CIRCULATION PATTERNS IN THE NORTH ATLANTIC AND POSSIBLE IMPACT ON POPULATION DYNAMICS OF *CALANUS FINMARCHICUS*

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ABSTRACT

Due to advective impact few consistent time-series describing the population development of the copepod *C. finmarchicus* exist. Quantitatively, the spring generation seems to be the most important, and especially in the northern areas one generation per year seems to prevail. A fecundity of 10^2-10^3 eggs female^{-1} and a sex ratio 1:1 then give a maximal reproductive rate of 3.9-6.2 year^{-1}. This low rate seems to be compensated by low mortality due to effective predator avoidance in terms of diurnal and seasonal vertical migrations. We have calculated that the advective renewal of the habitats of *C. finmarchicus* in the subpolar gyre and in the Nordic Seas are 0.13 and 0.29 year^{-1} respectively, while the birth and death rates of *C. finmarchicus* typically are above 3.9 year^{-1}. This means that the biological rates are likely to dominate over the advective rates in the two ocean areas, and that the *C. finmarchicus* development is facilitated by local production in both areas. Rough calculations for the Nordic Seas indicate that out of a total annual production of 74 mill. tonnes, 3.6 mill. tonnes are lost to adjacent seas by advection. Due to the flow of deep and cold waters southward and the seasonal migration of *C. finmarchicus* it is likely that the loss of individuals from the Nordic Seas southward to the North Atlantic is dominated by copepodite V, and that a higher proportion of younger life stages are carried in the south-north (Barents Sea) and west-east (Norwegian coast and the North Sea) directions with the warmer Atlantic Water.

INTRODUCTION

The change in numbers and biomass of a plankton stock in sub-areas of the ocean will always be influenced by physical transport of the organisms as well as by biological processes. With knowledge about the advective rates acting in the system, the rates of the biological processes and the spatial scale of the system, we may calculate to what extent physical versus biological processes govern local population dynamics. In the present paper we briefly review the large scale circulation of the North Atlantic and population dynamical charac-

teristics of *C. finmarchicus* such as generation time, recruitment, mortality and vertical distribution. By use of a simple model, advective and biological rates are made comparable by scaling (Aksnes et al. 1989).

Timokhina (1964) estimated the biomass and production of *C. finmarchicus* in the Norwegian Sea (i.e. the Norwegian, Icelandic and Greenland Seas which correspond to our term the "Nordic Seas"). We have combined these data with published results on the population dynamics of *C. finmarchicus* to approximate a life-table for the *C. finmarchicus* stock in the Northern Seas. On this basis we have provided rough estimates of the production of different life stages together with estimates of advective losses from the Nordic Seas.

Rather than giving the answers to the many unknown aspects of the large-scale *C. finmarchicus* population dynamics, the scope of the present paper is to stimulate future research by summarising some physical and biological knowledge that we consider relevant for the dynamics of this very important oceanic and coastal species. As advection may easily invalidate any biological interpretation of *C. finmarchicus* time series, we have finally included a brief discussion on how this problem may be dealt with in future research programmes.

A SIMPLE MODEL OF ADVECTIVE INFLUENCE ON A LOCAL POPULATION

The dynamics of a local population that is distributed homogeneously over a habitat volume V (m^3) may be expressed:

$$dN/dt = (b-d)N - eN + iN_b \qquad (1)$$

where,

N:	abundance of animals of the local population (ind. m^{-3})
b:	birth rate of the local population (ind. ind.$^{-1}$ s^{-1})
d:	mortality rate of the local population (ind. ind.$^{-1}$ s^{-1})
e:	emigration rate from the local population (ind. ind.$^{-1}$ s^{-1})
i:	immigration rate from the boundary population into the local population (ind. ind.$^{-1}$ s^{-1})
N$_b$:	abundance of animals surrounding the local population - boundary population (ind. m^{-3})

If emigration and immigration relative to the local population are dominated by physical transport rather than by swimming, we may assume:

$$e = i = 0.5Av/V \qquad (2)$$

where v is the average water current (m s^{-1}) across the boundary areas (A, m^2) of the habitat volume (V, m^3). The figure 0.5 appears in (2) because we assume that the amount of water leaving the habitat volume equals the amount of water entering. Insertion of Eq. (2) into (1) gives:

$$dN/dt = (b\text{-}d)\ N + (0.5Av/V)\ (N_b\text{-}N) \tag{3}$$

Here, the dynamics of the local population (dN/dt) is expressed as a function of two biological parameters (b and d), and three parameters governed by hydrodynamics and the spatial scale under study (v. A, and V). Hence, we have a simple theoretical framework to analyse the population dynamics of plankton as a function of biological rates, water movements and the spatial scale of the habitat.

If the physical-spatial coefficient Av/V is much greater than the biological coefficients b and d, we have a stock whose dynamics is dominated by physics rather than biology. Eq. (3) has earlier been applied by Aksnes et al. (1989) to quantify the impact of zooplankton advection on resident planktivores in a coastal area of Norway.

CIRCULATION PATTERNS IN THE NORTH ATLANTIC

The current system which encircles and forms the subpolar gyre (Fig. 1) is a continuation of the Gulf Stream (Gu), the North Atlantic Current (Na), the northern part of which fans out into a gradually widening drift. South of Iceland it forms the Irminger Current (Ir) which continues northward along the Icelandic west coast with a transport of about 3 Sv (1Sv = 10^6 m^3 s^{-1}). In the Denmark Strait it divides into two branches of which the northern one flows along the Icelandic shelf into the Iceland Sea with a transport of 1-2 Sv to North Icelandic shelf waters (Kristmannsson 1991). The western branch turns west and southwest to flow along with, and partly mixing with the East Greenland Current (Eg) where it forms a warm intermediate layer. This current rounds Cape Farewell and continues along the coast of West Greenland as the West Greenland Current (Wg). In the Davis Strait it turns west and later south, to follow the Labrador coast to the Newfoundland banks where the circle is more or less closed.

