

OBSERVATIONS ON BEHAVIOUR AND DISTRIBUTION OF *NATATOLANA BOREALIS* (LILLJEBORG) (CRUSTACEA, ISOPODA)

PER-OTTO JOHANSEN & TORLEIV BRATTEGARD

SARSIA



JOHANSEN, PER-OTTO & TORLEIV BRATTEGARD 1998 10 09. Observations on behaviour and distribution of *Natanolana borealis* (LILLJEBORG) (Crustacea, Isopoda). – *Sarsia* 83:347-360. Bergen. ISSN 0036-4827.

Natanolana borealis were collected with baited traps at two localities near Bergen, Norway in 1977-78 and 1991-96, and faunistic surveys carried out with grab, detritus sledge and epibenthic sampler in Norwegian waters, including the northern Norwegian Trough, from 1981 to present, and in Faroese waters in the years 1987-90.

Catches of *N. borealis* by epibenthic sledge in the Norwegian Trough were significantly larger at night than in daylight. Laboratory observations and trap experiments indicate that feeding activity is regulated by *in situ* illumination and degree of hunger. The species appears to be an opportunistic omnivore scavenger and might use a combination of 'sit and wait' and 'swim across the current' foraging strategies. The content of the anterior hindgut averaged 42 % of the total body dry weight after unlimited access to food for 24 h. A full gut enabled survival without further feeding for > 6 months. The assimilation efficiency of *N. borealis* feeding on fish flesh was estimated to be > 90 %.

Recent records of *N. borealis* indicate a northern distribution limit at ca 70°N on the coast of Norway. At the Faroe Islands it was only found in water-masses dominated by Atlantic Water and not in water-masses dominated by the colder Arctic Intermediate Water or the cold Norwegian Sea Bottom Water. The usual temperature range of waters inhabited by *N. borealis* in the East Atlantic is about 5-14 °C. It occurs in a wide range of sediments (from gravelly sand to fine silty clay) into which it burrows.

Per-Otto Johansen, N-5240 Valestrandsfossen, Norway. – Torleiv Brattegard, University of Bergen, Department of Fisheries and Marine Biology, Bergen High-Technology Centre, N-5020 Bergen, Norway. E-mail: torleiv.brattgard@ifm.uib.no

KEYWORDS: *Natanolana borealis*; behaviour; distribution; feeding; isopod; scavenger.

INTRODUCTION

Natanolana borealis (LILLJEBORG, 1851) is a voracious scavenger, attacking any dying and dead fish, leaving only skin and skeleton (SCHJØDTE 1866; HANSEN 1890). It plagues long-line fisheries in the north-western North Sea (LØKKEBORG 1990) and severely affects catches of fish in bottom set gill-nets south-west of the British Isles (BERROW 1994).

A commercial company has investigated the possibility of using substances present in *N. borealis* as additives in feed pellets for young fish in culture (LARSEN 1991).

Recently WONG & MOORE (1995) examined aspects of the feeding of *N. borealis*, TAYLOR & MOORE (1995) the burrows and physiological adaptations to a burrowing lifestyle, and WONG & MOORE (1996) presented observations on the activity, and life history.

N. borealis has been reported from the coast of Norway to the coast of West Africa in the East Atlantic and off South Carolina and Florida in the West Atlantic

(KEABLE & BRUCE 1997). It has been reported frequently from Norwegian coastal waters south of Trondheimsfjorden (ca 64°N), but has been assumed to be absent (DONS 1935, as *Cirolana borealis*) or rare (NIELSEN 1967) north of Trondheimsfjorden.

In this paper we add some observations on the behaviour of *N. borealis* based on field and laboratory experiments. Records of *N. borealis* from the northern border of its distribution area in the northeastern Atlantic are reviewed and some aspects of the distributional ecology of *N. borealis* are discussed.

MATERIAL AND METHODS

Natanolana borealis was caught in baited traps deployed in 1977-78 and 1991 at 90-100 m depth in Skogsvågen (60°16'N, 5°06'E) south of Bergen, and at 40-90 m depth in Raknesvågen (60°34'N, 5°26'E) north of Bergen in 1992-96. The temperature in the near-bottom water was 6.6-9.9 °C in Skogsvågen and 7.4-8.5 °C in Raknesvågen (JOHANSEN 1980, 1996).

JOHANSEN & BRATTEGARD (1996) described the different traps used. The main trap used in Skogsvågen was a PVC-tube per-

forated with small holes (3 mm diameter) and an entrance funnel in one end. The main trap used in Raknesvågen was a cylinder-shaped metal trap with plankton net (1 mm mesh size) surrounding the funnels at both ends. The diameter of the entrance funnel holes were about twice the maximum width of adult *N. borealis*. The traps were usually baited with frozen fish (cod, saithe, ling, tusk, halibut, salmon or silvery pout) and retrieved from the bottom after 24 h.

Three baited traps were placed on hard bottom and on soft bottom, respectively, near Raknesvågen in September 1992. The distance between the soft and hard bottom collection sites was 500 m. The depth at both sites was 40 m. The bottom types of the localities were examined by grab sampling.

N. borealis was also searched for in samples of hyperbenthos and benthos taken along the coast of Norway using a modified Rothlisberg & Pearcy epibenthic sampler (RP-sledge; see BRATTEGARD & FOSSA 1991): 103 samples from the Norwegian shelf and Norwegian Trough taken between 87 and 517 m depth (near-bottom water temperature 4.0–10.0 °C), and 208 samples from Norwegian fjords taken between 31 and 1280 m depth (near-bottom water temperature 6.3–11.8 °C). Numbers of specimens were standardized to numbers per 1000 m haul length. The differences between day and night catches were tested using the Mann-Whitney U-test.

Per J. Johannessen and his co-workers at the Department of Fisheries and Marine Biology, University of Bergen have published 143 reports between 1990–96 (in the report series *IFM Rapport*, ISSN 0803-1924) containing species lists from 824 grab stations sampled from 4.5 to 1100 m depth on the western coast of Norway from ca 59°40' to 67°17'N (Per J. Johannessen pers. commn). These lists have been searched for records of *N. borealis*.

N. borealis was encountered near the Faroe Islands during the BIOFAR programme 1987–90 using a RP-sledge and a detritus sledge (SNELI 1998). The RP-sledge was deployed 76 times at depths between 35 and 2420 m, and the detritus sledge was deployed 165 times (between 70 and 1223 m). For data on the BIOFAR stations, see NØRRETVANG & al. (1994).

Survival

Survival of individuals kept separately in 10 × 4 × 5 cm glass jars was recorded. The jars were placed in running sea water. Survival was examined on 20 arbitrarily chosen individuals after unlimited access to food for 24 h. The temperature of the sea water varied between 6.5 and 10.0 °C during the observation period of 448 days.

Activity at day and night

N. borealis was caught in 20 separate day and night deployments in 1993–1994 at 40–50 m and 80–90 m in Raknesvågen. The day catches were caught under different light conditions (sunshine vs total cloud cover) in traps set after dawn and retrieved before sunset. Catch sizes were expressed as catch (number of individuals) per unit of effort (10 h on the bottom). During trap deployments daylight illumination 5 m above sea level was recorded automatically every third minute by a Silkeborg pyrheliometer (± 5 %) connected to a datalogger. The illumination sensitivity related to temperature variation of the pyrheliometer was automatically corrected. The amount of submarine daylight at 80 m was estimated roughly for a two-layer

situation (brackish water on top of normal sea water) following the procedures advocated by WEINBERG (1976). The differences between day and night catches were tested using Wilcoxon's non-parametric test.

Burrowing

The burrowing of 13 individuals from Skogsvågen was studied in a dark room in a tank (30 × 10 × 25 cm) carefully filled with a 20 cm thick layer of natural sediment from Skogsvågen. After 24 h one tank wall was removed and the digging depth of the isopods in the sediment measured. Burrowing behaviour of starved *N. borealis* from Raknesvågen was studied in a beaker filled with 8 cm coarse sand and sea water at 12 °C.

Feeding

Feeding of *N. borealis* was studied using specimens trapped with the bait enclosed in bags made of double plankton cloth (1 mm mesh size) to prevent direct access to the bait. Specimens from Skogsvågen were given fish flesh for 24 h two days after trapping. After feeding the anterior hindgut was removed from 27 randomly selected specimens and the body and the content of the anterior hindgut were dried separately. Two days after being trapped the feeding behaviour was observed on 8 specimens from Raknesvågen when given fish flesh in beakers filled with sea water at 12 °C. After feeding the anterior hindgut was removed and the content studied with a dissection microscope.

Fish fluid was produced by leaving fish flesh overnight in sea water and filtering the sea water through 0.168 mm mesh size.

Assimilation

Assimilation efficiency (U' , see CONOVER 1966) of *N. borealis* was estimated using the ratio between ash-free dry weight (AFDW) and dry weight (DW) in the ingested food (I') and the faeces (E'): $U' = (I' - E') \cdot 100 \% / [(I' - E') \cdot I']$. Nine out of ten specimens examined from the pool of individuals used had an empty anterior hindgut, while one had some food in the hindgut. After being offered flesh of saithe (*Pollachius virens*) without skin for 24 h, twice during a fortnight, 28 adult *N. borealis* were transferred to individual glass jars. The temperature of the laboratory sea water was between 5 and 9 °C during the experiment. Biological material was dried for 24 h at 70 °C and burned in a muffle furnace for 12 h at 500 °C. Biomass was determined with an accuracy of ± 0.02 mg.

RESULTS

Survival

N. borealis lived for long periods under laboratory conditions and even moulted. After being fed fish, 9 males and 11 females were kept in separate beakers without access to food. Males survived longer than females. The first male died on day 276 and the next on day 290, 324, 335, 339, 349, 395, and 407. The first female died on day 7, and the next on day 43, 101, 104, 122, 266, 290, 315, 328, and 429. When the experiment was terminated after 448 days, one individual of each sex was still alive.

