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Contribution to the knowledge of growth and postmarsupial development of *Natatolana borealis* (Crustacea: Isopoda)

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Postmarsupial development and growth of *Natatolana borealis* were studied from Skogsvåg and Raknesvåg on the western coast of Norway. Growth was determined from size and instar stage distributions. Growth was also examined in laboratory kept isopods that were collected from Skogsvåg. The postmarsupial instar stages were identified using the number of articles and the position of setae on the flagellum of the first antenna and other morphological features. The mean size of isopods in instar stages 1–3 did not show any significant seasonal variation in Raknesvåg. The estimated growth and mortality rates of males and females were not significantly different. Nine and 11 postmarsupial instar stages were found in material from Skogsvåg and Raknesvåg, respectively. The life span from instar stage 1 to 9 of male and female *N. borealis* from western Norway was estimated to be 3–4 y. Mortality rate increased significantly from instar stage 9 to 10 of both sexes. Isopods that attained instar stage 10 and instar stage 11 in Raknesvåg, may have lived 4–5 y. The mean size of instar stages 8 and 9 and the size-to-weight relationships were significantly higher in material from Raknesvåg relative to that from Skogsvåg and may have been caused by differences in food access and predation pressure at the two study sites. Specimens sampled from the Bay of Monaco attained smaller adult size than the isopods from the Norwegian population.

INTRODUCTION

Natatolana borealis (Lilljeborg) is found from the western Mediterranean to northern Norway in the eastern Atlantic and it is commonly collected from sediment substrates deeper than 20–40 m along the south and west coast of Norway (Johansen & Brattegard, 1998). The isopod is usually caught in small numbers in dredges, grabs and sledges, but often caught in large numbers in baited traps (Sars, 1899; Wong & Moore, 1996; Johansen & Brattegard, 1998). Wong & Moore (1996) studied the life history of *N. borealis* from 190 m depth in Loch Fyne, Scotland and Kaïm-Malka (1997) examined the life cycle of *N. borealis* from 500 m depth on the continental slope of north-west Mediterranean canyons, basing their studies on trapped specimens. Longevity of *N. borealis* from western Mediterranean was estimated to be more than twice the longevity in Loch Fyne. In an unpublished study, Johansen (1980) examined the growth and instar stages of *N. borealis* from the western coast of Norway. The low number of trapped young isopods and overlapping size distributions of adult isopods made the growth estimates uncertain. A trap that caught all the instar stages of *N. borealis* efficiently was constructed in 1992 (Johansen & Brattegard, 1996) and the instar stages described by Johansen (1980) and Wong & Moore (1996) were used to re-estimate the growth of the isopod.

The main goals of this study were to examine postmarsupial growth rate, weight and longevity of *N. borealis* from the coast of western Norway. The relative mortality rates of *N. borealis* from a Norwegian location were estimated. Growth and sexual maturation of *N. borealis* from the Norwegian coast were also compared to trapped specimens from the Bay of Monaco.

MATERIAL AND METHODS

Material from Norway

Routine samples of *Natatolana borealis* were collected in Skogsvåg (60°16′N 05°06′E), south of Bergen and in Raknesvåg (60°34′N 05°25′E), north of Bergen. The isopods were trapped from September 1977 to November 1978 in Skogsvåg, Raunefjord at 90–100 m depth and they were taken from January 1993 to June 1996 in Raknesvåg, Osterfjord at 80–90 m depth. The baited traps in Skogsvåg and Raknesvåg were usually deployed for 24 h with a few exceptions. Cannibalism or damage to the isopods was rarely observed in baited trap collections. The monthly trapping collections were usually finished after one deployment. When the trap was set out two or three times, the collections were finished within a week, except for February 1993 and September 1995 in Raknesvåg. The instar stage distribution of the first and last collection in February 1993, however, showed only slight differences to each other (Johansen & Brattegard, 1996). The catches of the monthly collections were sorted, frozen and then examined shortly after.

Traps

Two types of traps provided samples of *N. borealis* from Skogsvåg: a mesh-walled, cone-shaped trap with a funnel on the top and a PVC tube with a funnel in one end

(Johansen & Brattegard, 1996). The size distributions of *N. borealis* of these two different traps showed the same pattern after having been simultaneously deployed in Skogsvåg, August 1978. The trap that collected *N. borealis* from Raknesvåg was the most effective of seven examined traps. This trap was made of a metal cylinder with a funnel in each end surrounded by plankton gauze (1 mm mesh size). To prevent escape, the minimum funnel diameters of the traps used at both collection sites were small, 16–18 mm which is about twice the maximum width of the largest isopods.

The traps used in Skogsvåg were baited with 500–800 g fish flesh and those used in Raknesvåg with 125–650 g fish flesh. The bait was cut in pieces and packed in closed mesh bags (1 mm mesh size). The bags allowed the fish odour to leak out and prevented the scavengers from eating into the fish flesh. The use of mesh bags also made it easy to locate even the smallest isopods in the trap catches.

A small hole (3 mm diameter) occurred in the trap used in Raknesvåg in June 1996 and resulted in under-representation of instar stage 1–4 this month. This hole did not influence the interpretation of growth in later instars because isopods in instar stages 5–11 were too large to escape through the hole.

Laboratory conditions

Postmarsupial development and growth were studied using specimens collected in Skogsvåg and kept in a dark, temperature-regulated laboratory in separate glass jars (10×4×5 cm) containing less than 1 cm sediment with grain size 1–2 mm. The isopods were fed with flesh from silvery pout (*Gadiculus argenteus thori*) every fortnight. The temperature in the glass jars of running, filtered seawater varied between 6.5°C and 10°C and the salinity varied between 31.5 psu and 34.0 psu.

Laboratory observations—growth

Growth of crustaceans can be described by a combination of the moult increment (growth factor) and the intermoult period (moult interval) (Hartnoll, 1982). The length increase per moult was described by the eqn (I):

$$L_s = A + B\cdot b^s \qquad (1)$$

where $A - a/(1 - b)$ and $B = L_1 - A/b$ as used by Kurata (1962). The expressions A and B were calculated from the growth coefficients a and b that were found by linear regression of premoult/postmoult plot:

$$L_{s+1} = a + b\cdot L_s \qquad (2)$$

where L_s is the pleopod 1 length in the instar stage s.

