

Some effects of ultraviolet radiation and climate on the reproduction of *Calanus finmarchicus* (Copepoda) and year class formation in Arcto-Norwegian cod (*Gadus morhua*)

Stig Skreslet^{a,*}, Angel Borja^b, Luca Bugliaro^c, Georg Hansen^d, Ralf Meerkötter^c, Ketil Olsen^a and Jean Verdebout^{e,1}

^a Faculty of Fisheries and Natural Sciences, Bodø Regional University N-8049 Bodø, Norway, UK

^b Department of Oceanography AZTI, Pasaia, Spain

^c DLR-Institute for Atmospheric Physics, German Aerospace Center Oberpfaffenhofen, Germany

^d NILU, Polarmiljøsenderet Tromsø, Norway, UK

^e EC-JRC Space Applications Institute Ispra, Italy

*Correspondence to S. Skreslet: tel: +47 7551 7496; fax: +47 7551 7484. e-mail: stig.skreslet@hibo.no.

Zooplankton sampling in 1997 identified the frontal zone of the Norwegian Coastal Current as a reproduction habitat for *Calanus finmarchicus* in June–August. This area is subject to considerable ultraviolet radiation (UVR), as calculated from satellite observations of ozone and cloudiness. While *in situ* experiments indicated UVR-induced mortality in reproducing *C. finmarchicus*, monthly UVR doses during the actual reproduction period did not appear to affect the abundance of the resulting generation of adolescent copepodites (CIV-V) that accumulated in a fjord habitat during October 1983–2000. Local UVR in the spawning grounds of Arcto-Norwegian cod at the Lofoten Islands in March–May was positively correlated with the stock's 0-group index, which resulted in the rejection of the hypothesis that local UVR leads to high mortality of cod eggs or reduces the abundance of prey for cod larvae. Rather, the result suggests an indirect positive effect of UVR on the survival of cod eggs and larvae, possibly by controlling harmful microbes.

Keywords: bacteria, climate, freshwater, Norwegian Coastal Current, radiation, recruitment, trophodynamics, UV

Received 1 July 2004; accepted 28 May 2005.

Introduction

[Sømme \(1934\)](#) was the first to investigate the biology of *Calanus finmarchicus* in the Vestfjord, which is separated from the Norwegian Sea by the Lofoten Islands ([Figure 1](#)). The Lofoten Waters are the main habitat of adult Arcto-Norwegian cod (*Gadus morhua*) during spawning in April. [Wiborg \(1948\)](#) established that the nauplii of *C. finmarchicus* were the main food item of cod larvae. Since then, several have investigated this trophic relationship to establish whether or not it could play a role in the establishment of year-class strength in Arcto-Norwegian cod in accordance with the critical period concept of [Hjort \(1914\)](#).

Many factors are thought to affect the year-class strength of cod. Temperature is considered to affect recruitment through its influence on differences in the timing of the reproduction periods of cod and *C. finmarchicus* ([Ellertsen et al., 1989](#)), thereby supporting match and mismatch theory of [Cushing \(1969\)](#). [Sundby et al. \(1994\)](#) suggested that the survival of cod larvae was proportional to wind-generated micro-turbulence, which determined the rate of encounter with prey. Freshwater run-off from Norway has been suggested as an influence on cod recruitment through its effect on zooplankton ([Izhevskii, 1964](#); [Skreslet, 1976, 1988, 1997](#)). [Skreslet and Borja \(2003\)](#) suggested that positive correlations between *C. finmarchicus* abundance and the North Atlantic Oscillation (NAO) are linked through freshwater discharge, given that positive NAO causes northerly storm tracks and increased precipitation in Scandinavia ([Hurrell, 1995](#); [Greene and Pershing, 2000](#)).



Figure 1 The mid-Norwegian Shelf showing plankton sampling stations (circles). The rectangle encloses the assumed summer reproduction habitat of *C. finmarchicus* in the frontal zone of the Norwegian Coastal Current (NCC), and is the area where surface UVR was estimated from satellite measurements of ozone and cloud cover. The shelf current jet and the frontal jet of the NCC indicate current velocities $>40 \text{ cm s}^{-1}$, as observed by [Poulin et al. \(1996\)](#).

