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Density- and Sound Speed Contrasts in Sub-Arctic Zooplankton

Johannes W. Køgeler[1], Stig Falk-Petersen[2], Åge Kristensen[3], Fritz Pettersen[4] and John Dalen[5]

[1] Akvaplan A/S, Bankgt. 1, N-9000 Tromsø, Norway
[2] Institute of Fisheries, P.O.Box 3083 Guleng, University of Tromsø, N-9001 Tromsø, Norway
[3] Continental Shelf and Petroleum Technology Research Institute Ltd., P.O.Box 1883 Jarlesletta, N-7000 Trondheim, Norway
[4] EISCAT, 9027 Ramfjordbotn, N-9000 Tromsø, Norway
[5] Electronic Research Laboratory, University of Trondheim, N-7034 Trondheim, Norway

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Summary. The sound speed was determined for *Meganyctiphanes norvegica,* for a mixture of *Thysanoessa raschii* and *Thysanoessa inermis* and for a mixture of *Calanus finmarchicus* and *Calanus hyperboreus.* The sound speed contrasts ranged from 1.014 to 1.044. Seasonal variations in specific density were measured for *Thysanoessa inermis, Thysanoessa raschii, Meganyctiphanes norvegica, Calanus finmarchicus* and *Calanus hyperboreus.* The density of 20 mm *T. inermis* was lowest in November (1.052 g/cm^3) and highest in February–March (1.065 g/cm^3). For a 20 mm *T. raschii* the minimal density was determined in December (1.059 g/cm^3) and the maximum in February–March (1.074 g/cm^3). *M. norvegica* individuals of 35 mm also had their lowest density in December (1.060 g/cm^3), but reached their maximum density in July (1.076 g/cm^3).

The density of the euphausiids was found to be size dependent. The density increases as the size decreases. *C. finmarchicus* and *C. hyperboreus* had densities less than seawater (1.026 g/cm^3) during most of the year. Just before spawning the density increased to 1.028 g/cm^3 and 1.036 g/cm^3 for *C. finmarchicus* and *C. hyperboreus* respectively. The seasonal variations of the density were closely related to the lipid content of the animals.

Introduction

The majority of secondary production in the marine areas of the world is due to euphausiids (krill) and calanoid copepods (Mauchline and Fisher 1969). This production forms the basis of the energy channelled onwards through the food web to the major stocks of zooplanktivorous fish such as anchovetta, herring and capelin.

Estimation of zooplankton abundance has been dependent on net sampling, but the many disadvantages of this technique (Cassie 1968; Vannucci 1968) have led to the development of remote acoustical assessment techniques (Greenlaw 1977; Kristensen 1983). The major advantages of acoustic methods are their continuous nature of observation to meet requirements of high sampling frequency, large observation volumes and the possibility to make rapid *in situ* biomass estimates from a large geographical area.

Two basic approaches can be used in acoustic estimation of zooplankton. In the first one an empirical relation between biomass and volume backscattering strength is used (Pieper 1979; Sameoto 1980; Falk-Petersen and Hopkins 1981). The other method is based on scattering models of the investigated zooplankton species. These models can be empirical or mathematical (Anderson 1950; Johnson 1977; Greenlaw 1977, 1979; Kristensen 1983; Falk-Petersen and Kristensen 1985). The backscattering cross section predicted by these models is generally dependent on the acoustic frequency, the density contrast and the sound speed contrast between the organism and seawater. The physical shape and angular orientation of the organisms may also be introduced as a parameter.

The accuracy of acoustic assessment of zooplankton depends on the quality of the scattering model and the ability to measure the parameters required by the model (Kristensen and Dalen 1986).

Little is known about density and sound speed contrasts of zooplankton (Beamish 1971; Greenlaw 1977; Suzuki 1979; Kils 1979a). From the North-Atlantic no information is available. As the biochemical composition of zooplankton is known to change during the year, density and sound speed were measured for three euphausiid and two copepod species over a yearcycle.

In the present study the seasonal variations of the density and the sound speed together with the sound speed and the density contrasts are presented. The variations of the density are discussed in relation to the biochemical composition of the animals.