Growth converged towards a limit (since $b<1$, i.e. retrogressive geometric growth) and the theoretical pleopod 1 maximum length could be calculated by using the expression A. The intermoult period of *N. borealis* was described by the eqn (II):

$$D_s = c\cdot L_s^3 + d \qquad (3)$$

where D_s is the duration of the instar stage s and c and d are linear regression coefficients.

The growth curve of laboratory kept specimens was constructed by combining calculations from eqn I and II and by setting L_1 equal to the pleopod 1 mean length of the first instar stage.

Determination of instar stages and growth in field

Total body length measured from the front of cephalon to the tip of telson, can vary several millimeters on the same specimen of *N. borealis* because the connections between the pereonites are highly flexible. Total length will depend on the treatment before measuring (fresh, kept in alcohol or formaldehyde, or frozen and thawed) and how it was measured (degree of compression). In contrast to total body length, the pleopod 1 length can be measured exactly and also used on exuvia. The pleopod 1 length was determined by measuring the length from the proximal to the distal lobe on the exopod of the first pleopod. The pleopod 1 lengths of thawed material were measured and the sex and instar stage determined for pooled monthly samples from Raknesvåg and Skogsvåg, using a binocular microscope. The relationship (measured in mm) between pleopod 1 length (PLP1) and total length (TL) of isopods from Raknesvåg, October 1998 was roughly estimated to: $TL=6.52\cdot PLP1+0,3123$. Isopods from the Mediterranean and Loch Fyne were kept in formaldehyde or alcohol before pleopod 1 length was measured. Pleopod 1 length of *N. borealis* preserved in 70% ethanol or 4% formaldehyde for a week did not change significantly.

The growth of *N. borealis* from Skogsvåg was examined by separating the pleopod 1 length distribution into instar stages using the pleopod 1 mean length corresponding to each identified instar stage and following the successive peaks with time. The pleopod 1 length increment i.e. growth factor was calculated by dividing the postmoult pleopod 1 length by the premoult pleopod 1 length. The 95% confidence limits of pleopod 1 mean lengths ($\bar{X}$) were calculated using the formula:

$$\bar{X} \pm t\cdot (SD/\sqrt{N}) \qquad (4)$$

where SD is the standard deviation and t is the critical value of $(N-1)$ degrees of freedom (Schefler, 1969).

The instar stages of *N. borealis* from Raknesvåg were determined from the number of flagellar articles and the position of setae on the first antenna which is accompanied by development of pereopods and secondary male sexual characters (Johansen, 1980; Wong & Moore, 1996). The first flagellar article on the first antenna of *N. borealis* was identified using the method of Wägele (1983). The first flagellar article was firmly attached at the distal end of the third peduncle, and it was separated from the second flagellar article by a broad hinge. Injuries to the flagellum of the first antenna were rarely found in field material and only antennal flagella that were a normal shape and uninjured were used for instar stage determination. Trap catches taken at the same place and time containing more than 100–200 isopods gave almost identical instar stage distributions (Johansen & Brattegard, 1996). The duration of instar stages of *N. borealis* from Raknesvåg was determined by following the peaks of consecutive instar stages with time.

Male *N. borealis* were identified by the presence of fully developed appendix masculinum and genital papillae. Males and females could not be separated in the three first instar stages i.e. when the pleopod 1 length was less than 1.6 mm. Sexual maturation of male *N. borealis* was determined from the shape of the appendix masculinum (Johansen, 1996). Specimens that lacked secondary male sex characters were classified as females.

Weight in field

Wet weight was determined after the isopods were dried on a water absorbing cloth. The isopods were washed in distilled water, dried at 65–70°C for 24 h and burned in a Hereus MR 170 muffle-furnace at 500°C for 12 h. The isopods from Skogsvåg were weighted on a Mettler B6 (±0.02 mg) and the isopods from Raknesvåg were weighted on a Sartorius B310P (±1 mg). Comparison of regressions from large, sexed isopods indicated the difference in precision of the two weights was insignificant. The eqn:

$$\text{Weight} = a \cdot \text{Length}^b \qquad (5)$$

was used to describe the exponential relations between pleopod 1 length and wet weight (WW), dry weight (DW), ash-free dry weight (AFDW). To describe the linear relations between AFDW and DW the eqn:

$$\text{AFDW} = a \cdot \text{DW} + b \qquad (6)$$

was used. The non-linear regressions were logarithmic transformed and the regressions were tested using comparisons in pair on covariance, slope and elevation (Schefler, 1969; Zar, 1974).

Estimation of field mortality

Mortality of *N. borealis* was estimated from instar stage 1 to instar stage 9 using a vertical life table approach on the data from Raknesvåg in the period January 1993–May 1996. The main assumption of the vertical life table method is that daily recruitment rate to a stage is constant over a period that corresponds to the duration of the stage (Aksnes & Ohman, 1996). Widespread reproduction of *N. borealis* through the year (Johansen, 1996), indicates the fulfilment of this assumption. The results of Aksnes & Ohman (1996) indicated that moderate random Gaussian variability in the true recruitment, stage duration and mortality risk was not critical for mortality estimation by the vertical method. The ratio of the numbers of individuals in two consecutive instar stages was: $r_i = n_i/n_{i+1}$ (Aksnes & Ohman, 1996). A mortality estimate was obtained by solving the preceding eqn and the eqn:

$$r_i = (e^{ma_i} - 1)/(1 - e^{-ma_{i+1}}) \qquad (7)$$

iteratively. Mortality in the last instar stage was calculated using:

$$m = \ln(r_{q-1} + 1)/a_{q-1} \qquad (8)$$

Survival per day is described by the expression: $e^{(-m)}$. Mortality rate (per cent dead per day) was calculated using the formula: $(1 - e^{-m} \cdot 100)$. The estimated mortality rates from the collections were averaged and