In recent laboratory experiments, ultraviolet radiation (UVR) caused mortality of cod eggs as well as eggs of *C. finmarchicus* ([Kouwenberg et al., 1999a, b](#); [Browman et al., 2000](#)). In northern Norway, periodic depletion of ozone causes interannual variation in UVR ([Hansen et al., 1997](#)). Thus, the strength of cod year classes could be a direct function of both cod egg mortality and control of larval prey ontogeny by UVR damage. UVR acting on the parent copepod generation could also indirectly regulate the prey abundance during their ontogeny and adolescence, i.e. during the previous summer ([Skreslet et al., 2000](#)). In this paper, we investigate the possibility of negative effects of UVR on reproduction at the population level of *C. finmarchicus* and Arcto-Norwegian cod.

Methods

To establish that the Norwegian Coastal Current (NCC) is a reproduction habitat for *C. finmarchicus* during summer, monthly sampling was undertaken from June to August 1997, outside the archipelago of Træna ([Figure 1](#)). Seven fixed stations were distributed across the convergent front between the NCC and the shelf water. Double oblique tows were taken from 0 to 40 m with a 20-cm Bongo 100- μm net equipped with a calibrated flowmeter for calculation of the sampling volume. Hydrographic data were recorded by a SeaBird SBE25 Sealogger and salinities calibrated against standard seawater using a Guildline laboratory salinometer.

As *C. finmarchicus* in the upper 10 m experience the highest UVR exposure, we sampled the upper mixed layer during their summer reproduction period at Træna in July 2000 and 2001. Horizontal tows were made at discrete depths by a Clarke-Bumpus plankton sampler equipped with a 350- μm net and a calibrated flowmeter for calculation of the sampling volume. *C. finmarchicus* eggs and nauplii were sampled on a 100- μm sieve from 1 to 2 l of seawater contained in Niskin bottles, closed at discrete depths. Large samples were split by a Folsom plankton divider.

To observe effects of solar UVR on reproducing *C. finmarchicus*, a field experiment was performed at Træna, 5–6 July 2000, on females sampled in the NCC frontal zone by double oblique tows in the 0–40-m depth range, with a 20-cm Bongo of 180- μm net. A subset of live females was stored in bottled seawater immersed in ice slush (0°C). Later, live females were transferred to individual 10-cm-long quartz tubes that allowed transmission of UVR from outside. The 2.5-cm-diameter tubes were closed with a plastic stopper. Fifteen control tubes were wrapped in aluminium foil that prevented intrusion of any solar radiation, while another 15 tubes remained unshielded. All tubes were kept in ice slush until transferred to a rig submerged in a sheltered bay. The tubes were suspended horizontally in a frame at about 5-cm depth. They were left for 24 h from noon to noon exposed to a natural diurnal

light regime with no clouds. After recovery, the tubes were kept in ice slush until opened. The number of dead females was first recorded and the eggs were counted under a stereomicroscope. Eggs from individual females were kept in separate tubes, incubated at 10°C for 72 h, and then the eggs and nauplii were grouped according to stage and counted.

A time-series of monthly surface UVR intensity was constructed over the assumed NCC reproduction habitat ([Figure 1](#)) using radiative transfer modelling and satellite data to obtain the influencing atmospheric factors ([Verdebout, 2000](#)). Surface UVR is mainly determined by cloud optical thickness and total column atmospheric ozone, which is a very strong UV absorber. Cloud optical thickness was retrieved from METEOSAT data, the operational European geo-stationary meteorological satellite, while total column ozone is provided by the specialized space instruments TOMS (Total Ozone Monitoring Spectrometer), TOVS (Tiros Operational Vertical Sounder), or GOME (Global Ozone Monitoring Experiment). These time-series were extracted from an UVR climatology covering Europe (34°N–74°N 12°W–32°E) with daily dose maps since 1 January 1984 (with ~10% missing days because of lack of data). The UV spectrum was weighted with an action spectrum-specific to the UV-induced mortality of *C. finmarchicus* eggs ([Kouwenberg et al., 1999b](#)). The reconstructed UVR values were successfully validated by comparison with those modelled with the higher spatial resolution AVHRR (Advanced Very High Resolution Radiometer) satellite instrument and measurements performed in Tromsø ([Meerkötter et al., 2003](#)).