Water masses within the subpolar gyre are subarctic in the southern Labrador and Irminger Seas (t ~ 3-5°C, s ~ 34.8) while in the eastern Irminger Sea and in the area to the south of Iceland there are modified Atlantic Waters (t ~5 - 8°C, s ~ 35.1 - 35.25). Its southeastern border is the subarctic front in the North Atlantic which forms the border between the warm water masses of the North Atlantic Current (Na) to the south and subarctic and modified Atlantic water masses to the north. Along the coasts of Greenland and Labrador the Polar front forms the border toward the relatively narrow zones with Polar
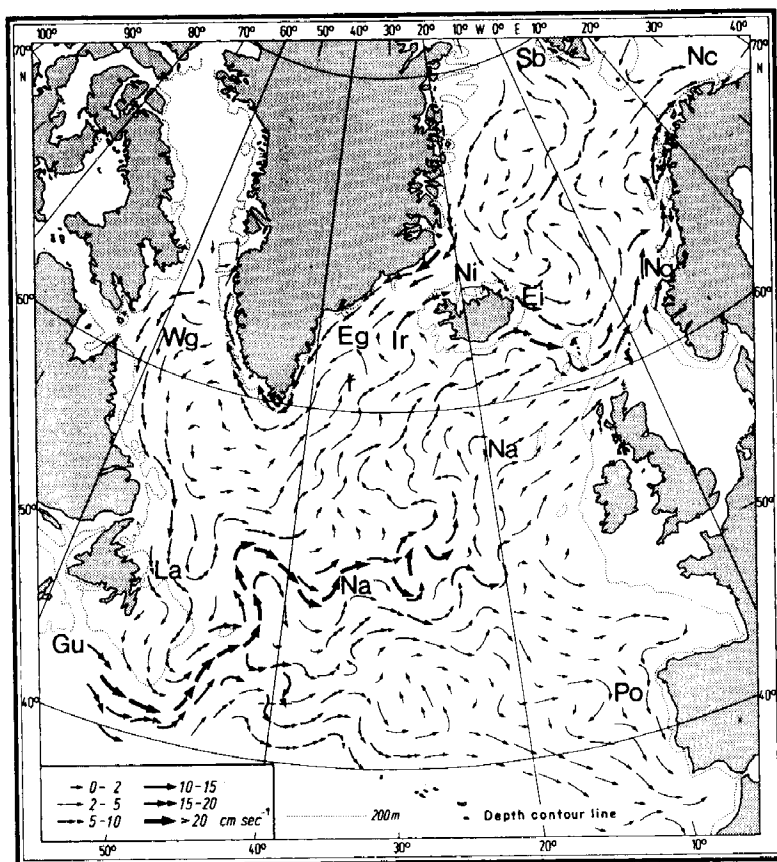
Fig. 1. Surface currents in the North Atlantic Ocean in the summer of 1958. **Eg**: East Greenland Current, **Ei**: East Icelandic Current, **Gu**: Gulf Stream, **Ir**: Irminger Current, **La**: Labrador Current, **Na**: North Atlantic Current, **Nc**: North Cape Current, **Ni**: Northern branch of the Irminger Current, **Ng**: Norwegian Atlantic Current, **Po**: Portuguese Current, **Sb**: West Spitsbergen Current, **Wg**: West Greenland Current (Dietrich et al. 1980).

waters in the East and West Greenland Current (Wg) as well as the Labrador Current (La). The fronts are indicated by the increased horizontal temperature gradients in Fig. 2 which shows temperatures at 200 m depth in the northern North Atlantic.

While the subarctic front weakens in the northeastern part of the North Atlantic, horizontal temperature gradients increase again between its extension in the Norwegian Sea, the Norwegian Atlantic Current (Ng), and Arctic water masses of the East Icelandic Current (Ei) and the cyclonic circulation in the Greenland Sea. This is the Arctic front between Arctic and Atlantic waters in the circulation system of the Nordic Seas. This system is connected to the subpolar gyre through the Atlantic inflow and the outflow of the East Green-
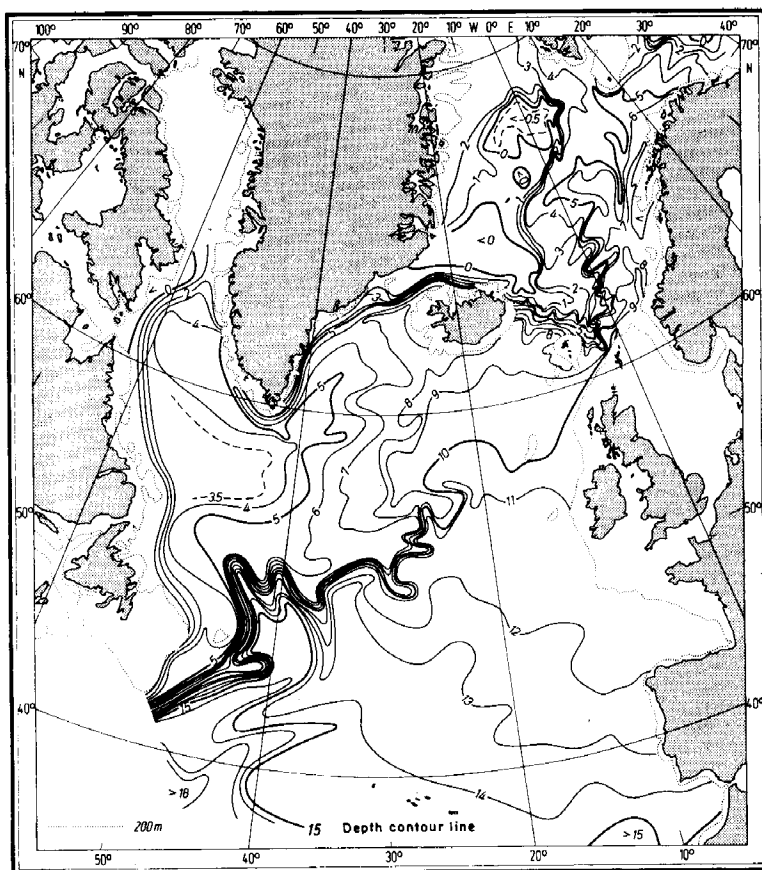
Fig. 2. Temperature at 200 m depth in the northern North Atlantic Ocean in the summer of 1958
(Dietrich et al. 1980).

land Current (Eg) in the Denmark Strait. Although the Norwegian Atlantic
Current (Ng) spreads out in the central Norwegian Sea, between mid-Norway
and Jan Mayen, most of its transport follows the continental shelf break,
where it ultimately continues as the West Spitsbergen Current (Sb) along the
west coast of Svalbard and into the Arctic Ocean. There is, however, continua-
tion to the south-flowing colder currents to the west as a considerable portion
of water from the West Spitsbergen Current (Sb) turns west and adds to the
East Greenland Current (Eg) as a relatively warm intermediate component. In
the Norwegian Sea, Atlantic waters fill the strata in the upper 500-800 m (t ~2-
9°C, s~35.0 - 35.3).

There is considerable exchange of water between the subpolar gyre and the
circulation system in the Nordic Seas, mainly through inflow of warm water
from the North Atlantic in the east and outflow of Arctic and Polar waters to
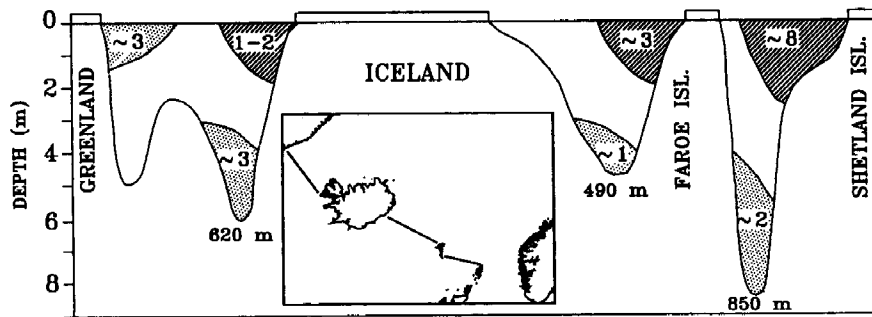
Fig. 3. Water transports (Sv, 1 Sv=10^6 m^3 s^{-1}) across the transects between Greenland-Iceland, Iceland- Faroe Islands and Faroe Islands - Shetland Islands. Flows from south to north are indicated by lines, while flows from north to south are indicated by dots. Depth is given in thousands.

the west. The main inflow of Atlantic water in the Faroe-Shetland area is assessed to be in the order of 10 Sv as an average (e.g. Gould et al. 1985; Hansen et al. 1988). The smaller Atlantic inflow of 1-2 Sv in the Irminger Current (Ig) is already mentioned. The outflow in the East Greenland Current (Eg) is in the order of 3 Sv (Worthington 1970). Most of the outflow from the Nordic Seas occurs, however, as overflow across the Greenland-Scotland Ridge (i.e. equatorward flow near the bottom). As summarised by Dickson et al. (1990), the overflow in the Denmark Strait is in the order of 3 Sv while the overflow through the Faroe Bank Channel is in the order of 2 Sv (Fig. 3). In addition, overflow through the deeper passages in the Faroe-Iceland Ridge is assessed at approximately 1 Sv. Here the lack of balance between inflow and outflow indicates that the various estimates are uncertain, but still it gives a reasonable overview of the circulation.