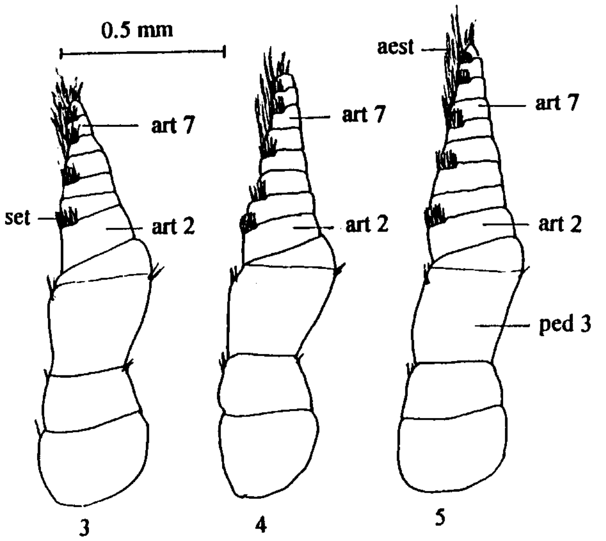

Figure 1. The structure of the peduncle and the flagellum of the first antenna is drawn with groups of setae and aestetascs. The position of setae groups and number of articles are illustrated from instar stage 3 to instar stage 5. The detailed structures of antennal setae are discussed in Kaïm-Malka et al. (1999).

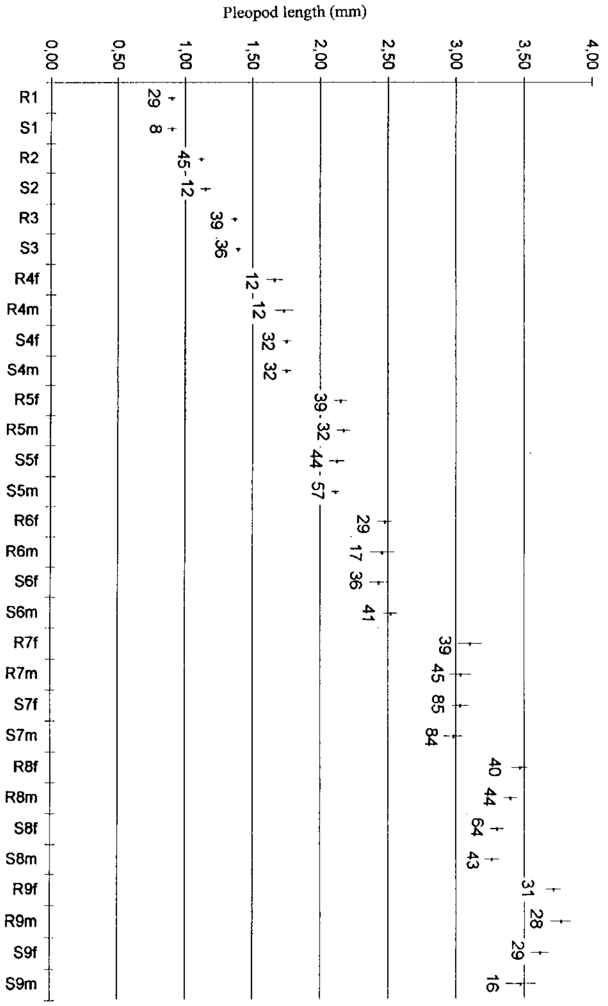

Figure 2. The mean size of female (f) and male (m) *Natatolana borealis* in instar stages 1–9 from Skogsvåg (S) and Raknesvåg (R) drawn with 95% confidence limits. The numbers of isopods measured in each instar stage are denoted beneath the mean sizes.

Table 1. *Estimated mean mortality rates of Natatolana borealis collected in Raknesvåg from January 1993 to May 1996.*

Instar stage	MMR	95% CI	Number of estimates	Instar stage	MMR	95% CI	Number of estimates
	Unsexed						
1/2	0.097	±0.279	41				
2/3	0.013	±0.227	41				
3/4	0.122	±0.281	41				
	Females				Males		
4/5	0.462	±0.223	41	4/5	0.262	±0.270	39
5/6	0.126	±0.142	39	5/6	0.080	±0.154	40
6/7	−0.304	±0.204	39	6/7	−0.310	±0.105	40
7/8	0.024	±0.086	41	7/8	0.118	±0.083	40
8/9	0.072	±0.079	41	8/9	0.113	±0.065	40
9/10	0.967	±0.186	17	9/10	1.332	±0.140	12

Mean mortality rate (MMR) was expressed as per cent isopods that died per day. 95% confidence limits (CI) are given.

95% confidence limits were calculated. The symbols used represent: a_i=estimate of duration of instar stage i; n_i=estimate of number of individuals in instar stage i; m_i=estimate of mortality in instar stage i; q=adult instar stage having infinite duration.

Material from the Mediterranean

Natatolana borealis was trapped at about 200 m depth in Bay of Monaco during January–February 1998 and December 1998.

RESULTS

Moulting in the laboratory

Shortly before release of the exuvium, a change in the red-brown dorsal and lateral body colour towards a slightly more greyish taint could be seen in laboratory kept specimens. The exoskeleton split during moulting between the fourth and fifth pereonite. The period between shedding of the posterior and anterior exuvia varied from 2 to 8 d, on average 4.6 d (N=36, SD=1.7). Of the 71 examined laboratory kept specimens, more than 45% died during moulting or shortly after ecdysis. Most of the specimens that died during ecdysis, failed to release the anterior exoskeleton. Twenty-two females and 24 males moulted once. Only five males and six females moulted more than once in the laboratory. The number of flagellar articles on the left and right first antenna increased with one article in six of eight observed cases after moulting in the laboratory. In two of the cases the number of articles increased with one article on one antenna while the number of articles remained constant on the other and was probably caused by difficulties in shedding of the anterior part of the exuvium.

Field instar stages

Postmarsupial instar stages 1 and 2 lacked the seventh pair of pereopods (manca 1 and 2). The seventh pereopod was rudimentary in postmarsupial instar stage 3 (juvenile 1) and became functional in instar stage 4 (juvenile 2) and in instar stage 5 (juvenile 3). The isopods could be sexually differentiated from instar stage 4. Some of the isopods became sexually mature from instar stage 6 (adult). Laboratory kept isopods that were released from the marsupium had six flagellar articles on the first antenna. Postmarsupial instar stage 1, 2, 3, 4, 5, 6, etc. were represented by 6, 7, 8, 9, 10, 11, etc. flagellar articles and 3, 4, 4, 5, 5, 6, etc. setae groups, respectively (Figure 1). The three first instar stages of *Natatolana borealis* formed three distinct size groups. The pleopod 1 length distributions of male and female *N. borealis* from Skogsvåg and Raknesvåg partly overlapped but the pleopod 1 mean length increased significantly ($P<0.05$) with instar stage (Figure 2).