Nine of the 11 females were developing eggs during this period. Through the transparent venter of the females the ripe eggs could easily be seen as a large, light yellow mass, different from the white, orange or yellow hepatopancreatic glands.

When well-fed *N. borealis* were handled, they often vomited some of the content of the alimentary tract, but they did not seem to suffer from this.

Search for food

More than 150 newly trapped *N. borealis* were kept in a tank without sediment and without access to food. All the animals were lethargic in daylight and none of the animals could be induced to swim by disturbing the surface water mechanically. In the evening and during the night most animals swam around.

After a frozen piece of herring (*Clupea harengus*) was put gently into the surface water, most of the animals were swimming about half a minute later. The search for the fish flesh seemed to be random within the relatively small space of the tank. Within a short time the piece of fish was almost completely covered by *N. borealis*. After feeding, the isopods became lethargic by day and night.

More than 200 newly trapped *N. borealis* were kept in a tank without sediment but with access to food. In daylight all were lethargic. After a frozen fish was lowered into the surface water only 3-4 individuals became active after several minutes. The low number of active individuals persisted for 30 minutes (the observation period).

The effect of fish odour was tested on 20 individuals of *N. borealis* kept in a small container without access to food. After five drops of sea water containing fish fluids were introduced to the test-group all individuals became very active within a few seconds. The activity lasted 5-10 minutes. When more drops were added the same intense response occurred again. Five drops of sea water without fish fluids introduced to the control group elicited no reaction. The experiment was repeated 24 h later. The former test-group was then the control-group, and vice versa. Once more, the test-group showed a very high activity for 5-10 minutes, while the control-group showed no activity.

Day and night activity

Baited traps deployed in April 1993 during the night, at depths of 40-50 m and 80-90 m, caught significantly more *N. borealis* than identical baited traps deployed during daytime (Table 1). During daytime none was caught at 40-50 m depth, but 1-2 specimens were caught at the darker site at 80-90 m depth.

The catches at 80-90 m were significantly lower on sunny days than at night ($p = 0.014$) (Fig. 1). On cloudy

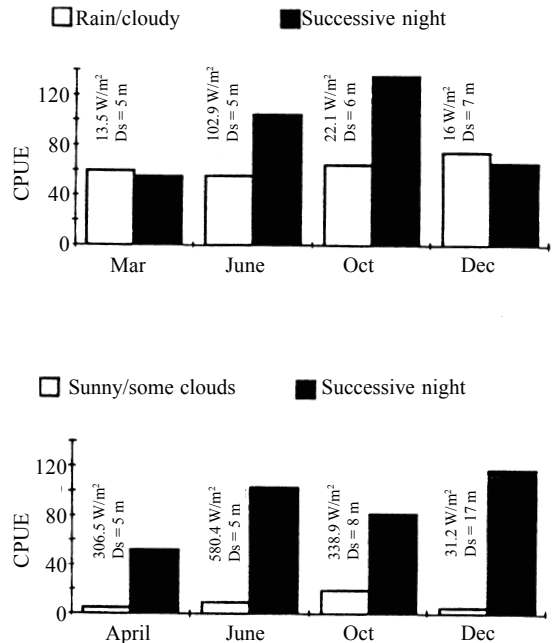


Fig. 1. Numbers (Catch Per Unit Effort) of *Natatolana borealis* caught in successive day and night deployments of baited traps at 80-90 m in Raknesvågen, western Norway in 1994. Average illumination (W/m²) and Secchi depth (Ds) are given for each daylight deployment.

days there was no significant difference between day- and night-catches ($p = 0.24$). Irradiance measured in Herdlafjorden (part of the fjord system in which Raknesvågen is situated) from 0 to 60-70 m and extrapolated to 80 m to in March, May, October, and December 1994 showed that 0.08-0.008 % of the surface irradiance (500 nm) remained at 80 m depth (Rune Rosland pers. commn). The average *in situ* day irradiance (500 nm) at 80 m in Raknesvågen was estimated roughly to be between 10^{-2} and 10^{-4} watt · m⁻².

The catches of *N. borealis* in successive day and night RP-sledge hauls along a transect in the Norwegian Trough at 135 to 382 m depth in March 1985 (BRATTEGARD & FOSSÅ 1991) were significantly higher at night ($N = 12, 0.01 < P < 0.025$), especially at 176 to 314 m depth ($N = 8, 0.0025 < P < 0.005$).

Table 1. Numbers of *Natatolana borealis* caught in baited traps at 40-50 m and 80-90 m depth at night and on sunny days in Raknesvågen, western Norway in April 1993.

Depth	Night 2-3 April	Day 3 April	Day 5 April	Night 5-6 April
40-50 m	98	0	0	84
80-90 m	56	1	2	100

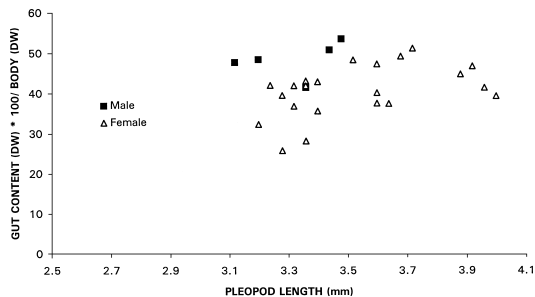


Fig. 2. *Natatolana borealis*: Relation between the capacity of the anterior hindgut and pleopod length of 27 specimens from Skogsvågen, Raunefjorden, western Norway.

Burrowing

The sediment taken by core sampler from Skogsvågen consisted of oxidized sandy silt through the entire sample depth (6 cm). The sediment in Raknesvågen at 40 m depth was coarser consisting of 46 % clay/silt, 30 % sand and 24 % gravel (TVEDTEN & al. 1993).

Three traps, which were placed on soft bottom at 40 m depth off Raknesvågen, trapped 28, 47, and 60 specimens. When the same traps were deployed at 40 m depth on a rocky hard bottom 0, 0 and 5 specimens of *N. borealis* were trapped.

When *N. borealis* began digging into sediment of sandy silt, the body was positioned at 30-40° inclination head down. This resulted from the posterior legs being significantly longer than the anterior. Initially the pleopods beat rapidly before the highly setose pereopods pushed the sediment sideways and backwards. The highly setose pereopods pushed away the compact sediment and the isopod was covered by sediment within 0.5-2 minutes.

N. borealis was found from 2.5-6.5 cm below the sediment surface in laboratory aquaria; on average their position was 4.4 cm (SD = 1.3, N = 13) from the surface. There was no correlation between depth and pleopod length ($r = 0.017$) and no significant difference between males and females in the positioning below the sediment surface. After having made a burrow in the sediment, some individuals were observed close to the opening of the burrow with the front part visible and the second antennae pointing upwards, above the sediment. *N. borealis* kept in a large aquarium with transparent walls under artificial light conditions for several months had made permanent burrows to about 10 cm below the sediment surface. Several brooding females were found among these animals.

The concealment of 10 individuals digging into coarse sand (Raknesvågen) was complete after 30-60 seconds but the burrows made collapsed when *N. borealis* emerged.

Feeding

N. borealis was sometimes observed eating dead or dying conspecifics in the laboratory. The soft parts were primarily ingested leaving most of the exoskeleton. Examination of gut contents of *N. borealis* kept in a storage tank together with amphipods (*Tmetonyx* spp.) confirmed the observations of cannibalism and that it also could eat *Tmetonyx* spp.

Keeping large numbers of *N. borealis* in containers without sediment was, however, never a problem as long as the isopods were fed dead fish. *N. borealis*, which was offered pieces of fish with skin, searched the piece until they reached exposed flesh. *N. borealis* was once observed eating along the edge of a wound in the fish skin and once along the lips of a cod after an unsuccessful attempt to penetrate the skin of the fish. They crawled slowly while they fed. The gut content of these individuals consisted of slender tissue slices with a length of 0.5-3 cm. Slender slices of food were occasionally observed in vomited gut contents of newly trapped *N. borealis*.

Specimens offered fish flesh without skin finished feeding in less time than those offered fish totally covered with skin. The observed feeding of *N. borealis* lasted 3-13 minutes. When the gut was filled with dark material the outline of the gut was visible from the dorsal surface. The digestive system of *N. borealis* narrows considerably at the mouth and in the pleon, with the broadest part being in the posterior pereon. The flexible anterior hindgut of *N. borealis* is slightly pigmented. When fish carrion was available, the animals filled the anterior hindgut. The internal organs were pressed against the body walls and the soft ventral integument swelled as a result of the full gut. None of the examined females had visible ova in their ovaries.

The relative amount of food ingested seems to be independent of the size of the animal (Fig. 2). The content of the gut varied from 25.7 to 53.4 % of the total body DW. The average content was 48.3 % for the males and 40.5 % for the females. For the total sample the average content of the anterior hindgut was 42 % (SD = 6.77) of the total body DW.

Some sediment was occasionally observed in the anterior hindgut of recently captured juvenile and adult *N. borealis*. This consisted of fine and coarse particles, including uncrushed specimens of some Foraminifera species. In some cases also polychaete setae and echinoid spine fragments were observed in the anterior hindgut.

Assimilation

The AFDW of fish flesh which was used to feed *N. borealis*, was on average 93.7 % (SD = 0.30, N = 5) of the total DW. When fish flesh was kept in sea water for

24 h, organic material leaked out resulting in relatively lower AFDW, on average 81.6 % (SD = 0.89, N = 10) AFDW. The first faeces of *N. borealis* were found 37 days after ingestion. The organic content of pooled samples of faeces averaged 21.6 % (SD = 3.35, N = 7). The assimilation efficiency calculated (formula of CONOVER 1966) from fish flesh which was not kept in sea water, was on average 98.1 % (SD = 0.39, N = 7). The assimilation efficiency calculated from fish flesh which was kept 24 h in sea water, was on average 93.7 % (SD = 1.32, N = 7).