The NCC time-series for monthly UVR was subjected to a Spearman correlation test (undertaken with a Statgraphics[®] software) with a time-series of *C. finmarchicus* abundance obtained by annual sampling in the Saltfjord ([Figure 1](#)) in October of most years from 1983. The samples were collected with a 0.1-m² Juday net with 180-µm mesh, towed vertically from 10 m above bottom (380 m) to the surface. Five replicate tows were conducted each day to take account of variance caused by patchiness. Here we present the averages from each sampling date. A more detailed presentation of the data is found in [Skreslet and Borja \(2003\)](#).

The *C. finmarchicus* time-series was also regressed against the 0-group abundance index for four- to five-month-old Arcto-Norwegian cod calculated from the international 0-group survey in the Barents Sea ([Anon., 2004](#)) and accessed from <http://www.imr.no/produkter/publikasjoner/toktrapper/2002>. A time-lag of one year was applied to test the hypothesis that the abundance of *C. finmarchicus* accumulating in the Vestfjord area during autumn influences the year-class strength of Arcto-Norwegian cod the following year.

The 0-group time-series was regressed against estimated UVR doses from 1973 to 2000 (Tromsø), using monthly doses (March, April, May), weekly doses (from weeks 10 to 21: days 64 to 147), and maximum doses (from an 11-day period around 1 April and 1 May). To construct a multi-decadal time-series of local UVR in the spawning area of cod in Lofoten, we used daily observations of the cloud cover fraction at Skrova, and total ozone measurements recorded at Tromsø, and, when not available, from other sites in Northern Fenno-Scandia (Andøya, Sodankyla, and Murmansk). Moreover, in the years 1979–2000, most ozone data were taken from TOMS. These agree quite well with the Tromsø Dobson measurements, but are much more frequent. The resulting UVR series have been published recently ([Engelsen et al., 2004](#)). Daily observations from Skrova were also used to construct a multi-decadal time-series of photosynthetic active radiation (PAR).

We recognized that single weekly doses of UVR might yield spurious correlation with other variables. Some correlations with monthly doses of UVR were significant at $p = 0.05$, apparently because of contributions from weekly doses that might be spurious. Accordingly, we only considered p values of 0.01 to be statistically significant.

Results

C. finmarchicus nauplii were present in the area between Træna and the outer Vestfjord during the sampling period from late June to August 1997, with a recorded maximum in July (Figure 2). Their abundance was negatively correlated ($r = -0.709$, $n = 21$, $p = 0.01$) with surface salinity (Figure 3). At Træna, the eggs, nauplii, and adults of *C. finmarchicus* were associated with the upper 40-m depth range, i.e. the upper mixed layer and pycnocline. Their vertical distribution varied between stations and dates, and was, on occasion, concentrated in the 0–10-m depth range (Figures 4 and 5).

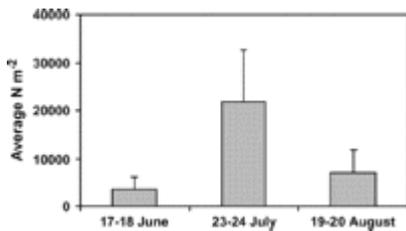


Figure 2 Average abundance of *C. finmarchicus* nauplii sampled during daytime by double oblique Bongo tows in the upper 40 m at seven stations in the NCC convergent front from 17 June to 20 August 1997. Bars: 95% confidence limits.

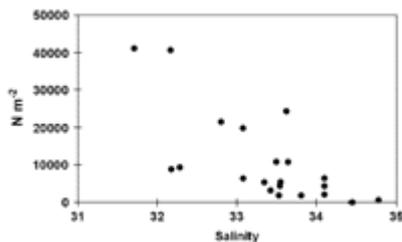


Figure 3 Abundance of *C. finmarchicus* nauplii sampled during daytime by double oblique Bongo tows in the upper 40 m related to salinity at 5-m depth in the NCC convergent front from 17 June to 20 August 1997 ($r = -0.709$, $n = 21$, $p = 0.001$, $\text{nauplii} = -10\,803 \text{ salinity} + 371\,383$).

