

Interactions between biological and environmental structures along the coast of northern Norway

Maria Fossheim^{1,*}, Meng Zhou², Kurt S. Tande¹, Ole-Petter Pedersen¹, Yiwu Zhu², Are Edvardsen¹

¹Norwegian College of Fishery Science, University of Tromsø, 9037 Tromsø, Norway

²EEOS Department, University of Massachusetts Boston, Boston, Massachusetts 02125, USA

ABSTRACT: Spatial and temporal variability in physical conditions off the northern coast of Norway may affect the 3D distribution of mesozooplankton and capelin larvae (*Mallotus villosus* Müller) during the early capelin recruitment period. To monitor distribution patterns, we sampled the water masses down to 100 m on 3 successive occasions in May 2001 with a SCANFISH-OPC-CTD-F platform. We found distinct differences between coastal and oceanic waters in the study area. The water masses were most clearly distinguished by salinity and there was a tendency for higher zooplankton abundance and biomass in water of oceanic origin. Our study area was characterised by mesoscale eddies, translating in an easterly direction which follow the Norwegian Coastal Current. Cyclonic eddies contained oceanic water, high zooplankton abundance and biomass, whereas anti-cyclonic eddies contained water masses of coastal origin and low abundance of zooplankton. The eddies found in the spawning and hatching habitat of capelin were relatively small and of short duration; however, their impact on the biological community in terms of mediating exchange of biotas across the shelf can be significant.

KEY WORDS: Optical plankton counter · Eddy · Barents Sea · Capelin larvae

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INTRODUCTION

Spawning sites of capelin *Mallotus villosus* Müller are often found in fjords and adjacent areas on the shelf of northern Norway (Gjøsæter 1998), where tidal-, wind- and density-driven currents and coastal up- or downwelling events interact (Harms 1992, McClimans & Nilsen 1993). The southern Barents Sea is dominated by interactions of 2 waters: coastal water and Atlantic water (Loeng 1991), and the mixing of these 2 waters prevails in the hatching and nursery areas of capelin larvae. Mesoscale hydrographical features such as fronts and eddies dominate in this area (Pedersen et al. 2005), and may affect larval survival and subsequently recruitment. After hatching, the fish larvae are transported offshore towards nurseries in the central part of the Barents Sea, and few larvae remain in the coastal area after 2 wk (Gjøsæter 1998, Pedersen et al. 2003). The strategic programme BASECOEX ('Capelin and

Herring in the Barents Sea—Coexistence or Exclusion') is a multidisciplinary research project attempting to understand capelin–herring interactions in the Barents Sea. During the project, field surveys were undertaken to resolve the 3D advection, migration and *in situ* population dynamic rates of capelin larvae and zooplankton in a core spawning area of capelin.

Mesoscale eddies have been observed within coastal current systems on numerous continental shelves, including within the Benguela Current (Bang 1973), the Florida Current (Lee & Mayer 1977), the Gulf Stream off North America (Csanady 1979), the Norwegian Coastal Current (Ikeda et al. 1989), the Irish Shelf front (Huang et al. 1991), the Gulf of Alaska (Bograd et al. 1994) and the Barents Sea (Pedersen et al. 2005). The length and timescales of eddies vary geographically but are typically between 10 and 50 km and 1 and 4 wk, respectively. Mesoscale eddies can contribute to the retention or dispersal of planktonic organisms

*Email: mariaf@nfh.uit.no

(Lobel & Robinson 1986, Boehlert et al. 1992, Bograd et al. 1994, Rodriguez et al. 2001, Halvorsen et al. 2003) and affect the biological productivity of coastal regions (Rey 1981, Kimura et al. 1997, Kasai et al. 2002). An eddy can concentrate buoyant passive materials when its secondary circulation converges. This mechanism may aggregate patches of plankton in confined areas and may provide favourable retention areas (Halvorsen et al. 2003). A divergent eddy on the other hand may increase primary production due to the upwelling of nutrient-rich deep water to the euphotic surface layer, which may further enhance zooplankton production (Kimura et al. 1997, Nakata et al. 2000).

Abundant fish larvae have previously been observed in both cyclonic (Okazaki et al. 2002) and anti-cyclonic (Schumacher et al. 1993) eddies. Canino et al. (1991) suggested that feeding and survival conditions may be better in eddies. Bograd et al. (1994) found that larvae retained within an eddy had a lower mortality rate than elsewhere. It has also been hypothesised that retention in eddies, that move downstream at slower rates than mean currents (Bograd et al. 1994), aid in delivering larvae to the nurseries. Eddies may aid in retention of fish larvae in coastal areas (Kasai et al. 2002) and may decrease the likelihood of them being transported into the oceanic regime (Bograd et al. 1994), or may function as a transport mechanism from coastal areas to offshore nursery grounds (Komatsu et al. 2002). Eddies are also important for larvae in helping them to avoid excessive transport (i.e. currents may carry them away from the nurseries) by retaining them in areas that are conducive to their survival (Hinckley et al. 2001). Young larvae are more likely to survive in

a healthy environment if that environment includes an eddy (Bograd et al. 1994, Okazaki et al. 2003).

The present study describes the physical and biological environment in an important spawning habitat of capelin during the period of larval hatching. The objective was to determine, in particular, how the spatial and temporal variability in physical conditions dictate the 3D distribution patterns of mesozooplankton and capelin larvae and investigate the possible role of mesoscale eddies in the along-shelf and offshore transport of capelin larvae after their release from the seabed.

MATERIALS AND METHODS

Survey and study area. The study area in the southern Barents Sea in May 2001 (Fig. 1) was chosen because of the high concentrations of capelin larvae detected by a MultiNet (MultiNet MiDi; Hydro-Bios Apparatebau). A grid (71 to 71° 20' N, 25 to 29° E) of approximately 6×10^3 km² outside the 2 fjords Porsangerfjord and Laksefjord was surveyed on 3 successive occasions (Phases 1, 2 and 3). During each phase, the area was sampled by a towed, undulating vehicle (MKII SCANFISH, GMI, Snekkersten, Denmark) that sampled the water column from 1 to 100 m. An optical plankton counter (OPC; Focal Technologies) (Herman 1988, 1992) was mounted on the SCANFISH together with a CTD (Sea-Bird 911; Sea-Bird Electronics) and a fluorometer (Seapoint chlorophyll fluorometer; Seapoint Sensors). The OPC detects particles in 4096 digital sizes within a range of 0.25 to 14 mm equivalent

