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## Age determination in the Antarctic shrimp *Notocrangon antarcticus* (Crustacea: Decapoda), using the autofluorescent pigment lipofuscin

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**Abstract** Determination of basic population parameters in long-lived Crustacea is hindered by a lack of appropriate methods for age determination. This study uses the pigment lipofuscin as an age marker in the common Antarctic decapod *Notocrangon antarcticus* (Pfeffer, 1887) from the eastern Weddell Sea. Resin brain sections of the lateral somacluster of the olfactory lobe of 189 specimens were digitally recorded by confocal microscopy and images were subsequently analyzed. A modal progression analysis of the lipofuscin concentration–frequency distribution revealed a total of eight regularly spaced modes presumed to reflect consecutive annual age classes. All eight modes contained females, and the first four contained males. No regular modes were obvious in the comparable length–frequency distribution. The average yearly pigment accumulation was nearly linear and estimated as 0.02% area fraction year<sup>-1</sup>, which is considerably lower than rates published for species from lower latitudes. This is probably explained by the effect of low water temperature on metabolism and lipofuscin accumulation rate. The growth parameters  $CL_{\infty}$  and  $k$  from the von Bertalanffy growth function were 22.3 mm and 0.79 year<sup>-1</sup> for females, respectively, and 16.9 mm and 0.64 year<sup>-1</sup> for males, respectively. Mortality, estimated from catch curves, amounted to 0.44 year<sup>-1</sup> in females and 0.92 year<sup>-1</sup> in males, whereas  $P/B$ , calculated from the mass specific growth rate method, was slightly lower. The results indicate that the lipofuscin-inferred population parameters are an improvement over what can be learned about *N. antarcticus* with traditional methods.

### Introduction

Insight into the community components of the Weddell Sea has increased immensely over the past two decades (Voß 1988; Priddle et al. 1992; Arntz et al. 1994, 1997; Brey et al. 1994; Brey and Gerdes 1998). Studies on population dynamics are, however, still rare, though needed to obtain a complete picture of the system's trophic flow, in which bottom-living Crustacea play an important role (Jarre-Teichmann et al. 1997). While Peracarida form the most diverse crustacean taxon (DeBroyer and Jazdzewski 1996), decapods, although low in species diversity (Yaldwin 1965; Kirkwood 1984), can reach considerable abundances. *Notocrangon antarcticus* (Pfeffer, 1887), the most common benthic circumantarctic shrimp species, was reported to occur at maximum densities of 73 individuals per 100 m<sup>2</sup> in water depths of 200–600 m (Gutt et al. 1991). Consequently, shrimps can have a marked impact on abundance and population structure of their prey taxa, as well as on food competitors, e.g. echinoderms (Jarre-Teichmann et al. 1997). Larval development of *N. antarcticus* has been described in detail (Bruns 1992), but information on population dynamics of the adults is lacking.

Data on individual age, which are important in studying growth and mortality in a population, are difficult to obtain for crustaceans due to the lack of permanent hard structures bearing potential age markers. The most common approaches so far attempted for age determination of Crustacea are: (1) to keep individuals in captivity while studying the growth increments associated with moltings (Plaut and Fishelson 1991; Hill 1992), (2) recapture of tagged specimens (Campbell 1983; Taylor and Hoenig 1990; Fitz and Wiegert 1991; Somers and Kirkwood 1991), and (3) analysis of length–frequency data (MacDonald and Pitcher 1979; Pauly et al. 1984; Fournier et al. 1991; France et al. 1991; Roa and Bahamonde 1993). Growth data derived from specimens in captivity are prone to error due to the artificial conditions (e.g. Lagardère 1982); moreover, such

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studies are time-consuming for longevous species. Although modern tags are retained through molting and probably do not inhibit growth (Fitz and Wiegert 1991; Bannister et al. 1994), tagging and recapture is not a feasible procedure in polar deep-water regions for logistical reasons. Pronounced variability of size at age and slow growth in long-lived polar invertebrates can provoke considerable overlap of modes in size-frequency distributions (France et al. 1991; Sheehy 1992; Bannister et al. 1994). We, therefore, tried to employ the approach proposed by Sheehy (1989, 1990a, b), i.e. the use of the physiological correlate lipofuscin as an age marker.

Free radical-induced lipid peroxidation processes induce the formation of lipofuscin, which seems to occur in all postmitotic eukaryotic cells (Sheldahl and Tappel 1974; Sohal 1981). Accumulation of the pigment in postmitotic cells over the lifespan of an individual has been shown to be a universal characteristic of animal senescence (Katz et al. 1984; reviewed in Terman and Brunk 1998). For calibrating the content of morphological lipofuscin against age, two approaches have been suggested. Preferably, wild-grown, marked and recaptured individuals of known age provide calibration, as demonstrated by Sheehy et al. (1999) for European lobsters. Alternatively, age groups may be derived from analysis of lipofuscin concentration–frequency histograms (Ettershank 1983; Sheehy et al. 1994, 1998), analogous to size-frequency distributions. A previous study demonstrated that a number of polar crustaceans showed lipofuscin concentrations considered sufficiently high to conduct lipofuscin analysis (Bluhm et al. in press). Based on the lipofuscin concentration–frequency distribution, we tried to assess maximum age and age distribution in the eastern Weddell Sea population of the shrimp *N. antarcticus*, and from that data inferred further population parameters.

## Materials and methods

### Sampling and study area

Samples were taken during the expedition ANT XV/3 (EASIZ II, January to March 1998) of R.V. “Polarstern” to the eastern Weddell Sea (Arntz and Gutt 1999) (Fig. 1). In the Weddell Sea average annual sea temperature close to the sea bottom ranges, depending on water depth, from 0.4 °C (Circumpolar Deep Water) to –1.88 °C (Antarctic Surface Water), with seasonal variability generally <0.8 °C (Hellmer and Bersch 1985; Fahrbach et al. 1992). Specimens of *Notocrangon antarcticus* (Pfeffer, 1887) were caught in water depths of 245–440 m in Agassiz and bottom trawls with mesh sizes of 1 cm by 1 cm in the cod end. One sample was taken with an epibenthic sledge with a mesh size of 500 µm, and 300 µm in the net bucket. The species was identified according to Kirkwood (1984). Specimens were subsequently fixed in 4% buffered formaldehyde-seawater solution until embedding in resin (summer 1999).

