipids). These general hypotheses could also guide the design of measurements to be made at each site. Recommendation

> ***TASC projects should select an indicator of diapause conditon and trace its appearance in the Calanus stocks they study as a function of season, temperature history, depth and photoperiod.***

There may be some clue in the interannual variation in the number of C5 that are found in the diapause stock. For example, interannual variation in the proportion of C4 to C5 in the Gulf of Maine varies. Apparently, either stage can respond to the signal to initiate diapause, and it is likely that in different years and sites the signal finds the stock at different points in the developmental progression. By comparing C5:C4 ratios to differences in timing of changes in the habitat, we may be able to guess at the signal. This leads to the following recommendation:

> ***TASC projects should sample resting stocks for stage composition over at least several years. Basic habitat data, particularly water column temperature patterns, should be recorded through the period prior to and during diapause onset.***

Field study sites and suite of measurements

- Fjords off Norway offer excellent opportunities to study overwintering behavior with sufficient frequency to respond in a rigorous manner to questions posed above.

- The Norwegian Sea, where overwintering depth distribution is deep.

- The sea off Iceland

- The Gulf of St. Lawrence, which is relatively shallow (200-400 m)

- The Newfoundland-Labrador shelf region

At each study site, time series of measurements should be made using a standard methodology. These measurements could include:

- Depth distribution with multi-net sampler (e.g. MOCNESS, BIONESS)

- Acoustic measurements for distribution and abundance of fish (as potential visual predators). The working group considers that the assessment of the predator field is an important part of the set of overwintering observations. This implies involvement of fisheries biologists in the study.

- Identification of molting stages, using mandibular gnathobase facies as described by Miller et al. 1991, and examination of gonad maturation status.

- Measurement of metabolic and feeding activity. Explore enzyme techniques (e.g. ETS, digestive enzymes) for rapid assessment of diapause state.

- Standardized measurement of dry weights and condition factor.

Experimental studies

A number of laboratory experiments could be conducted to determine the factors determining the initiation and termination of diapause. Attempts to rear *C. finmarchicus* and establish diapausing populations in the laboratory are encouraged. Recommendation:

> ***TASC should encourage laboratory studies on life cycle phenomena, and care should be taken so that the experimental setup is designed in order to mimic the variation in the environmetal variables found during the period of study. Future experimental studies should pursue the effect of dynamic environmental varibles on life cycle phenomena in Calanus.***

Experiments should try to simulate the range in the change of, for instance, temperature and light climate, during the most likely period relevant for studies on the diapause phenomenon. This might prove more ecologically relevant compared to experiments designed where the environmental conditions (i.e. light and temperature) are kept constant with time.

5.1.2. Reproduction: general problem and research goals

In several regions within its distributional range, the eggs and nauplii of *Calanus finmarchicus* are the principal prey of the larvae of resident fish stocks. Variability in egg production might therefore substantially influence larval growth rates and consequently their survivorship. Study of *Calanus*-larval fish interactions requires research along several lines, including models of larval fish growth rate as a function of ration. Several specific questions related to *Calanus* spawning activity have a bearing on the structure and output of these models:

1. What is the winter-spring spawning cycle and how does it relate to the cycle of primary production? Heinrich (1962) concluded that the onset of spawning is well correlated with the start of the spring phytoplankton bloom, and that subsequent spawning episodes occur during periods of phytoplankton growth later in the season. However, there is evidence for sustained egg production supported by feeding on

microzooplankton in low chlorophyll waters. The hypothesis implicit in Heinrich's analysis and its alternatives can be tested for each region.

2. What are the relative roles of female abundance and egg production rate (eggs/female/d) in determining cohort structure of the regional *Calanus* population? The production of cohorts is a function of the recruitment rate and the mortality of eggs and naupliar stages. The relative importance of these factors may vary among regions and years.

3. Under what conditions is the egg production rate food limited? What is the extent of variability in egg production rate once spawning has started in spring?

4. Is there significant seasonal variability in hatching success of eggs? This could be a significant source of variability in the recruitment of new individuals into the population.

5. Is there a diel periodicity in spawning? In general, it is considered that *C. finmarchicus* spawns in the night and early morning. However, spawning may not be on a diel cycle in certain regions, such as boreal sites with long daylengths.