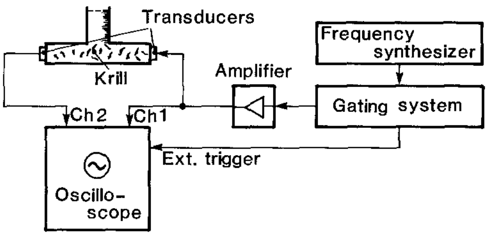

Fig. 1. Instrumentation for sound speed measurement of zooplankton

Material and Methods

Zooplankton was caught with a 1 m^2 rectangular (Tucker trawl) mid-water trawl (mesh size 1 mm^2) during 10 cruises with *RV Johan Ruud* in the Tromsø area (Northern Norway) between November 1982 and September 1983. The zooplankton was kept in big sea water filled containers until the measurements were made. Details of the physical environment of the fjords in the Tromsø area are given in Sælen 1950 and Eilertsen et al. 1981.

The measurements of the sound speed were performed using a T-shaped plexiglass velocitymeter with two ceramic transducers mounted at the ends of the horizontal tube (Fig. 1. Greenlaw 1977; Kristensen 1983). The volume displaced by the zooplankton introduced into the horizontal tube was measured to calculate the exact volume fraction of the animals in the medium between the transducers. A maximal volume fraction of plankton of approximately 65% could be obtained.

The 10 µs sinus pulse at 500 kHz was transmitted from one of the transducers and received at the other. The transit time of the pulse was measured and the sound speed of the medium between the transducers was calculated for various concentrations of zooplankton.

For a volume of fluid containing objects of slightly different sound speed and density, a good approximation of the sound speed of the mixture is a weighted sum of the sound speed of the components (Greenlaw 1977).

This yields:

$$c_m = (1 - V_p)\, c_f + V_p \cdot c_p$$

where

c_m – sound speed ($m \cdot s^{-1}$) of the mixture,
c_f – sound speed ($m \cdot s^{-1}$) of the fluid,
c_p – sound speed ($m \cdot s^{-1}$) of the injected objects, and
V_p – volume fraction of the objects.

A first order regression equation was calculated for the sound speed of the mixture versus the volume fraction of zooplankton. The sound speed of the zooplankton, at $V_p = 1$, was estimated from this regression equation. Thereafter the sound speed contrast was obtained by dividing the sound speed of zooplankton by that of sea water determined in the same experiment.

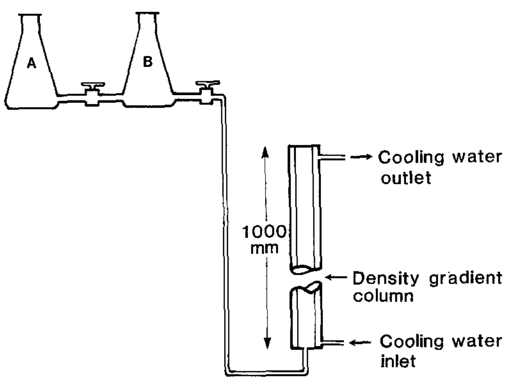

Fig. 2. Sketch of the density gradient column methods. Bottles A and B contain NaCl-water with different densities

The density was determined using Pharmacia 50/1000 water cooled column filled with sea water having a linear salinity gradient of 80 cm total height (Payne and Stephenson 1964). No measurements were made in the top 10 cm of the column so as to exclude any effects that might be caused by turbulence when introducing animals into the column (Fig. 2). Each column was calibrated using a series of glass floats of precisely known density (Martin Instrument Company Ltd., Herts, England). A continuous density scale over the whole column, the density of the floats was regressed on depth using a first order linear model.

The animals were anaesthetized for a few seconds in a 50‰ saltwater solution. Immediately thereafter each specimen was identified, and the length was measured before it was brought into the column. The length of the euphausiids was defined as the distance from the behind anterior margin of the eye to the tip of the telson. For the copepods the length was defined as the length of the prosome. *Calanus finmarchicus* had a prosome length between 2.2 and 3.0 mm and *C. hyperboreus* between 3.5 and 5.5 mm. Only specimens positively evaluated to be clearly alive prior to the anaesthetation activity were used for the experiments.

The depth where the organism reached neutral buoyancy was used to determine it's specific density. The density contrast was obtained by dividing the calculated density by the specific density of sea water (1.026 g/cm^3).

Results

As the sorting of live animals is difficult, the sound speed were determined to mixed samples of *T. inermis* and *T. raschii* and mixed to samples of *C. finmarchicus* and *C. hyperboreus*. Pure samples could only be obtained of *M. norvegica*.