### Sample preparation

Carapace length (CL) from the rear of the eye socket to the posterior dorsal edge of the carapace was measured to the nearest

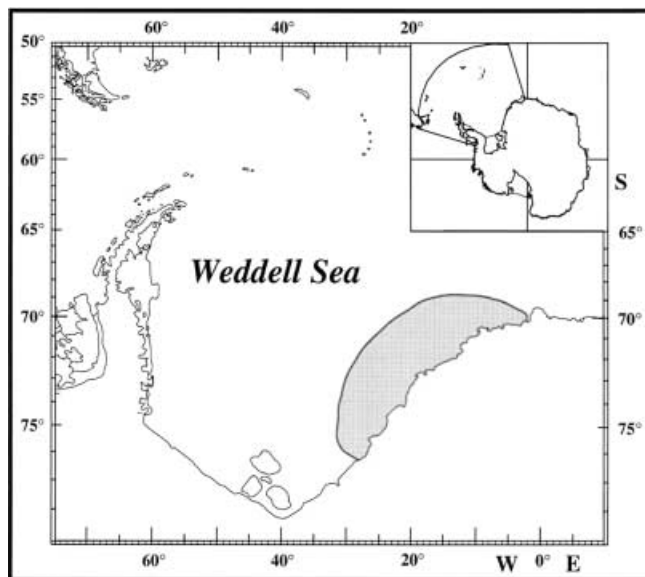


Fig. 1 Study area (shaded) in the eastern Weddell Sea

0.1 mm (rounded down) using vernier calipers. Wet body mass of formaldehyde-preserved specimens after blotting was determined to the nearest 0.1 g; weights were not corrected for preservation. Sex was determined using the gonads as indicators as well as the endopod of the first pleopod, which in males is shorter than that of the second pleopod; in females, both pleopods are equally long (Tiews 1954; Smaldon 1979). Specimens without detectable gonads were categorized as juveniles, as the endopod is not a reliable characteristic in very small specimens (Smaldon 1979). Brains were prepared for lipofuscin measurement as described for other decapod species by Sheehy (1989, 1990a) and Sheehy and Wickins (1994). The brains were dissected and dehydrated in ascending ethanol concentrations from 70% to 100%. Unstained, serial, horizontal, 6 µm thick resin sections (Technovit, Kultzer) were prepared following standard embedding procedures, however, excluding mounting medium and cover slip.

### Fluorescence confocal microscopy

Sections were analyzed with an inverted Leica TCS NT confocal microscope, using the 488 nm excitation wavelength of a KrAr laser (Omnichrome) combined with a 515 nm long pass filter. A 40× oil immersion lens (zoom factor 1) with a numerical aperture of 1.25 was applied. The posterior lateral somacluster of the olfactory lobe (nomenclature after Sandeman et al. 1992) was localized, as lipofuscin has proven to be especially dense in this area in decapod crustaceans (Sheehy 1989, 1990b; Sheehy et al. 1995a, 1998). Eight approximately equidistant sections of the entire cell mass were selected for lipofuscin analysis. Digital images of 1024 by 1024 pixel resolution (250 by 250 µm frame area) were recorded, applying Kalman averaging of four images each to reduce noise.

### Lipofuscin quantification

Image analysis was carried out using “Image” software (National Institute of Health). The outline of the cell mass area analyzed was traced manually, and the autofluorescent lipofuscin granules therein were discriminated using manual grayscale thresholding. The total area fraction (AF) of lipofuscin granules in the binarized selected area of the images was calculated by dividing the area of lipofuscin granules by the total area of analyzed tissue, and multiplied by 100. Each image was analyzed three times to reduce the impact of personal bias during analysis. The geometric average AF

over all sections examined for each individual was calculated (which – in line with stereological convention – corresponds to the volume fraction in percent lipofuscin). The image analysis was performed without prior knowledge of the body length of the specimens to avoid personal bias.

#### Age class identification

A length-frequency distribution (LFD) histogram was established from the size-data of 953 specimens, using class intervals of 0.5 mm. A lipofuscin concentration–frequency distribution (LCFD) histogram was constructed from the pigment concentration analysis of a subsample (189 specimens). For efficient comparison with the LFD, class intervals in the LCFD histogram were chosen such that the bulk of the data lay within a similar number of classes as in the length-frequency histogram. Potential age groups were identified by fitting normal components to modes in the LCFD histogram, using the modal progression analysis routine of FiSAT (FAO-ICLARM stock assessment tools, Gayanilo et al. 1996). Within this program, Bhattacharya's method (after Bhattacharya 1967) was applied to obtain initial values for mode means, which were refined using NORMSEP (after Hasselblad 1966). The latter method applies the maximum likelihood concept to SEPARation of the NORMally distributed components. Modes were only accepted when separated by a separation index above the critical value of 2 and when visually obvious. A  $\chi^2$ -test was performed to confirm the goodness-of-fit of observed and predicted frequency. In the case of overlapping normal components, normal distributions were generated using the normal probability density function (Sokal and Rohlf 1995), and individuals were designated to modes accordingly. Modes were assumed to reflect distinct broods, i.e. subsequent age classes separated by the age difference of 1 year, referred to as relative age (Pauly 1984). For this parameter, we use the dimension "years +": (1) to imply that exact age depends on what time of the year the sample was taken relative to the hatching period, (2) to account for natural spread of age in modes and (3) to account for the fact that detectable lipofuscin accumulation may start at some point after larval release. Therefore, 1+ means individuals between approximately 1 and 2 years of age. A yearly pigment accumulation rate was calculated from the regression of lipofuscin concentration against estimated age. Individuals used for lipofuscin analysis were not collected randomly from the available sample, but with the intention of covering the complete size range present. Hence, the age-frequency distribution (AFD) based on the lipofuscin sample is not representative for the population, but the distribution of age within each size class is likely to be representative. A corrected AFD was established by rearranging all individuals constituting the LFD into age classes according to this information. The corrected AFD was used to compute the catch curve.