6. Where do females spawn in the water column and what is the vertical distribution of egg abundance? In general, it is considered that females spawn in the surface layer, although spawning may also be concentrated in the chlorophyll maximum (Melle & Skjoldal 1989). Knowledge of the microstructure of egg distribution is important to models of *Calanus*-larval fish interaction.

7. What is the effect of turbulence on egg distribution?

On the basis of the above considerations, the following recommendations are given:

Regional TASC programs should produce winter-spring time series of egg production rate estimates. These rates are the basis of recruitment rate into Calanus populations.

The population egg production rate (eggs/m^2/d) is determined by the per female egg production rate (eggs/female/d) and the abundance of females (females/m^2). The former variable can be measured by incubation techniques and female abundance by net tows integrating the water column. These methods should be standardized to ensure comparable results among regions.

5.1.3. Prediction of egg production rates: annual vs. multigeneration patterns.

Interpretation of the field measurements requires knowledge of the relationship between temperature and maximum egg production rate? Maximum egg production rates should be obtained under different temperature regimes using high quality food (probably a dinoflagellate or a mixture of dinoflagellates and ciliated protozoans). Rates should be expressed in terms of µgC/µgC/d in order to standardize rates across the wide range of female body size. Conversions to carbon for egg and female body mass should be carefully determined. Observations by Melle & Skjoldal (1991) indicate that egg diameter varies with temperature. This variability must be understood, in order to properly calculate clutch output and carbon-specific egg production rates.

It should be possible to develop empirical relationships, perhaps specific to each region, that will allow reduction of the workload of monitoring variability in spawning cycles. For example, satellite data on surface chlorophyll may serve as a proxy for the start of the spring phytoplankton bloom and egg production. Egg production rates after the spring bloom may vary by a relatively small factor, in which case regional cohort structure and generation number will be determined by the abundance of reproductively active females. It may be possible to develop empirical relationships between the female-specific egg production rate and the state of reproductive maturity in preserved samples of females, as described in Runge (1987) and Plourde and Runge (1993). This would allow prediction of egg production rates from net tow samples, reducing the number of labor-intensive incubation measurements, which would then be used for periodic checking of the egg production to gonadal status relationship.

The measurement of egg production rate, hatching success and female abundance should be standardized among regional studies. There are methodological issues concerning the proper incubation technique for estimating egg production rates (time of capture, incubation container, incubation conditions) that should be resolved and standardized. An efficient method for estimating hatching success, perhaps involving enzyme activity or DNA marking for flow cytometry, needs to be developed. Bongo or vertical tow nets should be equipped with flow meters, and the depths from which females are collected should be standardized within each region.

6.1. THEME III: POPULATION COHERENCE AND LATITUDINAL IMPACT ON GROWTH PATTERNS

The working group considering Theme III, population coherence and latitudinal impact on growth patterns, treated the components of their topic separately. In asking about population coherence, the TASC sought to learn whether or not *C. finmarchicus* is one 'stock' in the fisheries sense, that is, a population moderately well mixed genetically with a single behavioral repertoire for dealing with the challenges of its habitat. Even across a range as large as from Georges Bank to the Barents Sea, gene flow may make such homogenization possible. In asking about the impact of latitude, we seek to know how the strong variations in the challenges of the habitat affect the life of this abundant copepod.

The group did not see growth as an isolated issue, stating also the importance of more general matters of life cycle control. Both the analysis of population genetics of *C. finmarchicus* and assessment of latitudinal patterns of growth and development will require a combined approach consisting of field observations of natural populations with emphasis on individual variability, ship-board experimental studies, and development of controlled culturing capabilities.