The first flagellar article seemed to be firmly attached to the distal end of the third peduncle and the broad hinge that made the flagellum movable was located between the first and the second flagellar article (Figure 1). The new article on the flagellum grew out between the second and third article. All of the articles except the first one had aesthetascs and the number of aestehetasc groups on the large second article increased with age. The few isopods collected in Raknesvåg that were instar stages 10 and 11 constituted less than 0.5% of the 9004 animals collected at this location during 3.5 y.

Field mortality

The mean mortality rates of male and female isopods in the same instar stage were not significantly different in instar stage 4–9 (Table 1). The calculated mean mortality rate was negative from instar stage 6 to 7, due to increasing number of isopods trapped in instar stage 7 relative to instar stage 6. The mortality rate of males and females increased significantly from instar stages 9–10.

Growth in field

The growth factors from instar stage 1 to instar stage 5 were 1.20–1.26 and 1.21–1.28 in Raknesvåg and Skogsvåg, respectively (Figure 3). The growth factors from instar stage 7 to instar stage 10 were less than 1.14 in Raknesvåg and less than 1.09 from instar stage 7 to instar stage 9 in Skogsvåg. An increase in female growth factors occurred between instar stages 6 and 7 in Skogsvåg and Raknesvåg.

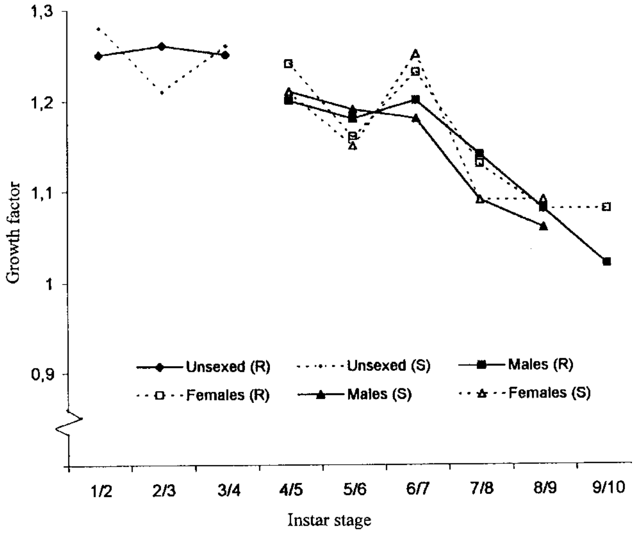

Figure 3. The growth factors from instar stages 1–9 of male, female and sexually undifferentiated *Natatolana borealis* from Skogsvåg and Raknesvåg.

The inflection points of premoult/postmoult pleopod 1 mean length plots of field data from Skogsvåg and Raknesvåg were approximately 2.5 mm and 3.0 mm premoult pleopod 1 length, which corresponded to instar stages 6 and 7, respectively.

The pleopod 1 mean lengths of instar stages 1, 2 and 3 of *N. borealis* from Raknesvåg sampled in the winter ($N_{1\text{-}3}$=148) were not significantly different ($P>0.05$) from the summer ($N_{1\text{-}3}$=126). The males in instar 5 and females in instar 9 were significantly different, but in each of these comparisons one of the samples consisted of a relatively low number of specimens.

The pleopod 1 mean lengths of males and females in instar stages 4–10 were not significantly different in Raknesvåg (Figure 2). Likewise, the pleopod 1 mean lengths of males and females in instar stages 4–9 were not significantly different in Skogsvåg. Comparisons of pleopod 1 mean lengths of unsexed specimens, males and females from Raknesvåg showed that instar stages 1–7 were not significantly different from the corresponding instar stages from Skogsvåg. The mean female and male pleopod 1 lengths of instar stages 8 and 9 were significantly larger in Raknesvåg than in Skogsvåg. The differences in instar stages 8 and 9 were also apparent when samples from only June and September were compared. Two more instar stages were also found in Raknesvåg.

The peak of an offspring cohort could be discerned in the pleopod 1 length distribution (Figure 4) in September 1977 at 2.12 mm and likewise at 3.2 mm in September 1978 for both males and females from Skogsvåg. This corresponds to growth from instar stage 5 to instar stage 8 in 12 months. The time spent to grow from postmarsupial instar stages 1–8 was estimated as 27 months at Skogsvåg. Assuming equal duration of instar stages 8 and 9, the longevity was 35 months from instar stages 1–9.

The peak of an offspring cohort is apparent in data from February, June and October 1993, February, June and November 1994, April and October 1995 and June 1996 in Raknesvåg (Figure 5), which gives a figure of about 41 months duration for the first eight instar stages. The average duration of postmarsupial instar stages 1–8 of *N. borealis* were estimated to 38 months in Raknesvåg. The duration of consecutive instars showed an increasing tendency. Assuming that the duration of instar stage 9 was at least similar to the duration of instar stage 8, the longevity of *N. borealis* was estimated to 45 months in Raknesvåg (Figure 6).