The connection in circulation system between the Nordic Seas and the subpolar gyre in the North Atlantic was clearly demonstrated by the so-called "mid seventies anomaly" which has attracted much attention since its occurrence and its propagation has been summarised by Dickson et al. (1988). As indicated in Fig. 4 it was initiated by increased supply of fresh, cold Polar waters to the East Greenland Current (Eg) from the Arctic Ocean during the 1960s. It was first observed as an extremely cold period in North Icelandic waters when the surplus of cold water in the East Greenland Current (Eg) partly spread into the East Icelandic Current (Ei). Later on this pulse proceeded through Denmark Strait and came into the subpolar gyre where it was observed off West Greenland in 1969-1970, off Newfoundland in 1971-1972. As it propagated toward northeast it probably more or less followed the Subarctic front into the North Atlantic Drift. In 1976 it was observed in the Atlantic inflow to the Nordic Seas where a time series of sections revealed that the salinities during the anomalous period were the lowest on record since the time series was

Fig. 4. Water transports (in Sv; see Fig. 3) in the North Atlantic with dates of the salinity minimum (the mid-seventies salinity anomaly) superimposed (Dickson et al. 1988).

initiated in the beginning of this century. Thereafter the anomaly was observed at the entrance to the Barents Sea in 1979 and in 1981-1982 it could be observed as a slight salinity anomaly in the intermediate return flow of the East Greenland Current (Eg). This forms a closed circulation system with cycle time on the order of 15 years. This means that properties of the water masses will need about 15 years to drift around the system.

We have approximated the area of the subpolar gyre as $2.1 \ 10^6 \ km^2$. We assume that the major renewal of the water in this gyre is facilitated by the East Greenland Current (Eg, 2 Sv) and by a branch from the North Atlantic Current (2 Sv) (see Fig. 3). Under the assumption that the advective layer is con-

Table 1. Advective rates of the Nordic Seas and the subpolar gyre. The biological rates indicate the maximal reproductive rate (r_{max} =ln b/ T_g, where b is egg no., T_g is generation time, and a sex ratio 1:1 is assumed). Sv = $10^6 m^3 s^{-1}$

Ocean Area	Area x10^6 km^2	Volume 500-0m x 10^{15} m^3	Transport into the area		Advective renewal rate y^{-1}	Biological rate (y^{-1})			
			Sv	x 10^{15} m^{3}y^{-1}		Egg no.	No. of generations		
							1	2	3
Nordic Seas	2.6	1.3	12	0.38	0.29	100	3.9	7.8	11.7
Subpolar gyre	2.1	1.1	4	0.13	0.12	500	5.5	11.0	16.6
Nordic Seas+ subpolar gyre	4.7	2.4	7	0.22	0.09	1000	6.2	12.4	18.6

strained to the upper 500 m, the estimated renewal rate (or frequency) of the volume of the subpolar gyre above 500 m then becomes 0.13 y^{-1}. For the Nordic Seas (2.6 10^6 km^2) having a high inflow of Atlantic Water, we arrived at the higher rate, 0.29 y^{-1} (Table 1).

POPULATION DYNAMICS OF *C. FINMARCHICUS*

As reviewed by Conover (1988), *C. finmarchicus* is distributed both in the subpolar gyre and in the Nordic Seas. Before discussing possible implications of transport, we need to assess the typical biological rates of *C. finmarchicus*. The growth of a population is primarily governed by generation time, fecundity and mortality (and all the variables nested within them). In zooplankton, vertical distribution and migration have also turned out to be an important aspect of the population dynamics as vertical positioning in zooplankton is an efficient way of regulating predation risk, temperature and feeding opportunities (McLaren 1963; Dagg 1985; Ohman 1988). Hence, large gain in fitness may be achieved by relatively small adjustments in vertical positioning (Aksnes & Giske 1990; Ohman 1990; Giske et al. 1994). Finally, vertical positioning also has large impact on the horizontal transport of the organisms.

Generation time

There is substantial evidence that most *C. finmarchicus* enter a diapause at large depths during autumn and winter, and it is therefore generally easy to identify the G_0 (the overwintering population) and the G_1 generations from data obtained during winter and spring. Later on, however, advective influence complicates the identification of new generations. As traditional time series of marine zooplankton are likely to describe animals of different origin over time, it is hard to demonstrate whether recruiting individuals during summer

and autumn represent true new generations or another cohort of late G_0-survivors originating elsewhere. A simulation study by Slagstad & Tande (1996) demonstrates how population development measured at a fixed station becomes highly biased due to advection and different spatial timing of population events. Nevertheless, although two and three yearly spawnings (often interpreted as new generations) have been reported by several authors (see Conover 1988 for a review), it seems likely that the recruitment during summer and autumn is minor compared to the spring recruitment. This is especially true for the northern regions where a yearly generation prevails (Ussing 1938; Manteufel 1941; Digby 1954; Fontaine 1955; Lie 1965, 1968; McLellan 1967; Tande 1982; Aksnes & Magnesen 1983). Also the observations of Wiborg (1954) and Østvedt (1955) in the Norwegian Sea indicate that only a part of the spring generation took part in spawning later in the year. Hence, the proportion of the population that undergoes a second and a third generation is an important population characteristic.

Mortality

C. finmarchicus populations having yearly generations and a life-time fecundity of 10^2-10^3 eggs (discussed later) and 1:1 sex ratio may tolerate an average instantaneous mortality rate of 0.011- 0.017 d^{-1} in order to sustain a constant population size from one year to another. Little is known about zooplankton mortality, however, and as pointed out by Ohman & Wood (1995) more attention should be given to mortality estimation of zooplankton.