6.1.2. Population Coherence and Population Genetics

A good start has been made on genenetic analysis by Bucklin and colleagues, as shown in her position paper. This paper identifies what will be needed to fully complete the task. A work plan for comprehensive population genetic analysis of *Calanus finmarchicus* across the N. Atlantic will require extensive and intensive sample collection with appropriate preservation, development of new techniques, and time and funding for analysis of many individuals. Recommendation:

> ***TASC projects should be underpinned by detailed molecular genetic analyses of C. finmarchicus stocks across its range with the aim of establishing the rates of genetic mixing and degree of genetic isolation within the species. Among the wide array of pelagic species, C. finmarchicus is an ideal study subject for issues of population vagility and genetic differentiation.***

The more specific requirements for future research will be:

1. We need genetic markers with more resolution. We are not sure exactly which spatial and temporal scales are appropriate to sampling for these markers. Scales will need to be chosen relative to generation time and advective transfer. A suite of genetic characteristics will be needed to allow both large-scale mapping and paired genetic/physiological studies. Mitochondrial DNA may be the most appropriate source of markers for large-scale mapping to recognize genetically distinctive populations. Coding regions of nuclear DNA, especially for glycolytic enzymes, may be useful markers for genetic/physiological analyses. Non-coding nuclear regions, which tend to be highly variable, may be useful to evaluate the level of individual genetic variation.

2. We need a marker for which the variation is selectively driven, i.e., one that reflects the ecology of the species. Those enzymes exhibiting allozymic variation may be especially useful, since some allozymic variants have already been shown to be under selective control. Studies of such markers should help us to understand the ecological meaning of genetic variation. For example, does higher genetic variation imply greater ecological and environmentally flexibility?

Two examples of studies were discusssed that might be undertaken with this question in mind. First, *C. hyperboreus* can endure long periods without food in cold temperatures. Is this endurance due solely to its larger body size, or is there a genetic strategy that accompanies this pattern? Second, *C. finmarchicus* may differ between Atlantic and Arctic regions, which may constitute a pattern in selection.

We will also want to observe genetic changes that are caused by selection and occur in populations as they are transported. During transport, changing environmental conditions may drive directional selection. The question is: how fast do genetic changes occur relative to the generation times and the circulation patterns. Appropriate sites for these studies are in gyres and recirculation patterns (see below).

3. We need quantitative estimates of advection of *C. finmarchicus* based on genetic characteristics. The goal is to distinguish between local recruitment and advected individuals. For example, can we quantify population exchange across the Iceland/Faroes front? It separates Arctic/Atlantic mixed water from Atlantic water. Genetic analysis will need to be paired with distributional studies and excellent hydrography.

The overall goal of this effort is to identify "core stocks" of *C. finmarchicus* and to determine their transport and exchange. Ultimately, we should be able to identify individuals according to their geographic lineage, and a model will be feasible of the interaction of genetic and advective mixing.

4. We will need genetic characteristics that allow the partitioning of individual variation into genetic, physiological, and environmental components. We should pair the genetic studies with physiological analyses of condition and nutritional state. It will also be interesting to compare individuals from different regimes.

Possible Approaches:

The first step is to map the population genetic structure, using presumably neutral markers that reveal the large-scale structure of the populations. Next is to determine whether individuals that differ in genetic characters also are ecologically different in adaptive characteristics. In other words, what are the ecological implications of genetic variation?

In order to do this, we will need new genetic characteristics that may be linked directly to the physiological condition of the individual. Also, we will need laboratory experiments to discriminate the effects of genetic variation under controlled conditions. In particular, the effects of genetic character on the relationship between temperature and growth, the timing and duration of diapause, and the duration of the feeding period. How do individuals of different genetic character differ in behavior, especially feeding and swimming behavior?

These experiments should simulate natural conditions in controlled conditions. Since for the moment we can only determine the genetics of dead copepods, there is likely to be substantial developmental work before such experiments are undertaken.

6.1.3. Latitudinal Patterns of Growth

A strategy is required for separating the effects on growth of temperature and food within regions to provide the means for comparing among regions. As for genetic analyses, we will need an integrated approach. We would begin with mapping studies to determine geographic patterns of variation in individual weight and biochemical composition (including, lipid and protein), in comparison with environmental conditions. Field mapping studies cannot answer the question: how much of the effect of temperature is directly due to temperature and how much is mediated through effects on the food chain leading to *Calanus*? This will be addressed in laboratory experiments to determine the nature of the direct effect of temperature on growth and its mechanism.

Requirements for Future Research:

1. We will need a compilation of data to demonstrate the relationship between temperature and growth, including both biomass and lipid reserves. These studies must be correlated with environmental conditions, since the timing of growth in relation to environmental conditions (especially the rapid accumulation of lipid reserves) is critical. The growth studies should be set in the context of the ecosystem, including the availability of phytoplankton and prey species and the abundance of predators.