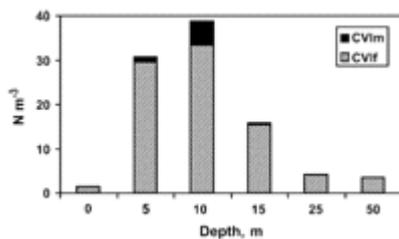


Figure 4 Depth distribution of *C. finmarchicus* CVI females and males sampled during daytime by Clarke-Bumpus plankton sampler at one of the stations at Træna, 6 July 2000.

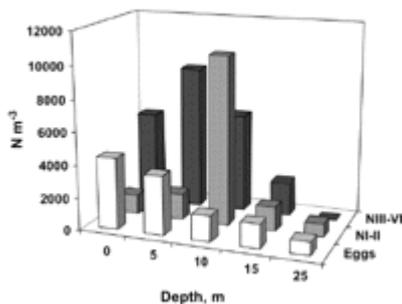


Figure 5 Depth distribution of *C. finmarchicus* eggs and NI-VI sampled during daytime by Niskin bottles at one of the stations at Træna, 4 July 2001.

Seven of 15 *C. finmarchicus* females died after 24-h exposure to natural light under cloud-free conditions at Træna, while none of the 15 females kept in dark control chambers died. Seventy-two hours after the termination of the field experiment, most of the eggs from unexposed females had developed into NIII-VI. A larger fraction of eggs from exposed females had not hatched or still remained as NI-II (Figure 6). The sums of unhatched eggs and nauplii were smaller than the number of eggs incubated, which was attributed to autolysis of dead embryos and nauplii.

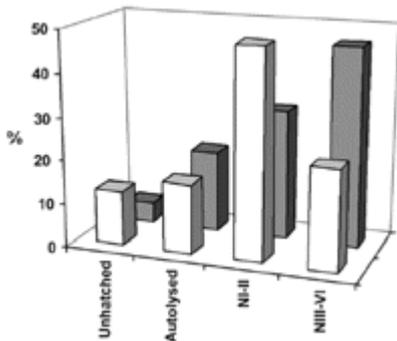


Figure 6 Development of eggs and nauplii produced by *C. finmarchicus* females kept for 24 h in individual chambers at about 5 cm below sea surface at Træna, 5–6 July 2000. White columns: exposed to solar UVR. Dark columns: controls.

The average abundance of *C. finmarchicus* CIV-V sampled in the Saltfjord during October was not correlated with monthly biologically weighted doses of UVR on *C. finmarchicus* eggs on the inner mid-Norwegian Shelf in June, July, and August. However, it was negatively correlated with the monthly dose in May ($r = -0.832$, $n = 15$, $p = 0.01$). There was no significant correlation between abundance of *C. finmarchicus* and cloud cover in May.

The 0-group index for Arcto-Norwegian cod was not correlated with the October abundance of *C. finmarchicus* in the previous year. However, it was positively correlated with surface UVR in the main spawning area of Arcto-Norwegian cod in Lofoten ($r = 0.667$, $n = 28$, $p = 0.01$), calculated as the average of maximum doses from two 11-day periods, around 1 April and 1 May, respectively (Figure 7). Correlations with monthly and weekly doses in March–May were not significant, except for week 13 ($r = 0.523$, $n = 28$, $p = 0.01$). The 0-group index was not correlated with PAR.

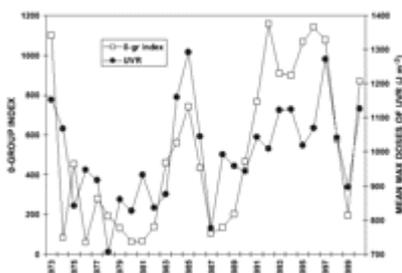


Figure 7 Interannual variation in 0-group abundance of Arcto-Norwegian cod and average maximum doses of UVR in Lofoten. Regression: 0-group cod = $1.8474 \text{ UVR doses} - 1326.7$, $r = 0.677$, $n = 28$, $p = 0.01$.

Discussion

The abundance of *C. finmarchicus* nauplii in the NCC frontal zone identifies the inner mid-Norwegian Shelf as a summer reproduction habitat of the species.