  C. finmarchicus time series not ruled by advection (e.g. Cushing & Tungate 1963; Aksnes & Magnesen 1983) clearly indicate a higher mortality in early life than later on. This is demonstrated in Fig. 5 where mortality rates higher than 20 % per day (corresponding to an instantaneous rate higher than 0.22 d^{-1}) were obtained in May, while rates below 0.01 d^{-1} were obtained most of the year (Aksnes & Magnesen 1983). In the same study the average instantaneous mortality rate was estimated in the range 0.15-0.18 for the first three copepodite stages, 0.04 for stage IV, and <0.01 d^{-1} for stage V. No estimate was given for the adult stage, but the original data (Aksnes 1981) indicate a mortality of 0.05 d^{-1} during March. Cushing & Tungate (1963) followed a *C. finmarchicus* patch in the North Sea from March to April where they obtained a unique time series of a homogeneous ocean population. In the last period of their study the recruitment to copepodite I (and also to stage II) had ceased, and the decrease in total numbers corresponded to an instantaneous mortality rate of 0.07 d^{-1} for the combined stages III, IV and V (calculated from fig. 3 in Cushing & Tungate 1963). Hence, from these studies it may be concluded that the mortality of *C. finmarchicus* is quite high during the intensive surface-exposed growth period in spring. Unfortunately, eggs and nauplii were not included in the above studies. Miller & Tande (1993) suggested an instantane-
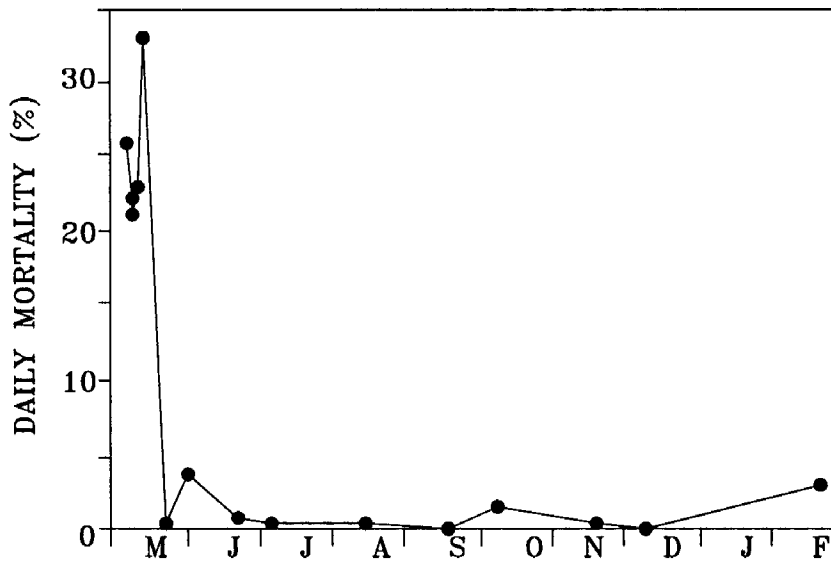
Fig. 5. The daily mortality rate (%) of *C. finmarchicus* in Lindåspollene, Norway (Aksnes & Magnesen 1983). The estimates are based on the observed decrease in total numbers of copepodites after the recruitment to copepodite stage I has ceased and are therefore not dependent on assumptions about stage durations. Daily mortality in % (M) is related to the daily instantaneous mortality (d) by the following relationship: $M = (1\text{-}e^{-d})\ 100\%$.

ous mortality for eggs and nauplii of 0.16 d^{-1} and 0.08 d^{-1} by fitting modelled stage abundances to observations.

The mortality rates obtained by Matthews et al. (1978) for *C. finmarchicus* in Korsfjorden, western Norway, are on average very high (see Table 2) and it is not likely that a *Calanus*-population can tolerate such high rates for a very long period. Korsfjorden is very exposed to advection and it seems likely that the high rates obtained for the *Calanus*-stock in this fjord are partly due to changes governed by exchanges with the coastal waters outside the fjord (Aksnes et al. 1989). This is also in accordance with the conclusion of Matthews & Heimdal (1980) that Korsfjorden is heavily influenced by advective production.

Vertical distribution , mortality and overwintering

It is now commonly accepted that an important adaptive value of vertical migration is decreased predation risk from visually guided predators in the illuminated zone (Zaret & Suffern 1976; Clark & Levy 1988; Ohman 1988; Aksnes & Giske 1990). Thus, it is tempting to consider mortality risk as a function of depth rather than a function of developmental stage or age. As the potential for feeding of visual predators is likely to be exponentially related to

Table 2. Some population characteristics of *Calanus finmarchicus* (modified after Aksnes & Magnesen 1983 and Tande 1988).

	Egg	N	CI	CII	CIII	CIV	CV	CVI	Temp.°C	Source
Stage duration (d)			3-5	2-4	3-11	3-13	4-19		14-15	1
					2-9	5-12	12-13		Spring	2
					8-10	1-11	61-159		Summer	2
			2	3	3-5	4-5	2-5		6.2	3
			2	4	6	13	250		>4	4
			6.8	5.4	6.4	7.6	9.6		7.6	5
				16	18				0	6
				8.4	10.5	11.8	16.7		5	6
				4.0	8.5	8.0	10.0		10	6
				4.0	8.2	8.9	9.3		15	6
					5	5.5	11		7	7
				4	5	7	5		8.2	8
			2.4	4.6	5.8	19			6	9
Mortality (d⁻¹)	GI				.04-.14	.07-.23	.04-.46	.06-.5		2
	GII				.02-.10	.02-.16	.02-.16	.03-.15		2
			.16	.18	.15	.04	<.01			4

1. Marshall & Orr (1955), Clyde Sea UK, Field
2. Matthews et al. (1978), Korsfjorden Norway, Field
3. Williams & Lindley (1980), North Sea, Field
4. Aksnes & Magnesen (1983), Lindåspollene Norway, Field
5. Thompson (1982), North Sea, Laboratory
6. Matthews (1966), Firth of Clyde, Laboratory
7. Runge et al. (1985), Novia Scotia Canada, Laboroatory
8. Corkett et al. (1986), Novia Scotia Canada, Laboratory
9. Tande (1988), Northern Norway, Laboratory

depth (Aksnes & Giske 1993), it is also likely that the predation risk of the prey, being hunted by visually guided predators, is decreasing exponentially with depth. Accordingly, Aksnes & Giske (1990) fitted mortality rates obtained for *Paracalanus parvus*, *Temora longicornis*, *Pseudocalanus elongatus* and *C. finmarchicus* (Aksnes & Magnesen 1983, 1988) to the following equation:

$$M = 0.23\ e^{-0.04D} \qquad n=10,\ r^2=0.89 \tag{4}$$

where M is the instantaneous mortality rate (d⁻¹) and D is depth (m) giving mortality rates of 0.22 and 0.006 d⁻¹ at one and 90 m respectively. Also non-visual predators contribute to the mortality of zooplankton. As such, Ohman (1983, 1990) found that the mortality of the copepod *Pseudocalanus newmani* in a deep fjord location was mainly influenced by non-visual rather than visual

predators. Then, reversed migration (i.e. avoiding surface layer at night rather than at daytime) became advantageous. Such reversed migration has to our knowledge not yet been reported for the larger *C. finmarchicus.*, and we therefore (as Aksnes & Giske 1990) hypothesise that reduced visual predation risk is the main adaptive significance of avoiding the surface layer in this species. Aksnes & Giske (1990) calculated that *C. finmarchicus* was "allowed" (in order to keep constant population size) to be exposed to the daytime predation risk in the upper 20 m for 22-38 days if the rest of the year was spent at 90 m depth. In contrast, under the same mortality regime, *Paracalanus parvus* had no benefit from vertical migrations (actually it represented a cost) as the calculations indicated that the highest reproductive output was realised in the upper 5 m (due to high temperature and food availability giving short generation time and high fecundity in this species).

The above relationship between mortality rate and depth (Eq. 4) was obtained in a fjord, Lindåspollene, with a bottom depth of only 90 m, and is hardly representative for the ocean environment. Probably, the predation risk for *C. finmarchicus* at 90 m depth in oceans (and also in deep fjords) is much higher than in Lindåspollene, and *C. finmarchicus* has to move deeper in order to reduce the predation risk. In deep fjords and oceanic environments, mesopelagic fishes such as *Maurolicus muelleri* and *Benthosema glaciale* (Kaartvedt et al. 1988; Giske et al. 1990; Baliño & Aksnes 1993; Giske & Aksnes 1992) probably add significantly to the predation risk down to several hundred meters depth.