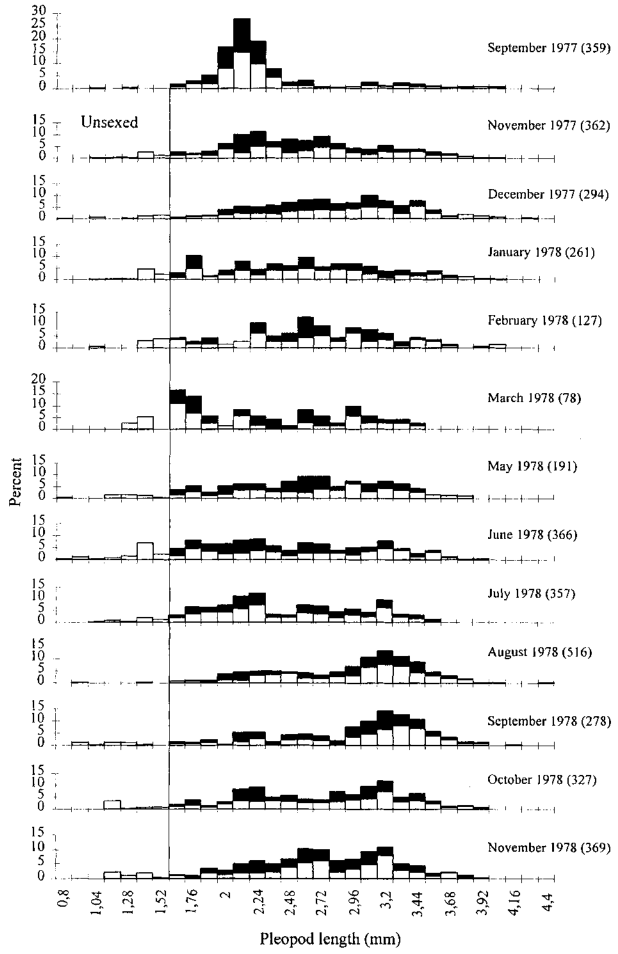

Figure 4. The pleopod 1 length distribution of unsexed (<1.6 mm), male (black) and female (white) *Natatolana borealis* from Skogsvåg from September 1977 to November 1978 drawn for 31 size groups, ranging from 0.8 to 4.52 mm. The number of examined isopods is given in brackets.

Weight in field

The exponential relationships between DW and pleopod 1 length of male and female *N. borealis* from Raknesvåg were significantly larger ($P>0.05$) than all the regressions from Skogsvåg, except for the males in October 1977 (Figures 7 & 8). The DW of all of the 479 measured isopods from Skogsvåg was less than 200 mg, while the DW of eight of the 163 isopods collected in Raknesvåg in October 1998 varied from 207 to 426 mg. The female regressions from Skogsvåg were significantly larger than male regressions within the same month, with the exception of July 1978. Both the male and female exponential regressions from January 1978 were significantly

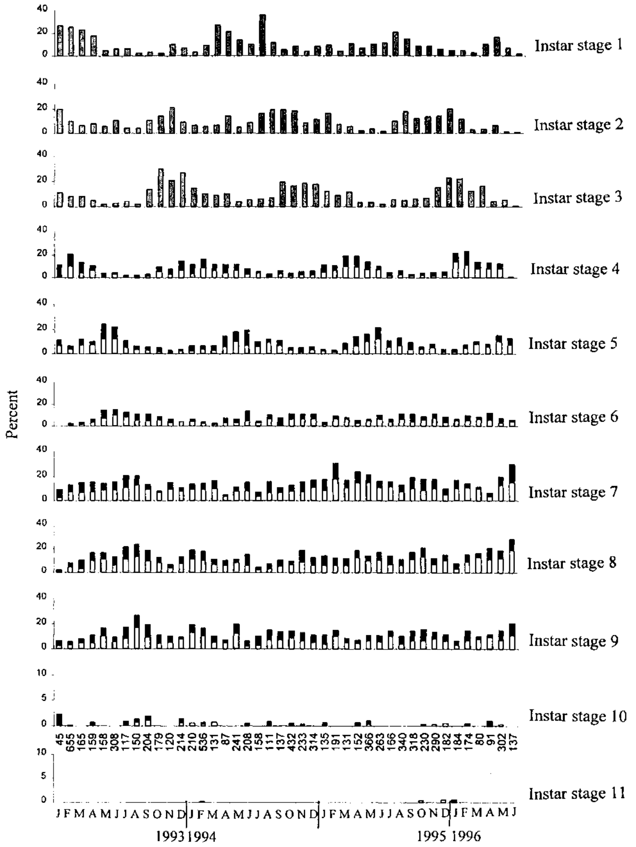

Figure 5. The frequency distribution of sexually undifferentiated (grey), male (black) and female (white) *Natatolana borealis* in instar stages 1–11 from Raknesvåg in the period from January 1993 to June 1996. The number of isopods examined per month is given beneath the distribution of instar stage 10.

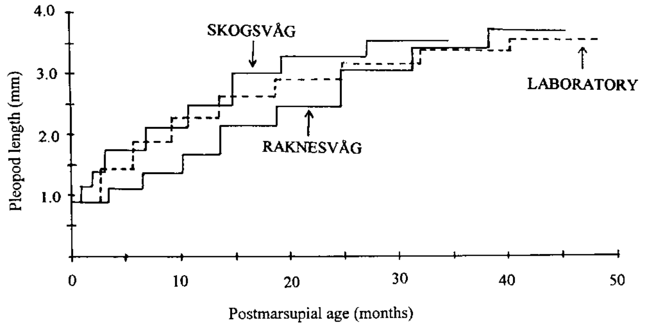

Figure 6. The growth curves from laboratory and field data of *Natatolana borealis* collected from two localities from western Norway. The *in situ* graphs were constructed from pleopod 1 mean lengths and mean intermoult periods.

lower than the regressions from the other months ($P<0.05$) and deviated at pleopod 1 lengths larger than 2.5 mm.

The linear relationship between DW and AFDW of males and females from Skogsvåg were significantly different ($P<0.05$) within the same months, except for July 1978 (Table 2). The highest slopes of the regression lines were found in October 1977, 1978 and April 1978.

The water content of *N. borealis* from Raknesvåg in October 1998 varied between 59–92% and was on average 76.6% (SD=4.7; N=163) (Figure 9).

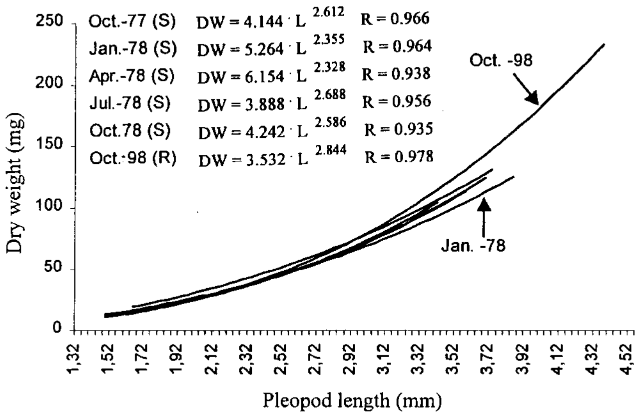

Figure 7. Exponential regresssion lines between pleopod 1 length (L) and DW of male *Natatolana borealis* from Skogsvåg (S) and Raknesvåg (R). The correlation coefficient of logarithm transformed data is denoted by R=.