2. We will require an understanding of the mechanism(s) linking food availability to spawning and development. The understanding we need will answer a string of related questions:

   > To what extent is spawning under control of the females; do they "decide" when and where to spawn?
   > Is spawning mediated by food availability and/or lipid reserves?
   > Is the number of offspring critical of is the quality of offspring also important?

3. We should focus on studies of the control of the inception of diapause. How do individuals decide whether to begin diapause or produce another generation? What are the critical environmental cues? Can individuals in very northern regions diapause at earlier stages? How does the implied delay for resumed development in spring influence the timing of spawning of the stock the following spring and the numerical abundance of the species? Is *C. finmarchicus* more or less flexible in its growth and diapause pattern than other representatives of the Calanidae?

4. We will need to learn the role of genetic variation in determining individual size. How do the genetic character, physiological condition, age in stage, and environmental conditions interact to control growth processes?

5. All experiments on growth and development processes of *C. finmarchicus* should focus on the individual: individual size and stage should be measured as part of all studies. Processes should be measured for all stages of development, including especially nauplii, which tend to be ignored. Length/weight regressions must be standardized in order to allow comparisons among areas. We will need to determine how tightly linked growth (biomass increase) is to stage progression (development).

6. Standardization of methods for studies of growth and development is very much needed. In addition, new techniques proposed for use must be evaluated. Some of this need is being met through ICES Study Group on Zooplankton Production, but the need for standardization should be emphasized here also.

7. There are a number of requirements for field sampling. These include:

    a. Location of a fixed site(s) for frequent observations during the winter/spring transition. We will need to quantify advection at these sites.

    b. Nets for collecting must be in two mesh sizes in order to catch all developmental stages. For the larger stages, we should comply with the ICES and GLOBEC standard 150 μm mesh size. For smaller sizes, there are various approaches, including: fine mesh nets, pump sampling with screening on 60-70 μm, or the use of 30 liter Niskin bottles.

9. We will require controlled rearing conditions. Laboratory and culture facilities should be developed to allow simulation of natural conditions and natural behaviors.

Possible Approaches:

Three approaches are useful and should be developed further:

Direct methods: Growth and development should be observed directly in incubation studies that simulate real growth conditions. We should also do ship-board experiments. An important type of direct experiment is "food spiking": increasing food availability, keeping the temperature constant, and observing growth rate.

Egg production: Growth can be inferred from the measurement of egg production. These methods especially are in need of standardization.

Indirect methods: Instantaneous measurements of growth processes via biochemical indices may be very useful but they must be evaluated.

Proposed Study Sites for Population Genetic and Growth Studies

1. Gyres and recirculation systems:
   - Norwegian and Greenland Seas for gyre studies
   - Northern N. Atlantic Circulation System
   - Gulf of St. Lawrence
   - Gulf of Maine/Georges Bank system in western N. Atlantic

2. Transition zones between Arctic and Atlantic regions:
   - Atlantic (south of Iceland) compared to
   - Arctic/Atlantic mixture (north of Iceland)
   - Denmark Strait
   - polar front in the Barents Sea
   - polar front off west Greenland
   - deep overflow in the Faroes/Shetland Channel
   - polar front in the Labrador Sea

7. *THEME IV: TROPHIC INTERACTIONS AND MORTALITY*

Concern with *Calanus* derives in part from its importance to fish and fisheries. Therefore, the fourth working group was asked to consider *C. finmarchicus* as a link between the particulate food web of the North Atlantic pelagial and the predatory food web of larger animals. This led the group to both direct consideration of the role of *C. finmarchicus* in supporting fishery stocks and to review of the problem of mortality rate estimation.

7.1. *Does Calanus production drive the production of commercially important fish stocks?*

It is essential that TASC projects address this question, since it is the practical basis likely to justify much of our support. An ideal approach can be postulated in which a full analysis of *Calanus* productivity is undertaken in a substantial number of years and compared to the survival or year-class strength of important fishes (e.g., Gulf of St. Lawrence Redfish, Georges Bank Cod and Haddock, North Sea Herring). By full analysis we mean a dense time series of stagewise growth and biomass measures suitable for summing as

$$P=\sum_{time}\sum_{i} G_i B_i \ ,$$

(sum over time and stage of stage growth rate and stage biomass). Survival of fish might, then, be found to depend upon *Calanus* production in specific time intervals or *Calanus* abundance in specific stages.