A full 24 h near-surface exposure to natural solar radiation during our *in situ* experiment at Træna during summer caused increased mortality among female *C. finmarchicus* and retarded the development of their eggs and nauplii, in accord with the experimental results of [Kouwenberg et al. \(1999b\)](#). In the field, we observed cases with abundant eggs, nauplii, and adults in the upper 10 m where UVR is supposed to be harmful. However, free-living copepodites, including adult females, have the option of vertical diurnal migration and avoidance of detrimental radiation ([Aarseth and Schram, 1999](#)). Their eggs and nauplii may avoid surface UVR levels by wind mixing and tidal turbulence that can move them deeper in the mixed layer. Also, they contain screening pigments and may mobilize photo-repair reactions ([Browman et al., 2000](#)). The lack of correlation between our calculated surface UVR in the reproduction habitat of *C. finmarchicus* in June–August and the abundance of CIV-V in one of the population's accumulation habitats during October ([Heath et al., 2000](#)) seems to indicate that solar UVR to the mixed layer in the open sea has little or no direct effect on egg production, fertilization, embryonic ontogeny, and growth of nauplii.

The significant negative correlation of October abundance of *C. finmarchicus* with UVR in May could be random but deserves some discussion. Fjords along the mid-Norwegian Shelf serve as habitats for reproducing *C. finmarchicus* in April ([Sømme, 1934](#); [Strømgren, 1976](#); [Skreslet and Rød, 1986](#); [Skreslet et al., 2000](#)). In May, the first generation has developed mainly into CIVs and CVs ([Skreslet et al., 2000](#)) that may be observed in swarms that ripple the surface film at noon on calm, sunny days (unpublished data). Their behaviour possibly exposes them to UVR-induced effects. This spring generation leaves the fjords, probably by flushing of freshwater outflow ([Strømgren, 1976](#)) that normally starts in May–June and lasts for a month or two ([Skreslet, 1976](#); [Skreslet et al., 2000](#)). This first generation possibly matures into adults and occupies the NCC reproduction habitat in June–August. Thus, there is the possibility that reproductive inability due to UVR damage in first generation adolescent stages in May might regulate the size of the second generation that accumulates in the Saltfjord in October.

Variation in sea surface UVR on the inner mid-Norwegian Shelf in late spring and summer is mainly caused by cloud cover, while the ozone variation is much smaller than, e.g., in March–April. Thus, the observed negative correlation between UVR in May and *C. finmarchicus* in October might be an effect of cloudiness rather than protection from UVR. However, we found no significant correlation between October abundance of *C. finmarchicus* and cloudiness recorded by satellite, either in May or in the following months.

Clouds mainly develop along the Norwegian coast during periods of westerly winds from the Northeast Atlantic. The coastal mountains cause humid air to rise and become subject to adiabatic cooling that condenses vapour and causes precipitation, which results when the NAO ([Hurrell, 1995](#)) is positive ([Greene and Pershing, 2000](#)). Water vapour contains large amounts of potential energy that is released as heat when clouds form and generate precipitation, which in May–July favours melting of snow and generation of freshwater run-off from Norwegian mountain ranges ([Skreslet, 1976](#)). On the other hand, the absence of clouds means clear sky and sunshine, which results in sublimation of the snow cover, i.e. direct loss of water vapour to the atmosphere rather than melt-water run-off. Our calculated UVR may be a proxy for intensive solar radiation and also for sublimation that possibly regulates the vernal freshwater discharge to the coast. Thus, the observed negative correlation with UVR in May and *C. finmarchicus* in October may indicate that freshwater outflow to the mid-Norwegian Shelf stimulates plankton productivity according to the theory of [Izhevskii \(1964\)](#). We observed that *C. finmarchicus* produced nauplii for two months during the seasonal freshwater outflow that peaks in June–July ([Skreslet, 1976](#)). The negative correlation between salinity and abundance of nauplii in the NCC frontal system possibly indicates that physical processes forced by freshwater outflow could stimulate the reproduction of *C. finmarchicus* as reported from UK waters by [Hay \(1995\)](#).