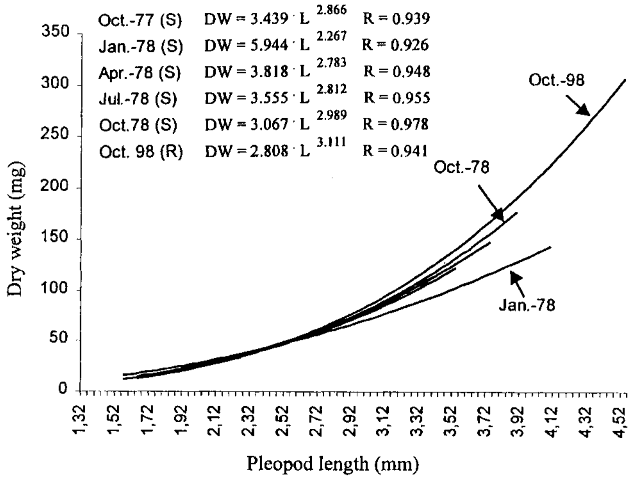

Figure 8. Exponential regresssion lines between pleopod 1 length and DW of female *Natatolana borealis* from Skogsvåg and Raknesvåg. For abbreviations see Figure 7.

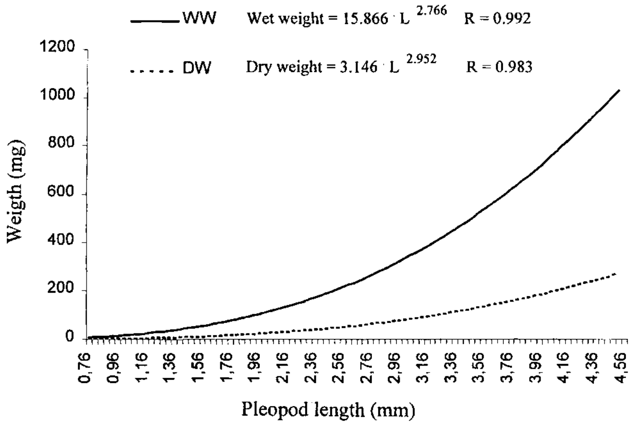

Figure 9. Exponential regresssion lines between pleopod 1 length, DW and WW of unsexed, male and female *Natatolana borealis* from Raknesvåg. For abbreviations see Figure 7.

Table 2. *Linear regressions between DW (mg) and AFDW (mg) of* Natatolana borealis *from Skogsvåg.*

Date	Males	R	N	Females	R	N
Oct 1977	AFDW=0.673·DW−1.685	0.986	52	AFDW=0.784·DW−7,168	0.989	42
Jan 1978	AFDW=0.607·DW+0.571	0.990	35	AFDW=0.676·DW−3.099	0.986	53
Apr 1978	AFDW=0.710·DW−2.713	0.989	42	AFDW=0.765·DW−6.070	0.985	55
Jul 1978	AFDW=0.720·DW−3.288	0.990	53	AFDW=0.716·DW−2.224	0.991	47
Oct 1978	AFDW=0.712·DW−1.609	0.989	46	AFDW=0.761·DW−3.690	0.996	54

R, correlation coefficient; N, number of isopods.

Table 3. *Linear regressions of length increment (mm) and intermoult period (days) from laboratory kept* Natatolana borealis.

	Length increment	R	N	Intermoult period	R	N
Males	Post=0.908·Pre+0.489	0.976	29	IP=4.386·PLP+76.952	0.830	5
Females	Post=0.826·Pre+0.768	0.974	30	IP=4.362·PLP+77.008	0.925	9
Total	Post=0.857·Pre+0.660	0.973	59	IP=4.379·PLP+76.887	0.888	14

Pre and Post are the premoult and postmoult lengths of pleopod 1. PLP, (pleopod 1 length)^3 and corresponding intermoult period (IP). R, correlation coefficient; N, number of isopods.

Table 4. *Pleopod 1 mean length (PML) of* Natatolana borealis *in instar stages 5–9 from the Bay of Monaco. The isopods were caught in January–February 1998 (nine specimens) and December 1998 (98 specimens). 95% confidence intervals (CI) were calculated. The percentage of sexually mature males within an instar stage is given. One sexually mature female wearing oostegites was found in instar stage 8.*

	Males				Females		
Instar stage	PML (mm)	CI	N	% mature	PML (mm)	CI	N
5	—	—	0	—	1.63	—	1
6	2.29	±0.13	3	0	2.17	±0.70	3
7	2.62	±0.09	27	55.6	2.84	±0.17	7
8	2.87	±0.06	29	93.1	2.96	±0.13	12
9	3.13	±0.07	21	100.0	3.34	±0.30	4
Total	—	—	80	—	—	—	27

Laboratory observations—growth

The linear correlation between (pleopod 1 length)^3 and intermoult duration that was found for *N. borealis* was better than the correlation of logarithmic, first and second degree. Both the length increment regressions and the intermoult period regressions were not significantly different ($P > 0.05$) between male and female laboratory kept isopods (Table 3). Potential differences in growth rate between young and adult isopods could not be discerned in the laboratory data because 56 of the 59 measured isopods had pleopod 1 lengths larger than 2.00 mm (i.e. ⩾instar stage 5). The increase in pleopod 1 length of laboratory kept isopods was reduced from 20% in case of the smallest measured specimen (1.6 mm pleopod 1 length) to about 1–2% in case of the largest measured specimens (3.6–3.7 mm). Increase of pleopod 1 length could vary 10% between isopods of the same size.

The age of laboratory kept animals with pleopod 1 lengths from 0.9 to 3.3 mm, which corresponded to instar stages 1–8, were calculated to 40.4 months (Figure 6). When instar stage 9 was included, the longevity of laboratory animals was 49.6 months.

Material from the Mediterranean

The structure of the first antenna and positions of setae on the flagellum in the material of *N. borealis* from Loch Fyne and Bay of Monaco, were both identical to the structures of the Norwegian isopods.