#### Growth parameters

The growth constant  $k$  and the asymptotic carapace length  $CL_\infty$  of the von Bertalanffy growth function were approximated by fitting the Powell–Wetherall function (FiSAT, Wetherall 1986) to the size-frequency data. This fit does not require modes but uses the pure size frequencies to estimate  $Z/k$  and  $L_\infty$ . Mortality rate  $Z$  was estimated as described below, and, thus, values for  $k$  could be calculated. A cut-off length  $L'$  (length not smaller than the smallest length fully represented in the sample) of 12 mm CL was applied. Von Bertalanffy growth curves (VBGF),

$$CL_t = CL_\infty \left( 1 - e^{-k(t-t_0)} \right)$$

and Gompertz growth curves,

$$CL_t = CL_\infty \left( e^{-e^{-k(t-t_0)}} \right)$$

[ $CL_t$  = carapace length at age  $t$  (years),  $t_0$  = theoretical age at which  $CL = 0$  mm] were fitted to the size at lipofuscin-estimated age data by the iterative non-linear Levenberg–Marquardt algorithm (Marquardt 1963).

#### Mortality $Z$

Annual mean mortality was expressed by the parameter  $Z$  of the single negative exponential mortality model (Ricker 1979). It was estimated by linear regression as the slope (with sign changed) of the descending right arm of the catch curve, i.e. plotting the natural logarithm of the number of specimens in each age group (corrected as described above) against their corresponding (in this case lipofuscin-estimated) age. In addition, we applied Brey's (1995, 1999) empirical function established from data for benthic invertebrates:

$$\log Z \approx \log(P/B) = 1.646 + 0.995 \cdot \log(1/A_{\max}) \\ - 0.034 \cdot \log(M_{\max}) - 292.039 \cdot 1/T$$

[ $A_{\max}$  = maximum age (years+, as defined for this paper),  $M_{\max}$  = maximum body mass (in kJ),  $T$  = temperature (K)]. For this estimate, wet body mass in grams was converted to body mass in kilojoules using a factor of 3.31, composed of conversion factors suggested by Salonen et al. (1976), Rumohr et al. (1987) and Brey et al. (1988). As for temperature, a value of  $-1.0$  °C = 172.15 K was used.

#### Productivity, biomass and production

Mean annual biomass was calculated based on abundance data by Gutt et al. (1991) derived from a photographic survey in the eastern Weddell Sea ( $0.064$  ind.  $m^{-2}$ ), and the mean body mass from our data for 935 specimens of *N. antarcticus*. Annual production and productivity ( $P/B$  ratio) was, first, estimated from  $Z \approx P/B$  (Allen 1971; Brey 1995, 1999). Secondly, the mass-specific growth rate method (MSGRM, Crisp 1984) was applied, which combines the information provided by the LFD, the growth function and the size–body mass relationship.