The successful overwintering shallower than 90 m (> 4000 stage V m^{-2}) reported by Aksnes & Magnesen (1983) suggests that *C. finmarchicus* does not depend on a depth requirement *per se* for overwintering. It is more likely that the overwintering success is related to the predation risk of the overwintering habitat. In Masfjorden, a 494 m deep fjord of western Norway, high numbers of overwintering *C. finmarchicus* (> 300 ind. m^{-3}) have been found between 120 and 200 m, and in lesser concentrations below 200 m (Giske et al. 1990, Baliño & Aksnes 1993). Surface integrated winter abundances (January) of *C. finmarchicus* have repeatedly been found above 30 000 ind. m^{-2} in this fjord. Such concentrations are obviously not due to local production, but rather to the severe advective influence on zooplankton abundances in this fjord system (Aksnes et al. 1989). Miller et al. (1991) observed that the resting stock of *C. finmarchicus* centred near 500 m in the North Atlantic Slope Water with abundances (5000-10000 stage V m^{-2}, about 30 ind. m^{-3}), which is comparable to the overwintering stock observed above 90 m by Aksnes & Magnesen (1983) in the shallow Lindåspollene. The biomass estimate (about 3 tonnes wetweight km^{-2}) of Timokhina (1964) for the Norwegian Sea indicates an average overwintering stock of approximately 4000 ind. m^{-2}. These data, however, were obtained on the basis of sampling above 500 m and probably underestimate the real abundance. Overwintering animals have been observed as deep

as 1000-1500 m in the Greenland Sea (Hirche 1991), and in 600-1000 m in the Norwegian Sea (Østvedt 1955). Hence the overwintering depth of *C. finmarchicus* seems to span an order of magnitude. If the adaptive significance of seeking deep water is to reduce predation risk from visually oriented predators, part of this variation in resting depth may be due to differences in water clarity of the upper waters and predator presence (Kaartvedt 1996) which may be quite pronounced between coastal and oceanic water masses.

Egg production and reproductive potential

The egg production rate of *C. finmarchicus* may vary considerably (Hirche 1996; Runge & Plourde, 1996). While average rates seem to be in the range 0-30 eggs female^{-1} day^{-1} depending on factors such as food availability, temperature and body-size, maximum rates as high as 80 eggs female^{-1} day^{-1} have been reported. Although daily egg production (b) is important for calculating the potential fecundity, female survival (exp(-Mt), where M is instantaneous mortality) is the key-factor for realising the total fecundity (f):

$$f = \int_{0}^{\infty} be^{-Mx}dx = b/M \qquad (5)$$

Hence, females of a population suffering from an instantaneous mortality rate of 0.2 d^{-1} and an egg production rate of 20 eggs d^{-1} female^{-1} will on the average have a realised fecundity of (20/0.2=) 100 eggs female^{-1}, while a mortality of 0.01 gives a fecundity of 2000 eggs female^{-1}. While the fecundity is positively correlated with food, temperature and body size, it is according to Eq. (5) negatively correlated with predation risk. As large body size and surface water exposure is likely to promote predation risk (as in Eq. 4), individual maximisation of daily egg production rate does not necessarily mean maximisation of the fecundity.

It seems likely that the average fecundity of *C. finmarchicus* is of order 10^2-10^3 eggs. Combined with a yearly generation time (as in high latitudes), the reproductive potential, corresponding to $r_{max} \approx 3.9$-6.2 y^{-1} (assuming a sex ratio of 1:1), must be considered low (but see Table 1, where shorter generation times are considered). Especially, in comparison with predators such as capelin having a generation time of two years and an egg number of 10^4 ($r_{max} \approx 4.3$ y^{-1}), and cod having an even higher egg number of 10^6 (furthermore, cod is iteroparous) and a generation time of about three years ($r_{max} \approx 4.4$ y^{-1}). Hence, over large ocean areas the small herbivore *C. finmarchicus* seems to have a reproductive potential, comparable to the predatory fishes of the same ocean.

The C. finmarchicus stock of the Nordic Seas

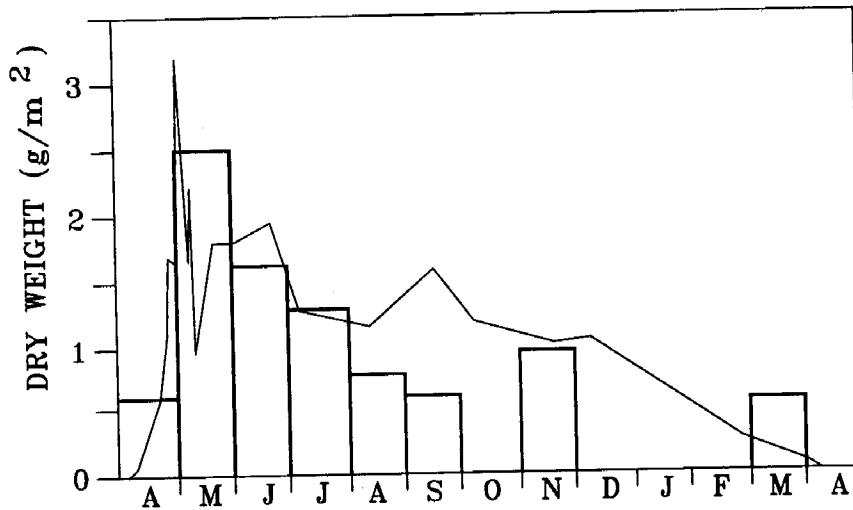By assuming a dry-weight to wet-weight ratio of 0.2 we have compared the

Fig. 6. Biomass development of the 1979-generation of *Calanus finmarchicus* in a landlocked fjord, Lindåspollene, in Western Norway (solid line, after Aksnes & Magnesen 1983) compared with the development in the Norwegian Sea (bars). The data from the Norwegian Sea are based on Timokhina (1964) and represent the average values of 1959 and 1960. Totally 1148 samples were obtained along standard oceanographic sections in the Norwegian Sea over the depth range 0-500 m. We have assumed that dry-weight corresponds to 20% of the wet weight estimates given by Timokhina (1964).

extensive biomass data (obtained from 1148 zooplankton samples) given by Timokhina (1964) for the Nordic Seas with the time-series given by Aksnes & Magnesen (1983) for Lindåspollene (Fig. 6). Surprisingly, the biomass levels during the year of the shallow fjord system compared well with the oceanic system. Although somewhat speculative we have applied the dynamics of the Lindåspoll population and the results of Miller & Tande (1993) to estimate recruitment and production of the different copepodite stages in Nordic Seas (Table 3). Recruitment and production of the different developmental stages are calculated by assuming: 1) that the overwintering stock of *C. finmarchicus* corresponds roughly to the values for the Nordic Seas according to Timokhina (1964); 2) that each female produces 400 eggs (which correspond to a female mortality of 0.05 d^{-1} and an average egg laying rate of 20 $female^{-1}$ day^{-1}); 3) that individual wet-weights, developmental times and mortality rates may be approximated according to the references given in Table 3. We then calculated a yearly *C. finmarchicus* production of 74.5 million tonnes wet-weight, while Timokhina (1964) arrived at a production estimate of 50 million tonnes *C. finmarchicus* per year in the Norwegian Sea (corresponding to our term the "Nordic Seas").