In all experiments the correlation coefficient of the linear regression of the sound speed data was greater than 0.96. The calculated sound speed contrasts are given in Table 1. The variability of the data makes it impossible to detect seasonal trends. A mean sound speed contrast of 1.030±0.01 is calculated for *M. norvegica*. For the *Thysanoessa* and *Calanus* these mean contrasts are 1.026±0.005 and 1.027±0.007, respectively.

Table 1. Sound speed contrast (h) in *Thysanoessa, Meganyctiphanes norvegica* and *Calanus*

Date	*Thysanoessa*	*M. norvegica*	*Calanus*
6. 11. 82	1.031	1.038	–
	1.023	–	–
16. 11. 82	1.029	1.028	–
15. 12. 82	1.021	1.027	1.036
			1.027
			1.026
20. 1. 82	–	1.039	–
		1.044	
10. 3. 83	–	1.014	–
		1.018	–
6. 4. 83	1.023	–	–
	1.021		
27. 5. 83		1.033	
	1.030	1.029	1.021
30. 7. 83	1.028	–	–
Mean contrast	1.026±0.005	1.030±0.01	1.027±0.007
No. of measuring series	(7)	(10)	(4)

The densities of the euphausiids are found to decrease linearly with increasing size. (Tables 2, 3 and 4). Both slope and intercept of the calculated regression equation changed during the year. To make comparisons possible between the estimated values, the density of a reference-sized animal was calculated from the regression equation. This is to eliminate size as a variable in the comparison between months. As reference size, a length of 20 mm for the *Thysanoessa* spp. and 35 mm for *M. norvegica* was chosen.

The density of *T. inermis* increased between November 1982 and March 1983 from 1.052 to 1.065 g/cm^3 before decreasing again during the spring and summer period. *T. raschii* showed similar variations, but the densities were higher than those of *T. inermis*. The density of *T. raschii* increased from 1.059 g/cm^3 in December 1982 to 1.074 g/cm^3 in March 1983 before decreasing to 1.061 g/cm^3 in September 1983.

M. norvegica also had its lowest density (1.060 g/cm^3) in December 1982, but did not reach its maximum before August 1983 (1.076 g/cm^3).

The density of *C. finmarchicus* and *C. hyperboreus* also varied with the season (Fig. 4). It is interesting to note that most of the year *Calanus* spp. are slightly lighter than sea water. *C. finmarchicus* had a density of 1.025 to 1.026 g/cm^3 from May to January, while in the same period *C. hyperboreus* had densities between 1.022 and 1.025 g/cm^3. Only in March, just before spawning, both species had densities greater than sea water (respectively 1.029 and 1.036 g/cm^3).

Table 2. *Thysanoessa inermis*. Specific density (s) and density contrasts (g). Linear regression between density/density contrasts, Y, and length (L); Y = aL + b, a = regression coefficient, b = intercept and r = correlation coefficient

Data	No.	Range (mm)	Density (g/cm^3)			Density contrast g	
			b	a·10^{-3}	r	b	a·10^{-3}
5. 11. 82	33		1.093	−1.81	−0.766	1.065	−1.76
17. 11. 82	21	16−22	1.091	−1.91	−0.951	1.063	−1.86
15. 12. 82	17	11−25	1.074	−0.90	−0.752	1.047	−0.88
20. 1. 83	12	12−23	1.101	−2.05	−0.899	1.073	−2.00
28. 2. 83	17	11−25	1.101	−1.77	−0.929	1.073	−1.73
28. 5. 83	15	17−25	1.060	−0.01	−0.140	1.033	−0.01
28. 7. 83	15	10−23	1.106	−2.50	−0.895	1.078	−2.44
21. 9. 83	17	12−22	1.088	−1.35	−0.765	1.060	−1.32

Table 3. *Thysanoessa raschii*. Specific density (s) and density contrast (g). Linear regression between density/density contrast, Y, and length (L); Y = aL + b, a = regression coefficient, b = intercept and r = correlation coefficient

Data	No.	Range (mm)	Density (g/cm^3)			Density contrast g	
			b	a·10^{-3}	r	b	a·10^{-3}
5. 11. 82	17		1.083	−0.87	−0.503	1.056	−0.85
17. 11. 82	12	16−21	1.080	−0.71	−0.687	1.053	−0.69
15. 12. 82	11	10−24	1.079	−0.99	−0.714	1.052	−0.96
20. 1. 83	10	11−20	1.097	−1.49	−0.729	1.069	−1.45
28. 2. 83	6	10−23	1.105	−1.52	−0.743	1.077	−1.48
28. 5. 83	15	13−22	1.086	−0.92	−0.420	1.058	−0.90
21. 9. 83	9	14−24	1.077	−0.81	−0.593	1.049	−0.79