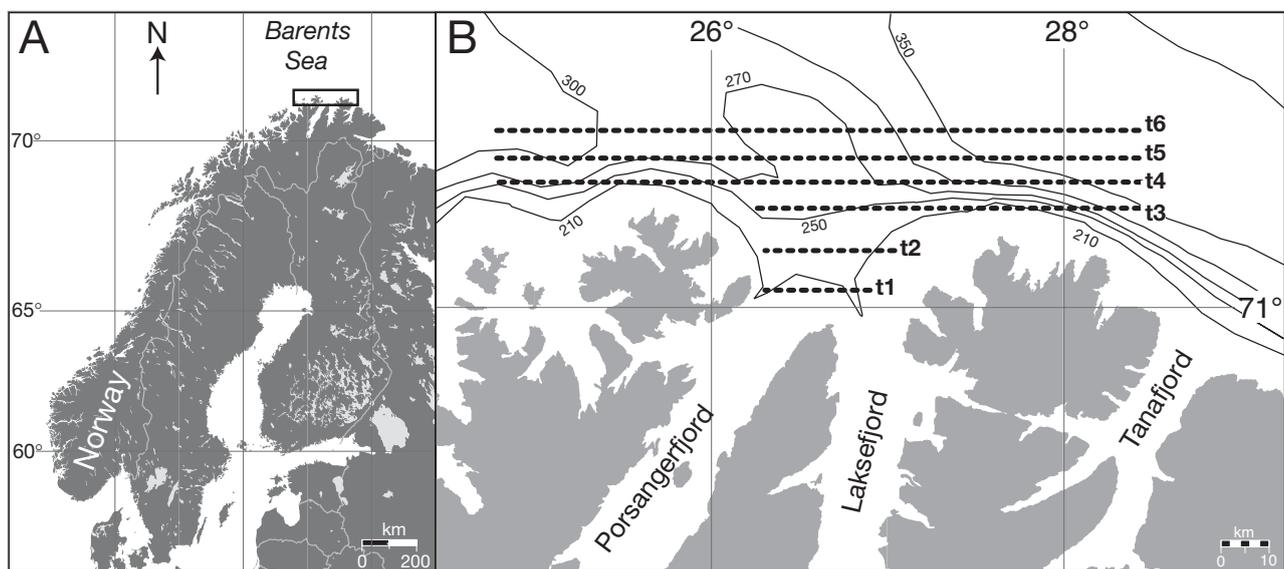


Fig. 1. (A) Map of Scandinavia showing location of study area (box); (B) study area in the southern Barents Sea, showing the 3 fjords Porsangerfjord, Laksefjord and Tanafjord and idealised Transect Lines t1 (inner) to t6 (outer)

spherical diameter (ESD), and measures abundance of zooplankton (individuals m^{-3}) and individual sizes (see Edvardsen et al. 2002 for further details). The CTD measures conductivity (i.e. salinity), temperature and depth. The flow was monitored outside the OPC by a flowmeter (Model 2135; General Oceanics).

Each phase lasted for approximately 5 d, consisting of 1 or 2 d of the SCANFISH coverage followed by 3 d of conventional sampling of hydrography and plankton using vertical CTD-F casts and MOCNESS (multiple opening–closing nets and environmental sensing system) (Wiebe et al. 1976, 1985) at approximately 9 stations covering the survey area in each phase. Phase 1 (17 May) was terminated after 3 transects due to OPC failure. In Phases 2 (21 to 23 May) and 3 (28 to 30 May), all 6 transects (from t1, closest to the coast, to t6, furthest from the coast) were sampled (Fig. 1). The survey area varied between phases: Phase 2 transects reached further to the west while Phase 3 transects reached further to the southeast, including the area outside Tanafjord.

Data processing. Data from the various instruments onboard the ship and the SCANFISH were integrated to provide a data set containing spatial (i.e. latitude, longitude, depth) and environmental (temperature, salinity, fluorescence, zooplankton abundance) variables. After processing the raw data, each variable of the data set represented an average over a period of 5 s. In addition to the abundance of zooplankton (individuals m^{-3}), the biomass in carbon was also estimated. The zooplankton carbon weight (W) was calculated from body length (L) given by the ESD (Huntley et al. 1995) and the relation of Rodriguez & Mullin (1986): $\log W [\mu\text{gC}] = 2.23 \log L [\mu\text{m}] - 5.58$. This relation is applicable to zooplankton in our study area at the first order of approximation. For interpolation and smoothing the measured field objective analysis (OA) was applied (Gandin 1963, Bretherton et al. 1976). OA is basically a contemporary synonym for statistical estimation based on the Gauss–Markov theorem. The correlation function applied is the same as that presented in Zhou (1998). The major advantage of OA is that the method yields an estimate at every point (x, y, z, t) which is optimal to the least square error. Abundance and biomass estimates for the 3 phases are shown.

The digital size spectrum measured by the OPC was integrated into 60 size classes of equal log (ESD) increments. We use the definition of a normalised biomass spectrum (simply referred to as a biomass spectrum) used in previous literature (Sheldon & Parsons 1967, Platt & Denman 1978, Silvert & Platt 1978, Zhou & Huntley 1997), i.e.

$$\text{biomass spectrum} = \frac{\text{biomass in the size interval } \Delta w}{\text{the size interval } \Delta w} \text{ (in } \text{m}^{-3}\text{)}$$

where the size (w) of zooplankton is the body biomass in carbon. Because an OPC provides ESD measurements of zooplankton, the body volumes of zooplankton can be converted directly from ESD. The biovolume spectrum (b) is defined as

$$\text{biovolume spectrum } (b) = \frac{\text{biovolume in the size interval } \Delta v}{\text{the size interval } \Delta v} \text{ (in } \text{m}^{-3}\text{)}$$

where the size (v) of zooplankton is the body volume in mm^3 . Although the relation between the body biomass and volume can vary between species, the biovolume spectrum should be equivalent to the biomass spectrum on the first order of approximation. To avoid further complication and uncertainty in the relations between the body biomass and volume for different species compositions, we simply use biovolume and biovolume spectra in our computations and discussion. We present the biovolume spectra vs. corresponding ESD instead of individual biovolume to better visualize plankton sizes.