The sample from Bay of Monaco in December 1998 consisted of 74.5% males, which is significantly different from the expected unity ($P < 0.005$, χ^2 test). Sexually mature males were found in instar stages 7, 8 and 9 (Table 4). The pleopod 1 mean lengths of male *N. borealis* in instar stages 7, 8 and 9 were significantly smaller ($P < 0.05$) than the corresponding instar stages from both Skogsvåg and Raknesvåg (Figure 2). Females in instar stage 8 were significantly smaller than females from the Norwegian coast. The confidence limits of female pleopod 1 lengths in instar stages 6, 7 and 9 were relatively large due to the low number of females in the sample.

One female of instar stage 8, bearing an empty marsupium, was found in the sample from the Bay of Monaco from December 1998. The oocytes in the ovary were undeveloped and the anterior hindgut was filled with fish flesh.

DISCUSSION

Moulting and instar stages

As in most isopods, *Natatolana borealis* follows the normal biphasic pattern during ecdysis where the posterior cuticle is lost first and after a while the anterior part is shed. The time between posterior and anterior ecdysis of *N. borealis* varied from 2 to 8 d in the laboratory. The observed interecdysis of three laboratory kept *N. borealis* collected off Monaco were 3–4 d (Carvalho & Fowler, 1985). Interecdysis of *N. borealis* collected on the continental slope off Marseilles lasted from several hours to 4 d and increased with age (Kaïm-Malka, 1997). The moult cycle comprising nerve stimuli and hormones can be affected by factors like illumination, nourishment, temperature and possibility of hiding (Carlisle, 1956; Passano, 1960). The large variation in interecdysis and the high mortality during ecdysis of *N. borealis* that was kept in glass jars with little sediment may indicate unfavourable conditions relative to the deep sediment in the field.

Natatolana borealis underwent nine postmarsupial instar stages in Skogsvåg and 11 in Raknesvåg. The pleopod 1 mean length increased significantly with consecutive instar stages for both sexes at both localities. The growth factors for isopods varied between 1.28 and 1.08 and showed a decreasing trend after sexual maturation. The instar stage distributions changed through the year, but were identical when traps were deployed simultaneously (Johansen & Brattegard, 1996). *Natatolana borealis* from Loch Fyne underwent ten postmarsupial instar stages with observed mean body lengths from 5.7 to 26.1 mm (Wong & Moore, 1996).

Norwegian *N. borealis* in instar stages 1, 2 and 3 showed three distinct size groups (manca 1, manca 2 and juvenile 1) that all lacked secondary sexual characters. This agrees with the observations from Loch Fyne (Wong & Moore, 1996). These results do not accord with the five size classes that were described for sexually undifferentiated *N. borealis* from north-west Mediterranean (Kaïm-Malka, 1997).

Field mortality

Natatolana borealis breeds continuously through the year with occasional peaks (Johansen, 1996). The main drawback of the vertical life table approach is sensitivity to trends in recruitment, which makes it most applicable to populations with continuous breeding characterized by overlapping generations (Aksnes & Ohman, 1996). Negative estimates of mortality were found in instar stages 6–7 for *N. borealis*, this may indicate violation of assumptions of the model or, alternatively, high sampling variability (Aksnes & Ohman, 1996) resulting from more isopods being attracted to the trap in instar stage 7 than in instar stage 6. An increased need for energy of sexual mature isopods, better swimming ability and changed behaviour are possible causes for the estimated negative mortality as the maximum swimming speed of *N. borealis* generally increases with increasing instar stages (P.O. Johansen, unpublished data) and sexually mature females and males were found from instar stage 7 in Raknesvåg (Johansen, 1996).

Because the mortality rate of female and male *N. borealis* increased significantly from instar stage 9 to instar stage 10 it appears that only a small part of the study populations survived the ninth instar stage. The estimated mortality rate was the same for female and male *N. borealis* of the same age. Equal mortality of male and female *N. borealis* agrees with the observed sex ratios in instar stages 4, 5 and 10 from Raknesvåg that were not significantly different from unity (Johansen, 1996). However, the fact that ovigerous females were not caught in baited traps and were probably hiding in the sediment (Johansen, 1996; Nielsen & Strömberg, 1965; Taylor & Moore, 1995; Wong & Moore, 1996) may have influenced on the mortality estimate of sexually mature females.

Growth on the Norwegian coast

An increase in growth factors and inflection points in postmoult/premoult plots were seen for female *N. borealis* in instar stages 6–7 from Raknesvåg and Skogsvåg. Sexual maturation was reached for some male and female *N. borealis* from instar stages 6–7 (Johansen, 1996). The level of allometric growth in crustaceans often changes at the puberty moult (Hartnoll, 1982). Onset of sexual maturation seems to influence both the growth and the behaviour of female *N. borealis*.

Field and laboratory data indicated that male and female *N. borealis* from western Norway underwent the same number of instar stages, did not have significantly different mean sizes at the same instar stage, reached the same maximum size and had a growth rate which declined as the isopods aged. Similarily growth rate of *N. borealis* from Loch Fyne was the same for both sexes and slowest in adult isopods (Wong & Moore, 1996) and no differences were observed between the patterns of development of male and female *N. borealis* from the north-west Mediterranean (Kaïm-Malka, 1997).

Potential changes in growth due to changes in temperature might be expected in short lasting juvenile instar stages, but were not observed in Raknesvåg where the yearly temperature variation was 1.1°C (Johansen, 1996). The growth rate of *N. borealis* from Loch Fyne showed only moderate seasonal variation (temperature variation approximately 3.5°C) (Wong & Moore, 1996). Growth of *Serolis polita* Pfeffer in winter was significantly slower than in summer at Signy Island where the yearly temperature variations were less than 3°C, and the reduced growth was considered to be due to reduced food availability (Luxmoore, 1982). Low variablility of growth in *N. borealis* coupled with seasonally low temperature variation found in the deep water may indicate that food availability was not strongly pulsed seasonally in Raknesvåg.