Northern distribution

New and old records of *Natatolana borealis* made north of 61°N, from the Faroe Islands to northern Norway, are listed in Appendix 1. Most of the records are also shown in Fig. 3. The northernmost record of *N. borealis* is from 70°10'N, 17°53'E at 324–333 m, sandy mud, WNW of Rebbenesøy, Troms County.

N. borealis was caught more often by RP-sledge on the Norwegian shelf and in the Norwegian Trough than in Norwegian fjords (Table 2; Appendix 1). On the shelf and in the Trough the highest frequency of catches (34 %) and the largest catches (up to 135 specimens per 1000 m²) were taken in the 200–299 m depth zone. In Norwegian fjords it was caught only twice: in Risnefjorden at 110 m depth, and in Sulafjorden at 450 m.

The range of temperature of the near-bottom water at the deployment sites where *N. borealis* was caught was 6.5–8.2 °C.

N. borealis was present in samples at 37 out of 824 grab stations sampled by Per J. Johannessen's group. *N. borealis* occurred in samples from between 15 and 205 m depth. The northernmost record with grab was made 15 km west of Bodø at 67°17.1'N, 14°00.9'E.

At the 37 stations 125 samples were taken of which 49 contained a total of 70 specimens of the isopod: 41 samples with one specimen in each sample, 4 samples with 2 specimens, one sample with 3 specimens, 2 samples with 4 specimens, and one sample with 10 speci-

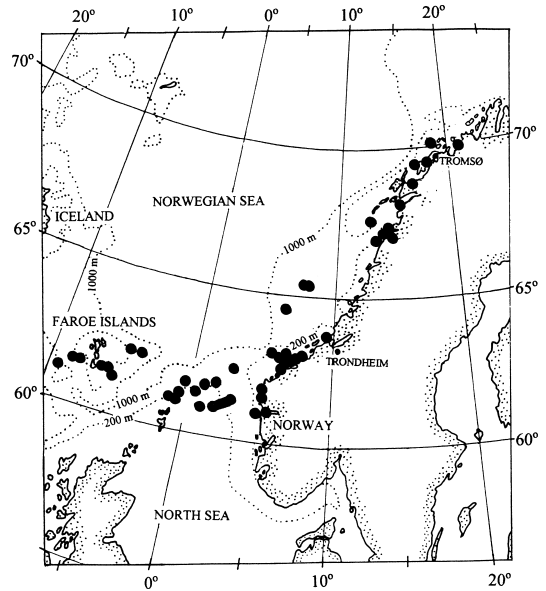


Fig 3. Records of *Natatolana borealis* from north of latitude 61°N, from the Faroe Islands to northern Norway. All records with details are listed in Appendix 1.

mens. The number of specimens per station where *N. borealis* was caught varied from 0.2 (SD = 0.447, N = 5) to 2.0 (SD = 4.47, N = 5) specimens per 0.2 m², or 1.0–10.0 per m².

The sediment of grab samples in which *N. borealis* occurred varied in its composition from silty clay (98 % clay/silt, 2 % sand) via sand (96 % sand, 4 % clay/silt) to gravelly sand (66 % sand, 26 % gravel, 8 % clay/silt) with organic content, measured as «loss on ignition», between 2.3 and 10.6 %.

The temperature of the near-bottom water at the grab stations where it was caught was between 5.0 and 13.8 °C.

In the area around the Faroe Isles specimens of *N. borealis* were caught in 3 RP-sledge hauls and 4 detritus

Table 2. Number of sites (S) and deployments (D) of Rothlisberg & Percy epibenthic sampler (RP-sledge) with number of records (R) of *Natatolana borealis* in depth zones in the Norwegian Trough and Norwegian shelf waters (T), and in Norwegian fjords (F) north of 61°N.

Depth zone (m)	ST	STR	DT	DTR	SF	SFR	DF	DFR
31–99	1	0	1	0	10	0	17	0
100–199	20	4	29	6	21	1	38	1
200–299	27	8	37	12	22	0	40	0
300–399	17	2	24	6	16	0	20	0
400–499	11	0	11	0	17	1	36	1
500–599	1	0	1	0	9	0	19	0
600–1280	0	0	0	0	21	0	38	0
Sum	88	14	103	24	116	2	208	2

sledge hauls during the BIOFAR programme. Catches of *N. borealis* were confined to depths between 235 and 350 m (see Appendix 1).

The average bottom temperatures at all the RP-sledge (76) and detritus sledge (165) hauls in the Faroe area ranged from -0.92 ± 0.02 to 9.1 ± 1.8 °C. *N. borealis* were collected from six stations in Faroese waters within a temperature range of 6.5 ± 1.6 to 7.9 ± 0.8 °C and from one station (Stn 174) where the estimated average temperature of the highly variable bottom water is 6.1 ± 6.5 °C.

DISCUSSION

Survival

After only one meal, *N. borealis* could live for long periods (more than 448 days) under laboratory conditions and even moult, and many females had produced almost ripe eggs. WONG & MOORE (1995) estimated from the trend in change of WW that the acquired weight from a single meal was reduced by 50 % in about 100 days. They also kept *N. borealis* separately for at least four months without feeding but the specimens became lethargic and in poor condition.

The observed vomiting can be explained as a reaction to unfavourable conditions in the laboratory. ZWAAN & SKJOLDAL (1979) noted that when *N. borealis* was subjected to experimental anoxia, they expelled their gut contents. If vomiting occurs in the habitat it could be a way of avoiding an attacking predator as the releasing of food may confuse a predator.

Search for food

Response to food odour involves sensory organs situated on the antennules and the antennae in *N. borealis* (WONG & MOORE 1995).

Introduction of diluted fish fluids to *N. borealis* resulted in immediate activity which ceased soon after. When more fluid was introduced, i.e. an increase in concentration, the activity recommenced. The gradual decrease of activity indicate olfactory fatigue at constant odour concentration level.

Presence of odour gradients may be necessary to stimulate search activity in *N. borealis*. JOHNSON (1976a) observed *Cirolana harfordi* LOCKINGTON swimming towards the bait in a characteristic zigzag pattern while waving the antennae rapidly. WONG & MOORE (1995) suggested a more haphazard swimming towards the bait *in situ* by *N. borealis*. The lysianassid amphipod *Boeckosimus affinis* (HANSEN) swam with a back-and-forth 'sweeping' pattern outside the odour plume and swam directly upcurrent towards the bait within the odour plume (BUSHDOSH & al. 1982). Olfaction, combined with

rheotactic swimming behaviour, is probably the principal means of detection and localisation of bait by lysianassid amphipods (SAINTE-MARIE 1992).

Day and night activity

The active search of *N. borealis* for bait in the traps, during April 1993, took place only at night at 40 m depth. Some specimens which were caught at 90 m in day-time, indicate a possible longer feeding period in deeper water. The active feeding period at 90 m seems to be further extended on cloudy, rainy days by low surface illumination and reduced transparency in the sea. An increased period of feeding activity should then be expected in deeper water. This agrees with WONG & MOORE'S (1996, table 4) catches at 190 m off Sgat Mohr which usually contained more than 150 specimens of *N. borealis* during mid-day after 2 h 45 min deployment.

The spectral sensitivity of the eye of *N. borealis* has a maximum between 495 and 528 nm corresponding to a visual pigment of 514 nm (LINDSTRÖM & NILSSON 1983). The threshold of damage of the retinula cells lies between 0.47 and 4.9 watt · m⁻² and thus the eye of *N. borealis* is strictly adapted to dim light environment (NILSSON & LINDSTRÖM 1983). *N. borealis* presumably avoids illumination above the level of retinula cell damage. The eye is well adapted to 0.001 % of the surface irradiance (500 nm), which in Norwegian northern latitudes can reach $4 \cdot 10^{-3}$ watt · m⁻² at noon in summer (LINDSTRÖM & NILSSON 1983). This corresponds roughly to the light level at 100 m depth in oceanic water.

Unfed specimens of *N. borealis* were attracted to carrion in daylight in the laboratory, while fed individuals were lethargic. Retinal damage (NILSSON & LINDSTRÖM 1983) of light-exposed individuals may have caused feeding activity in the laboratory during daytime.

The observed spontaneous nocturnal activity of unfed *N. borealis* at night in the laboratory accords with the endogenous circadian rhythm of spontaneous emergence from the substratum and swimming activity reported by MACQUART-MOULIN & KAIM-MALKA (1994). The irradiance level at 400 m in the northwestern Mediterranean appears sufficient to synchronise the endogenous rhythm.

The catches of *N. borealis* in RP-sledge from the Norwegian Trough and the shelf (Buagrunden and Ona) between 136 and 314 m depth were significantly higher at night than in daylight indicating swimming activity at night. Nightly swimming activity supports a 'swim across the current' strategy which will increase the chances of detecting up-current food falls.

The feeding activity of non-breeding *N. borealis* in the field seems to be mainly regulated by the *in situ* illumination and the degree of hunger. Breeding females do not feed *in situ* during incubation of eggs (JOHANSEN 1996).

Burrowing

N. borealis was caught on several kinds of soft bottom at the coast of Norway, such as clay, mud, sand and gravel and it seems to avoid hard bottoms. When baited traps were placed on hard bottom, fewer isopods were captured than on soft bottom. On hard bottom there is little, if any, sediment to hide in. The isopods must then swim a longer distance to reach the carrion. According to fishermen hooked fish attract more crustacean scavengers when the longlines are set on soft bottom than on rocky bottom.