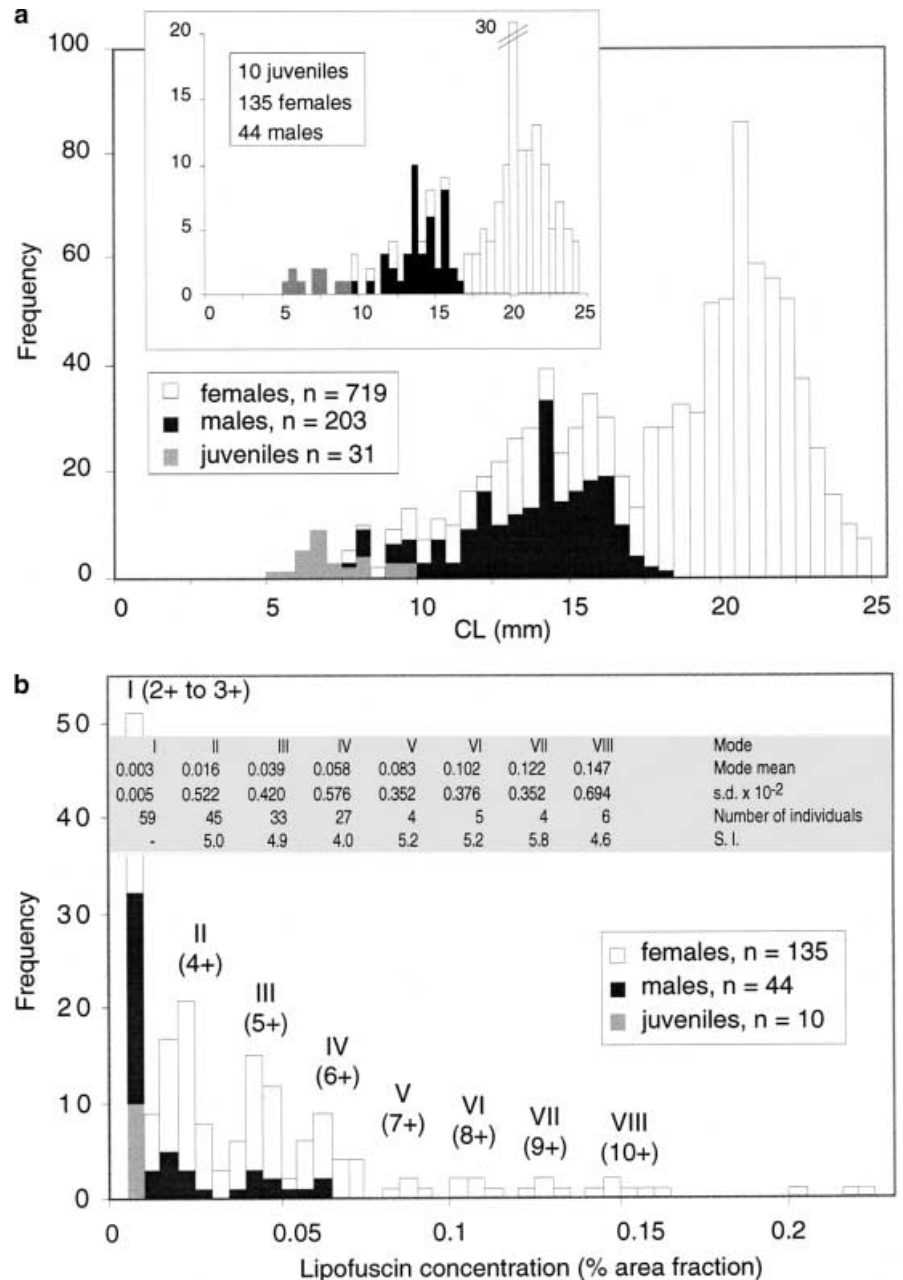
## Results

#### Age class identification

A representative subsample of the total catch ( $n = 953$  individuals) was measured, weighed and sexed. Numbers of females, males and juveniles were 719 (75.4%), 203 (21.3%) and 31 (3.3%), respectively. The carapace length (CL) ranged from 7.4 to 25.0 mm in female shrimps, from 7.5 to 17.6 mm in males and from 5 to 9.5 mm in juveniles. The size–body mass (WM) relation was  $\log(gWM) = 2.89 \cdot \log(mmCL) - 2.98$  ( $r^2 = 0.97$ ,  $P < 0.001$ ) in females and  $\log(gWM) = 2.97 \cdot \log(mmCL) - 3.07$  ( $r^2 = 0.97$ ,  $P < 0.001$ ) in males. The LFD was characterized by a pile up of large specimens in two modes (Fig. 2a). The first one (12–17 mm CL) represented approximately 80% of males in the catch and the second one (17–24 mm CL) represented about 75% of all females. No modes reflecting consecutive age classes were visually distinguishable, and modal components could not sensibly be fitted to the distribution.

A total of 135 females, 44 males and 10 juveniles of *Notocrangon antarcticus* were analyzed for their lipofuscin concentration in the lateral somacluster of the olfactory lobe. Pigment granules were found in most specimens, and ranged in size from  $< 1$  to 5  $\mu m$  diameter (Fig. 3). Lipofuscin concentrations varied between  $< 0.001$  and 0.216% ( $\pm SD = 0.065$ ) area fraction (AF) (females), 0.056% AF ( $\pm SD = 0.012$ ; males) and

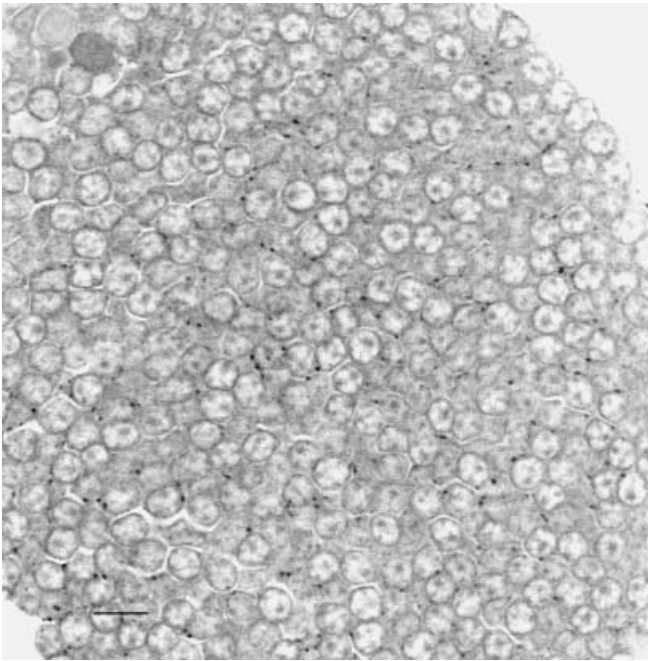
**Fig. 2a, b** *Notocrangon antarcticus* from the eastern Weddell Sea. **a** Length-frequency distributions of total catch and lipofuscin-analyzed specimens (*inset*). **b** Lipofuscin concentration–frequency distribution, including results from modal progression analysis. The frequency ( $n$ ) of one bar is  $n_{\text{total bar}} = n_{\text{females}} + n_{\text{males}} + n_{\text{juveniles}}$  (*s.d.* standard deviation; *S.I.* separation index; *Roman numerals* modes; *Arabic numerals* cohort designation in years +)



0.002% AF ( $\pm$ SD = 0.002; juveniles). Standard deviation between the eight analyzed sections of one individual was 25% on average in concentrations >0.015% AF (SD = 100% in concentrations  $\leq$  0.015% AF). Fitted modes were well resolved with high separation indices ( $\chi^2$  test,  $P < 0.001$ , Fig. 2b). Eight modes were separated, with females present in all eight while males were present in modes I–IV. Data from juveniles ranged within mode I. Three females had concentrations outside the range of mode VIII, suggesting the existence of more than eight age groups. The LCFD differed from the LFD in that the former had evenly spaced modes that were distinguishable by eye.

The relationship between lipofuscin content ( $L$ ) and lipofuscin-estimated age ( $A$ ) was highly significant

(Fig. 4a,  $P < 0.001$ ). Linear regressions defining the relationship were  $L = 0.021A + 0.022$  ( $r^2 = 0.98$ , females) and  $L = 0.017A + 0.014$  ( $r^2 = 0.94$ , males), corresponding to an annual lipofuscin accumulation rate of 0.021% AF (females) and 0.017% AF (males). There was a slight but statistically significant effect of sex on lipofuscin accumulation rate (ANCOVA,  $P < 0.001$ ). The relation between lipofuscin concentration and size or body mass, in contrast, showed substantial scatter (Fig. 4b, c), especially in females  $\geq 18$  mm CL and males  $\geq 14$  mm CL. Individuals with high lipofuscin content, though, tended to be large. For example, lipofuscin concentrations >0.1% AF were only measured in specimens >19.4 mm CL. Overall, higher pigment concentrations were found in females than in males.