The zooplankton community structure was known from conventional sampling with the MOCNESS. Since there is a growing evidence that the MOCNESS and the OPC sample the zooplankton community differently (Edvardsen et al. 2002), we have to be cautious when comparing the abundance of zooplankton from the MOCNESS with the abundance output from the OPC size spectra. Species present in more than 1% of the total abundance in the MOCNESS samples were considered to contribute to the OPC data, and the species was assigned to a size group as follows: in the laboratory, OPC size measurements were conducted on monocultures of all copepodite stages and adult females for *Calanus finmarchicus* together with *Thysanoessa* spp. furcilia and newly hatched capelin larvae (A. Edvardsen & M. Fossheim unpubl. data). Other groups were assigned to a size group based on literature sources describing their prosome sizes and body volumes. These gave a total of 6 new groups, all in size ranges much lower than capelin larvae, except for *Oikopleura* spp. whose actual body size was estimated to be within a size range similar to that of capelin larvae (M. Fossheim pers. obs.). In the following, we use the OPC data as size structured abundance information on zooplankton, bearing in mind that linking this type of data to species information must be done with great care.

Statistical analysis. To document spatial variation in the physical and biological structures, we compared the particle abundance in different eddies identified in the 3 outer transects (t4 to t6) in Phase 3. Because of strong autocorrelation, the data set was halved, and only the downward part of every SCANFISH profile (5 to 95 m) was chosen. An average for every profile was then calculated, 9 profiles ($n = 9$) were selected in the core of each physical structure, and a 2-factor (transect and

eddy) ANOVA was performed followed by post-hoc *t*-tests (with Bonferroni corrections). The null hypothesis (H_0) states that there are no differences in particle abundance between different physical structures (eddies).

RESULTS

The present paper provides a simultaneous analysis of the main hydrodynamic features together with biological information in terms of abundance and biomass. This information is presented below for each phase.

Phase 1 (Fig. 2)

The area close to the outlet of Porsangerfjord and Laksefjord was dominated by water of coastal origin (Fig. 2), of low temperature ($<5^{\circ}\text{C}$) and salinity ($<34.7\text{‰}$), along the 2 inner transects (t1 and t2). Along transect t3 ($26^{\circ}30'$ to $27^{\circ}00'$ E), coastal water occupied its middle west section while oceanic water of high temperature ($>5^{\circ}\text{C}$) and salinity ($>34.8\text{‰}$) occupied both sides. The abundance of zooplankton was highest (max. 7×10^3 ind. m^{-3}) in the deeper part of the water column (below 50 m), particularly in the inner transects (t1 and t2), where temperature and salinity were low. In contrast, the biomass was high throughout the whole water column (max. $\sim 1.5 \times 10^5 \mu\text{g C m}^{-3}$).

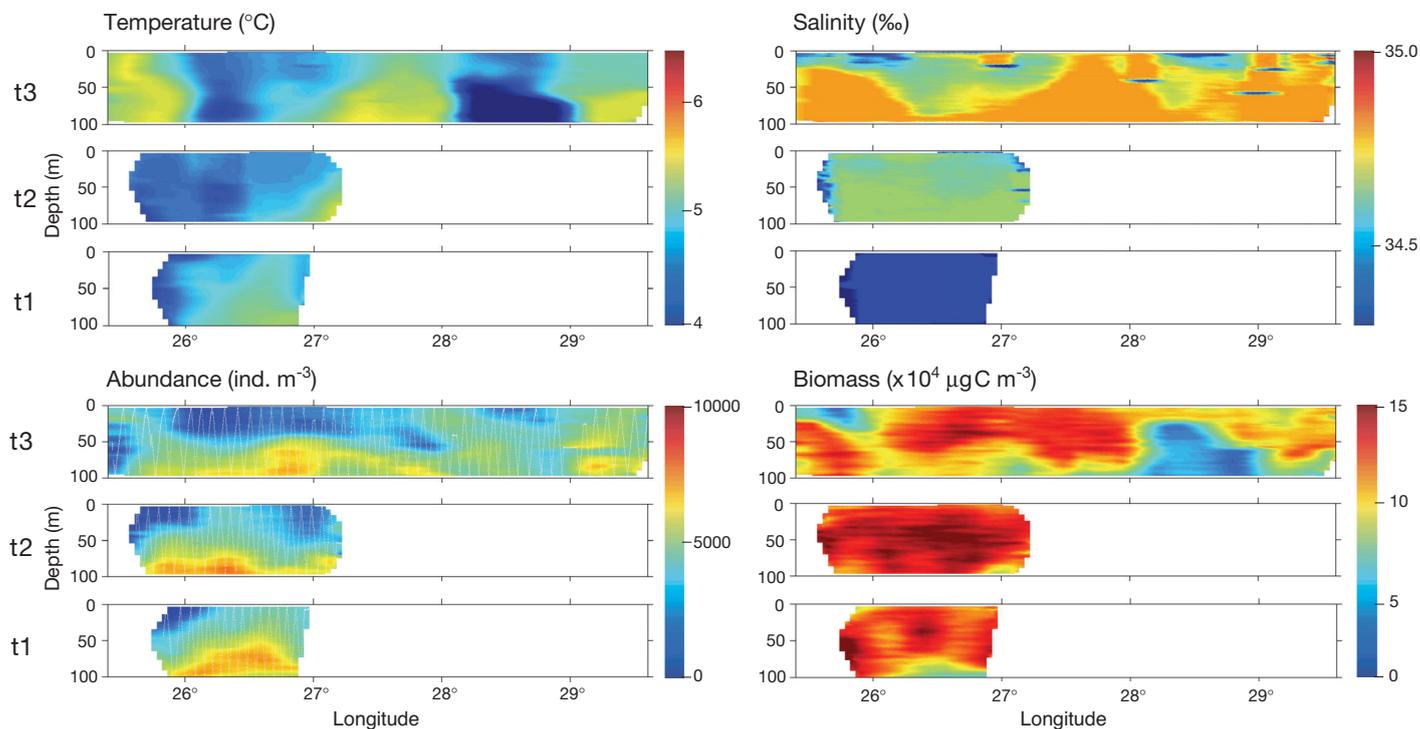


Fig. 2. Temperature ($^{\circ}\text{C}$), salinity (‰), abundance (ind. m^{-3}) and biomass ($\mu\text{g C m}^{-3}$) of zooplankton along the major transects (t1 to t3) in the southern Barents Sea in Phase 1 (17 May)

Phase 2 (Fig. 3)

In the inner part of the study area, which was surveyed during all phases, hydrographic conditions changed between Phases 1 and 2 (Fig. 3). More saline water ($>34.8\text{‰}$) now dominated the inner shelf (t2 and t3). Oceanic water (temperature $>5^{\circ}\text{C}$, salinity $>34.9\text{‰}$) dominated in the outer area, but was interspersed by several wedges of coastal water. The abundance of zooplankton was low ($\sim 3 \times 10^3$ ind. m^{-3}) in the western area of the study region, concurrent with relatively low salinity coastal water. High zooplankton abundance (max. 7.5×10^3 ind. m^{-3}) was found in oceanic water in outer transect t6 and on the eastern rim of inner transect t3 (max. 8×10^3 ind. m^{-3}). Biomass distribution showed the same pattern as abundance (maxima $\sim 2 \times 10^5 \mu\text{g C m}^{-3}$ in t3, and $1.7 \times 10^5 \mu\text{g C m}^{-3}$ in t6).