N. borealis is able to dig in sediment varying from clayey silt to sand and can make burrows in sandy silt to silty sand reaching down to 10 cm below the sediment surface. It seems to dig in the same manner as WÄGELE & BRUCE (1989) reported for *N. pastorei* (GIAMBIAGI, 1925): the anterior pereopods push the sediment laterally and caudally and the posterior pereopods push the sediment caudally.

N. borealis from Loch Fyne swam rapidly head-first into consolidated mud, with sediment expelled behind them, helped by the beating activity of the pleopods (TAYLOR & MOORE 1995). Initial concealment was rapid, often taking no longer than 5 seconds, but the construction of the hole burrow took up to 24 h. The permanent U-shaped burrows extended 7–10 cm into the sediment (TAYLOR & MOORE 1995). The sediment from Sgat Mohr, Loch Fyne was a sandy mud (TAYLOR & MOORE 1995; WONG & MOORE 1996) finer than that in Skogsvågen. The disparities in digging speed and digging behaviour of *N. borealis* reported from Loch Fyne and western Norway may be caused by the differences in the sediment composition.

TAYLOR & MOORE (1995) reported that *N. borealis*, within an artificial laboratory burrow, usually remained quiescent close to the opening. We observed individuals in the laboratory with their antennae raised extending from the opening in the sediment. This position may also indicate a 'sit and wait' foraging strategy. *N. borealis* may thus use a combination of 'sit and wait' and 'swim across the current' foraging strategies.

Feeding

Various food items have been reported in the literature: bony fishes (see TATTERSALL 1905; NIERSTRASZ & STEKHOVEN 1930; ANON. 1969; BERROW 1994; WONG & MOORE 1996), cartilaginous fishes (NIERSTRASZ & STEKHOVEN 1930; BERROW 1994), and invertebrates (WONG & MOORE 1995). The occurrence of remains of slow-moving species such as infaunal polychaetes in the gut of *N. borealis* (WONG & MOORE 1995) may indicate opportunistic predation. Foraminifera found in the gut were not crushed but swallowed intact. This may indicate accidental swallowing of detritus when it is feeding

on bait on the bottom.

N. borealis consumed any food item that it was offered in the laboratory unselectively. It fed primarily on the soft parts of the fish and used more time to consume intact fish than fish cut into pieces. In spite of its powerful mandibles with sharp teeth, *N. borealis* finds tough skin and hard material of fish-scales difficult to cut. When it has a choice between several fish species it seems to prefer those with delicate or soft epidermis (BERROW 1994; P.-O.J. own obs.).

N. borealis has been found in fish roe several times (cod (RAITT 1929; HALVORSEN 1965; VADER & ROMPPAINEN 1985); saithe (BERLAND 1983); tusk (ANON. 1969)) and BERLAND (1983) reported it from the body cavity of a spurdog (*Squalus acanthias*). Fish infested by *N. borealis* do not always show any exterior signs of damage. It seems able to enter the opening of the anus and thereby the ovaries and other organs in the body cavity of living fishes (RAITT 1929; HALVORSEN 1965; also reported for *Cirolana diminuta* MENSZIES by STEPHEN & BRUSCA 1985).

Cannibalism of damaged or moulting individuals of *N. borealis* was frequently observed in traps and in tanks, as also observed by WONG & MOORE (1995). Intraspecific feeding might be an artifact due to crowding of unfed animals in the traps and the tanks. On the other hand, dead or dying conspecifics may be a possible resource in food-scarce environments.

We conclude that *N. borealis* should be classified as an opportunistic omnivorous scavenger.

Laboratory observations of *N. borealis* from western Norway showed that they needed only 3–13 min to fill their guts with fish flesh. This accords with 3–5 min reported by WONG & MOORE (1995). The time needed to fill the gut may depend partly on the pre-fed condition and partly on the condition of the food (soft vs. tough tissue). The food capacity of the anterior hindgut in relation to the total body DW of *N. borealis* was on average 42 % after feeding on de-skinned fish flesh. With the gut empty before the meal, *N. borealis* was able to increase the body DW by 73 %, on average. The body WW of *N. borealis* increased, on average, by 52 % (33–78 %); WONG & MOORE (1995) reported that the body volume in one animal expanded by 35.4 % and that return to pre-fed volume took some six weeks. When the alimentary tract was empty, the gut did not fill the visceral cavity of *N. borealis* (P.-O. J. own obs.). It may be expected that *N. borealis* is able to fill the anterior hindgut to some extent before the body volume increases. The proportion of the increased volume of *N. borealis* will then be less than the increase in WW after a single meal. CARVALHO & FOWLER (1985) found an average WW increase 26 ± 17 % ($N = 20$) in *N. borealis* from the Mediterranean. The variation in the measurements of increased WW may depend on the amount of food in the gut before the meal.

N. borealis is able to store large amounts of food in the gut. Such ability has also been reported for other scavenging crustaceans like the intertidal *Cirolana harfordi* (JOHNSON 1976a) and some deep-sea bait-attending lysianassid amphipods (DAHL 1979; SAINT-MARIE 1992).

Assimilation

The assimilation efficiency of carnivorous isopods seems to be high: assimilation of food energy by *Cirolana harfordi* feeding on fish muscles averaged 88% (JOHNSON 1976b), the isopod *Glyptonotus antarcticus* EIGHTS assimilated over 90% of ingested benthic shrimps (CLARKE 1979), and *Cirolana imposita* (BARNARD) assimilated 88-98% of polychaetes (SHAFIR & FIELD 1980). If *N. borealis* ingested the food efficiently, the assimilation efficiency was calculated to be 98.1%. When 12% loss of organic solubles to the sea water from the fish flesh was accounted for, the assimilation efficiency was 4.4% lower. The mean loss to the sea water of protein by maceration of the food item when *Glyptonotus antarcticus* was feeding, was on average 13% of the AFDW (CLARKE 1979). Because *N. borealis* usually fed quickly and cut the food into slices, the organic loss from the food should be expected to be low. Loss of organic substances from faeces to the sea water increases the estimation of assimilation efficiency. If the fish flesh was consumed immediately by *N. borealis* and the loss of organic solubles from the faeces to the sea water was 12%, the assimilation efficiency was on average 99.2% (SD = 0.29). Assimilation of some ash in the gut of *N. borealis* might be expected to vary with the moult cycle. The assimilation efficiency was, on average, 96.6 (SD = 0.55) and 94.1% (SD = 0.87) when the loss of ash from the faeces was calculated to 12% and 25%, respectively. When organic assimilation is > 90%, ash assimilation must be > 50% to have any marked effect on the value of organic assimilation as calculated by Conover's method (CLARKE 1979).

Estimation of the energetics of a female *N. borealis* which had filled the gut with fish-flesh, showed that survival, the development of ova and maintenance of postmarsupial development for 6-7 months was possible without need of additional feeding (JOHANSEN 1980). This explains the consistent lack of ovigerous females in trap catches. Covert hiding in burrows by ovigerous female *N. borealis* is probably favourable for survival of the species. When feeding is extremely sporadic, the ability to store large quantities of food is an important survival factor.

Our findings support the theory that a beneficial survival strategy for scavengers consists of rapid response and localisation of food, consumption of a large quantity in a short time, ability to store food over long peri-

ods, and efficient assimilation (DAHL 1979; SMITH & BALDWIN 1982; WONG & MOORE 1995). The high assimilation efficiency of *N. borealis* may give some energy-gain from a poor food-item like sediment in times when no carrion is available.

Northern horizontal distribution

SARS (1899, appendix p. 248) refers to HOEK (1882) writing: 'Distribution. - The Barents Sea (Hoek)'. HOEK (1882), however, actually wrote that the R/V *W. Barents* caught four individuals on 24 May 1878 at 61°52.5'N, 1°42.1'E, northwest of Shetland Islands. The 'Barents Sea record' of *N. borealis* from the Barents Sea Expedition thus seems to be erroneous. KEABLE & BRUCE (1997) refers to a specimen in Nationaal Natuurhistorisch Museum, Leiden collected by 'Barents Sea Expedition, 1878'. This specimen is probably from the same material as HOEK (1882) reported (C. Fransen, pers comm).

GURJANOVA (1933) mentioned that *N. borealis* was occasionally found north of the Arctic Circle (66°33'N), but she listed no localities.

The earlier records of *N. borealis* along the coast of northern Norway have mainly been linked to reports of isopods found in cod roe at the dinner table. The reliability of these reports has been questioned because of the mobility of the host fishes. BERLAND (1983) surmised that only fishes caught in bottom nets and long-lines may become infested, while all free swimming fishes caught by hand-line, trawl, purse-seine and probably drift-net will be 'clean' of *N. borealis*, implying that *N. borealis* live at or near the site where the fish was caught.

N. borealis has now been found in northern Norway on the continental shelf off Troms County (70°10'N, 17°53'E), and in the subarctic fjord Malangen (69°20'N, 18°30'E) (Wim Vader pers. comm) (Fig. 4). These records support the supposed presence of the species in northern Norway. LoppHAVET, at ca 70°30'N, is now regarded as the geographical boarder area between the West Norwegian Sub-Province and the colder Finnmark Sub-Province (see BRATTEGARD & HOLTHE 1997).

The northern distribution of *N. borealis* is from ca 70°N off the coast of northern Norway and south along the Norwegian shelf and coast to the continental edge north and east of the Shetland Islands and west to the Faroe Islands. It is probably common in the Faroe area because the scavenger is well known by Faroese fishermen. It has not been found on the Icelandic shelf or coast (STEPHENSON 1938; Jörundur Svavarsson pers. comm) (Fig. 4).