**Fig. 3** *Notocrangon antarcticus*. Fluorescent lipofuscin granules in the olfactory lobe somacluster in a presumably 7+ year old female shrimp. Excitation = 488 nm, emission  $\geq 515$  nm, digital confocal inverted image. Scale bar 20  $\mu\text{m}$

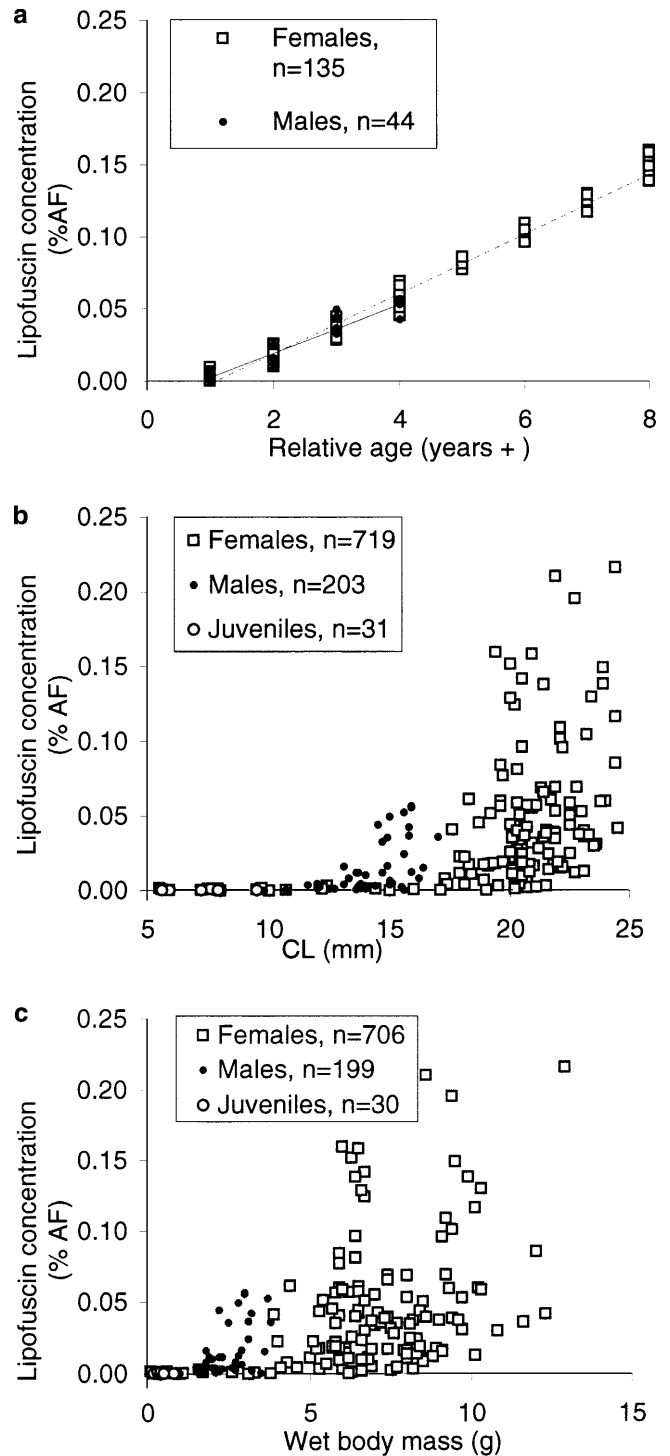
Males, on the other hand, showed higher lipofuscin values at a smaller size than females (Fig. 4b).

### Growth parameters

The Wetherall plot estimated  $CL_{\infty} = 22.3$  mm in females and 16.9 mm in males;  $k$  was approximated as  $1.05 \text{ year}^{-1}$  in females and  $0.63 \text{ year}^{-1}$  in males, derived from  $Z/k = 0.37$  and  $0.94$ , respectively. The size-at-estimated age data were modified prior to growth analysis by first adding information for zoea II-stage larvae, which are about 1 year of age at an average CL of 2.5 mm (Bruns 1992; Gorny et al. 1992). These zoea are designated as the 1+ age group. Secondly, based on the assumption that mode I is not homogeneous due to the lack of resolvable lipofuscin in the youngest individuals, juveniles lacking gonads were removed and designated as a 2+ age class. The remaining mature individuals in mode I were classed as 3+ years. Remaining modes are treated as sequential homogeneous age classes. The underlying assumption is that mode I does not represent 1-year-old specimens if detectable lipofuscin accumulation does not start right after larval release (Sheehy 1990a, c; Nakano et al. 1993; Sheehy et al. 1995a). The fit of the corrected VBGF growth curves (Fig. 5a, b) resulted in:

$$CL_t = 22.34 \left( 1 - e^{-0.79(t+0.76)} \right), \quad r^2 = 0.72 \text{ (females, Fig. 5a)}$$

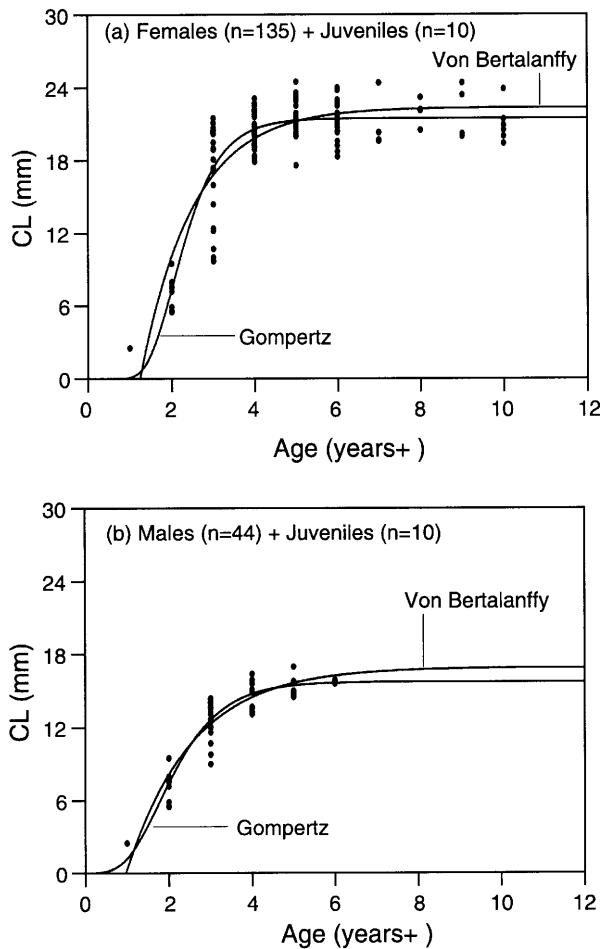
(standard errors:  $CL_{\infty} = 0.38, k = 0.07, t_0 = 0.08$ )



**Fig. 4a-c** *Notocrangon antarcticus* from the eastern Weddell Sea. Lipofuscin concentration in relation to: (a) lipofuscin-based estimated age ( $L = 0.021A + 0.022$ ,  $r^2 = 0.98$ , females;  $L = 0.017A + 0.014$ ,  $r^2 = 0.94$ , males;  $L =$  lipofuscin concentration,  $A =$  age), (b) body size as carapace length (CL) and (c) wet body mass

$$CL_t = 16.93 \left( 1 - e^{-0.64(t+1.03)} \right), \quad r^2 = 0.84 \text{ (males, Fig. 5b)}$$

(standard errors:  $CL_{\infty} = 0.74, k = 0.09, t_0 = 0.12$ ).