Table 4. *Meganyctiphanes norvegica*. Specific density (s) and density contrasts (g). Linear regression between density/density contrasts, Y, and length (L); Y = aL + b, a = regression coefficient, b = intercept and r = correlation coefficient

Data	No.	Range (mm)	Density (g/cm^3)			Density contrast g	
			b	a·10^{-3}	r	b	a·10^{-3}
5. 11. 82	12		1.098	−0.87	−0.865	1.070	−0.85
17. 11. 82	11	23−45	1.080	−0.47	−0.719	1.053	−0.45
15. 12. 82	13	27−45	1.072	−0.33	−0.429	1.045	−0.32
20. 1. 83	14	24−44	1.090	−0.66	−0.802	1.062	−0.64
28. 2. 83	12	23−39	1.091	−0.57	−0.622	1.063	−0.56
28. 5. 83	13	25−41	1.086	−0.27	−0.330	1.058	−0.26
28. 7. 83	6	29−41	1.087	−0.28	−0.603	1.059	−0.27
21. 9. 83	6	22−44	1.099	−0.90	−0.965	1.062	−0.88

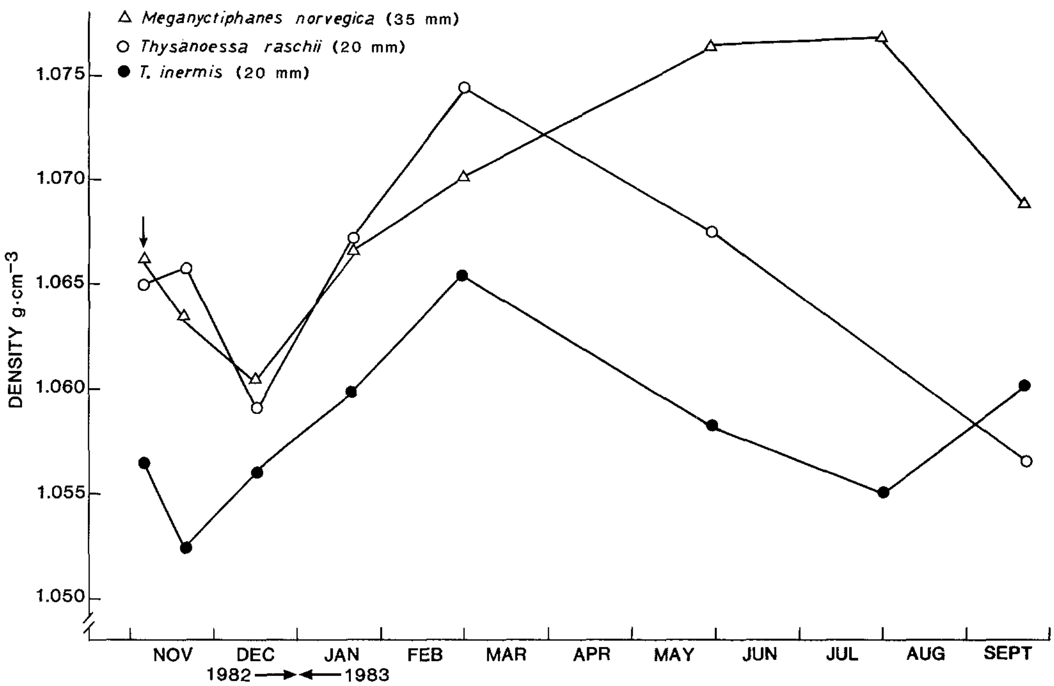

Fig. 3. Seasonal variation of density for animals of *Thysanoessa inermis, Thysanoessa raschii* and *Meganyctiphanes norvegica.* The densities for the reference animals were calculated from the monthly regression equations

Discussion

The mathematical models used in acoustical estimation of zooplankton biomass are very sensitive to changes of density and sound speed contrasts (Johnson 1977; Greenlaw 1977; Kristensen and Dahlen 1986). A one percent change in one of these parameters results in a approx. 2.0 dB change of the backscattering cross section (Kristensen 1983, page 27; Johnson 1977).