Phase 3 (Fig. 4)

The hydrographic conditions changed again between Phases 2 and 3. Conditions in the area just outside the 2 fjords now resembled those during Phase 1, with more coastal water close to the outlet of Porsangerfjord and Laksefjord (Fig. 4). The inner transects (t1 and t2) covered an area containing coastal water (temperature $<5^{\circ}\text{C}$, salinity $<34.5\text{‰}$). This coastal water plume

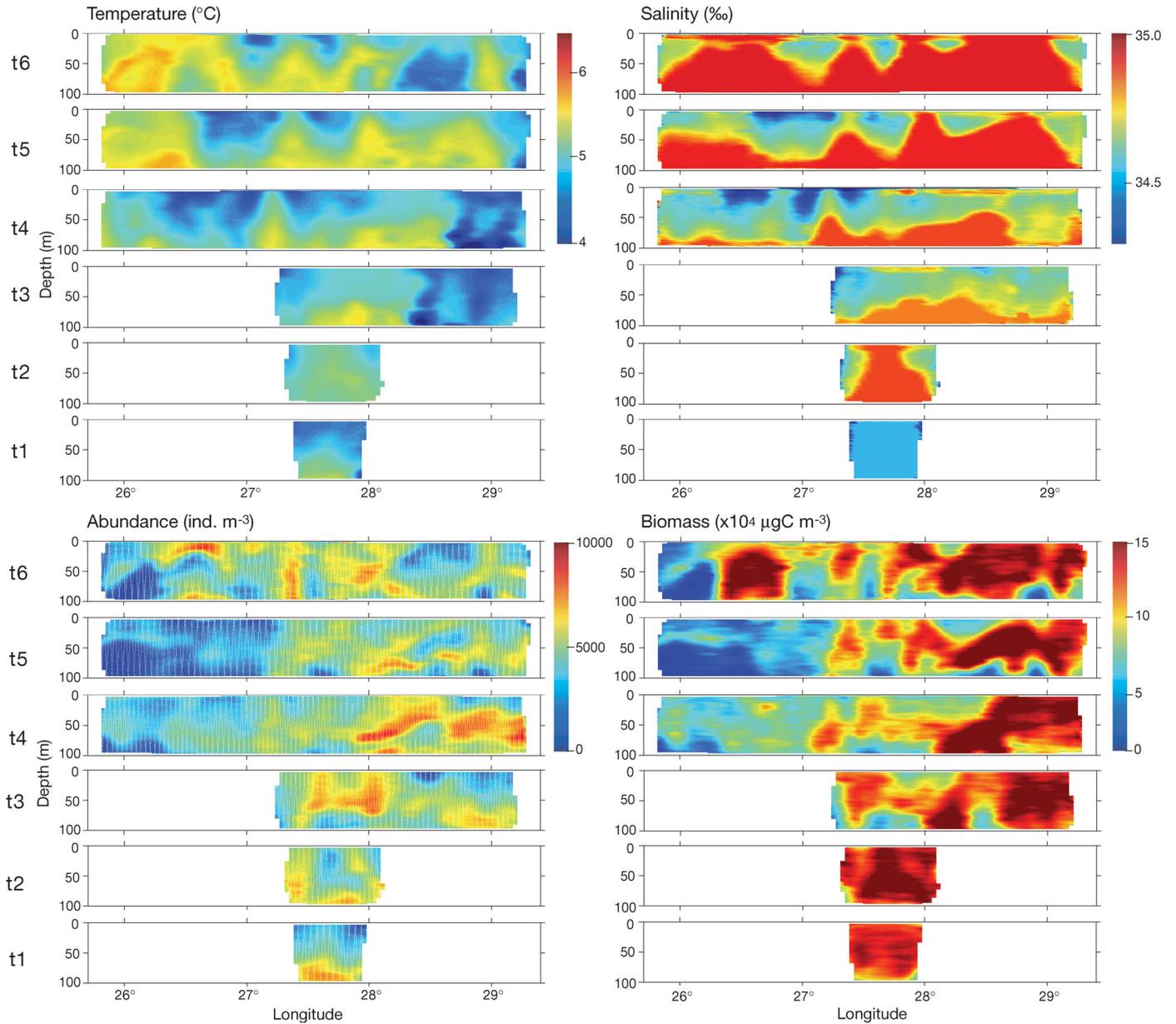


Fig. 3. Temperature ($^{\circ}\text{C}$), salinity (‰), abundance (ind. m^{-3}) and biomass ($\mu\text{g C m}^{-3}$) of zooplankton along the major transects (t1 to t6) in the southern Barents Sea in Phase 2 (21 to 23 May)

continued through the middle of all transects. On both sides of this coastal water in transects 4 to 6, oceanic waters were found (temperature $>5^{\circ}\text{C}$, salinity $>34.9\text{‰}$). Along the eastern rim of the study area, from t3 to t6 just outside Tanafjord, the water became less saline and colder (temperature $<5^{\circ}\text{C}$, salinity $<34.7\text{‰}$). The abundance of zooplankton was generally higher in oceanic waters, with maximum numbers of $\sim 6 \times 10^3 \text{ ind. m}^{-3}$. The biomass (maxima $\sim 1.5 \times 10^5 \mu\text{g C m}^{-3}$) mirrored the abundance pattern, except for the coastal water outside Tanafjord, where the biomass was high (1 to $1.5 \times 10^5 \mu\text{g C m}^{-3}$) and low abundance (~ 2 to $3 \times 10^3 \text{ ind. m}^{-3}$).