Northern depth distribution

From Norwegian waters *N. borealis* has been reported from 30 to 270 m by DONS (1935) and from 40 to 690 m (Korsfjorden) by NIELSEN (1967). Despite extensive sam-

pling efforts in Norwegian and Faroese waters from 5 to 2420 m depth, samples of *N. borealis* were obtained only from depths of 235 to 350 m in Faroese waters and 15 to 450 m in Norwegian waters.

N. borealis occurs rarely in shallow water. Quantitative catches of adults at 40–50 m and 80–90 m in Raknesvågen, western Norway were not significantly different (JOHANSEN & BRATTEGARD 1996). However, the catches of postmarsupial instars 1–3 were significantly lower at 40–50 m than those at 80–90 m. LINDSTRÖM (1990) suggested that the eyes of *N. borealis* are better adapted to the dim light of deep water and are probably damaged when they are exposed to daylight in shallow water. The occasional occurrence in shallow water might be a result of nightly swimming from deeper water in search of food.

The deepest records of *N. borealis* are from 1478 m southwest of Ireland (NORMAN 1904), 1000 m in the Bay of Biscay (Jean-Claude Sorbe pers. commn), and 1210 m in the Mediterranean (DOLLFUS 1903). Being able to live in such deep waters but only down to 390 m in Faroese waters, ca 400 m in Norwegian shelf waters and 690 m in Norwegian fjords indicates that hydrostatic pressure is not the factor limiting vertical distribution along its northern boundary.

Northern temperature conditions

The range of near-bottom temperature at the epibenthic sampler and detritus sledge stations during the fauna surveys off the Faroe Islands and the Norwegian shelf and coast was from -0.92 to 11.8 °C, and for the grab stations on the Norwegian coast it was from ca 4 to 15 °C (Per J. Johannessen pers. commn). HANSEN (1916) reported *N. borealis* at the Faroes in 7.8 °C and the BIOFAR samples were collected from stations in water of 4.9 to 9.1 °C which means water masses dominated by Atlantic Water. It was never found at stations within water masses dominated by Arctic Intermediate Water (1.5 – 3.5 °C) nor Norwegian Sea Bottom Water (< 0 °C). In Norwegian waters *N. borealis* was found in bottom water of 5.0 to 13.8 °C. The temperature of the basin water at 400–650 m depth in Korsfjorden varied between 5.3 and 7.4 °C in the period 1968–1977 (MATTHEWS & SANDS 1973; BAKKE & SANDS 1977). The minimum temperature (March–May) of the basin water of the fjord Malangen, northern Norway (3.3 – 5.4 °C, SÆLEN 1950) is usually 2 – 4 °C lower than the more stable basin water temperature of deep fjords in western Norway. The low temperatures in the spring in Malangen may retard the reproduction of *N. borealis* (see below).

It is interesting that on the west coast of Morocco *N. borealis* is present in the area of relatively cool upwelling water (GRUNER 1966) with temperature less than 15 °C. In the western Mediterranean the temperature is between 12.8 and 13.0 °C below 200 m (FREDJ & LAUBIER 1985)

where it seems to be common (CARTES & ABELLÓ 1992; CARTES 1993, 1994).

Laboratory experiments (JOHANSEN 1996) showed that the development of embryos and larvae were arrested or slow at temperatures from 3.7 to 6.5 °C. This, and that the usual temperature range of this species in the field seems to be between 5 and 14 °C, indicate that temperature might be an important factor limiting its ability to live in deep, cold water masses and its distribution towards north.

Northern distribution – abundance

Patchiness in the distribution of scavengers might be expected since a foodfall will aggregate the scavengers (RICE & LAMBSHEAD 1994). However, endogenous night activity (MACQUART-MOULIN & KAIM-MALKA 1994) and postprandial activity (WONG & MOORE 1995) will disperse aggregations of *N. borealis*.

The catches of *N. borealis* with van Veen grab in Norwegian coastal waters were low except for one single instance when the grab contained 10 specimens (0.2 m²). The grab is not suitable to catch actively swimming animals just off the bottom. The specimens caught in the grab were presumably lodged in their burrows within the sediment. Grab catches probably underestimate the abundance of *N. borealis*.

The RP-sledge is theoretically able to sample *N. borealis* swimming above the sediment in a stratum 26–59 cm above the bottom provided the sledge does not sink into the sediment (BRATTEGARD & FOSSÅ 1991). In reality the sledge is not a quantitative sampling gear. It will catch less than 30 % of the hyperbenthic animals, and even fewer of the fastest swimmers, and it usually also catches some of the fauna in the uppermost part of the sediment. Animals living in burrows are only occasionally caught. To estimate abundance from catch figures obtained by the RP-sledge the numbers should probably be multiplied with a correction factor higher than 3. A corrected estimate, but still an underestimate, points to an abundance in places of up to 0.4 specimen of *N. borealis* per m².

The catch of *N. borealis* by an epibenthic sledge (different from the RP-sledge) in the Bay of Biscay was 0.258 specimen per m² 10–40 cm above the bottom and 0.313 specimen per m² 10–145 cm above the bottom (ELIZALDE & al. 1993). These values may also be underestimated.

The catches of *N. borealis* from Sgat Mohr were occasional in an epibenthic sledge, but abundant in baited traps at 190 m (WONG & MOORE 1996, table 1). Baited trap catches of *N. borealis* from Raknesvågen at 80–90 m were from 45 to > 200 specimens after 24 h. Increasing amounts of bait seemed to increase the catch of *N. borealis* (JOHANSEN & BRATTEGARD 1996) and up to 1230 specimens were caught in Skogsvågen (JOHANSEN 1980).

If the initial density was 0.4 specimens per m² the bait attracted the whole population from an area of over 3000 m². Use of baited traps seems to result in higher total catches of scavengers than it is possible to obtain with grabs and sledges.

N. borealis has been recorded from the western Atlantic from off South Carolina and Florida, and (KEABLE & BRUCE 1997) reported only slight morphological differences between populations of *N. borealis* in the eastern and the western Atlantic. It has not been found between the Faroe Islands and northeastern America and seems, therefore, to have a discontinuous geographical distribution. *N. borealis* avoids shallow water but can live down to 1500 m depth. It seems to avoid water with temperature below 4-5 °C and to require silty sediments in which it can make burrows to hide in while digesting the usually large meal.

The depth of the Faroe-Iceland Ridge is mainly less than 450 m. Sill depths of ca 450 m are found near the Faroe shelf and the Iceland shelf (AKEN & EISMA 1987). The depth, as such, is probably not a hindrance for *N. borealis* to reach from the Faroe area to Icelandic waters. Sediments of the right kind are probably present. Water with temperatures near zero overflows the ridge (LEE 1963). The temperature below 500 m is higher (2-7 °C) on the southern slope of the ridge than on the northern slope (< 0 °C) (AKEN & EISMA 1987, fig. 5). The cool overflowing bottom water along the Faroe-Iceland Ridge may, thus, prevent the distribution of *N. borealis* to Iceland. At times when bottom water with temperature above 4-5 °C was present at suitable depths (less than 1500 m) the southern slope of the Faroe-Iceland Ridge might have acted as an east-west corridor for dispersal of *N. borealis*. Later cooling of the North Atlantic may have separated East and West Atlantic populations of *N. borealis* and eliminated populations in Icelandic waters.

SUMMARY

Trap catches of *Natanolana borealis* were usually larger at night than during daytime. Trap catches in daylight at 80-90 m depth seemed to depend on the *in situ* illumina-

tion. Catches by epibenthic sledge were larger at night than during daytime in the Norwegian Trough.

Laboratory observations and trap experiments indicate a combined 'sit and wait' and 'swim across the current' feeding strategy. Feeding activity of non-breeding *N. borealis* may be regulated by hunger and illumination. The presence of odour gradients was necessary to maintain search activity for food. *N. borealis* seems to feed primarily on soft tissues of carrion but can feed opportunistically on available food items. Feeding was accomplished after 3-13 minutes depending on the nature of the food (soft vs. tough tissues). *N. borealis* increased its dry weight with 73 % on average after one meal. *N. borealis* kept in laboratory tanks entered a lethargic state after a full meal. A filled anterior hindgut enabled all the males and more than 50 % of the females to survive more than 7 months without access to food. The assimilation efficiency of *N. borealis* was estimated to be higher than 90 %.

In the northeastern Atlantic the northern distribution borderline of *N. borealis* seems to run from the Faroe Islands, along the continental edge north and east of Shetland to 70°N on the coast of northern Norway. It was not caught deeper than 350 m at the Faroes and 450 m at the Norwegian coast. The recorded range of *in situ* temperature where *N. borealis* has been caught in the northeastern Atlantic was about 5-14 °C.

N. borealis has been collected from bottom types ranging from fine clayey/silty sediments to gravel. Both the pleopods and the pereopods were involved in digging in sediments suitable for making burrows.

ACKNOWLEDGEMENTS

We are grateful to Torgeir Bakke as an initiator to the study of *Natanolana borealis* in 1977, the crews of R/V *Magnus Heinason* (Fiskirannsóknaströvan, Faroe Islands) and R/V *Håkon Mosby* (University of Bergen) for good service at sea. We also thank Børre Bjørnsen for translation from a Russian publication, and Robert Barrett, Svein-Rune Erga, Audun Fosshagen, Charles Fransen, Per J. Johannessen, Stephen Keable, Rune Rosland, Jean Claude Sorbe, Jörundur Svavarsson and Wim Vader for valuable information, and Niel L. Bruce and two anonymous referees for critical and constructive comments on the MS, and Elin Holm for drawing the figures.