Recognizing UVR as a possible mortality factor for juvenile stages of cod and *C. finmarchicus* ([Kouwenberg et al., 1999a, b](#); [Browman et al., 2000](#)), the production and survival of cod larvae could

be expected to suffer in periods of high UVR. The Lofoten Islands are situated in an area that, in the past two decades, has been subject to periodic thinning of atmospheric ozone (e.g. [Hansen et al., 1997](#)). The area is also subject to periodic variation in albedo effects from snow cover, as well as to a variable cloud cover, which causes extensive short-term variation in solar radiation. However, rather than observing a negative correlation of the 0-group index of cod with local UVR, we observed positive correlation. This was contrary to our expectations and while it may be a result of statistical randomness, we consider some other possible explanations.

As UVR is influenced by both clouds and ozone levels, we considered the possibility that the positive correlation between UVR and 0-group cod might not be directly related to solar UVR, but rather to cloud-induced changes of the photosynthetic active radiation (PAR). PAR stimulates the production of food for female *C. finmarchicus*, which would lead to increased fecundity and more prey for cod larvae. However, we found no correlation between PAR and the 0-group index and rejected this possibility.

In experimental and hatchery designs for incubation of cod eggs, [Hansen and Olafsen \(1989\)](#) observed that bacterial growth on the egg membrane was a serious mortality factor. The problem is likely to occur in nature as well. Solar UVR may keep microbial infection of cod eggs at a low level, thereby leading to improved embryo survival and higher abundance of cod larvae. In tropical waters, UVR damages bacterial DNA in the upper 5 m ([Visser et al., 2002](#)). Considering that cod eggs at the Lofoten Islands are kept in suspension close to the sea surface ([Ellertsen et al., 1989](#)), seawater bacteria in suspension or attached to cod eggs may be directly inactivated by UVR. However, an alternative is that viruses may cause lysogeny of microbes in the marine environment when exposed to UVR ([Jiang and Paul, 1998](#); [Weinbauer and Suttle, 1999](#)). Taking into account that our best significant correlation was with maximum daily doses and not averaged over days, brief periods of particularly high UVR may be responsible for this effect.

We have been reluctant to accept a significant correlation between 0-group index and average UVR dose in week 13 (i.e. around 1 April), suspecting that it might be spurious. However, this result is supported by the significant correlation between the 0-group index and UVR maximum doses in two 11-day periods around 1 April and 1 May. The results are consistent with maximum cod spawning in Lofoten (cf. [Ellertsen et al., 1989](#)) around 1 April (week 13), and the period around 1 May is when most cod larvae hatch and first-feed. All are crucial events that perhaps benefit from effects of UVR on microbes.

From the MARMAP time-series 1977–1987, [Morse \(1994\)](#) observed that recruitment of Atlantic cod (*G. morhua*) on Georges Bank, as measured by abundance of one-year olds, was positively correlated with the production index of 6-mm cod larvae of the same year class, i.e. in the previous year. Accordingly, the year-class size seems to be largely established around the end of the yolk-sac stage, which indicates that food limitation may be critical only within a very short time frame, possibly being less important than hatching success. Thus, UVR strengthens its role as a generally positive environmental factor for cod reproduction, whether this relates to DNA damage or viral lysis of bacteria.

In summary, the Norwegian Coastal Current that flows northwards on the inner mid-Norwegian Shelf towards the Lofoten Islands is a reproduction habitat for *C. finmarchicus* in June–August. The production of *C. finmarchicus* progeny does not appear to be directly affected by UVR. Their abundance in autumn near the Lofoten Islands does not seem to control 0-group abundance in Arcto-Norwegian cod hatched during the following spring. There was no supporting evidence that local UVR on the spawning grounds of cod controls the 0-group abundance by causing mortality in cod eggs, cod larvae, or their prey. However, UVR may influence the 0-group abundance of cod positively by direct or indirect forcing of the microbial environment of cod eggs and larvae.

Acknowledgements

The UVAC project was financed by the European Commission Contract No. EVK3-CT-1999-00012. Some of the biological data originated from TASC, European Commission Contract No. MAS3-CT95-0039, and the Norwegian Research Council for Science and the Humanities, Grant No. 457.91/008. Our sincere thanks go to Morten Krogstad and the crew of R/V "Oscar Sund" for assistance during the fieldwork, and to Runar Thyrrhaug for drawing our attention to UVR effects on microbial lysogeny.