**Fig. 5a, b** *Notostrangon antarcticus* from the eastern Weddell Sea. Growth curves fitted to size at lipofuscin-estimated age data in (a) females and (b) males. Von Bertalanffy:  $CL_{\infty} = 22.34$  mm,  $k = 0.79$  year<sup>-1</sup>,  $t_0 = -0.76$  years,  $r^2 = 0.72$  (females),  $CL_{\infty} = 16.93$  mm,  $k = 0.64$  year<sup>-1</sup>,  $t_0 = -1.03$  years,  $r^2 = 0.84$  (males); Gompertz:  $CL_{\infty} = 21.46$  mm,  $k = 1.62$  year<sup>-1</sup>,  $t_0 = 0.04$  years,  $r^2 = 0.78$  (females),  $CL_{\infty} = 15.74$  mm,  $k = 1.22$  year<sup>-1</sup>,  $t_0 = -0.23$  years,  $r^2 = 0.87$  (males)

The Gompertz growth curves (Fig. 5a, b) estimated:

$$CL_t = 21.46 \left( e^{-e^{-1.62(t-0.04)}} \right), r^2 = 0.78 \text{ (females, Fig. 5a)}$$

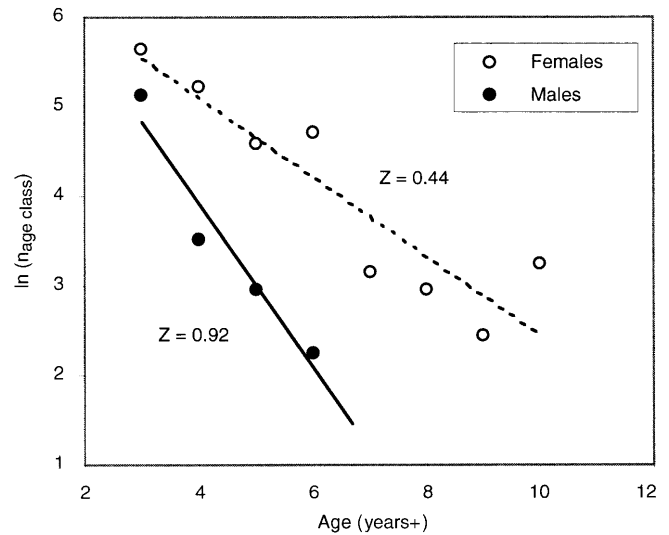
(standard errors:  $CL_{\infty} = 0.25$ ,  $k = 0.15$ ,  $t_0 = 0.05$ ).

$$CL_t = 15.74 \left( e^{-e^{-1.22(t+0.23)}} \right), r^2 = 0.87 \text{ (males, Fig. 5b)}$$

(standard errors:  $CL_{\infty} = 0.44$ ,  $k = 0.16$ ,  $t_0 = 0.07$ ).

### Mortality

Mortality, estimated from the catch curve, amounted to 0.44 year<sup>-1</sup> for female shrimps and 0.92 year<sup>-1</sup> for males (Fig. 6). Data from juveniles were not included in the regression (according to Ricker 1979; Pauly 1984). Using Brey's (1995, 1999) empirical relationship, mortality was



**Fig. 6** Catch curve of *Notostrangon antarcticus* from the eastern Weddell Sea. Females:  $\ln(n_{\text{age class}}) = 5.97 - 0.442 \cdot \text{age}$ ,  $r^2 = 0.83$ ; males:  $\ln(n_{\text{age class}}) = 5.76 - 0.918 \cdot \text{age}$ ,  $r^2 = 0.94$ . The number of individuals per age class ( $n_{\text{age class}}$ ) was adjusted from lipofuscin-analyzed subsample to total sample size (see "Materials and methods")

estimated to range between 0.33 and 0.41 year<sup>-1</sup> in females ( $A_{\text{max}} = 8$  and 10 years+,  $M_{\text{max}} = 42.74$  kJ) and between 0.57 and 0.85 year<sup>-1</sup> in males ( $A_{\text{max}} = 4$  and 6 years+,  $M_{\text{max}} = 15.24$  kJ).