Zooplankton size spectra (Fig. 5)

In Phase 1 there was a difference in abundance below and above 50 m depth in the coastal water just outside the 2 fjords Porsangerfjord and Laksefjord. We therefore plotted the size spectra for the 2 depth intervals 0 to 50 m and 50 to 100 m (Fig. 5A,B). The higher abundance of zooplankton below 50 m was mostly due to small zooplankton, as indicated by the increased biovolume in the size range 0.25 to 1 mm ESD (Fig. 5B). In Phase 2, the size spectrum in oceanic water on the eastern side increased from 0.5 to 2 mm ESD, and was 1 order of magnitude higher than the size spectrum in

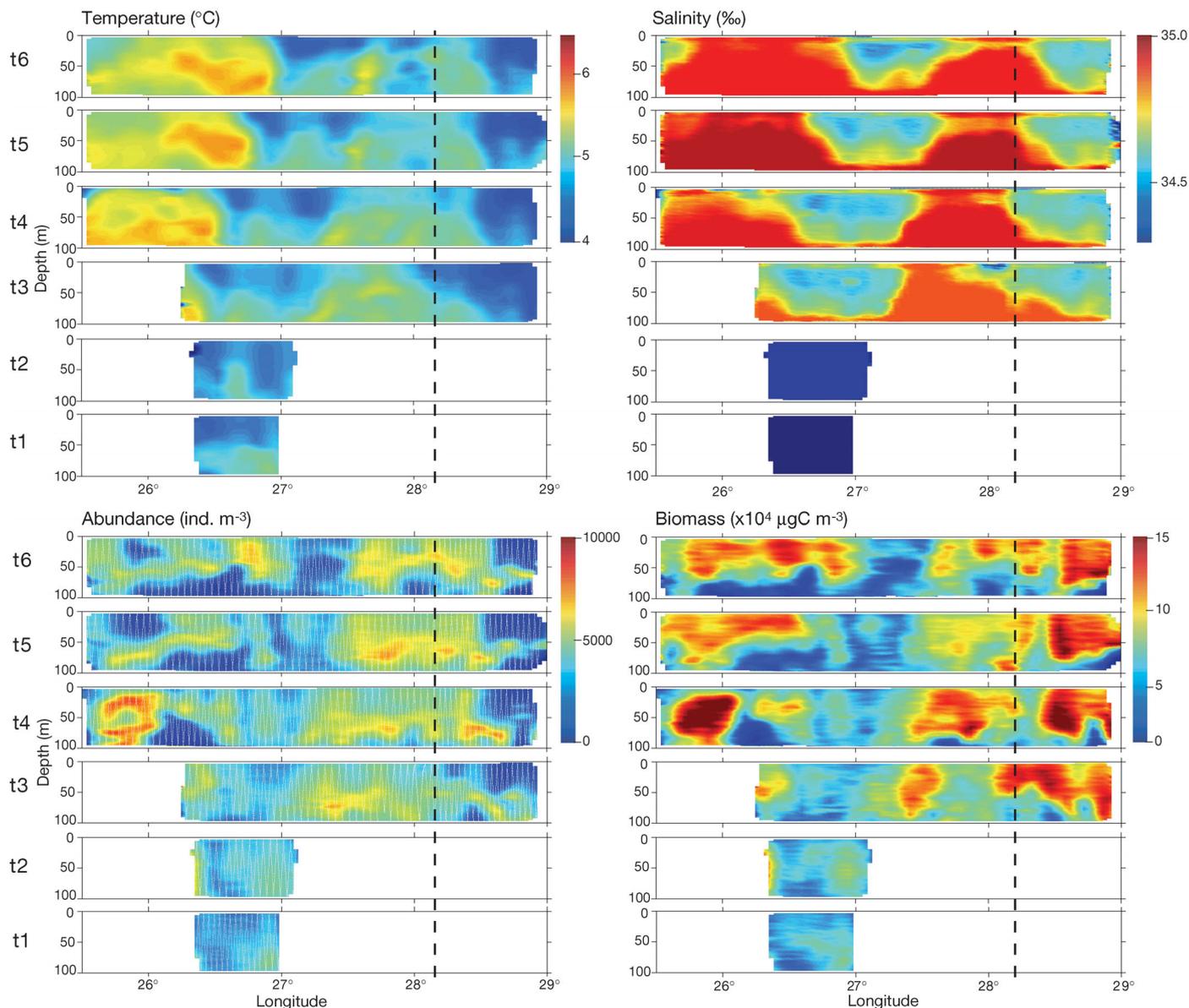


Fig. 4. Temperature (°C), salinity (‰), abundance (ind. m⁻³) and biomass (µgC m⁻³) of zooplankton along the major transects (t1 to t6) in the southern Barents Sea in Phase 3 (28 to 30 May). Vertical dashed line indicates where transects continued S-E outside Tanafjord

the coastal water on the western side, which was relatively linear (Fig. 5C,D). In Phase 3, the size spectra of the 2 outer areas with oceanic water (data not illustrated) was similar to the spectrum of the oceanic part of the outer area in Phase 2 (Fig. 5D). All these spectra peaked around 1 mm ESD. On the other hand, the size spectra of the 2 coastal waters (outside the 2 fjords) were quite different from each other (Fig. 5E,F) and also from the spectra of oceanic waters. The spectrum of the coastal water outside Porsangerfjord was linear from 0.5 to 2.5 mm ESD and lower than that of oceanic water (Fig. 5E). It was similar to the spectrum of the coastal part of the outer area in Phase 2 (Fig. 5C), but

different from the spectrum of the coastal water at the same location in Phase 1 (Fig. 5A,B). The size spectrum of the coastal water outside Tanafjord was more similar to the spectra in oceanic water. However, the peak was around 1.3 mm ESD in the size spectrum of the coastal water outside Tanafjord (Fig. 5F), while it was around 1 mm ESD in the size spectra typical of oceanic water.

Currents and abundance in eddies (Fig. 6)

Pedersen et al. (2005) calculated the relative geostrophical current for the study area (based on den-