Footnotes

¹ Present address: EC-JRC Institute for Health and Consumer Protection, Ispra, Italy.

References

- Aarseth K.A. and Schram T.A. (1999) Wavelength-specific behaviour in *Lepeophtheirus salmonis* and *Calanus finmarchicus* to ultraviolet and visible light in laboratory experiments (Crustacea: Copepoda). *Marine Ecology Progress Series* **186**: 211–217.
- Anon. (2004) Report of the international 0-group fish survey in the Barents Sea and adjacent waters in August–September 2002. *Institute of Marine Research, Bergen, Norway, Toktrapport Nr. 22*: 1–26.
- Browman H.I., Alonso Rodriguez C., Béland F., Cullen J.J., Davis R.J., Kouwenberg J.H.M., Kuhn P., McArthur B., Runge J.A., St-Pierre J.F., Vetter R.D. (2000) The impact of ultraviolet radiation on marine crustacean zooplankton and ichthyoplankton: a synthesis of results from the estuary and Gulf of St. Lawrence, Canada. *Marine Ecology Progress Series* **199**: 293–311.
- Cushing D.H. (1969) The regularity of spawning season of some fishes. *Journal du Conseil International pour l'Exploration de la Mer* **33**: 81–92.
- Ellertsen B., Fossum P., Solemdal P., Sundby S. (1989) Relation between temperature and survival of eggs and first-feeding larvae of northeast Arctic cod (*Gadus morhua* L.). *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **191**: 209–219.
- Engelsen O., Hansen G., Svenøe T. (2004) Long-term ultraviolet and photosynthetically active radiation doses at a North-Norwegian location in spring on the basis of total ozone and cloud cover. *Geophysical Research Letters* **31**: L12103 10.1029/2003GL019241.
- Greene C.H. and Pershing A.J. (2000) The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: basin-scale forcing associated with the North Atlantic Oscillation. *ICES Journal of Marine Science* **57**: 1536–1544.
- Hansen G.H. and Olafsen J.A. (1989) Bacterial colonization of cod (*Gadus morhua* L.) and halibut (*Hippoglossus hippoglossus*) eggs in marine aquaculture. *Applied Environmental Microbiology* **55**: 1435–1446.
- Hansen G., Svenøe T., Chipperfield M.P., Dahlback A., Hoppe U.P. (1997) Evidence of substantial ozone depletion in winter 1995/96 over northern Norway. *Geophysical Research Letters* **24**: 799–802.