The problem with this ideal approach is likely to be the expense of such ambitious data on a recurring basis. Instead, we recommend concentration on those cases where fish larvae are shown to feed primarily on *Calanus* eggs and nauplii. All the example cases listed above fit this criterion. So do the larvae of many other fish stocks. Then we can produce recurring series of *Calanus* egg production data (female egg output X female abundance) for comparison to fish survival or year-class strength information. Clearly direct field estimates of egg and/or naupliar abundance might be substituted for production estimates. This approach, too, is labor intensive, but it is less demanding than full production studies.

We note that these studies are almost certain to be coastal in character, since the high time frequency that they require is only likely relatively close to shore.

There are a number of exciting sites for match/mismatch studies like this (accepting that the issue of the importance of timing matches between the timing of fish spawning and *Calanus* abundance is not settled). An excellent example is the spawning of Labrador Sea cod beneath ice in February/March. The median spawning time in a given area does not vary year to year, while extent of ice cover and the timing of the ice-retreat is highlay vaiable year to year. It follows then that the spring bloom of both phytoplankton and the subsequent spawing of *Calanus* is also variable. At these cold temperatures, fish eggs may take 3-4 weeks to hatch, and are subjected to drift onto northern Grand Bank due to Labrador current. The post-hatch survival time before the larvae reach the point of no return is 10-11 days. This could potentially allows frequent failures due to imprecise timing bwteen the larvae and their food supply. This site has been selected for a prolonged study by Canadian Department of Fisheries and Oceans. TASC-related projects cold address other, similar situations.

Study of the relation of *Calanus* production (particularly egg and naupliar output) to fish success is going to require multiple-year time series. Reducing the cost of obtaining such series is an important consideration. The only way to speed up time to obtain such series is to work with old data and old samples to extend information into the past. Canadian reevaluation of historical continuous plankton recorder data is one example of the benefit to be derived from this approach.

7.2 Acoustics as a basis for improved abundance estimation

The data base for evaluating the trophic impact of fluctuations in *Calanus* productivity on observed growth variations in pelagic fish (such as herring and capelin) is meager. The lack of equipment adequate for sampling zooplankton on the required scales has hampered the development of such a data base. Recent developments in acoustical detections of plankton have opened this field for innovative research, leading to the following recommendation:

> ***TASC should include acoustic technology in order to monitoring currents and copepod distribution so that Calanus abundance can be considered in the management of marine biotas as resources. This must be parallel to continuous research on improved acoustic instrumentation.***

7.3. The overwintering stock as an index of population size of C. finmarchicus.

In order to correlate possible fluctuations in recruitment and growth of important fish stocks with fluctuations in *C. finmarchicus* availability it is crucial to establish a reliable stock size estimator of *C. finmarchicus*. Due to the large distributional range of *C. finmarchicus*, assessment of the stock size with a high frequency and full spatial coverage is likely to be prohibitively expensive. It will be most efficient to undertake sampling in periods characterized by small changes in numbers and biomass, both temporally and spatially. This will allow for a smaller number of geographical stations and make year-to-year comparisons more reliable than if the sampling were carried out in periods with high biological rates and spatial patchiness. The time period that spans from late autumn (October?) to winter/early spring (February?) is probably the period where rates are at the lowest and the stocks are most homogeneously distributed horizontally. In this period, *C. finmarchicus* undergoes diapause with low metabolic activity (Hirche, this workshop). This diapause-period is spent at relatively great depths that probably also facilitate a low mortality rate (< 1% per day according to a fjord study by Aksnes & Magnesen 1983).