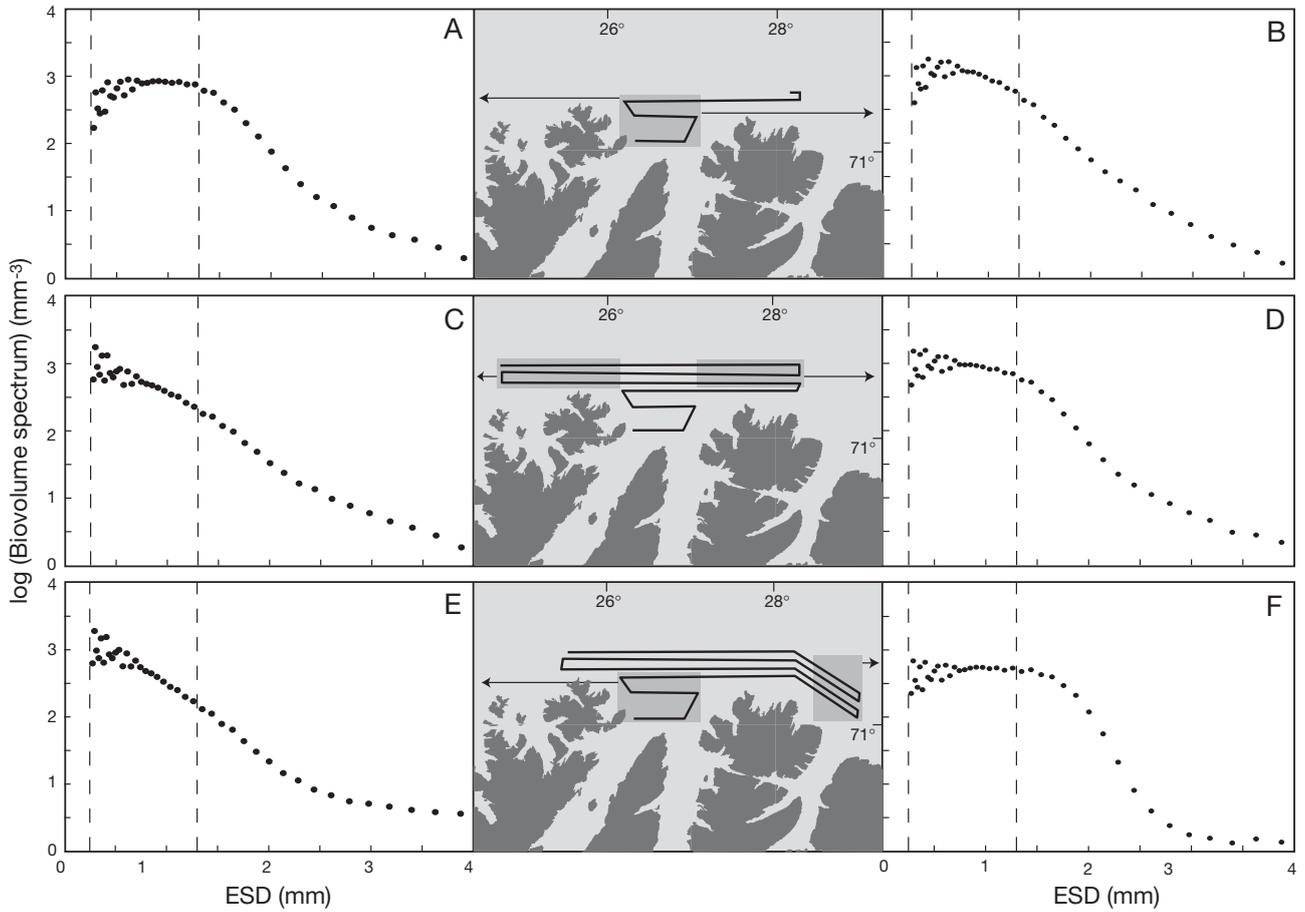


Fig. 5. Biovolume size spectra during Phases 1 to 3 (top, middle and lower rows, respectively) in coastal water outside Porsanger and Laksefjord at (A) 0 to 50 m and (B) 50 to 100 m depth; in outer area (C) coastal water and (D) oceanic water; and in (E) coastal water outside Porsanger and Laksefjord and (F) coastal water outside Tanafjord. Vertical dashed lines indicate ESD at 0.25 mm (detection limit of optical plankton counter) and at 1.3 mm (mean size for capelin *Mallotus villosus* larvae)

sity measurements from the CTD on the SCANFISH, see their paper for more details). Their results show the presence of several mesoscale eddies. Anti-cyclonic eddies contained water of low salinity, while cyclonic eddies contained water of higher salinity. We overlaid the zooplankton abundance field with the current field at 50 m depth from Phases 1, 2 and 3 to show the correlation between the biological information and the mesoscale circulations (Fig. 6).

In Phase 1 an anti-cyclonic eddy with coastal water was apparent close to the outlet of the 2 fjords (Fig. 6: top panel). The abundance of zooplankton in this eddy was low above 50 m depth, with values around 3 to 4×10^3 ind. m^{-3} , and high below 50 m depth, with values around 6.5×10^3 ind. m^{-3} (Fig. 2). In the east, 2 cyclonic eddies with oceanic water was identified, and along the western rim of our study area strong currents prevailed. In Phase 2 (Fig. 6: middle panel) a cyclonic eddy in the central area consisted of oceanic water and high zooplankton abundance, with maximum values ~ 7 to 8×10^3 ind. m^{-3} (Fig. 3: t3), while meanders

occurred further offshore. Abundance of zooplankton in the meanders varied with depth and area, being lower on the western side (Fig. 3: t4 west, 3×10^3 ind. m^{-3}) where coastal water dominated, and higher on the eastern side (Fig. 3: t4 east, 7×10^3 ind. m^{-3}) within oceanic water. The abundance was also high (6 to 7×10^3 ind. m^{-3}) in the frontal zone between the meanders and the cyclonic eddy.

In Phase 3 (Fig. 6: bottom panel) an anti-cyclonic eddy with coastal water and low abundance (Fig. 4: 3 to 4×10^3 ind. m^{-3}) was present just outside the 2 fjords. Further offshore (Fig. 4: t4 west, 8×10^3 ind. m^{-3} ; and t4 east, 6×10^3 ind. m^{-3}) 2 cyclonic eddies with oceanic waters and high zooplankton abundances were found. A fourth eddy was also identified in the eastern part of the study area, outside Tanafjord. This anti-cyclonic eddy consisted of coastal water and had a low abundance of zooplankton (1 to 2×10^3 ind. m^{-3}). Statistical tests show that the 2 cyclonic eddies contained significantly higher abundances of zooplankton than the 2 anti-cyclonic eddies (ANOVA, $p < 0.05$, Tables 1 to 3).