REFERENCES

- Aken, H.M. van & D. Eisma 1987. The circulation between Iceland and Scotland derived from water mass analysis. – *Netherlands Journal of Sea Research* 21:1-15.
- Anonymous 1969. New items. Scavengers in a tusk. – *Scottish Fisheries Bulletin* 32:29-30.
- Bakke, J.L.W. & N.J. Sands 1977. Hydrographical studies of Korsfjorden, western Norway, in the period 1972-1977. – *Sarsia* 63:7-16.
- Bakke, T., B. Enger, S. Johnsen, G.H. Maisey & Ø. Stokland 1989. Baseline Environmental Survey of the Heidrun Field, June 1988. – *NIVA-Report* No. O-88113. Vol. 2: Appendices. 195 pp.
- Berland, B. 1983. Sjølus i fiskerogn og pigghå. – *Fiskets Gang* 6/7:175-179.
- Berrow, S. 1994. Fish predation by the marine crustaceans *Orchomene nana* (Krøyer) and *Natanolana borealis* (Lilljeborg). – *Irish Naturalists' Journal* 24:514.

- Botnen, H.B., Ø.F. Tvedten & P.J. Johannessen 1993. Resipientundersøkelse i Rysjedalsvika, Hyllestad kommune. – *IFM Rapport* Nr. 31-1993. 20 pp.
- Botnen, H.B., Ø.F. Tvedten, P.J. Johannessen & H. Hagen 1994. Resipientundersøkelse ved Stokkeneset, Selje kommune. – *IFM Rapport* Nr. 15-1994. 20 pp.
- Botnen, H.B., Ø.F. Tvedten, O. Grahl-Nielsen, O. Mjaavatten & P.J. Johannessen 1996. Miljøundersøkelse i Dalabukta og Kristiansund havneområde. – *IFM Rapport* Nr. 19-1996. 83 pp.
- Brattegard, T. & J.H. Fosså 1991. Replicability of an epibenthic sampler. – *Journal of the Marine Biological Association of the United Kingdom* 71:153-166.
- Brattegard, T. & T. Holthe (eds) 1997. Distribution of marine, benthic macro-organisms in Norway. A tabulated catalogue. Preliminary edition. – *Research Report for DN 1997-1*. Directorate for Nature Management. 409 pp.
- Brattegard, T. & W. Vader 1972. A collection of Peracarida from Møre and Romsdal, northwestern Norway. – *Sarsia* 49:33-40.
- Bushdosh, M., G.A. Robilliard, K. Tarbox & C.L. Beehler 1982. Chemoreception in an arctic amphipod crustacean: a field study. – *Journal of Experimental Marine Biology and Ecology* 62:261-269.
- Cartes, J.E. 1993. Feeding habits of pasiphaeid shrimps close to the bottom on the Western Mediterranean slope. – *Marine Biology* 117:459-468.
- 1994. Influence of depth and season on the diet of the deep-water aristeid *Aristeus antennatus* along the continental slope (400 to 2300 m) in the Catalan Sea (Western Mediterranean). – *Marine Biology* 120:639-648.
- Cartes, J.E. & P. Abelló 1992. Comparative feeding habits of polychelid lobsters in the western Mediterranean deep-sea communities. – *Marine Ecology Progress Series* 84:139-150.
- Carvalho, F.P. & S.W. Fowler 1985. Biokinetics of plutonium, americium and californium in the marine isopod *Cirolana borealis*, with observations on its feeding and moulting behaviour. – *Marine Biology* 89:173-181.
- Clarke, A. 1979. Assimilation efficiency of the Antarctic marine isopod *Glyptonotus antarcticus*. – *Marine Biology* 52:157-160.
- Conover, R.J. 1966. Assimilation of organic matter by zooplankton. – *Limnology and Oceanography* 11:338-345.
- Dahl, E. 1979. Deep-sea carrion feeding amphipods: evolutionary patterns in niche adaptation. – *Oikos* 33:167-175.
- Dollfus, A. 1903. Note préliminaire sur les espèces du genre *Cirolana* recueillies pendant les campagnes de 'l'Hirondelle' et de la 'Princesse Alice' sous la direction de S.A. Prince Albert 1^{er} de Monaco. – *Bulletin de la Sociétés Zoologique de France* 28:5-10.
- Dons, C. 1935. Zoologiske Notizen 28. Isopoden aus der Møre-Küste und Nord-Norwegen. – *Kongelige Norske Vitenskabers Selskab Forhandlinger* 8(13):1-4.
- Elizalde, M., J.C. Sorbe & J.C. Dauvin 1993. Las comunidades suprabentónicas batiales del golfo de Vizcaya (margen sur del cañón de Cap-Ferret): composición faunística y estructura. – *Publicacion Especial Instituto Español Oceanográfico* 11:247-258.
- Fredj, G. & L. Laubier 1985. The deep-sea Mediterranean benthos. – Pp. 109-146 in: Moraitou-Apostolopoulou, M. & Kiortsis V. (eds) *Mediterranean marine ecosystems*. Plenum. New York.
- Gruner, H.-E. 1966. Krebstiere oder Crustacea. V. Isopoda. 2. Lieferung. – *Die Tierwelt Deutschlands* 53.Teil. Pp. 151-380. VEB Gustav Fischer Verlag. Jena.
- Gurjanova, E. 1933. Die Marinen Isopoden der Arktis. – *Fauna Arctica* 6:391-470.
- Halvorsen, O. 1965. Isopoder i torskerogn. – *Fauna* 19:90-91.
- Hansen, H.J. 1890. Cirolanidae et familiae nonnullae propinque Musei Hauniensis. – *Kongelige Danske Vitenskabernes Selskab Skrifter, Ser. 6, Naturvidenskabelig og Mathematisk Afdeling* 3:239-426.
- 1916. Crustacea Malacostraca III. Isopoda. – *The Danish Ingolf-Expedition* 3B(5):1-262.
- Hoek, P.P.C. 1882. Die Crustaceen gesammelt während den Fahrten des 'Willem Barents' in den Jahren 1878 und 1879. – *Niederländisches Archiv für Zoologie. Supplementbind 1. Lief 3*. Pp. 21-75.
- Johannessen, P.J. & A.M. Stensvold 1987. Resipientundersøkelse i Flora kommune. – Institutt for marinbiologi. Rapportserie: Rapp. nr. 52 1987. 27 pp.
- Johansen, P.-O. 1980. Vekst, reproduksjon, energiinnhold og ernæringsbiologi hos *Cirolana borealis* Lilljeborg (Crustacea: Isopoda) i Skogsvåg, Raunefjorden. – Unpubl. cand. real. thesis, University of Bergen, Norway. 141 pp (in Norwegian).
- 1996. Reproduction and sexual maturation of the scavenging deepwater isopod *Natatolana borealis* (Lilljeborg) from Western Norway. – *Sarsia* 82:297-306.
- Johansen, P.-O. & T. Brattegard 1996. Fangst av *Natatolana borealis* Lilljeborg (Crustacea: Flabellifera) med ulike typer feller med åte. – *IFM Rapport* nr. 15, 1996. Institutt for fiskeri- og marinbiologi, Universitetet i Bergen. 29 pp.
- Johnson, W.S. 1976a. Biology and population dynamics of the intertidal isopod *Cirolana harfordi*. – *Marine Biology* 36: 343-350.
- 1976b. Population energetics of the intertidal isopod *Cirolana harfordi*. – *Marine Biology* 36:351-357.
- Keable, S. & N.L. Bruce 1997. Redescription of the North Atlantic and Mediterranean species of *Natatolana* (Crustacea: Isopoda: Cirolanidae). – *Journal of the Marine Biological Association of the United Kingdom* 77:655-705.
- Larsen, P.-M. 1991. Minikreps-prosjekt avsluttet: Trenger fangstteknologi for store kvanta. – *Fiskets Gang* 77(12):17-18.
- Land, J. van der (ed.) 1966. *Verslag van een zoölogische excursie naar Noorwegen en Zweden in 1965, waaraan toegevoegd een deel van de resultaten van excursies in 1961 en 1963*. – Rijksmuseum van Natuurlijke Historie en Afdeling Systematische Dierkunde der Rijksuniversiteit - Leiden. Mimeographed report. 116 pp.
- Lee, A. 1963. The hydrography of the European Arctic and Subarctic seas. – *Oceanography and Marine Biology Annual Review* 1:47-76.