Table 3. Calculated stock size and production of the G1 *Calanus finmarchicus* in the Nordic Seas (corresponding to an area of 2.6 10^6 km^2). We have assumed an initial breeding stock giving rise to 1.6 mill eggs m^{-2} which corresponds to 4000 females m^{-2} producing 400 eggs each. Wet weights are based on unpublished measurements by K.F. Wiborg (Ellingsen 1973). Egg and nauplii development times are approximated by the temperature relationship given by Corkett et al. (1986). Mortality rates for eggs and nauplii are based on the values suggested by Miller & Tande (1993). Duration and mortality estimates for the copepodites are based on Aksnes & Magnesen (1983). The number of individuals represent the number recruited into each developmental stage, while the production estimates represent the weight of dead animals within a particular stage (see text for further explanation).

Stage	Wet weight (μg)	Duration (d)	Inst. mortailty (d^{-1})	Number of individuals per m^2	Number of individuals Nordic Seas	Productions (mill. tonnes)
Eggs	3.5	2	0.16	1600000	4.16E+18	3.99
Nauplii	3.5	20	0.08	1161838	3.02E+18	8.44
Copepodid I	10	20	0.16	234571	6.10E+17	1.53
Copepodid II	30	3.5	0.18	175872	4.57E+17	6.41
Copepodid III	100	6	0.15	93668	2.44E+17	14.45
Copepodid IV	250	13	0.04	38083	9.90E+16	10.04
Copepodid V	520	300	0.005	22641	5.89E+16	23.78
Adult	750			5052	1.31E+16	9.85
				Total production		74.50

POSSIBLE IMPACT OF CIRCULATION PATTERNS ON POPULATION DYNAMICS

Table 1 indicates that the subpolar gyre is "slow enough" to sustain local populations of *C. finmarchicus* as the calculations indicate a much higher biological (>3.9 y^1) than advective (0.13 y^1) rate. In this gyre, retention of *C. finmarchicus* is facilitated by the circulating water masses (Fig. 4). Individuals drifting out of the system may also meet adequate conditions and form self-sustained sub-populations. Also the Nordic Seas, having an estimated advective renewal of 0.29 y^1 (Table 1), seem to offer adequate space for one or more self-sustained population(s) of *C. finmarchicus* (Table 3). Due to the relatively large amounts of inflowing Atlantic water, animals are likely to be supplied from the North Atlantic and the subpolar gyre to the Nordic Seas. A return transport of animals from the Nordic Seas to the subpolar gyre is also possible through the East Greenland Current (Eg, restricted occurrence of *C. finmarchicus* in this current, however, is indicated by Conover 1988), but also through the deep overflow water (Fig. 3). Transport with the deep overflow water is most likely during periods when *C. finmarchicus* is distributed at large (overwintering) depths.

Given the assumptions in Table 4, about 1.1 mill. tonnes *C. finmarchicus* are advected with the deep water (mainly as copepodite V) from the Nordic Seas

Table 4. Calculated advective losses of *C. finmarchicus* from the Nordic Seas. Calculations are based on the transport values (Sv = 10^6 m^3 s^{-1}) of the dominant currents leading out of the Nordic Seas where surface transports are assumed to prevail above 300 m depth and the transport associated with the deep overflows below 300 m depth. The biomass values (wet-weight) are based on the measurements of Timokhina (1964) and represent an average for the entire Nordic Seas. "Concentration in current" is obtained by assuming that the biomass of *C. finmarchicus* is distributed in the upper 300 m in the period March-June and in the depth 300-800 m in the period July-February. Transects and currents correspond to those given in Figs 1 and 3.

Transect	Current	Transport Direction (Sv)		Biomass March-June (tonnes km^{-2})	Biomass July-Feb. (tonnes km^{-2})	Concentration in current (g m^{-3})	Loss of *C. finmarchicus* March-June (mill. tonnes)	Loss of *C. finmarchicus* July-Feb. (mill. tonnes)
Greenland-Iceland	Eg	3	Out	6.5		0.02	0.78	
	I r	1.5	In					
Iceland-Faroe Isl.	Deep overflow	3	Out		4.3	0.01		0.54
	Na	3	In					
Faroe Isl.-Shetland Isl.	Deep overflow	1	Out		4.3	0.01		0.18
	Na	8	In					
	Deep overflow	2	Out		4.3	0.01		0.36
Shetland Isl.-Norway	North Sea	1	Out	6.5		0.02	0.26	
	North Sea	1	In					
Norway-Spitsbergen	Ng	3	Out	6.5		0.02	0.78	
	Deep	1	In					
Spitsbergen-Greenland	Sb	3	Out	6.5		0.02	0.78	
	Eg	4	In					
						Total loss	2.60	1.08

to the North Atlantic per year. This amounts to about 3% of the calculated recruitment to copepodite stage V in the Nordic Seas (Table 3). The younger stages are presumably lost from the Nordic Seas in the period March-June, and the total loss in this period is estimated as 2.6 million tonnes. Hence, a total loss from the Nordic Seas to adjacent waters (North Atlantic, North Sea, Barents Sea and the Arctic Ocean, see Table 4 and Fig. 4) of 3.7 mill. tonnes amounts to 5 % of the production in the Nordic Seas. Much of this biomass (being young developmental stages) will grow further in the adjacent seas such as the North Sea and the Barents Sea and make substantial impact on these ecosystems. In the Barents Sea, *C. finmarchicus* is probably transported into the area by the North Cape Current (Nc), a branch of the Norwegian Atlantic Current (Ng) which supplies temperate water into the southern and central Barents Sea. Although *C. finmarchicus* may survive overwintering in this shelf sea, it is a risk for the spawning products to be transported east and northeastwards to hostile Arctic and Polar environments. The North Sea is probably too shallow (apart from the Norwegian Trench) for *C. finmarchicus* to avoid visual predation, and the presence of *C. finmarchicus* depends probably on advective supply.

The possible communication between the *C. finmarchicus* stocks in the subpolar gyre and the Nordic Seas is probably not important in terms of number and biomass. Although this means that the short-term dynamics of the populations are not severely influenced by such communication, the genetical exchange between the areas may be significant as indicated by Bucklin et al. (1996). On longer climatic time scales, the Nordic Seas cannot always have been a favourable habitat, and transport from the south may have been important for possible recolonization of *C. finmarchicus* in the Nordic Seas.

The above discussion has primarily dealt with the entire stocks of the two seas. In more restricted regions, and especially in the border-regions of the two areas, advection may have substantial impact on observed population dynamics. This is evident in North Icelandic waters where *C. finmarchicus* was abundant during a long period prior to the mid 1960s. Conditions changed drastically, however, during the extremely cold period from 1965-1971 (giving rise to the mid- seventies anomaly). Since then, conditions have been changing with varying transport of warm Atlantic water from the Irminger Current (Ig). During the colder periods *C. finmarchicus* has decreased, more genuinely Arctic species have dominated, and the plankton abundance has generally been lower (Ástthórsson et al. 1983; Anon. 1992). *C. finmarchicus* has been more dominant during periods with Atlantic water on the Icelandic shelf than in periods with Arctic shelfwaters.