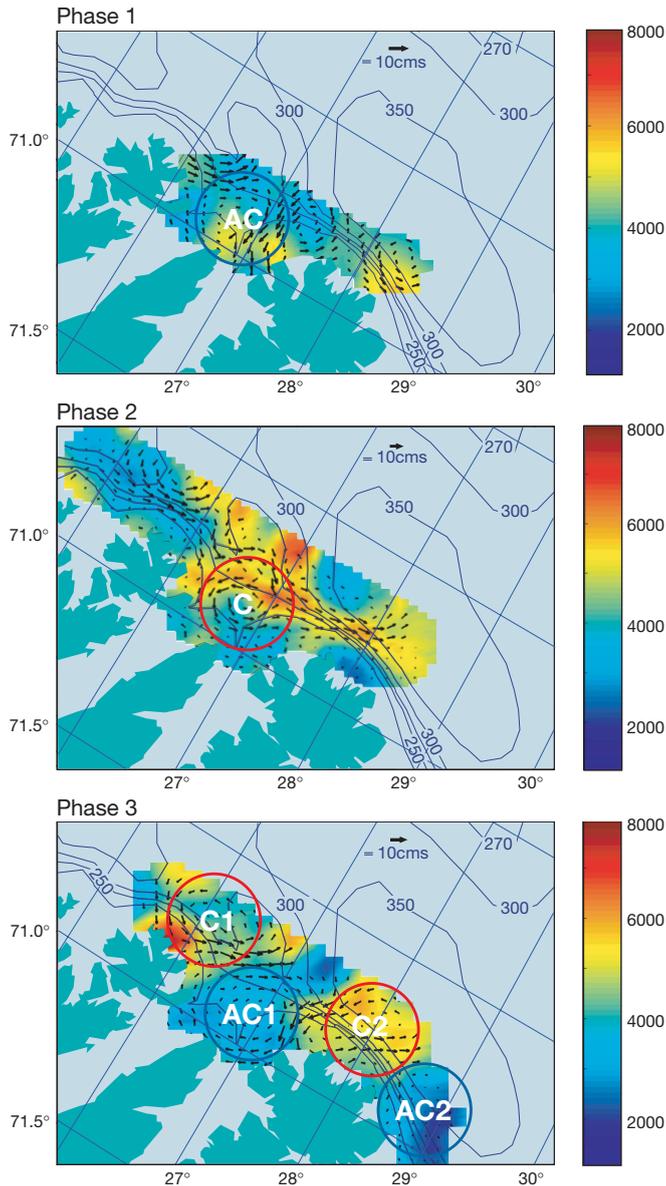


Fig. 6. Geostrophical current (arrows) and abundance (right colour bar, ind. m⁻³) of zooplankton at 50 m depth outside Porsanger, Laksefjord and Tanafjord in Phases 1 to 3. AC: anti-cyclonic eddy; C: cyclonic eddy

Zooplankton species in MOCNESS

In the study area, the zooplankton consisted essentially of copepods, which made up 82.2% of total abundance and comprised mainly *Calanus finmarchicus* (55.6%), *Oithona similis* (11.8%) and copepod nauplii (10.8%). *Metridia* spp. CI to III (2.2%) and *Oncaea borealis* F (1.8%) were found in low proportions. Other groups were *Oikopleura* spp. (5.7%), euphausiids (3.8%), echinoderm larvae (2.1%) and capelin larvae (~1%). The remaining group of species (>20) accounted for 5.2% of the total abundance in the net tows.

Table 1. Results of 2-factor ANOVA (transect and eddy) on physical structures identified during Phase 3 (28 to 30 May) (see Fig. 6). H₀: there are no differences in particle abundance between different physical structures (eddies)

Source of variation	SS	df	MS	F	p	F _{crit}
Transect	5381093	2	2690547	4.99	0.00866	3.09
Eddy	91010167	3	30336722	56.29	0.00000	2.70
Interaction	16174238	6	2695706	5.00	0.00017	2.19
Within	51739139	96	538949			
Total	164304637	107				

Table 2. Mean (±SE) abundance of particles (ind. m⁻³) in eddies (C: cyclonic; AC: anti-cyclonic) along Transects t4, t5 and t6 during Phase 3

Transect	Eddy			
	C1	AC1	C2	AC2
t4	5295 ± 564	3664 ± 193	4669 ± 141	2777 ± 288
t5	3850 ± 141	3141 ± 194	5647 ± 117	2408 ± 131
t6	3917 ± 158	2861 ± 153	4671 ± 253	2793 ± 243

Table 3. Student's t-tests (with Bonferroni corrections) comparing particle abundance in eddies (C: cyclonic; AC: anti-cyclonic) in Transects 4 to 6. *Significant difference at p < 0.05 between eddies; ns: no significant difference

Eddy	AC1		C2			AC2			
	t4	t5	t6	t4	t5	t6	t4	t5	t6
C1	ns	ns	*	ns	*	ns	*	*	*
AC1				*	*	*	ns	ns	ns
C2							*	*	*

DISCUSSION

Zooplankton abundance and biomass

We found distinct differences in zooplankton abundance and biomass between coastal and oceanic waters in our study area. The water masses were distinguished by temperature and salinity. Zooplankton abundance and biomass were higher in oceanic waters than in coastal waters (Figs. 2 to 4). This trend is consistent with the findings of Dalpadado et al. (2003), who found the highest abundance and biomass of zooplankton in Atlantic water, followed by mixed coastal and Atlantic water (termed 'oceanic' in the present study), while coastal water displayed low abundances. Dalpadado et al.'s (2003) study was conducted in the Barents Sea from August to October in 1986 to 2000, and although their data are from autumn and ours from spring, we can assume that there may be persistent

abundance and biomass differences between these 2 water types throughout the year. Falkenhaus et al. (1997) examined the zooplankton community within a fjord in northern Norway during spring and found that the community structure changed from the innermost to the outermost stations concurrent with changes in the hydrographic structure. They also found that the abundance of the recruiting generation of *Calanus finmarchicus* steadily increased from the outer to the inner stations during the productive season (minimum in March to maximum in July/August), demonstrating that *C. finmarchicus* was advected from the outer area into the fjord during this time. In the early part of the productive season, the abundant *C. finmarchicus* has its source area offshore and is transported steadily onto the shelf, i.e. the source populations of zooplankton clearly differ between coastal and oceanic waters, explaining the differences in abundance and biomass in different types of water. On-shelf transport of zooplankton biomass (primarily composed of *C. finmarchicus*) is a unique feature of northern Norwegian coastal regions, which enhances coastal biomass build-up during the early part of the productive summer season (Tande 1991). This may differ from other coastal productive areas, such as the California Current and the Benguela Current, where local zooplankton productivity is driven by upwelling and enhanced primary production.

Eddies

The area investigated was highly dynamic, with rapid changes in currents and in the properties of the water masses. The hydrodynamic conditions are described by Pedersen et al. (2005), whose study revealed non-linear mesoscale eddies translating eastward, following the shelf break. Anti-cyclonic eddies contained coastal water, while cyclonic eddies contained oceanic water. In further offshore areas, meanders and mesoscale jets were found. The properties of the water masses indicated mixing between warm, saline Atlantic water and cold, less saline Norwegian coastal water. The translation speed of these mesoscale eddies was approximately 7 km d^{-1} . Their formation is due to interactions between the Norwegian Coastal Current and bathymetric irregularities (Ikeda et al. 1989).