- Hay S. (1995) Egg production and secondary production of common North Sea copepods: field estimates with regional and seasonal comparisons. *ICES Journal of Marine Science* **52**: 315–327.
- Heath M.R., Astthorsson O.S., Dunn J., Ellertsen B., Gaard E., Gislason A., Gurney W.S.C., Hind A.T., Irigoien X., Melle W., Niehoff B., Olsen K., Skreslet S., Tande K.S. (2000) Comparative analysis of *Calanus finmarchicus* demography at locations around the Northeast Atlantic. *ICES Journal of Marine Science* **57**: 1562–1580.
- Hjort J. (1914) Fluctuations in the great fisheries of northern Europe. *Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer* **20**: 1–228.
- Hurrell J.W. (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* **269**: 303–313.
- Izhevskii G.K. (1964) Forecasting of Oceanological Conditions and the Reproduction of Commercial Fish Translated from Russian by the Israel Programme for Scientific Translations, Jerusalem (1966), 95 pp.
- Jiang S.C. and Paul J.H. (1998) Significance of lysogeny in the marine environment: studies with isolates and a model of lysogenic phage production. *Microbial Ecology* **35**: 235–243.
- Kouwenberg J.H.M., Browman H.I., Cullen J.J., Davis R.F., St-Pierre J.F., Runge J.A. (1999) Biological weighting of ultraviolet (280–400 nm) induced mortality in marine zooplankton and fish. I. Atlantic cod (*Gadus morhua*) eggs. *Marine Biology* **134**: 269–284.
- Kouwenberg J.H.M., Browman H.I., Runge J.A., Cullen J.J., Davis R.F., St-Pierre J.F. (1999) Biological weighting of ultraviolet (280–400 nm) induced mortality in marine zooplankton and fish. II. *Calanus finmarchicus* (Copepoda) eggs. *Marine Biology* **134**: 285–293.
- Meerkötter R., Verdebout J., Bugliaro L., Edvardsen K., Hansen G. (2003) An evaluation of cloud affected UV radiation from polar orbiting and geostationary satellites at high latitudes. *Geophysical Research Letters* **30**: 181956 10.1029/2003GL017850.
- Morse W. W. (1994) Atlantic cod, *Gadus morhua*, larvae: an analysis of the MARMAP time series, 1977–1987. US Northeast Fisheries Science Center Reference Document, 94–08: 1–44.
- Poulin P.M., Warn-Varnas A., Niiler P.P. (1996) Near-surface circulation of the Nordic Seas as measured by Lagrangian drifters. *Journal of Geophysical Research* **101**: 18237–18258.
- Skreslet S. (1976) Influence of freshwater outflow from Norway on recruitment to the stock of Arcto-Norwegian cod (*Gadus morhua*). In Skreslet S., Leinebø R., Matthews J.B.L., Sakshaug E. (Eds.). Fresh Water on the Sea (Association of Norwegian Oceanographers, Oslo) pp. 233–237 246 pp.
- Skreslet S. (1988) Fat indices and stock features of marine carnivores in relation to freshwater inflow to Norwegian coastal waters. In Wyatt T. and Larrañeta M.G. (Eds.). Proceedings of the International Symposium on Long Term Changes in Marine Fish Populations, Vigo 1986 Instituto de Investigaciones Marinas de Vigo pp. 69–82 554 pp.
- Skreslet S. (1997) A conceptual model of the trophodynamical response to river discharge in a large marine ecosystem. *Journal of Marine Systems* **12**: 187–198.
- Skreslet S. and Borja A. (2003) Interannual correlation between hemispheric climate and northern Norwegian wintering stocks of two *Calanus* spp. *ICES Marine Science Symposia* **219**: 390–392.
- Skreslet S., Olsen K., Mohus Å., Tande K.S. (2000) Stage-specific habitats of *Calanus finmarchicus* and *Calanus helgolandicus* in a stratified northern Norwegian fjord. *ICES Journal of Marine Science* **57**: 1656–1663.
- Skreslet S. and Rød N.Å. (1986) Advection of *Calanus finmarchicus* between habitats in Norwegian coastal waters. *NATO ASI Series G* **7**: 375–387.

- Sømme J.D. (1934) Animal plankton of the Norwegian coast waters and open sea I. Production of *Calanus finmarchicus* (Gunner) and *Calanus hyperboreus* (Krøyer) in the Lofoten area. *Fiskeridirektoratets Skrifter Serie Havundersøkelser* **4**: 1–163.
- Strømgren T. (1976) Relationship between freshwater supply and standing crop of *Calanus finmarchicus* in a Norwegian fjord. In Skreslet S., Leinebø R., Matthews J.B.L., Sakshaug E. (Eds.). *Freshwater on the Sea*(Association of Norwegian Oceanographers, Oslo) pp. 173–177 246 pp.
- Sundby S., Ellertsen B., Fossum P. (1994) Encounter rates between first-feeding cod larvae and their prey during moderate to strong turbulent mixing. *ICES Marine Science Symposia* **198**: 393–405.
- Verdebut J. (2000) A method to generate surface UV radiation maps over Europe using GOME, Meteosat, and ancillary geophysical data. *Journal of Geophysical Research* **105**: 5049–5058.
- Visser P.M., Poos J.J., Scheper B.B., Boelen P., van Duyl F.C. (2002) Diurnal variations in depth profiles of UV-induced DNA damage and inhibition of bacterioplankton in tropical coastal waters. *Marine Ecology Progress Series* **228**: 25–33.
- Weinbauer M.G. and Suttle C.A. (1999) Lysogeny and prophage induction in coastal and offshore bacterial communities. *Aquatic Microbial Ecology* **18**: 217–225.
- Wiborg K.F. (1948) Investigations on cod larvae in the coastal waters of northern Norway. Occurrence of cod larvae and occurrence of food organisms in the stomach contents and in the sea. *Fiskeridirektoratets Skrifter Serie Havundersøkelser* **9(3)**: 31–27.