- Lindström, M. 1990. Light tolerance in crustaceans especially the opossum shrimp *Mysis relicta* (Mysidacea) and the isopod *Cirolana borealis* (Flabellifera). – *Acta Academiae Aboensis Series B Mathematica et Physica Naturvetensk. Tek.* 50:113-120.
- Lindström, M. & Nilsson, H.L. 1983. Spectral and visual sensitivities of *Cirolana borealis* Lilljeborg, a deep water isopod (Crustacea: Flabellifera). – *Journal of Experimental Marine Biology and Ecology* 69:243-256.
- Løkkeborg, S. 1990. Utbredelse og årsvariasjoner i forekomster av åtselsetende krepsdyr - en intervju-undersøkelse blant fiskeskippere. – *FTFI-Notat* 20.09.90
- Macquart-Moulin, C. & R.A. Kaïm-Malka 1994. Rythme circadien endogène d'émergence et d'activité nataoïre chez l'isopode profond *Cirolana borealis* Lilljeborg. – *Marine Behaviour and Physiology, London* 24:151-164.
- Matthews, J.B.L. & N.J. Sands 1973. Ecological studies of the deep-water pelagic community of Korsfjorden, western Norway. The topography of the area and its hydrography in 1968-1972, with a summary of the sampling programmes. – *Sarsia* 52:29-52.
- Nielsen, S.-O. 1967. *Cironiscus dahli* gen. et sp. nov. (Crustacea Epicaridea) with notes on host-parasite relations and distribution. – *Sarsia* 29:395-412.
- Nierstrasz, H.F. & J.H. Schuurmans Stekhoven 1930. Isopoda genuina. - *Die Tierwelt der Nord- und Ostsee* (Grimpe & Wagler eds) X. e:57-133.
- Nilsson, H.L. & M. Lindström 1983. Retinal damage and sensitivity loss of a light-sensitive crustacean compound eye (*Cirolana borealis*): electron microscopy and electrophysiology. – *Journal of Experimental Biology* 107:277-292.
- Nørrevang, A., T. Brattegard, A.B. Josefson, J.-A. Sneli & O.S. Tendal 1994. List of BIOFAR stations. – *Sarsia* 79:165-180.
- Norman, A.M. 1904. British Isopoda of the families Aegidae, Cirolanidae, Idotheidae and Arcturidae. – *Annals and Magazine of Natural History* Ser.7. 14:430-448.
- Ohlin, A. 1901. Arctic Crustacea collected during the Swedish Arctic Expeditions 1898 and 1899 under the direction of Professor A.G. Nathorst. 1. Leptostraca, Isopoda, Cumacea. – *Bihang till Kungliga Svenska Vetenskaps-Akademiens Handlingar*. Band 26. Afd.4. Nr 12. pp 1-54.
- Raitt, D.S. 1929. Cod roe attacked by amphipod crustaceans. – *Scottish Naturalist Edinburgh* p. 57-58.
- Rice, A.L. & P.J.D. Lamshead 1994. Patch dynamics in the deep-sea benthos: the role of a heterogeneous supply of organic matter. – Pp. 469-497 in: *Aquatic Ecology: Scale, pattern and process*. The 34th Symposium of the British Ecological Society. Blackwell Scientific, Oxford.
- Sælen, O.H. 1950. The hydrography of some fjords in Northern Norway: Balsfjord, Ulfsfjord, Grøtsund, Vengsøyfjord and Malangen. – *Tromsø Museums Årshefter, Naturhistorisk Avdeling* Nr. 38, 70:1-103.
- Saint-Marie, B. 1992. Foraging of scavenging deep-sea lysianassoid amphipods. – Pp. 105-124 in: Rowe, G.T. & V. Pariente (eds) *Deep-sea food chains and the global carbon cycle*. NATO ASI Series. Series C. Mathematical and Physical Sciences Vol. 360.
- Sars, G.O. 1885. Zoologi. Crustacea, II. – *The Norwegian North-Atlantic Expedition 1876-1878 (Den Norske Nordhavs-Expedition 1876-1878)* 6(15):1-96. Printed by Grøndahl & Søn, Christiania (Oslo).
- 1899. *An Account of the Crustacea of Norway. Vol. II. Isopoda*. – Bergen Museum, Bergen. 270 pp., 100 + 4 pl.
- Schiøtde, J.C. 1866. Krepsdyrenes sugemund. – *Naturhistorisk Tidsskrift*. 3. Række 4:169-206.
- Shafir, A. & J.G. Field 1980. Importance of a small carnivorous isopod in energy transfer. – *Marine Ecology Progress Series* 3:203-215.
- Smith, K.L. Jr. & R.J. Baldwin 1982. Scavenging deep-sea amphipods: effect of food odor on oxygen consumption and a proposed metabolic strategy. – *Marine Biology* 68:287-298.
- Sneli, J.-A. 1998. A simple benthic sledge for shallow and deep-sea sampling. – *Sarsia* 83:69-72.
- Stephensen, K. 1938. Marine Isopoda & Tanaidacea. – Part 27, 26 pp. in: Fridriksson, A. & S. L. Tuxen (eds). *Zoology of Iceland*. Vol. 3. Lewin & Munksgaard. Copenhagen and Reykjavik.
- Stensvold, A.M., K. Sjøtun & P.J. Johannessen 1987. *Kartlegging av marinbiologiske forhold og bunnsforholdene ved vei- og brusamband Gamlemshaug - Lepsøy, Møre og Romsdal*. – Institutt for marinbiologi. Rapportserie: Rapp. nr. 60. 63 pp.
- Stephien, C.A. & R.C. Brusca 1985. Nocturnal attacks on nearshore fishes in southern California by crustacean zooplankton. – *Marine Ecology Progress Series* 25:91-105.
- Tattersall, W.M. 1905. The marine fauna of the coast of Ireland. Part 5. Isopoda. – *Reports of the Department of Agriculture and Technical Instruction for Ireland, Scientific Investigations of the Fisheries Branch 1904*. 2:53-142.
- Taylor, A.C. & P.G. Moore 1995. The burrows and physiological adaptations to a burrowing lifestyle of *Natatolana borealis* (Isopoda: Cirolanidae). – *Marine Biology* 123:805-814.
- Tvedten, Ø.F., H.B. Botnen & P.J. Johannessen 1995. Miljøundersøkelse ved Stolt Sea Farm's fiskeoppdrettsanlegg i Gildekal kommune, Nordland fylke. – *IFM Rapport* Nr. 8-1995. 52 pp.
- Tvedten, Ø.F., P.J. Johannessen & H.B. Botnen 1993. Resipientundersøkelse ved Raknes, Osterøy. – *IFM Rapport* No. 23-1993. 26 pp.
- Vader, W. & K. Romppainen 1985. Notes on Norwegian marine Amphipoda. 10. Scavengers and fish associates. – *Fauna norvegica, Serie A, Oslo* 6:3-8.
- Wägele, J.W. & N.L. Bruce 1989. *Natatolana pastorei* (Giambiagi, 1925) from the straits of Magellan, South America: redescription and notes on functional morphology. – *Proceedings of the Biological Society of Washington* 102:95-105.
- Weinberg, S. 1976. Submarine daylight and ecology. – *Marine Biology* 37:291-304.
- Williams, G. 1938. On the occurrence of *Scopelocheirus hopei* and *Cirolana borealis* in living *Acanthias vulgaris* (spiny dogfish). – *The Irish Naturalists' Journal* 7:89-91.

- Wong, Y.M. & P.G. Moore 1995. Biology of feeding in the scavenging isopod *Natatolana borealis* (Isopoda: Cirolanidae). – *Ophelia* 43:181-196.
- 1996. Observations on the activity and life history of the scavenging isopod *Natatolana borealis* (LILLJEBORG) (Isopoda: Cirolanidae) from Loch Fyne, Scotland. – *Estuarine, Coastal and Shelf Science* 42:247-262.
- Zirwas, C. 1910. Die Isopoden der Nordsee. – *Wissenschaftliche Meeresuntersuchungen, Abteilung Kiel* 12:73-119.
- Zwaan, A. de & H.R. Skjoldal 1979. Anaerobic energy metabolism of the scavenging isopod *Cirolana borealis* LILLJEBORG. – *Journal of Comparative Physiology* 129:327-331.

Accepted 23 February 1998
 Editorial responsibility: Ulf Båmstedt

Appendix 1. Records of *Natatolana borealis* from north of latitude 61°N, from the Faroe Islands to northern Norway, listed according to longitude from west to east, see also Fig. 3.

Near Faroe Islands:

- 61°06'N, 09°21'W, SW of the Faroe Islands, 395 m (= 210 Danish fms), 7.8 °C. Nine specimens, on bait on long-lines, 14 August 1902, 'Michael Sars'. Coll. A. Jensen (HANSEN 1916; KEABLE & BRUCE 1997).
- 61°35.0'N, 08°05.4'W, SW of the Faroe Islands, 322 m, soft bottom, 7.9 ± 0.8 °C. 10 specimens, Sneli detritus sledge, daylight sample, 20 July 1987, BIOFAR Stn 65.
- 61°39.3'N, 07°48.9'W, SW of the Faroe Islands, 350 m, fine sand, silt, clay, 7.9 ± 0.8 °C. Seven specimens, epibenthic sampler (= RP-sledge), daylight sample, 20 July 1987, BIOFAR Stn 62.
- 61°25.6'N, 06°17.3'W, SE of the Faroe Islands, 235 m, soft bottom, 7.1 ± 2.0 °C. One specimen, Sneli detritus sledge, daylight sample, 19 July 1987, BIOFAR Stn 52.
- 61°24.3'N, 06°10.9'W, SE of the Faroe Islands, 235 m, soft bottom, 7.1 ± 2.0 °C. One specimen, RP-sledge, daylight sample, 19 July 1987, BIOFAR Stn 51.
- 61°17'N, 05°24.9'W, SE of the Faroe Islands, 201 m, hard bottom with sand and cobbles, 7.5 ± 1.4 °C. Seven specimens, Sneli detritus sledge, night sample, 13 May 1988, BIOFAR Stn 235.
- 62°10'N, 04°41.6'W, E of the Faroe Islands, 251 m, fine sand, coarse cobbles and stones, 6.5 ± 1.6 °C. Two specimens, Sneli detritus sledge, 5 October 1990, BIOFAR Stn 764.
- 62°16.1'N, 04°09.9'W, E of the Faroe Islands, 300 m, gravel, 6.1 ± 6.5 °C. One specimen, RP- sledge, night sample, 9 May 1988, BIOFAR Stn 174.

Near Shetland, north of 61°N:

- 61°18'N, 01°22'W, N of Shetland, 210 m (NIELSEN 1967).
- 61°18'N, 01°12'W, N of Shetland, 197 m, sand with shell fragments (ZIRWAS 1910).
- 61°31'N, 00°39'W, N of Shetland, 196 m. Seven specimens, 21 July 1905, 'Thor' Stn 121 (HANSEN 1916; KEABLE & BRUCE 1997).
- 61°49'N, 00°09'W, NE of Shetland, 224 m. 'M. Sars' 1906 (NIELSEN 1967).
- 61°31'N, 00°34'E, NE of Shetland, depth not noted. Two specimens (KEABLE & BRUCE 1997).
- 61°43'N, 01°16'E, NE of Shetland, 190 m. «M. Sars» 1906 (NIELSEN 1967).
- 61°16'N, 01°18'E, NE of Shetland, 150 m, sand, some stones and shells. 31 May 1899 (OHLIN 1901; KEABLE & BRUCE 1997).