The pleopod 1 mean lengths of instar stages 8 and 9 from Raknesvåg were significantly larger than in Skogsvåg and instar stages 10 and 11 were not found in Skogsvåg. The measured DW of *N. borealis* confirmed the size differences between Raknesvåg and Skogsvåg. *Natatolana borealis* were collected at similar depths at both collection sites. The salinity was above 33.6 psu at the collection sites (Johansen, 1999). The yearly average temperatures at 100 m depth were calculated to be 7.6°C in Skogsvåg and 7.9°C in Osterfjord, respectively. Neither temperature nor salinity seems to explain the observed size differences between Skogsvåg and Raknesvåg. The isopods from these two locations are probably belonging to the same population because of the high mobility of the species and any differences may be caused by temporal or spatial differences. Differential mortality, migration, longevity or growth rate might alter the sex ratio of a population (Wenner, 1972). Of the total catch of *N. borealis*, 45.5% from Raknesvåg and 52.6% from Skogsvåg were females, and both being significantly different from unity (Johansen, 1996). Reproduction of *N. borealis* depends probably largely on food availability (Johansen, 1996). Onset of sexual maturation of *N. borealis* was attained a little later in Raknesvåg than in Skogsvåg (Johansen, 1996). Since only the latest instar stages were affected in Raknesvåg, it is reasonable to suggest that differences in food availability and sexual maturation may have been of importance to the observed size differences in Skogsvåg and Raknesvåg. Alternatively, large sizes could be reached due to lower predation risk on intermediate and large specimens. Differences in occurrence of demersal fishstocks and hyperbenthic crustaceans that feed on *N. borealis*, may at least partly explain the size and instar stage differences between Raknesvåg and Skogsvåg.

Longevity on the Norwegian coast

The pleopod 1 mean length of laboratory reared *N. borealis* in postmarsupial instar stage 1 was 0.803 ±0.015 mm, N=20 (Johansen, 1980) which is significantly smaller than the observed *in situ* sizes in Raknesvåg and Skogsvåg. Temperature variation or other unfavourable laboratory rearing conditions that differ from the natural deep-water environment, may have caused observed differences. The life span of *N. borealis* was estimated to last about 7–14 months longer in the laboratory than in Skogsvåg. Unfavourable conditions can impede ecdysis (Passano, 1960) and the intermoult period of crustaceans is always likely to last longer in the laboratory than in the wild (Hartnoll, 1982). The temperature and the salinity variations were only slightly different in Skogsvåg (6.6–9.9°C; 33.6–34.8 psu) from the laboratory (6.5–10.0°C; 31.5–34.0 psu). The isopods were kept in the dark as *in situ*, but with too little sediment to dig into. The age calculations were mostly based on specimens $\geqslant$instar stage 5. Accounting for possible bias, the calculated duration of instar stages 1–9 from laboratory data was probably overestimated.

About 32% of the 8036 isopods caught in Raknesvåg (1993–1995) were in instar stages 1–3 and 5% of the total catch (5374 specimens) in Skogsvåg (1977–1978) were in instar stages 1–3 (Johansen, 1980; Johansen & Brattegard, 1996). The relatively low number of *N. borealis* in instar stages 1–3 that were trapped in Skogsvåg made the intermoult estimates of the three first instar stages in Skogsvåg uncertain. Assuming that the three first instars stages lasted ten months as in Raknesvåg, the estimated longevity of *N. borealis* in Skogsvåg was 42 months. The field data indicate that the age of *N. borealis* in instar stage 9 from the Norwegian coast was 3–4 y. Specimens of *N. borealis* in instar stages 10 and 11 may have attained a maximum age of about 4–5 y. Longevity of *N. borealis* from Loch Fyne was estimated by following peaks in size–frequency distributions with time to be about 2.5 y (Wong & Moore, 1996). Longevity of *N. borealis* trapped off Marseille, was estimated using size-frequency distributions and total length (15 size classes) to be 4.6–6 y (Kaïm-Malka, 1997). The intermoult stages of *N. borealis* were estimated to last about 2–6 months off Marseille (Kaïm-Malka, 1997) and about 3–7 months on the Norwegian coast. The differences in longevity between the Norwegian and Mediterranean populations were probably mainly caused by the differences in number of estimated stages. The sample from Bay of Monaco, however, indicated nine instar stages, as observed for the greater part of Norwegian isopods.

Field weight

The DW regression lines of females from Skogsvåg varied more and the females were generally heavier than the males. Ripe ovarian oocytes in female *N. borealis* constituted 31.9% of the animals' DW and 38.3% of the animals' AFDW, on average (N=40) (Johansen, 1980). During the moult cycle organic and inorganic substances are accumulated in tissue, blood and hepatopancreas (Passano, 1960), however the growth of female gonads is probably more important to the DW than accumulated reserves for ecdysis. A large part of the female population in Skogsvåg was breeding in April–May and August–December (Johansen, 1996) and the organic content of female *N. borealis* was high in April and October and low in January. Seasonally changing DW of female *N. borealis* from Skogsvåg agrees with the observed peak reproduction periods through the year. Similarily, seasonal variation in length and weight of pooled samples of male and female *N. borealis* was indicated for Mediterranean *N. borealis* (Kaïm-Malka, 1997). However, these isopods had access to food during trapping and the reduced length-to-weight relationships in the spring was thought to be partly caused by reduced food intake associated with reproduction.

Material from the Mediterranean

In Raknesvåg, instar stages 7, 8 and 9 were represented by respectively 57.7, 91.2 and 100% sexually mature male *N. borealis* (Johansen, 1996). The distribution of sexually mature males caught in the Bay of Monaco was in agreement with the observations from Raknesvåg. The low number of examined *N. borealis* in instar stage 6 from the Bay of Monaco does not exclude the possibility that some of the males became sexually mature from this instar stage. The sex ratio of sexually mature *N. borealis* from the trap catches from the Norwegian coast tended towards a dominance of males during reproduction (Johansen, 1996). Therefore the large portion of males and the occurrence of a spent female in the sample from the Bay of Monaco indicate that many females were breeding in December 1998.

The pleopod 1 mean lengths of males and females from the Bay of Monaco were significantly smaller than the Norwegian *N. borealis* in samples containing more than 12 specimens. Both temperature and salinity at 100–200 m depth are higher in the Mediterranean than at the coast of Norway. Therefore either a different food regime or inenvironmental conditions may explain the size differences between the populations from the Mediterranean and the Norwegian coast, unlike the situation found at the two Norwegian localities.

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