Advection of water masses does not only make impact on population dynamics by means of physical transport of organisms, but also through the influence on the physical environment and the local productivity itself. The relatively low reproductive potential of *C. finmarchicus* means that the population

Table 5. Indication of the sampling length scale (L) that is necessary to obtain time-series that are dominated by biological rather than advective processes, $L=10v/(dN/(Ndt))$, where N is the population number, v is the advective rate and t is time). We have assumed that the biological rate $dN/(Ndt)$ corresponds to that of the early life stages of *C. finmarchicus.*, i.e. rates on the range 0.05 -0.2 d^{-1} (see text).

v (cm s^{-1})	L (km)
10	430 - 1728
50	2160 - 8640
100	4320 - 17280

cannot readily compensate for great reductions in stock size due to changes in the physical oceanic environment (nor to increased predation pressure). Thus, alterations of the local environment (such as temperature in the case of the mid-seventies anomaly) as a result of advection may be more important for the *Calanus* stock in the Nordic Seas than the direct impact of advective losses and supplies of the animals themselves.

Implications for sampling time series of C. finmarchicus

Time series of marine zooplankton are often likely to be influenced by advection so that estimation of population parameters such as generation time, recruitment, death rates and stage developmental times becomes impossible. Assumptions about synchronised development and invariant abundances over large spatial scales are most often unrealistic and do not help the analysis. It seems that the only way out of this problem is to undertake sampling that covers the relevant temporal and spatial scales adequately. The terms of Eq. (3) may illustrate this. If

$$b\text{-}d \gg 0.5 \; Av/V \tag{6}$$

is satisfied, we have a good chance to obtain time series dominated by biology rather than physics. According to this simple expression we have three ways to reduce the advective influence in a sampling design: 1) reduce the boundary surface against other systems (A). For a fjord system this simply means that the fjord with the smallest possible cross-sectional area above the sill should be selected (the semi-enclosed Lindåspollene has an $A=20 \; m^2$, while the highly advective Masfjord has an $A>10^4 \; m^2$). 2) Reduce the exchange rate with other systems (v). 3) Increase the volume to be covered by sampling (V).

In ocean studies, Av should be minimised by an appropriate selection and location of V. In Table 1, we see that the advective renewal rate of the subpolar gyre is calculated as 0.12 y^{-1} (0.5Av=4 Sv, $V=1.1 \; 10^{15} \; m^3$). If an area more to the south-east (but with the same volume, V) were selected as sampling location instead of the subpolar gyre, the Av would have been much higher because of the higher advective influence of the North Atlantic Current (Na) in this area (see Fig. 4). With 35 Sv crossing through our $V=1.1 \; 10^{15} \; m^3$, the

advective renewal would have been 0.8 y^{-1}. This means that a time series obtained from this last area would have been 6 times more influenced by advection than a time series obtained from sampling within the subpolar gyre.

Consider a *C. finmarchicus* stock with a biological change in numbers of 1 % per day. If we want to obtain a time series reflecting this rate, the advective rate should be much less than the biological rate, let us say one order of magnitude. Given a transport of 12 Sv into what we consider to be the habitat volume of *C. finmarchicus*, the sampling locations should ideally cover a volume (V) as large as 2.6 10^{15} m^3 in order to minimise advective influence. This volume corresponds to the entire Nordic Seas above 1000 m. This calculation applies to a rather low biological rate. The spring development in *C. finmarchicus* is characterised by alterations in population numbers much higher than 1% per day (Table 2), and as the biological rate increases the requirement for spatial sampling coverage decreases. In Table 5 we have used the simple "1D"-version of Eq. (5),

$$L \gg v/(b\text{-}d) \tag{6}$$

to indicate at which length scales (L) biological processes (b,d) are expected to dominate over advective processes (v) in time series of eggs, nauplii and the younger copepodite stages. If homogeneous distribution over large areas can be assumed, the criteria given in (5) and (6) may be relaxed accordingly. However, such assumptions are generally hard to justify.

REFERENCES

Aksnes, D. L., 1981. Undersøkelse av zooplankton populasjonsdynamikk i Lindåspollene, 1979. Unpubl. cand. real. thesis, Univ. of Bergen, Norway. 122 pp.

Aksnes, D. L. & T. Magnesen, 1983. Distribution, development, and production of *Calanus finmarchicus* in Lindåspollene, western Norway, 1979. – Sarsia **68**: 195-208.

Aksnes, D. L. & T. Magnesen, 1988. A population dynamics approach to the estimation of production of four calanoid copepods in Lindåspollene, western Norway. – Mar. Ecol. Prog. Ser. **45**: 57-68.

Aksnes, D. L., J. Aure, S. Kaartvedt, T. Magnesen & J. Richard, 1989. Significance of advection for the carrying capacities of fjord populations. – Mar. Ecol. Prog. Ser. **50**: 263-274.

Aksnes, D. L. & J. Giske, 1990. Habitat profitability in pelagic environments. – Mar. Ecol. Prog. Ser. **64**: 209-215.

Aksnes, D. L. & J. Giske, 1993. A theoretical model of visual aquatic predation. – Ecological modelling **67**: 233-250.

Anon., 1992. State of marine stocks and environmental conditions in Icelandic waters 1992. – Haffrannsóknir Fjölrit **29**, 147 pp.

Ástthórsson, Ó. S., I. Hallgrimsson & G.S. Jónsson, 1983. Variations in zooplankton densities in spring during the years 1961-1982. – Rit Fiskideildar **7**: 73-113.

Baliño, B & D. L. Aksnes, 1993. Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden, western Norway. – Mar. Ecol. Prog. Ser. **102**: 35-50.

Bucklin, A., R. Sundt & G. Dahle, 1996. The population genetics of *Calanus finmarchicus* in the North Atlantic. – Ophelia **44**: 29-45.

Clark, C. W. & D. A. Levy, 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. – Am. Nat. **131**: 271-290

Conover, R. J., 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. – Hydrobiologia **167/168**: 127-142.

Corkett, C. J., I. A. McLaren & J. M. Sevigny, 1986. The rearing of the marine calanoid copepods *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov and *C. hyperboreus* Krøyer with comment on the equiproportional rule. – In Schriver, G., H.K. Schminke & C.T. Shih (eds): Proceedings of the 2nd Int. Conference on Copepoda, Ottawa, Syllogeus No 58, Ottawa, p. 539-546.

Cushing, D. H. & D. S. Tungate, 1963. Studies of a *Calanus* patch. I. The identification of a *Calanus* patch. – J. mar. biol. Ass. U.K. **43**: 327-337.

Dagg, M. J., 1985. The effects of food limitation on diel migratory behavior in marine zooplankton. – Arch. Hydrobiol. Beih. Ergebn. Limnol. **21**: 247-255.

Dietrich, G., K. Kalle, W. Krauss & G. Siedler, 1980. General oceanography, an introduction. Second edition. John Wiley&Sons. New York: 626 pp.

Dickson, R. R. ,J. Meincke, S. A. Malmberg & A. J. Lee, 1988. The "Great salinity anomaly" in the northern North Atlantic 1968-1982. – Prog. Oceanogr. **20**: 103-151.

Dickson, R. R., E. M. Gmitrowitch & A.L. Watson, 1990. Deep-water renewal in the northern North atlantic. – Nature **344** (No. 6269): 848-850.

Digby, P. S. B., 1954. The biology of the marine plankton copepods of Scoresby Sound, East Greenland. – J. Anim. Ecol. **23**: 298-338.

Ellingsen, E., 1973. Kvantitative og kvalitative zooplankton undersøkelser i Lindåspollene. Unpubl. cand. real. thesis, Univ. of Bergen, Norway, 84 pp.

Fontaine, M., 1955. The planktonic copepods (Calanoida, Cyclopoida, Monstrilloida) of Ungava Bay, with special reference to the biology of *Pseudocalanus minutus* and *Calanus finmarchicus* – J. Fish. Res. Bd Can. **12**: 858-898.