Norwegian Trough north of 61°N:

- 61°52.5'N, 01°42.1'E, SE of Stadt, 130 fathoms = 238 m, mud (feiner Schlick) (HOEK 1882).
- 61°30.0'N, 02°00.1'E, 311 m, soft bottom, 8.2 °C. 23 specimens, RP-sledge, night sample, 17 November 1983. Coll. T. Brattegard. Each of the following six localities were sampled with RP-sledge twice at night (n) and twice in daylight (d) during 20-23 March 1985 by T. Brattegard:
- 61°00'N, 02°19'E, 136-137 m, soft bottom, 7.7 °C. Specimens: 0 (d), 2 (d), 0 (n), 9 (n).
- 61°04'N, 02°27'E, 174-176 m, soft bottom, 7.8 °C. Specimens: 0 (d), 0 (d), 5 (n), 8 (n).
- 61°06'N, 02°31'E, 209-213 m, soft bottom, 7.8-8.0 °C. Specimens: 1 (d), 3 (d), 11 (n), 15 (n).
- 61°08'N, 02°35'E, 255-260 m, soft bottom, 7.7-8.0 °C. Specimens: 0 (d), 2 (d), 19 (n), 22 (n).
- 61°12'N, 02°43'E, 314-317 m, soft bottom, 7.7 °C. Specimens: 3 (d), 4 (d), 5 (n), 44 (n).
- 61°14.6'N, 02°50.2'E, 382 m, soft bottom, 7.3 °C. Specimens: 0 (d), 0 (d), 0 (n), 1 (n).

Norwegian shelf, coast and fjords north of 61°N:

- Somewhere between 62°26' - 62°56'N, 02°48' - 03°42'E, NW of Stad (= Stadt, Statt), 150 m (NIELSEN 1967).
- 61°35.7'N, 05°05.8'E, Solheimsfjorden near Florø, 54 m, shell sand and stones. One specimen, 0.2 m², 0.2 m² van Veen grab, 6 August 1986 (JOHANNESSEN & STENSVDOLD 1987; KEABLE & BRUCE 1997).
- 61°06.7'N, 05°16.7'E, outer Sognefjorden, 151 m, sandy silt, ca 7.7 °C. One specimen in 0.4 m², 0.2 m² van Veen grab, 5 May 1993 (BOTNEN & al. 1993).

Appendix 1. continued

- Ca 63°05'N, 05°20'E, Storegga, two localities at 38 n.m. and 39 n.m. WNW of Ona, 200 m and 220 m. Year 1931 (DONS 1935).
- 61°01.3'N, 05°28.6'E, Risnefjorden, side-arm to Sognefjorden, 110 m, soft bottom, 8.0 °C. One specimen, RP-sledge, day-sample, 23 November 1984. Coll. T. Brattegard.
- 62°03.2'N, 05°28.8'E, Vanylvsfjorden, 46 m, silt and sand, between 6.1 and 6.8 °C. One specimen in 0.6 m², 0.2 m² van Veen grab, 30 April 1993 (BOTNEN & al. 1994).
- 63°04'N, 05°47'E, Kalvholå W of Buagrunnen, 217 m, soft bottom, 7-8 °C. 83 spec., RP- sledge, night sample, 15 March 1981. Coll. T. Brattegard.
- 63°05.7'N, 05°46.8'E, Kalvholå W of Buagrunnen, 210 m, soft bottom, 7-8 °C. 51 spec., RP-sledge, day sample, 18 March 1981. Coll. T. Brattegard.
- 62°25'N, 06°02.3'E, Sulafjorden, 450 m, soft bottom, 7.2 °C. One specimen, RP-sledge, night sample, 19 March 1981. Coll. T. Brattegard.
- 63°00.3'N, 06°20.3'E, Buagrunnen, 160 m, sand, gravel and stones, 7-8 °C. Seven specimens, RP-sledge, day sample, 16 March 1981. Coll. T. Brattegard.
- 63°24.9'N, 06°04.9'E, NW of Buagrunnen, 272 m, sandy silt, 7-8 °C. 15 specimens, RP- sledge, night sample, 17 March 1981. Coll. T. Brattegard.
- 62°58.7'N, 06°28.0'E, Buagrunnen, 147 m, sand, gravel and stones, 7-8 °C. 49 specimens, RP-sledge, night sample, 18 March 1981. Coll. T. Brattegard.
- 62°36.2'N, 06°16.4'E, Vigrafjorden, E of Lepsoy, 25 m, soft bottom, some stones and shells, 8.5 °C. Two specimens in 1.0 m², 0.2 m² van Veen grab, 10 November 1986, Stn LR1 (STENSULD, SJØTUN & JOHANNESSEN 1987).
- 62°55.1'N, 06°27.8'E, NW of Ona, 201 m, soft bottom, 6.8 °C. 23 specimens, RP-sledge, night sample, 10 June 1981. Coll. T. Brattegard.
- Ca 62°55'N, 06°28'E, NW of Ona, 215 m, soft bottom, 7-8 °C. One specimen, RP-sledge, day sample, 15 March 1981. Coll. T. Brattegard.
- Ca 62°40'N, 06°30'E, Harøyfjorden, two localities, 30-40 m and 50-100 m (DONS 1935).
- 64°48'N, 06°32'E, W of Haltenbanken, 283 m, sand-clay, 6.9 °C. Number of specimens not noted, 21 August 1876, The Norwegian North-Atlantic Expedition 1876-1878, Stn 79 (SARS 1886).
- Ca 62°50'N, 06°50'E, near Aukra, two localities, 60-70 m and 70-80 m. Year 1931 (DONS 1935).
- 65°19.44'N, 07°15.16'E, NW of Haltenbanken, 339 m, clay/silt, sandy (f), some gravel and small stones, 7.0 °C. One specimen in 0.5 m², 0.1 m² van Veen grab, 24 June 1988, Stn 6 (BAKKE & al. 1989).
- 65°19.93'N, 07°18.17'E, NW of Haltenbanken, 338 m, silt/clay some sand, 6.9 °C. One specimen in 0.5 m², 0.1 m² van Veen grab, 25 June 1988, Stn 15 (BAKKE & al. 1989).
- 65°18.60'N, 07°21.36'E, NW of Haltenbanken, 335 m, clay/silt, 6.9 °C. One specimen in 0.5 m², 0.1 m² van Veen grab, 25 June 1988, Stn 17 (BAKKE & al. 1989).
- 63°07'N, 07°41'E, Bremnesfjorden, between Klubbneset and Staveneset, 200-180 m, stones, gravel and sand. One specimen, rectangular dredge, 9 July 1970 (BRATTEGARD & VADER 1972).
- 63°07.8'N, 07°43.8'E, near Kristiansund, 70 m, silty sand, 5.0 °C. One specimen in 1.0 m², 0.2 m² van Veen grab, 27 March 1996 (BOTNEN & al. 1996).
- 63°09.8'N, 07°51'E, Hammersund, Talgsjøen near Kristiansund, 120-80 m, stones and sand. One specimen, triangular dredge, 9 July 1970 (BRATTEGARD & VADER 1972).
- 63°41'N, 09°23'E, N of Storfosna outside Trondheimsfjorden, 50 m. One specimen, dredge, 23 August 1961, Leiden Biol. Exped. Stn 16, (LAND 1966; KEABLE & BRUCE 1997).
- 63°42'N, 09°27'E, Grandeviken outside Trondheimsfjorden, 70-20 m, sand with shell fragments and stones. Dredge, 26 August 1965, Leiden Biol. Exped. Stn 114 (LAND 1966).
- 67°21.1'N, 12°02.1'E, S of Røst, outer Lofoten islands, 185-190 m (NIELSEN 1967).
- Ca 67°05'N, 13°40'E, Sørfugløy, from cod roe (BERLAND 1983).
- 67°17.1'N, 14°00.9'E, near Bliksvær W of Bodø, 190 m, fine sand, 6.3 °C. Two specimens in 0.6 m², 0.2 m² van Veen grab, 31 August 1994 (TVEDTEN & al. 1995).
- Ca 67°17'N, 14°20'E, Bodø, from cod roe. Coll. K. Andersen (KEABLE & BRUCE 1997).
- Ca 67°03'N, 14°35'E, Beiarn, two old samples, identified by G.O. Sars (KEABLE & BRUCE 1997).
- Ca 68°10'N, 15°30'E, Hamarøy, the newspaper 'VG', Oslo 7 April 1990, probably *N. borealis*.
- 69°11.38'N, 16°11.94'E, Andfjorden, E of Andøya, 250 m. Ca 100 specimens, R/V *Johan Ruud* Stn 468-97 (Wim Vader pers. commn).
- Ca 68°50'N, 16°40'E, Harstad, from cod roe. Ident. P.-O. Johansen.
- Ca 69°40'N, 17°40'E, Husøy, in cod roe (Wim Vader & Robert Barrett pers. commn).
- 70°09.6'N, 17°53.0'E, WNW of Rebbenesøy, 324-333 m. Three specimens, Sneli detritus sledge, sampled at 0200 hr on 9 June 1993, R/V *Håkon Mosby*. Ident. T. Brattegard.
- Ca 69°30'N, 18°E, Malangen, 300-400 m ?, dredge ? (Wim Vader pers. commn).
- Ca 69°50'N, 21°E, Storslett, Nordreisa, from cod roe. Ident. Ola Vahl (the newspaper 'Nordlys' 12 & 13 December 1978).