Samples from resting stocks in particular ocean gyres (e.g., the slope waters south of Georges Bank, in subpolar gyre south of Greenland, in the Nordic Seas) and in particular coastal basins (e.g., Gulf of Maine basins, Nova Scotian shelf basins, Norwegian fjords) can provide time series representing the integral of population production in the previous winter-spring. Both stock numbers and individual size (length, weight, lipid depot content) must be measured. They should be indicative of (1) the net outcome of birth rate and survivorship and of (2) growht conditions. Interpretation will require study of prior winter-spring production processes and food availability. However, the necessary burden of data may be less in light of the time series of resting stage output than it would be otherwise. The full potential of this sort of investigation needs to be studied and ultimately proved in practice.

Another reason to assess the size of the overwintering stock is due to the evidence that egg production and later productivity are heavily influenced by the numbers of females (papers by Harris, Slagstad & Tande, and others). Hence, estimates that represent the large scale overwintering stock of *C. finmarchicus* may be indicative of the large scale production the following year. It is important that we find sites for which estimates of the overwintering stock size will be representative for large sections of the distributional range of *C. finmarchicus*. The subpolar gyre and the Nordic Seas are especially important regions to cover adequately. Two estimates, one in autumn and one in winter, will facilitate mortality estimates for the overwintering period and will therefore be advantageous.

7.4. Food

A standardized method for estimating in situ feeding in parallel studies in different key environments throughout the latitudinal range of *C. finmarchicus* should be adopted. It is felt that the gut fluorescence method remains the most practical approach to obtaining information on in situ grazing on phytoplankton, and for estimating feeding periodicity. A standard measurement protocol should be employed. Recommendation:

> *TASC projects should provide for evaluation of food available to C. finmarchicus in order to interpret differences in reproduction, growth rate, and life history variations. If need be, this could be simply chlorophyll data. Ideal evaluations will consider phytoplankton and microzooplankton composition and nutritive value in detail.*

Despite the fact that the majority of our understanding of copepod feeding biology is based on studies of the genus *Calanus*, there are still important gaps in our knowledge. Two key aspects, demanding further quantitative study are:

1) Naupliar feeding ecology: Almost nothing is known of the food requirements of the naupliar stages, and yet these early developmental stages may be critical in population dynamics, and in model development. There is a need to evaluate the food conditions necessary for maximal naupliar growth and survival and to compare them with those established for later copepodites. Can nauplii feed on smaller food particles? Are feeding thresholds lower? Quantitative laboratory experiments are required to answer such questions, and to provide critical model parameters. Development of innovative approaches to the study of in situ naupliar biology should be encouraged.

2) Dietary diversity: Despite *Calanus* being classically viewed as an effective grazer of spring diatom blooms, there is increasing evidence of the importance of non-algal components, particularly microzooplankton, in the diet. The development of new techniques for assessing the role of microzooplankton in the diet should be encouraged. The analysis of astaxanthin-like pigments in copepod guts and immunoassay of ciliate proteins are promising approaches, which might be further developed for field use. At present, incubation studies using microscopic identification and counting remain the best (but most labor intensive) method for obtaining detailed information on the microzooplankton-*Calanus* link.

Quantitative studies of food and feeding, both in the field and in the laboratory, should be strongly interactive with modelling and model development. Models should provide hypotheses, and experimental work should be directed to the parameters of highest sensitivity.

7.5. Mortality Rate Estimation

TASC has a strong ecological emphasis on the relationship between life history events and habitat "challenges". Progress toward understanding this relationship will be expedited through careful use of mathematical models - especially population models. Thus the program for mortality rate estimation should be integrated with other population studies through the use of common models (e.g. Carlotti's stage structure model).

> ***TASC projects should invent and adopt strategies for determining the partitioning of mortality among the developmental stages of C. finmarchicus cohorts.***

We propose two approaches:

1. Use recent methods (e.g. Wood & Nisbet 1991) for estimating stage-specific mortality rates from stage population data. These are likely to be applicable in "nearly closed" systems such as fjords. An important open issue is to determine the necessary conditions for them to work when applied to spatially averaged data over a large enough area that advective contributions to total population change are relatively small.

2. Tackle the "inverse problem" (i.e. estimate stage specific mortality rates by demanding that measured population data be a solution to population dynamic equations) for appropriate structured population models starting with that of Carlotti.

Three further problems require research:

1. Importance of the vertical distribution. It may be that the depth-dependence of mortality rate is comparable in importance with life-stage-dependence. It will then be necessary to develop a structured population model which takes account of the vertical distribution of both copepods and their food.