Giske, J., D. L. Aksnes, B. M. Baliño, S. Kaartvedt, U. Lie, J. T. Nordeide, A. G .V. Salvanes, S. M. Wakili & A. Aadnesen, 1990. Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. – Sarsia **75**: 65-81.

Giske, J. & D. L. Aksnes, 1992. Ontogeny, season and trade-offs: vertical distribution of the mesopelagic fish *Maurolicus muelleri.* – Sarsia **77**: 253-261.

Giske, J., D. L. Aksnes & Ø. Fiksen, 1994. Visual predators, environmental variables and zooplankton mortality risk. – Vie Milieu **44**: 1-9.

Gould, W. J., J. Loynes & J. Backhaus, 1985. Seasonality in slope current transports N.W. of Shetland. – ICES C.M. 1985/C:7: 13 p. [Mimeo].

Hansen, B., O. H. Sælen and S. Østerhus, 1988. The passage of Atlantic water east of the Faroes. ICES C.M. 1988/C:29: 12 p. [Mimeo].

Hirche, H. J., 1991. Distrubution of dominant calanoid copepod species in the Greenland Sea during late fall. – Polar Biol. **11**: 351-362.

Hirche, H.-J., 1996. The reproductive biology of the marine copepod *Calanus finmarchicus* – a review. – Ophelia **44**: 111-128.

Kaartvedt, S., 1996. Habitat preference during overwintering and timing of seasonal vertical migration of *Calanus finmarchicus.* – Ophelia **44**: 145-156.

Kaartvedt, S., D. L. Aksnes & A. Aadnesen, 1988. Winter distribution of macroplankton and micronekton in Masfjorden, western Norway. – Mar. Ecol. Prog. Ser. **45**: 45-55.

Kristmannsson, S. S. 1991. Flow of Atlantic water into the northern Icelandic shelf area, 1985-1989. – ICES C.M. 1991/C:11: 20 pp [mimeo].

Lie, U., 1965. Quantities of zooplankton and propagations of *Calanus finmarchicus* at permanent stations on the Norwegian coast and at Spitsbergen, 1959-1962 – FiskDir. Skr. Ser. HavUnders. **13**: 5-19.

Lie, U., 1968. Variations in the quantity of zooplankton and the propagation of *Calanus finmarchi-cus* at station "M" in the Norwegian Sea, 1959-1966. – FiskDir. Skr. Ser. HavUnders. **14**: 121-128.

Manteufel, B. P., 1941. Plankton and herring in the Barents Sea – Polar Sci. Inst. Seafish. and Oceanogr. **7**: 125-218.

Marshall, S. M. & A. P. Orr, 1955. The biology of *Calanus finmarchicus* (Gunnerus). Oliver & Boyd, Edinburgh. 188 pp.

Matthews, J. B. L., 1966. Experimental investigations of the systematic status of *Calanus finmarchi-cus* and *C. glacialis* (Crustacea: Copepoda). – *In* Barnes, H. (ed.): Some contemporary studies in marine sciences, p. 479-492. Allen & Unwin, London.

Matthews, J. B. L. & B. R. Heimdal, 1980. Pelagic productivity and food chains in fjord systems. – *In* Freeland, H. J., D. M. Farmer & C. D. Levings (eds): Fjord Oceanography, p. 337-398 Plenum Publ. Corp., New York.

Matthews, J. B. L., L. Hestad & J. L. W. Bakke, 1978. Ecological studies in Korsfjorden, western Norway. The generations and stocks of *Calanus hyperboreus* and *C. finmarchicus* in 1971-1974. – Oceanol. Acta **1**: 274-284.

McLaren, I. A., 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. – J. Fish. Res. Board Can. **20**: 685-727.

McLellan, D. C., 1967. The annual cycle of certain calanoid species in western Greenland. – Can. J. Zool. **45**: 101-115.

Miller, C. B., T. J. Cowles, P. H. Wiebe, N. J. Copley & H. Grigg, 1991. Phenology in *Calanus finmarchicus*; hypotheses about control mechanisms. – Mar. Ecol. Prog. Ser. **72**: 79-91.

Miller, C. B. & K. S. Tande, 1993. Stage duration estimation for *Calanus* populations, a modelling study. – Mar. Ecol. Prog. Ser. **102**: 15-34.

Ohman, M. D, 1983. Reverse diel migration: An escape from invertebrate predators. – Science **220**: 1404-1407.

Ohman, M. D., 1988. Behavioral responses of zooplankton to predation. – Bull. Mar. Sci. **43**: 530-550.

Ohman, M. D., 1990. The demographic benefits of diel vertical migration by zooplankton. – Ecological Monographs **60**: 257-281.

Ohman, M. D. & S. N. Wood, 1995. The inevitability of mortality. – ICES. J. Mar. Sci. **52**: 517-522.

Østvedt , O. J. ,1955. Zooplankton investigations from weathership "M" in the Norwegian Sea, 1948-49. – Hvalråd. Skr. **40**: 1-93.

Runge, J. A., I. A. McLaren, C. J. Corkett, R. N. Bohrer & J. A. Koslow, 1985. Moulting rates and cohort development of *Calanus finmarchicus* and *C. glacialis* in the sea off southwest Nova Scotia. – Mar. Biol. **86**: 241-246.

Runge, J. A. & S. Plourde, 1996. Fecundity characteristics of *Calanus finmarchicus* in coastal waters of eastern Canada. – Ophelia **44**: 171-187.

Slagstad, D. & K. S. Tande, 1996. The importance of seasonal vertical migration in across shelf transport of *Calanus finmarchicus*. – Ophelia **44**: 189-205.

Sverdrup, H. U., M. W. Johnson & R. H. Flemming, 1942. The oceans, their physics, chemistry, and general biology. Prentice-Hall. New York: 1060 pp.

Tande, K., 1982. Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: generation cycles, and variation in body weight and body content of carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus finmarchicus* (Gunnerus). – J. Exp. Mar. Biol. Ecol. **62**: 129-142.

Tande, K. S., 1988. Aspects of developmental and mortality rates in *Calanus finmarchicus* related to equiproportional development. – Mar. Ecol. Prog. Ser. **44**: 51-58.

Timokhina, A. F., 1964. On zooplankton production in different water masses of the Norwegian Sea. – Trudy PINRO **16**: 165-182. (in Russian).

Thompson, B. M., 1982. Growth and development of *Pseudocalanus elongatus* and *Calanus* sp. in the laboratory. – J. mar. biol. Ass. U.K. **62**: 359-372.

Ussing, H. H., 1938. The biology of some important plankton animals in the fjords of East Greenland. – Meddr Grønl. **100**: 1-108.

Wiborg, K. F., 1954. Investigations of zooplankton in coastal and offshore waters off western and northwestern Norway. – Rep. Norw. Fish. Invest. **11**: 1-246.

Williams, R. & J. A. Lindley, 1980. Plankton of the Fladen Ground during FLEX 76. III. Vertical distribution, population dynamics and production of *Calanus finmarchicus* (Crustacea: Copepoda). – Mar. Biol. **60**: 47-56.

Worthington, L. W., 1970. The Norwegian Sea as a mediterranean basin. – Deep-Sea Research **17**:77-84.

Zaret, T. M. & J. S. Suffern, 1976. Vertical migration in zooplankton as a predator avoidance mechanism. – Limnol. Oceanogr. **21**: 804-813.