A 2-factor (transect and eddy) ANOVA revealed significant abundance differences in the 4 eddies identified in Phase 3 (Table 1). The 3 outer transects (Factor 1) were also significantly different ($p < 0.01$) from each other, probably representing a change from a coastal (fewer particles) to an oceanic (more particles) regime. More importantly, the eddy factor

(Factor 2) was highly significant ($p < 0.000$), representing synchrony between cyclonic eddies and particle abundance, and the post-hoc *t*-test pattern is close to an optimal diagonal diagram: $(C1 = C2) \neq (AC1 = AC2)$, where C = cyclonic and AC = anticyclonic (Table 3). The interaction term (transect \times eddy) was also significant, probably due to the fact that the 2 anti-cyclonic eddies are closer to the coast (see Fig. 6, bottom panel).

Cyclonic eddies have been shown to affect abundance and distribution of plankton and fish larvae by entrapment of planktonic organisms (Nakata et al. 2000, Okazaki et al. 2002), and can play an important role in primary production through upwelling of nutrient rich deep water to the euphotic surface layer. This may then cause enhanced zooplankton production followed by increased ichthyoplankton survival and recruitment (Kimura et al. 1997, Nakata et al. 2000). For an upwelling event to have any effect on secondary production, the cyclonic eddies would have to endure for several weeks (Dower & Mackas 1996), whereas the eddies in our study area are believed to endure over a temporal scale of days (or at most 1 to 2 wk: Dag Slagstad, SINTEF, Trondheim, Norway, pers. comm.). Consequently, any upwelling and subsequent phytoplankton growth in these cyclonic eddies would be too short-lived to induce development and growth of zooplankton.

Biological composition of eddies

During our study, the cyclonic eddies all contained oceanic water, high zooplankton abundance and biomass (for Phase 3, see Table 2). The shapes of the size spectra found in cyclonic eddies were also similar, and it is therefore probable that their biological composition was similar, since the waters in these eddies were of the same origin. The 3 anti-cyclonic eddies were all near-shore and contained water of coastal origin, with low abundance of zooplankton. However, as there was a clear variation in biomass and the shape of their size spectra also differed, their biological composition must also have differed (Fig. 5A,B,E,F). What is the cause for differences in zooplankton composition within coastal waters? A variable degree of mixing between coastal and oceanic waters may play a role, since the abundant zooplankton in cyclonic eddies eventually will be mixed with those in coastal waters as these eddies erode and disintegrate (Dalpadado et al. 2003). By definition, coastal water has salinities below 34.5‰, while Atlantic water has salinities higher than 34.95‰ (Rey 1981), and shelf water is a mixture of the two. During Phase 3, the coastal water outside Porsanger-

fjord and Laksefjord (Fig. 5E) was not influenced by oceanic water (as can be inferred from the salinity of <34.5‰: see t1 and t2 in Fig. 4), and biomass was low. The coastal water in the same position in Phase 1 was influenced more strongly by oceanic water (salinity ~34.7‰: see t1 and t2 in Fig. 2), and abundance and biomass were higher (Fig. 5B). Contrary to the effect of advection, we believe that in the coastal water outside Tanafjord in Phase 3 (Fig. 5F), the enhanced biomass derives from the coastal area through variable hatching of capelin larvae (see next subsection).

Capelin larvae

In the anti-cyclonic eddy, consisting of coastal water near the outlet of Tanafjord in Phase 3, the OPC size spectrum differed from that of other areas (Fig. 5F). It showed low abundance, but high biomass and a distinct peak around 1.3 mm ESD, which, based on our findings in net tow samples, we interpret as being due to newly hatched capelin larvae. The average size of capelin larvae just after hatching is approximately 1.21 (± 0.17) mm ESD (measured using the same field-OPC in our laboratory). Net tows were conducted in the area occupied by the anti-cyclonic eddy 3 d prior to the OPC transects in Phase 3. Capelin larvae were found in the net samples at all stations outside Tanafjord. The net tow samples confirm the patchy distribution of the capelin larvae, which contributed 5 to 38% of total abundance at the various stations. There were only a few net tows covering a very limited area, which may well have missed dense capelin larvae patches, whereas the towed SCANFISH-OPC measurements covered a much larger area, and provided more accurate estimates of their distribution. Since this area is highly dynamic, with coastal jets and translating eddies (Pedersen et al. 2005), the water mass can be replaced in certain areas within a few days. However, it is likely that larvae were continuously hatching in the area throughout the whole sampling period in May.

Within the size range of capelin larvae (1.21 \pm 0.17 mm), only *Calanus finmarchicus* CIV, *Oikopleura* spp. and capelin larvae contributed to zooplankton abundance. When zooplankton in coastal water are enriched by a cohort of recruiting *C. finmarchicus*, consisting of Stages CI to CIV in a parcel of oceanic water, a peak should occur between 0.5 and 1.5 mm ESD (the ESD range of CI to CIV larvae). As no such peak occurred in the size spectrum (which remained low at <1 mm ESD), we therefore believe that the increased biomass was not due to a pulse of *C. fin-*

marchicus CIV (i.e. mixing of waters). The larvaceans *Oikopleura* spp. are fast-growing opportunists that can double their abundance in a period of a few days (Dower & Mackas 1996), but patches of *Oikopleura* spp. have not previously been recorded in the southern Barents Sea (Henriksen 2000). Thus, we conclude that capelin larvae predominately contributed to this size range in the size spectrum (Fig. 5F).

Importance of eddies for capelin recruitment

The eddies in the spawning and hatching habitat of capelin in the southern Barents Sea are formed by different mechanisms (Ikeda et al. 1989, Johannessen et al. 1989) and are relatively small and of short duration (Loeng & Sætre 2001, Ingvaldsen et al. 2002). However, their impact on the biological community can be significant, by transporting biota into the region as food supplies, or transporting larvae out of this region. On the east coast of North America, meandering fronts along the shelf break create rings and eddies which carry large volumes of waters offshore into the Sargasso Sea, significantly reducing the successful recruitment of fish species on the shelf (Wroblewski & Cheney 1984). Meanders and eddies also exist in our study area. Although the most significant eddy transport follows the shelf, it is also clear that mesoscale eddies are translated on-shelf (Pedersen et al. 2005). The intrusion of eddies of oceanic water and plankton (both meso- and protozoan) onto the shelf may increase the temperature, provide food for fish larvae and seed the shelf water, before being eroded. The anti-cyclonic eddies are most probably formed through the interaction of fronts, jets and topographic steering. The absolute impact of these eddies on growth and survival conditions of the entrapped capelin larvae are still unknown. However, it is clear that these physical features will transport capelin larvae to offshore regions, where mortality may be minimised through higher growth rates due to elevated food supply and temperature (Pepin 1991). Thus, the number of springtime eddies formed and their phasing with the spawning and hatching cycle can be important to capelin recruitment variability (Logerwell & Smith 2001, Logerwell et al. 2001).

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