2. Life history strategies. Knowledge of variations of mortality rate with age and stage are key to testing any interpretation in terms of fitness of observed strategies for (a) entering diapause and (b) seasonal vertical migration. Such calculations should be attempted.

3. Natural mortality in crustacean larvae has recently been found to decrease, more, when the cohorts are subjected to a continous increase in temperature, than can be calculated based on a convetional obtained temperature function of mortality vs. temperature. Only limited data is available on *Calanus* (Tande 1988, Pedersen & Tande 1992), but further studies are encouraged.

7.5. Mortality due to predation

In addition to mortality rate estimation, it is valuable to know the causes of death. It is certain that a very large fraction of deaths occur when *Calanus* are eaten by predators. We developed an outline for studies of predation.

Key Issues:

1. What are the predators feeding on *Calanus*?
   a) Visual predators: fish. These can be studied using acoustics during zooplankton sampling in order to find their distributions relative to that of *C. finmarchicus* stocks. This requires multidisciplinary cooperation.

   b) Non-visual predators: carnivorous copepods and chaetognaths. These can be estimated in fixed samples. Gelatinous predators (ctenophores, jellyfish) should be sorted out from fresh samples before preservation.

2. How does predation pressure vary with depth? We need vertical distribution data for predators and *Calanus* from the whole water column.

3. Seasonal variation in predation pressure and in type of predation. Different predators develop large stocks at different times of the year. We need time-series of the predators, especially for gelatinous predators where such data are missing. There should be a routine to always record the amount (volume/number) of gelatinous zooplankton in fresh samples. How large is the predation on the overwintering stock, and what kind of predators are active during this period? For example, carnivorous copepods and chaetognaths feed during the whole winter-period.

4. Stage-specific mortality due to predation. Vulnerability to predation varies with stage of *Calanus*, and depends on the type of predator. Here we will probably make the most progress through experimental work: behavior, swimming patterns, escape-responses.

5. Predation rates. Can we develop a strategy for measuring predation rates? Is gut content coupled with gut clearance rate estimates appropriate? Developmental experimentation is required in this area for predators already demonstrated to be significant to *Calanus* on a population scale.

7.7. Reanalysis of historical data

Historically, the marine laboratories located around the Atlantic rim have collected zooplankton samples over many years. Most of these samples were probably collected for a dedicated project and have probably been discarded after the analysis. However, there probably remain a large quantity of data and samples archived in various laboratories.
Reanalysis of such data and samples would be useful to establish long-term trends in the patterns of abundance, distribution and life history events of *Calanus*. The US Globec program has initiated reanalysis of samples collected in the MARMAP program and new information on the stage distribution of *Calanus* on the NE shelf of USA is becoming available. Another set of data collected in 1930-40 have yielded information on depth

distribution of younger stages of *Calanus* on the Georges Bank. Similarly, reanalysis (Myers et al. 1994) of CPR data (1959-79) from the NW Atlantic, particularly from Newfoundland Shelf and the Grand Banks clearly show changes in the annual cycle of *Calanus*, along the north-south latitudinal gradient, presumably in response to the timing of the spring bloom. There may be more such data available from other parts of the North Atlantic, especially data collected by Russian scientists in the past in the Barents Sea, Greenland Sea, Laborador Sea and the Grand Bank. We recommend that:

> ***TASC should encourage that retrospective analysis of archived data should be initiated, so that the information can be applied to optimal design of new field studies.***

8. RECOMMENDATIONS TO THE COUNCIL

The ICES Workshop on the TransAtlantic Studies of *Calanus finmarchicus* (TASC) have identified a series of scientific topics in order to highlight future research on this species in the North Atlantic. The Workshop concluded on each topic by formulating **TASC recommendations** in order to focus on gaps in our knowledge and provide directional momentum for future studies on this species in the North Atlantic. These recommendations are considered building blocks for an implementation plan for a coherent study on the species in the North Atlantic.

The meeting recommended that: 1) a multidisplinary, internationally cooperative research programme on *Calanus finmarchicus* be initiated for the North Atlantic, and 2) a planning Group be established to develop the implementation of TASC.