### Production and productivity

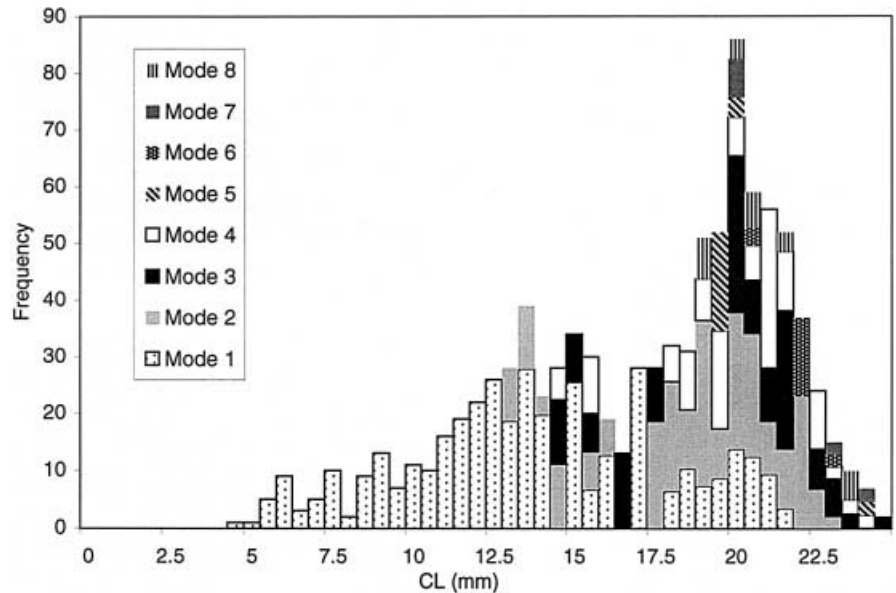
Average annual biomass was approximated at 0.043 g ash free dry mass (AFDM) m<sup>-2</sup> (0.039 g AFDM m<sup>-2</sup> female biomass, 0.004 g AFDM m<sup>-2</sup> male biomass) according to the body mass–frequency distribution. Productivity, estimated from  $Z$ , amounted to 0.44 and 0.92 year<sup>-1</sup> for females and males, respectively. The MSGRM resulted in lower  $P/B$  estimates (females: 0.30 year<sup>-1</sup> VBGF, 0.39 year<sup>-1</sup> Gompertz; males: 0.44 year<sup>-1</sup> VBGF, 0.46 year<sup>-1</sup> Gompertz). Annual production estimates based on  $P/B \approx Z$  amounted to 0.017 and 0.004 g AFDM m<sup>-2</sup>, respectively, for females and males.

### Discussion and conclusions

The size-frequency distribution of *Notostrangon antarcticus* was characterized by a pile-up of individuals in two modes comprising mature males and females, respectively. This pattern is typically observed in long-lived benthic invertebrates (e.g. Brey et al. 1995; Dahm 1996; Piepenburg and Schmid 1996; Bluhm et al. 1998; Gatti, personal communication), including crustaceans (Brewis and Bowler 1982; Phillips 1990; Gorny et al. 1992; Bannister et al. 1994; Sheehy et al. 1998). Declining

**Fig. 7** *Notocrangon antarcticus* from the eastern Weddell Sea. Distribution of modes derived from the modal progression analysis of the lipofuscin concentration–frequency histogram in the length–frequency distribution histogram. The number of individuals per age group was adjusted from lipofuscin-analyzed subsample to total sample size (see “Materials and methods”).

$$\text{Frequency}_{\text{total bar}} = n_{\text{mode1}} + n_{\text{mode2}} + \dots + n_{\text{mode8}}$$



growth with age as well as considerable scatter in size of individuals of the same age (Fig. 7) may be responsible for this pattern, which is apparently typical for Crustacea and usually unsuitable for modal progression analysis aiming at age determination (Chittleborough 1976; Pauly et al. 1984; France et al. 1991; Phillips et al. 1992). Positive examples can be seen among comparatively short-lived shrimp species, e.g. in Pauly et al. (1984), Jeri (1999, and references therein), and Oh et al. (1999). The size range and sex ratio in the studied population, discussed below, are in accordance with findings from the same area in other years (Arntz and Gorny 1991). The lack of small shrimps may be explained by gear selectivity and potential migration of juveniles as proposed and discussed by Arntz and Gorny (1991).

Modal separation of the lipofuscin concentration–frequency data revealed well-resolvable modes. Their regular bell shape and even spacing suggest: (1) a non-random distribution and (2) a nearly linear accumulation of the pigment with age (Fig. 4a). Although the number of individuals in modes V (6+ years) to VIII (10+ years) is low, several reasons encouraged us to treat those as modes in further calculations, i.e. (1) the high separation index, (2) significant  $\chi^2$ , (3) decreasing number of individuals with increasing lipofuscin concentration and (4) mode means lying 2.5–3 times the components’ standard deviations apart, as suggested by Grant et al. (1987) and Grant (1989) for reliable mode separation. There are no indications that spatial and temporal environmental as well as genetic variability, which potentially affects lipofuscin formation and accumulation (Sheehy et al. 1995b; O’Donovan and Tully 1996), evoked any obscuring overlaying rhythm of pigment formation, nor did it eradicate modes. As in most studies, however, those factors remained unquantified in our study. As discussed earlier the stable environmental temperature in the study area in combination with pre-

dominantly long life spans integrating short-term variations are more likely to favor the application of the lipofuscin method than to hamper it (Bluhm et al. in press). Low temperature, however, resulted in overall low pigment accumulation rates and, hence, low concentrations in *N. antarcticus*. Variation between sections of the same individual could be reduced by higher sample size and increased number of analyzed sections per individual. We are aware that our study lacks age calibration to validate modes as age classes, a shortcoming which is, however, also the flaw in most studies using size frequencies for age determination. To our knowledge, though, all studies to date quantifying lipofuscin as an age marker in crustaceans, have found little variability of lipofuscin at age as opposed to high size-at-age variability (e.g. O’Donovan and Tully 1996; Belchier et al. 1998; Sheehy et al. 1998). Evidence strongly supports Sheehy et al. (1998) who summarized that it is “difficult to conclude other than that the modes represent annual cohorts”.

In the modal progression analysis, males and females were not treated separately as no sexual differences in accumulation rates were found in previous studies (Sheehy 1990a, c; Sheehy et al. 1994, 1996). Although ANCOVA gave a statistically significant difference in lipofuscin accumulation rate between males and females, close inspection of Fig. 4a shows that this is driven by a difference in the mean of age group IV (6+ years). The number of sampled males in this group is small, and there may be some selective mortality of the physiologically oldest individuals, with highest lipofuscin concentrations. Due to lower survival of males, there is no information on lipofuscin concentrations for age groups older than mode IV (6+ years). The average accumulation rate of 0.02% AF year<sup>-1</sup> (0.021% AF year<sup>-1</sup> in females, 0.017% AF year<sup>-1</sup> in males) lies well below rates measured for other crustaceans, which range from



0.07% AF year<sup>-1</sup> in the long-lived European lobster (Sheehy et al. 1996) to 2.0% AF year<sup>-1</sup> in the relatively short-lived freshwater crayfish *Cherax quadricarinatus* (Sheehy et al. 1994). These findings reflect that the rate of physiological aging may be inversely correlated with longevity (Sheehy et al. 1995b). The main governing factor of physiological processes and metabolic rates is temperature (Parry 1983; Alongi 1990). Obviously, the lipofuscin accumulation rate also depends on temperature, which in our study is below 0 °C, and 8 and 23 °C in the investigations of the European lobster and *C. quadricarinatus*, respectively.