The mean sound speed contrast of 1.03 for the euphausiids we examined, agrees well with the 1.033 for *Euphausia pacifica* (Greenlaw 1977). It should be noted that Greenlaw used preserved krill from another geographic region. The sound speed contrast he found for *Calanus marshallae,* 1.007, is however lower than our observation of 1.027 for in the mixture of *C. finmarchicus* and *C. hyperboreus.*

The largest source of error in determining the density of zooplankton by the applied method was the measurement of the exact point of neutral buoyancy of the specimen in the column. The high salinities were lethal for the animals. A subsequent increase in density was observed, probably induced by osmotic processes. Before this happened, the animals did however maintain a stable position in the column for a shorter period of time. This position was defined as the point of neutral buoyancy. Further, the salinity gradient is very small and a 20 mm error in depth reading leads to an inaccuracy of the calculated density of less than 0.1%, i.e. a rather small error (Kristensen 1983). The difference in density between individuals of the same size was assumed to be due to dif-

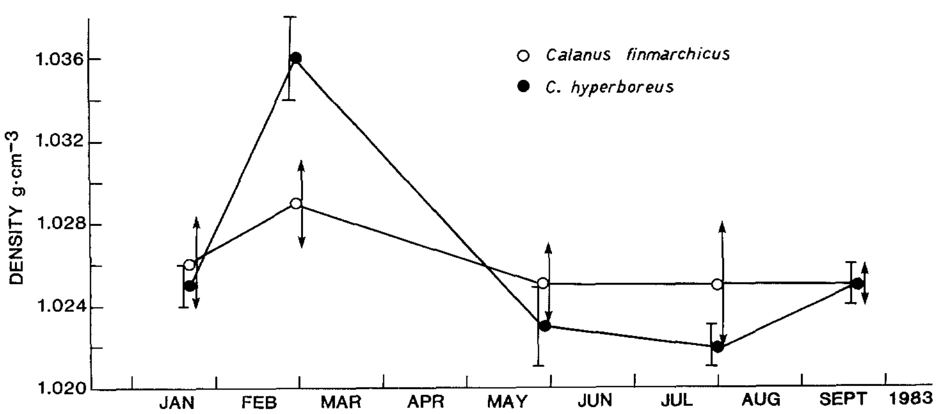

Fig. 4. The monthly mean density of *Calanus finmarchicus* and *Calanus hyperboreus.* The means are based on average of 5 to 13 animals

ferences in the biochemical composition among the organisms. The regression equations found for the densities of the euphausiids are therefore believed to express the mean density as a function of cn size. The differences in density between the species, sizes and season are closely related to changes in the lipid composition of the investigated species.

T. inermis contains more lipids and lipids of lower density (wax esters) than *T. raschii* which contains mainly triacylglycerols (Falk-Petersen 1981; Falk-Petersen et al. 1981). It has also been shown that the lipid content is higher in large krill than in small krill (Falk-Petersen 1981). This will contribute to the observed decrease in density with increasing length. The seasonal variations in density corresponding to changes in the lipid composition of the investigated zooplankton species as described by Falk-Petersen (1981), Falk-Petersen et al. 1981, Falk-Petersen et al. (submitted to Polar Biology).

Greenlaw (1977) calculated a mean density of 1.063 g/cm^3 for *Euphausia pacifica* of 19–23 mm total length, and Sheldon in Beamish (1971) reported a density of approx. 1.06 g/cm^3 for *Euphausia superba.* As season and size dependency of these values should also be taken into account, it is difficult to make a direct comparison with our results. Kils (1979b) also found a length density relation for *M. norvegica,* but in contrast to our observations, he found that the density increased with increasing size. He calculated the density in January for a reference sized animal (35 mm) to be 1.057 g/cm^3. This is lower than our observation, 1.067 g/cm^3. These differences might be due to the different biochemical compositions of the animals, and the fact that he used nitrogen frozen krill while we used living animals.

C. finmarchicus and *C. hyperboreus* have densities of less than 1.026 g/cm^3 from June to January. Only in February these two species had higher densities than sea water. This means that both species have a slightly positive buoyancy during most of the year. This was also observed by the fact that the animals had a slightly positive buoyancy in surface seawater with a density of 1.026 g/cm^3. This contradicts with observations of Greenlaw (1979) who found a density of approx. 1.04 g/cm^3 for *Acartia clausi* and *C. marshallae.* This difference can probably be explained by differences in the lipid levels.

The observed seasonal changes of the density contrasts of zooplankton are of such magnitudes that when a mathematical model is used for acoustic assessments of zooplankton abundances, the parameters of this model should be tuned for the actual seasons. The densities of the euphausiids are also so strongly size dependent (i.e. lipid dependent) that the relevant parameters of the model should reflect this.

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