The building blocks of the implementation plan for this programme should include a substantial part of the TASC recommendations given as follows:

* TASC projects should provide a combined budget for population development and advective transfer to establish whether individuals entering the deep-water resting habitat have grown primarily over the shelves or in the open oceanic.

* TASC projects should sample resting stocks for stage composition over at least several years. Basic habitat data, particularly water column temperature patterns, should be recorded through the period prior to and during diapause onset.

* TASC should include acoustic technology in order to monitoring

currents and copepod distribution so that *Calanus* abundance can be considered in the management of marine biotas as resources. This must be parallel to continuous research on improved acoustic instrumentation.

* TASC projects should study what determines whether a given generation matures and reproduces or enters diapause.

* TASC projects should select an indicator of diapause conditon and trace its appearance in the *Calanus* stocks they study as a function of season, temperature history, depth and photoperiod.

* Regional TASC programs should produce winter-spring time series of egg production rate estimates. These rates are a key component of the rate of recruitment into *Calanus* populations.

* TASC should encourage laboratory studies on life cycle phenomena, and care should be taken so that the experimental setup is designed to mimic the variation of environmetal variables during the period of study. Future experimental studies should persue the effect of dynamic environmental varibles on life cycle phenomena in *Calanus*.

* TASC projects should contribute to detailed molecular genetic analyses of *C. finmarchicus* stocks across its range with the aim of establishing the rates of genetic mixing and degree of genetic isolation within the species. Among the wide array of pelagic species, *C. finmarchicus* is an ideal study subject for issues of population vagility and genetic differentiation.

* TASC projects should provide for evaluation of food available to *C. finmarchicus* in order to interpret differences in reproduction, growth rate, and life history variations. If need be, this could be simply chlorophyll data. Ideal evaluations will consider phytoplankton and microzooplankton composition and nutritive value in detail.

* TASC projects should invent and adopt strategies for determining the partitioning of mortality among the developmental stages of *C. finmarchicus* cohorts.

* TASC should encourage that retrospective analysis of archived data should be initiated, so that the information can be applied to optimal design of new field studies.

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10. POSITION PAPERS PRESENTED

Section I:
THE INTERPLAY BETWEEN GENERATION CYCLES AND LARGE SCALE CIRCULATION PATTERNS IN OCEANIC AND SHELF AREAS

J. Blindheim & D. Aksnes
Circulation patterns in the North Atlantic and the possible impact on the population dynamics of Calanus finmarchicus.

J. O. Backhaus, I. H. Harms, M. Krause & M. Heath
Hypothesis on the space-time succession of Calanus finmarchicus in the range of the NW European Shelves.

E. Gaard
Life cycle, abundance, and transport of Calanus finmarchicus in Faroese Waters.

A. Gislason & O. Asttorson
Development of Calanus finmarchicus along an inshore-offshore gradient SW of Iceland.

D. Slagstad & K. Tande
The impact of SW and NE winds for advection of Calanus finmarchicus across the shelf break in North Norway during spring and summer. A model study.

Section II:
STRATEGIES FOR OVERWINTERING AND REPRODUCTION

S. Kaartvedt
Differences in habitat preference and the timing of descent and ascent with respect to the seasonal vertical migration in C. finmarchicus in the North Atlantic.

J. Runge
Factors affecting fecundity variability in Calanus finmarchicus.

H. J. Hirche
Overwintering physiology and reproduction in Calanus finmarchicus.

Section III:
POPULATION COHERENCE AND LATITUDINAL IMPACT ON GROWTH PATTERNS
A. Bucklin
Population genetics of Calanus finmarchicus in the North Atlantic.

F. Carlotti
A realistic physical-biological model for Calanus finmarchicus in the North Atlantic. A conseptual approach.

B. Hansen
Comparative productivity studies on Calanus finmarchicus from West Greenland and the Barents Sea.

Section IV:
TROPHIC INTERACTIONS, MORTALITY AND PROBLEMS RELATED TO FIELD SAMPLING

Roger Harris
Feeding ecology of Calanus.

R. Nisbet
Mortality rate estimation for Calanus finmarchicus in the North Atlantic.

C.B. Miller
Goals and potential of a Trans-Atlantic Calanus finmarchicus research program.

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