Growth parameters are among the prominent characteristics of a species' population dynamics. Our results show, however, that size and age are to a considerable extent decoupled (Figs. 4b, 7), so that the parameter values of the growth functions should be interpreted with caution. Estimates of  $k$  of the VBGF (0.79 year<sup>-1</sup> in females, 0.64 year<sup>-1</sup> in males) lie in the upper range of what has been published for other deep-water carideans ( $k \approx 0.2$ – $0.7$ , e.g. Dailey and Ralson 1986; Bergström 1992; Baelde 1994; Santana et al. 1997) but below most estimates for tropical and subtropical penaeids ( $k \approx 0.7$ – $1.6$  year<sup>-1</sup>; cited in Pauly et al. 1984; Jerí 1999). As reported for *Crangon crangon* (Oh et al. 1999) and several penaeids (García and Le Reste 1981; Baelde 1994), males reach a lower CL<sub>∞</sub> and grow slightly slower than females, while the opposite trend was observed in other penaeid shrimps (compiled in Jerí 1999). Growth performance of *N. antarcticus* as measured by the index  $\phi = \log(k) + 2 \cdot \log(\text{CL}_{\infty})$  (Pauly and Munro 1984) was 2.59 in females and 2.26 in males. These values lie within the range of published values for other carideans (2.1–3.1; Dailey and Ralston 1986; Hopkins and Nilssen 1990; Bergström 1992; Gorny et al. 1993; Roa and Ernst 1996; Santana et al. 1996; Oh et al. 1999) and penaeids (2.2–3.5; Pauly et al. 1984; Jerí 1991, 1999; Baelde 1994).

Maximum life span of *N. antarcticus* was estimated as at least 8–10 years for females and 4–6 years for males. The average specimen should attain reproductive maturity with sufficient time for successful production of offspring, consequently exceeding the age of first maturity for some time to account for potential errors. All berried females, except for three, fell into modes  $\geq \text{II}$ , presumably corresponding to an age of 4+ years at first spawning, thus 6+ years at second spawning, etc. This seems reasonable considering that development of headroe (visible eggs under the carapace) needs almost 1 year before eggs are attached to the pleopods, and hatch the following year (Gorny et al. 1992). Most gains in size and body mass happen prior to the first spawning event, when energy starts being allocated to reproduction. At this point continuing accumulation of pigment is not reflected in body growth any longer (Fig. 5). The comparatively late onset of first spawning is reflected in the small share of berried females in the total catch (<12%). As males lack the long incubation period they undergo the same number of reproductive events in half the females' life span. Life span differences between sexes

may explain the sex ratio observed in Arntz and Gorny (1991) and in the present study, although migration and catch effects cannot be excluded. *N. antarcticus* reach high ages compared to inshore shallow-water Caridea and Penaeidea from lower latitudes. The common shrimp *Crangon crangon*, e.g., attains a maximum age of 3.3 years (Oh et al. 1999), and many penaeids reach an age of 2–3 years (compiled in Jerí 1999). In contrast, other cold- and deep-water shrimps such as *Heterocarpus reedi* (Roa and Ernst 1996), *Pandalus borealis* (Teigmark 1983; Hopkins and Nilsson 1990; Bergström 1992) and *Chorismus antarcticus* (Gorny et al. 1992) obtain maximum ages of 5–10 years. Note, however, that these longevities may be subject to error due to limitations of size-based and artificial rearing studies. Pearl (1928) suggested in his "rate of living theory" that greater longevity arises from slowed rates of aging processes at low temperatures, whereas Brey and Clarke (1993) correlated longevity of marine benthic invertebrates with water depth, reflecting food availability. Indeed, studies on a variety of terrestrial taxa ranging from nematodes and flies to rats (e.g. Weindruch and Walford 1982; Sohal and Weindruch 1996) supported the prolonging effect of relatively low caloric intake on life span. This relationship also seems conclusive for marine invertebrates in seasonally food-limited habitats such as the Antarctic and the deep-sea (Clarke 1988, 1991).

The calculated  $P/B$  ratios match with Brey and Clarke's (1993) compilation of  $P/B$  ratios of Antarctic invertebrates. As expected, the results obtained from the catch curve range above those from MSGRM, as the latter does not include the portion of fast-growing productive young specimens not sampled by the net. Nevertheless, values from both methods lie within the same range and thus validate our results obtained from the VBGF. Brey and Clarke (1993) suggest that under food-limited conditions there would be a balance between low biomass and relatively high metabolic costs or vice versa. In motile species such as in the two common Antarctic shrimps *Chorismus antarcticus* (Gorny et al. 1993) and *N. antarcticus*, biomass seems to be rather low, while productivity is in the upper range of what the authors estimated for Antarctic benthic invertebrates when effects of body mass are accounted for. Concluding from  $P/B$  ratio and production estimates, a fishery on *N. antarcticus* would be ecologically and economically unsustainable. Brey and Gage (1997) attribute the relation between growth rate and mortality to a mortality–growth continuum of predator–prey relations. According to their empirical relation, *N. antarcticus* ranges at the bottom end of the low-mortality populations, which they interpret as well protected against predation. Indeed, only small amounts of shrimp have been found in stomachs and feces of representatives of higher trophic levels such as Weddell seals (Green and Burton 1987; Casaux et al. 1997; Burns et al. 1998), leopard seals (Green and Williams 1986) and emperor penguins (Klages 1989; Piatkowski and Pütz 1994; Pütz 1995).

To conclude:

1. Modal progression analysis of lipofuscin concentration frequencies allows estimates of population parameters which, for *N. antarcticus*, are inaccessible with traditional methods.
2. The fit of a growth function to size at lipofuscin-based age data is complicated if the beginning of lipofuscin accumulation is unknown, young age classes are lacking, and size and age are largely decoupled.
3. The results indicate that *N. antarcticus* corresponds to “the typical polar benthic invertebrate” with regard to high longevity and low mortality, production, and productivity.

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